The Agricultural Transition in Upper Nubia: An Analysis of Mandibular Morphology and Oral Health

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This thesis is submitted for the degree of Doctor of Philosophy

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Declaration

This thesis is the result of my own work and includes nothing which is the outcome of work done in collaboration, except as declared in the Preface and specified in the text. I further state that no substantial part of my thesis has already been submitted, or, is being concurrently submitted for any such degree, diploma or other qualification at the University of Cambridge or any other University or similar institution except as declared in the Preface and specified in the text. It does not exceed the prescribed word limit for the relevant Degree Committee.

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Research has shown that the biological and morphological effect of the transition to agriculture varied widely by population and geographical region. In Upper Nubia, the shift to full-scale agriculture included transitional phases with varying dependence on pastoralism and farming, alongside continued hunting and gathering. Therefore, Upper Nubia is an ideal region to study the relationship between subsistence strategy, mandibular morphology and oral health. This study analysed the mandibles and dentition from 102 adult individuals from ancient Nubian populations. The sample contained a Late Palaeolithic hunter-gatherer population from Lower Nubia (C. 13,000–9000 BC), as well as samples representing four cultural periods in Upper Nubia (Sudanese Neolithic c. 5000–4000 cal BC, Kerma Ancien c. 2500–2050 BC, Kerma Classique c. 1750–1500 BC and Meroitic c. 350 BC–AD 350). Mandibular osteometrics and cross-sectional geometric properties were calculated from 3D laser scanned models to explore the relationship between diet-induced biomechanical force and variation in mandibular shape and strength between samples. Dental pathology and wear were used to assess diachronic changes in oral health and dietary composition. Dental size was also measured to compare the relationship between mandibular and dental size over time.

The intensive agricultural population from the Kerma Classique period had the highest prevalence and severity of dental pathology and wear, which may reflect a highly cariogenic and abrasive diet. Oral health improved in the subsequent Meroitic sample, possibly due to an increase in dietary heterogeneity and/or improved hygienic practices. Overall, mandibles from the Late Palaeolithic hunter-gatherers were longer, wider, and had more upright and larger rami than subsequent agricultural populations. Mandibular size continued to decrease within the subsequent Upper Nubian samples, most notably in the overall length, body height in the molar region and width of the ramus. The gonial angle also became more obtuse over time. Changes in mandibular size were not accompanied by consistent evidence of dental size reduction. In addition, there were significant differences between the Late Palaeolithic and Upper Nubian samples in mandibular biomechanical properties. Most notably, molar I_x and I_{max} continued to decrease through agricultural intensification in the Upper Nubian samples, suggesting a reduction in the sagittal bending rigidity of the mandible in response to an increasing reliance

on softer agricultural food products. The timing of the mandibular morphological changes indicate that the overall size of the mandible began to decrease before strength relative to size.

Overall, this study used a novel combination of methodologies to identify major biological changes in the dentition and mandible during the transition to agriculture in Upper Nubia. Importantly, the results demonstrate that changes in masticatory loading magnitude, as a result of dietary shifts, specifically influence mandibular morphology and robusticity in anatomical regions associated with masticatory function, such as the molar region of the mandibular corpus and the ramus. The findings support the masticatory-functional hypothesis and show that dietary changes are an important factor influencing observed mandibular morphological variation between populations. This study contributes to a better understanding of the biological changes that accompanied the agricultural transition in Ancient Nubia.

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TABLE OF CONTENTS

DECL	ARATIO	۷	iii	
ABSTRACTv				
ACKNOWLEDGEMENTS				
TABL	E OF CO	NTENTS	ix	
LIST (OF TABL	ES	xv	
LIST (of Figur	RES	xvii	
1 INTRODUCTION			1	
1.1	Intro	DUCTION	1	
1.2	2 AN INT	RODUCTION TO ANCIENT NUBIA	3	
1.3	THE P	RESENT RESEARCH	4	
1.4	STRUC	CTURE OF THE THESIS	6	
2 AN		UBIAN CHRONOLOGY	7	
2.1	Intro	DUCTION	7	
2.2	Histo	RY OF ARCHAEOLOGICAL RESEARCH IN ANCIENT NUBIA	7	
2.3	G EOG	RAPHICAL CONTEXT AND ECOLOGICAL PERSPECTIVE	10	
2.4	CHRO	NOLOGY OF ANCIENT NUBIAN POPULATIONS	13	
	2.4.1	Late Palaeolithic (c. 15000–8500 BC)	15	
	2.4.2	Epipalaeolithic (c. 8500–5700 BC)	16	
	2.4.3	Sudanese Neolithic (c. 5700–3000 BC)	20	
	2.4.4	Pre-Kerma (c. 3500–2500 BC)	25	
	2.4.5	Kerma (c. 2500–1500 BC)	27	
		2.4.5.1 Kerma Ancien (c. 2500–2050 BC)	27	
		2.4.5.2 Kerma Moyen (c. 2050–1750 BC)	29	
		2.4.5.3 Kerma Classique (c. 1750–1500 BC)	30	
	2.4.6	Kerma Recent and Egyptian Occupation (c. 1500–1050 BC)	31	
	2.4.7	The Kushite Period (c. 750 BC–AD 350)	32	
		2.4.7.1 The Napatan Period (c. 750-350 BC)	33	
		2.4.7.2 The Meroitic Period (c. 350 BC-AD 350)	34	
2.5	SUMM	ARY	37	
3 MA	3 MANDIBULAR ANATOMY			
3.1	Intro	DUCTION	39	

	3.2	THE HUMAN MASTICATORY COMPLEX		
	3.3	MASTICATORY MUSCLES		
	3.4	INCISION AND MASTICATION	45	
	3.5	MANDIBULAR GROWTH AND DEVELOPMENT	48	
	3.6	SUMMARY	50	
4	SAM	PLE POPULATIONS AND RESEARCH OBJECTIVES	51	
-	4.1	INTRODUCTION		
	4.2	ANCIENT NUBIAN POPULATIONS		
		4.2.1 Jebel Sahaba (JSA) – Late Palaeolithic (c. 13000–9000 BC)	53	
		4.2.2 NDRS R12 (R12) – Neolithic (c. 5000–4000 cal BC)	54	
		4.2.3 NDRS P37 (KAW) – Kerma Ancien (c. 2500–2050 BC)	57	
		4.2.4 Kerma (KER) – Kerma Classique (c. 1750–1500 BC)	59	
		4.2.5 Kawa R18 (KUS) – Meroitic (c. 350 BC–AD 350)	61	
	4.3	RESEARCH OBJECTIVES AND HYPOTHESES	62	
		4.3.1 Mandibular osteometrics (Chapter 5)	63	
		4.3.2 Mandibular cross-sectional geometry (Chapter 6)	64	
		4.3.3 Oral health (Chapter 7)	66	
		4.3.4 Dental metrics (Chapter 8)	68	
		4.3.5 Discussion (Chapter 9)	69	
	4.4	SUMMARY	69	
5	MAN	DIBULAR OSTEOMETRICS	71	
	5.1	INTRODUCTION	71	
	5.2	MANDIBULAR OSTEOMETRIC RESEARCH	71	
		5.2.1 Animal studies	71	
		5.2.2 Clinical evidence	73	
		5.2.3 Archaeological evidence	75	
	5.3	MATERIALS AND METHODS	76	
		5.3.1 Materials	76	
		5.3.2 Methods	77	
		5.3.3 Statistical analysis	82	
	5.4	RESULTS	82	
		5.4.1 Mandibular length	84	
		5.4.2 Mandibular breadth	92	
		5.4.3 Ramus	97	
		5.4.4 Mandibular corpus	. 102	
	5.5	DISCUSSION	.114	

	5.6	CONC	LUSIONS	125
6	MAN	DIBUL	AR CROSS-SECTIONAL GEOMETRY	127
	6.1	INTRODUCTION		
	6.2	Mandibular stress and strain		128
		6.2.1	Symphyseal morphology	129
		6.2.2	Patterns of symphyseal stress and strain	131
		6.2.3	Patterns of mandibular corpus stress and strain	133
	6.3	SOLID	VS. OPEN CROSS-SECTIONAL MODELS	134
	6.4	MATER	RIALS AND METHODS	136
		6.4.1	Materials	136
		6.4.2	Methods	137
		6.4.3	Cross-sectional properties	140
		6.4.4	Statistical analysis	142
	6.5	Resul	_TS	145
		6.5.1	Symphysis	145
		6.5.2	Molar region	157
	6.6	Discu	SSION	160
	6.7	CONC	LUSIONS	165
7	ORA	L HEA	LTH	167
7	ORA 7.1	L HEA	LTH	 167 167
7	ORA 7.1 7.2	L HEA Intro Study	LTH DUCTION /ING ORAL HEALTH IN ARCHAEOLOGICAL POPULATIONS	 167 167 168
7	ORA 7.1 7.2 7.3	L HEA Intro Study Dent <i>i</i>	LTH DUCTION YING ORAL HEALTH IN ARCHAEOLOGICAL POPULATIONS AL PATHOLOGY BACKGROUND	167 167 168 168
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENTA 7.3.1	LTH DUCTION YING ORAL HEALTH IN ARCHAEOLOGICAL POPULATIONS AL PATHOLOGY BACKGROUND Dental wear	167 167 168 168 168
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENT 7.3.1 7.3.2	LTH DUCTION YING ORAL HEALTH IN ARCHAEOLOGICAL POPULATIONS AL PATHOLOGY BACKGROUND Dental wear Dental caries	167 167 168 168 168 170
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENTA 7.3.1 7.3.2 7.3.3	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus	167 167 168 168 168 170 172
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENTA 7.3.1 7.3.2 7.3.3 7.3.4	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH)	167 167 168 168 178 170 172 173
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENTA 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL)	167 167 168 168 168 170 170 172 173 174
7	ORA 7.1 7.2 7.3	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL)	167 167 168 168 170 170 172 173 174 175
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENTA 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER	LTH DUCTION YING ORAL HEALTH IN ARCHAEOLOGICAL POPULATIONS AL PATHOLOGY BACKGROUND Dental wear Dental vear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS	167 167 168 168 178 172 173 174 175 176
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials	167 167 168 168 168 170 172 173 174 175 176 176
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENTA 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials Methods	167 168 168 168 170 172 173 174 175 176 178
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials Methods 7.5.2.1 Dental wear	167 167 168 168 178 170 173 173 175 176 176 178 179
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials Methods 7.5.2.1 Dental wear 7.5.2.2 Dental caries	167 167 168 168 168 168 170 172 173 174 175 176 176 176 178 179 179
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials Methods 7.5.2.1 Dental wear 7.5.2.2 Dental caries 7.5.2.3 Dental calculus	167 167 168 168 168 168 170 170 172 173 174 175 176 176 176 178 179 179 180
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT/ 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials 7.5.2.1 Dental wear 7.5.2.2 Dental caries 7.5.2.3 Dental calculus 7.5.2.4 Linear enamel hypoplasia (LEH)	167 167 168 168 168 168 170 172 173 174 175 176 176 176 178 179 180 180
7	ORA 7.1 7.2 7.3 7.4 7.5	L HEA INTRO STUDY DENT 7.3.1 7.3.2 7.3.3 7.3.4 7.3.5 SEX D MATER 7.5.1 7.5.2	LTH DUCTION AL PATHOLOGY BACKGROUND Dental wear Dental vear Dental caries Dental calculus Linear enamel hypoplasia (LEH) Periodontal disease and ante-mortem tooth loss (AMTL) IFFERENCES IN ORAL HEALTH RIALS AND METHODS Materials 7.5.2.1 Dental wear 7.5.2.2 Dental caries 7.5.2.3 Dental calculus 7.5.2.4 Linear enamel hypoplasia (LEH) 7.5.2.5 Periodontal disease	167 167 168 168 168 168 170 172 173 174 175 176 176 176 178 179 180 180 181

	7.6	RESUL	_TS	. 182
		7.6.1	Dental wear	. 182
		7.6.2	Dental caries	. 186
		7.6.3	Dental calculus	. 189
		7.6.4	LEH	. 194
		7.6.5	Periodontal disease	. 196
	7.7	Discu	SSION	. 199
		7.7.1	Dental wear	. 199
		7.7.2	Dental caries	.201
		7.7.3	Dental calculus	.205
		7.7.4	Periodontal disease	.207
		7.7.5	LEH	.209
	7.8	CONCL	LUSIONS	. 209
8			ETRICS	.213
	8.1	Introi		.213
	8.2	DENTA	AL REDUCTION MECHANISMS	.213
	8.3	MATER	RIALS AND METHODS	.218
		8.3.1	Materials	.218
		8.3.2	Methods	.218
		8.3.3	Statistical analysis	.220
	8.4	RESUL	_TS	. 221
		8.4.1	Mesiodistal and buccolingual metrics	.221
		8.4.2	Coefficient of variation analyses	.229
	8.5	Discu	ssion	. 231
	8.6	CONCL	LUSIONS	. 236
9	DISC	USSIO	N	.239
	9.1	Introi		.239
	9.2	REVISI	ITING HYPOTHESES AND RESULTS	.239
		9.2.1	Mandibular osteometrics	.239
		9.2.2	Mandibular cross-sectional geometry (CSG)	.241
		9.2.3	Oral health	.242
		9.2.4	Dental metrics	.244
	9.3	Mandi	IBULAR MORPHOLOGICAL CHANGE IN UPPER NUBIA	.246
		9.3.1	Sex-specific mandibular morphological trends	.251
	9.4	LIMITA	TIONS AND FUTURE DIRECTIONS	. 253
		9.4.1	Mandible and cranial integration	.253
		9.4.2	Internal mandibular morphology	.254

	9.4.3 Nubian population sample	254
9.5	CONCLUDING REMARKS	256
10	REFERENCES	257
APPEN	NDIX A GENERAL METHODOLOGY	315
A.1	SEX AND AGE DETERMINATION	315
A.2	STATURE AND BODY MASS	
A.3	3D LASER SCANNING	
APPEN	NDIX B MANDIBULAR METRIC DATA	
APPEN	NDIX C MANDIBULAR CROSS-SECTIONAL GEOMETRY	DATA 343
APPEN	NDIX D ORAL HEALTH DATA	
APPEN D.1	NDIX D ORAL HEALTH DATA	347 347
D.1 D.2	NDIX D ORAL HEALTH DATA DENTAL WEAR DENTAL CARIES	347 347 349
APPEN D.1 D.2 D.3	NDIX D ORAL HEALTH DATA DENTAL WEAR DENTAL CARIES DENTAL CARIES DENTAL CALCULUS	
APPEN D.1 D.2 D.3 D.4	NDIX D ORAL HEALTH DATA DENTAL WEAR DENTAL CARIES DENTAL CARIES DENTAL CALCULUS LINEAR ENAMEL HYPOPLASIA (LEH) DENTAL CALCULUS	347 347 349 353 357
APPEN D.1 D.2 D.3 D.4 D.5	NDIX D ORAL HEALTH DATA DENTAL WEAR. DENTAL CARIES DENTAL CARIES DENTAL CALCULUS. LINEAR ENAMEL HYPOPLASIA (LEH) PERIODONTAL DISEASE	347 347 349 353 357 358
APPEN D.1 D.2 D.3 D.4 D.5 APPEN	NDIX D ORAL HEALTH DATA DENTAL WEAR. DENTAL CARIES DENTAL CARIES DENTAL CALCULUS. LINEAR ENAMEL HYPOPLASIA (LEH) PERIODONTAL DISEASE NDIX E DENTAL METRIC DATA	
APPEN D.1 D.2 D.3 D.4 D.5 APPEN E.1	NDIX D ORAL HEALTH DATA DENTAL WEAR. DENTAL CARIES DENTAL CARIES DENTAL CALCULUS. LINEAR ENAMEL HYPOPLASIA (LEH) PERIODONTAL DISEASE NDIX E DENTAL METRIC DATA DENTAL METRIC DATA	
APPEN D.1 D.2 D.3 D.4 D.5 APPEN E.1 E.2	NDIX D ORAL HEALTH DATA DENTAL WEAR. DENTAL CARIES DENTAL CARIES DENTAL CALCULUS. LINEAR ENAMEL HYPOPLASIA (LEH) PERIODONTAL DISEASE NDIX E DENTAL METRIC DATA DENTAL METRIC SEX DESCRIPTIVE STATISTICS. DENTAL METRICS SEX-ADJUSTED DATA	

List of Tables

Table 7.12 Prevalence of LEH within each population and tooth class (tooth count) 1	95
Table 7.13 Periodontal disease sample size by population, tooth, sex and age 1Table 8.1 Descriptive statistics by sample for the mandibular mesiodistal crown	97
dimensions	.21
Table 8.3 ANOVAs and post-hoc tests for mesiodistal tooth measurements	27
Table 8.5 Percentage difference in mesiodistal and buccolingual mandibular dimensions between populations	28

List of Figures

Figure 2.1 Map of Northeast Africa
Figure 2.2 Ancient Nubia and the Nile Cataracts
Figure 3.1 Mandible (lower jaw) anatomy
Figure 3.2 Left mandibular dentition with identifying labels Error! Bookmark not
defined.
Figure 3.3 Superior view of the mandible with directional terms for dentition
Figure 3.4 Muscles of mastication 44
Figure 3.5 Muscle insertion sites on the mandible (a) lateral view and (b) medial
view
Figure 3.6 Movements of the mandible during the closing stage of mastication 47
Figure 4.1 Map of the sample population sites included in this study
Figure 4.2 Location of R12 Neolithic cemetery at the edge of the Seleim Basin 55
Figure 4.3 NDRS site P37 – Kerma Ancien graves visible after the removal of the
Surface Sanu
correspond to major tumuli
Figure 4.5 Kawa site R18 (a) Site R18 the eastern cemetery: descendaries of
tombs arranged in north-south rows and (b) Tumuli (45) and (46) after removal
of surface sand, looking south-west towards the town
Figure 5.1 Mandibular length linear measurements
Figure 5.2 Mandibular and dental arcade breadth linear measurements
Figure 5.3 Mandibular ramus linear measurements
Figure 5.4 Mandibular corpus height and breadth linear measurements
Figure 5.5 Mandibular length measurements by population (pooled sex) for (a) ML1,
(b) ML2, (c) ML3, (d) UML, (e) LML, (f) GML, and (g) DAL
Figure 5.6 Mean mandibular length measurements by sex and sample for (a) ML1,
(b) ML2, (c) ML3, (d) UML, (e) LML, (f) DAL and (g) GML
Figure 5.7 Mean mandibular breadth measurements by population (pooled sex) for
(a) BGoB, (b) BCoB, (c) BCP3B, (d) BM1B, and (e) BM2B
Figure 5.8 Mean mandibular width measurements by sex and population for (a)
BGOB, (D) BCOB, (C) BCP3B, (d) BM1B, and (e) BM2B
Figure 5.9 Mean manufoldular ramai measurements by population (pooled sex) for (a)
Figure 5 10 Moon mondibular ramus moosurements by say and sample for (a) LPR
(b) MRB (c) CrH (d) RH and (e) GA
Figure 5 11 Mean cross-sectional linear measurements by population (pooled sex)
for (a) SH (b) MH (c) LH (d) RH (e) SB (f) MB (g) LB (b) RB (i) SR (i) MR
(k) LR. (l) RR. (m) SS. (n) MS. (o) LS. and (p) RS
Figure 5.12 Mean mandibular body by sex and sample for (a) SH, (b) MH, (c) LH,
(d) RH, (e) SB, (f) MB, (g) LB, (h) RB
Figure 5.13 Mandibular length results for the pooled-sex sample and by sex 115
Figure 5.14 Mandibular breadth results for the pooled-sex sample and by sex 117
Figure 5.15 Corpus height results for the pooled-sex sample and by sex
Figure 5.16 Corpus breadth results for the pooled-sex sample and by sex
Figure 5.17 Ramus linear measurement results for the pooled-sex sample and by
sex
Figure 6.1 Bending stresses at the human mandibular symphysis (adapted from
Daegling 1993a, Trinkaus and Dobson 2002, Fukase 2007, Bonner 2013) 132

Figure 6.2 3D mandibular models and alignment planes in Rapidform (a) Inferior plane parallel to the inferior border of the mandibular body; (b) midline plane perpendicular to the inferior plane and bisecting the midline at LI ₁ /RI ₁ and the bicondylar chord; (c) right molar M ₁ /M ₂ cross-sectional plane perpendicular to the inferior and occlusal plane; (d) digital polyline highlighting the outline of the symphyseal cross-section
Figure 6.3 Mandibular cross-sections in Photoshop (a) symphyseal raw cross- section; (b) symphyseal closed-section model; (c) right molar raw cross-section; (d) right molar closed-section model
 Figure 6.4 Mandibular length measurement 1 (ML1)
 Figure 6.6 Mean standardised symphysear cross-sectional values for pooled-sex data by sample for (a) TA, (b) <i>I_x</i>, (c) <i>I_y</i>, (d) <i>I_{max}</i>, (e) <i>I_{min}</i> and (f) <i>J</i>
 Figure 6.8 Mean standardised right M₁/M₂ cross-sectional values (error bars 95% confidence interval) for pooled-sex data by sample for (a) TA, (b) <i>I_x</i>, (c) <i>I_y</i>, (d) <i>I_{max}</i>, (e) <i>I_{min}</i>, and (f) <i>J</i>
 Figure 7.4 Calculus severity for combined dentition by population (tooth count) 189 Figure 7.5 Calculus severity by sex within (a) R12, (b) KAW, (c) KER and (d) KUS populations
 Figure 7.6 Calculus severity by age (combined dentition) within (a) R12, (b) KAW, (c) KER and (d) KUS populations
Figure 7.10 Prevalence of periodontal disease by (a) sex and (b) age (tooth count) 198 Figure 8.1 Mesiodistal and buccolingual posterior dental measurements
 Figure 8.2 Mesiodistal crown measurement (mm) for R12, KAW, KER and KUS populations (a) I₁, (b) I₂, (c) C₁, (d) P₃, (e) P₄, (f) M₁, (g) M₂ and (h) M₃ 223 Figure 8.3 Mean buccolingual crown measurement (mm) for the R12, KAW, KER, and KUS populations (a) I₁, (b) I₂, (c) C₁, (d) P₃, (e) P₄, (f) M₁, (g) M₂ and (h) M₃
Figure 8.4 Population dental metric CV for mesiodistal and buccolingual measurements by (a) anterior dentition (I ₁ , I ₂ , C ₁) and (b) posterior dentition (P ₃ , P ₄ , M ₁ , M ₂ , M ₃)

1 INTRODUCTION

1.1 Introduction

The emergence and spread of agriculture was one of the most significant events in recent human history, initiating major biological and cultural change globally (e.g. Bellwood, 2004; Childe, 1936; Diamond, 2002; Pinhasi and Stock, 2011; von Cramon-Taubadel, 2017). During the agricultural transition, populations shifted from a reliance on hunting and gathering to the cultivation of domesticated plants (e.g. wheat, barley, rice and maize) and animals (e.g. cattle and caprines) (Diamond, 2002; von Cramon-Taubadel, 2017). Changes in food consumption, the accompanying modifications in activity patterns and an overall increase in disease exposure all had a substantial effect on the physiology of agricultural populations (Dufour and Piperata, 2018; Gignoux et al., 2011; Pinhasi and Stock, 2011; Wells and Stock, 2007). With time, major advances in farming technology led to an increasingly reliable and abundant agricultural yield, resulting in a food surplus that initiated social stratification, political centralisation and ultimately a rise in the global human population (Diamond, 2002; Gignoux et al., 2011; Wells and Stock, 2007).

The agricultural transition occurred simultaneously and independently in different populations, and the nature of each transition varied considerably between regions (Asouti and Fuller, 2013; Bar-Yosef and Meadow, 1995; Bellwood, 2004; Diamond, 2002; Pinhasi and Stock, 2011; Smith, 2001a,b; Thorpe, 1996). As a result of the local environment, some populations adopted a sudden shift to agriculture, whereas other populations progressed gradually through several intermediary subsistence phases before becoming fully reliant on food production. In many areas, populations practiced a variety of subsistence strategies concurrently, influenced in part by regional climate and resource availability, but also in response to political and cultural affiliations (Bradley, 1992; Cavalli-Sforza, 1996; Fratkin et al., 1999; Turner, 2004).

The effect of the agricultural transition on global human populations from a genetic, cultural and biological perspective has been well-studied (e.g. Beckett and Lovell, 1994; Bridges, 1991; Childe, 1936; Cohen and Armelagos, 1984; Cohen and Crane-Kramer, 2007; Diamond, 2002; Goodman et al., 1984; Larsen, 1995; Macintosh et al., 2014; Martin et al., 1984; Pinhasi and Stock, 2011; Starling and Stock, 2007; Wells and Stock, 2007; Zabecki, 2006; Zakrzewski, 2003). Specifically, biological anthropologists have examined the

relationship between changes in dietary composition and human biological variation, especially with regards to overall health and skeletal morphology. Generally, early agricultural diets were less diverse, higher in simple carbohydrates and lower in protein compared with the diets of hunter-gatherers (Larsen, 2006). Research has shown that the combination of agricultural diets and associated cultural changes led to a variety of health problems in early farming populations, such as poor oral health, vitamin deficiencies and an overall higher frequency of infectious disease (Beckett and Lovell, 1994; Cohen and Armelagos, 1984; Larsen, 2006, 2015; Martin et al., 1984; Starling and Stock, 2007). However, the assertion that plant and animal domestication had a universally negative impact on human health is debated, and the observed biological repercussions vary by population studied (Dufour and Piperata, 2018). As such, when investigating health across the agricultural transition, it is important to adopt a biocultural perspective that considers any observed biological change within the cultural context of the population.

Morphologically, anthropologists have observed that early farmers had more gracile cranial features compared with their hunter-gatherer predecessors. Carlson and Van Gerven (1977) attributed the gracilisation of craniofacial morphology to reduced masticatory loading: the "masticatory-functional hypothesis" (Carlson and Van Gerven, 1977). Observations from populations around the world support a relationship between cranial gracilisation and agricultural intensification (e.g. Galland et al., 2016; Katz et al., 2017; Pinhasi et al., 2008; Sardi et al., 2006; Smith et al., 1984; von Cramon-Taubadel, 2011; Y'Edynak and Fleisch, 1983). Specifically, variation in masticatory load magnitude associated with changes in dietary composition has been shown to have had a greater influence on mandibular morphology compared with the rest of craniofacial region; morphological change is often observed in the mandibular regions associated with chewing musculature (Katz et al., 2017; von Cramon-Taubadel, 2011).

However, the causal relationship between dietary composition, biomechanical loading magnitude and craniofacial morphology remains unclear. Although many studies support the concept that dietary composition can influence the observed variation in mandibular morphology between populations, it may be that much of the morphological variation between populations instead reflects genetic relatedness and population history (von Cramon-Taubadel, 2017). Even when studies compare populations from a defined geographic area with evidence of population continuity to limit the likelihood that observed changes in morphology are reflective of genetic differences (Carlson and Van Gerven, 1977; Galland et al., 2016;

González-José et al., 2005; Paschetta et al., 2010; Pinhasi et al., 2008), it remains difficult to completely control for the confounding effect of migration (Galland et al., 2016). In addition, the observed pattern and degree of mandibular shape and size change observed in past populations can vary. Contrary to the conclusions of the masticatory-functional hypothesis, some comparisons have even demonstrated that farmer masticatory dimensions were larger and/or more robust than their hunter-gatherer predecessors (González-José et al., 2005; Paschetta et al., 2010; Pinhasi et al., 2008, 2015). These discrepancies highlight the importance of interpreting morphological change between populations alongside the local sociocultural and environmental context of each population (Pinhasi and Stock, 2011). There are still questions surrounding the ability of mandibular shape variation to reflect shifts in subsistence economies in past human populations, and the mechanisms that can drive such morphological change (von Cramon-Taubadel, 2017).

1.2 An introduction to ancient Nubia

The nature of the archaeological finds from ancient Nubia provides an opportunity to use time-successive populations to investigate how subsistence strategy transitions influenced human cultural and biological variation (Carlson and Van Gerven, 1977; Galland et al., 2016). The ancient civilisation of Nubia was located in the Nile Valley of Northeast Africa, spanning the geographical region between the First Cataract in Egypt and the confluence of the Blue and White Niles (beyond the Sixth Cataract) near present-day Khartoum, Sudan (Adams, 1977; Carlson and Van Gerven, 1979; Edwards, 2004; Greene, 1967; Vagn Nielsen, 1970). Nubia became a powerful economic state, in part through the occupation of a strategic geographical location and by controlling the trade of valuable raw materials such as gold; throughout its history, Nubia competed with ancient Egypt to the north (Adams, 1977; Edwards, 2004).

The Nile Valley is not considered to be an independent point of origin for agriculture (Diamond, 2002). There is evidence that the domesticated crops and animals present within the ancient Nile Valley originated in the Near East (Gatto and Zerboni, 2015; Smith, 1995). Within ancient Nubia, the transition to agriculture was incremental. Lithic, ceramic, funerary, settlement pattern and population size analyses indicate that Nubian populations practiced subsistence economy heterogeneity throughout their history; most likely in response to fluctuations in resource availability due to climatic instability and environmental change (Butzer, 1976; Caneva and Gautier, 1994; Clark, 1971; Gatto, 1997; Hassan, 1980, 1986; Hays,

1984; Wendorf, 1980b). Recent studies using archaeological, palaeobotanical and isotopic analyses have provided new information on the progression and biological effect of food production in Nubia (e.g. Fuller, 2004a; Galland et al., 2016; Iacumin et al., 1998; Madella et al., 2014; Out et al., 2016; Raue, 2019). However, research has often focused on evidence from Lower Nubia (e.g. Carlson and Van Gerven, 1977; Galland et al., 2016), and there has yet to be a targeted study of the relationship between craniofacial morphology and subsistence strategy in Upper Nubia. Research on Upper Nubian populations is needed in order to fully understand the biological impact of the adoption and intensification of food production throughout the ancient Nile Valley.

1.3 The present research

By using the regional continuity of the ancient Upper Nubian populations, this study explored the diachronic effect of agricultural intensification on mandibular shape and robusticity, dental size and oral health. Upper Nubia (or southern Nubia) refers to the area from the Second to Fourth Cataract along the Nile River (Carlson and Van Gerven, 1979; Vagn Nielsen, 1970). The excavation of time-successive populations from the Northern Dongola Reach in Upper Nubia provided a unique opportunity to study the effect of incremental shifts in subsistence economies on mandibular and dental morphology. Inferences regarding the diet of each population in this study was supported by evidence from archaeological, palaeobotanical and isotopic analyses. The Upper Nubian populations represent the following temporal periods: Sudanese Neolithic, Kerma Ancien, Kerma Classique and Meroitic. Unfortunately, an Epipalaeolithic hunter-gatherer population from Upper Nubia was not available for inclusion in this study. As such, a Late Palaeolithic hunter-gatherer population from Jebel Sahaba in Lower Nubia was included in the analysis.

The aim of this research was to explore the long-term relationship between diet, oral health and the mandibular and dental morphology of the ancient Nubian populations. Mandibular and dental linear measurements were used to quantify changes in the size and shape of the masticatory complex associated with concurrent shifts in subsistence strategy. Analysis of mandibular cross-sectional geometry, from 3D laser-scans, was used to identify the effect of diachronic variation in dietary biomechanical loading on the strength and robusticity of the mandible. Finally, dental pathology and wear were examined to identify patterns of oral health over time. These analyses addressed the following primary research questions:

- 1. How does mandibular size, shape and robusticity change over time between samples? Does the form of the entire mandible change, or is there a mosaic pattern of morphological change?
- 2. Are there significant changes in mandibular dental dimensions between samples? How do the observed trends vary between anterior and posterior dentition, and between mesiodistal and buccolingual dimensions?
- 3. How does the frequency and severity of mandibular dental wear and pathology change over time between samples?
- 4. How do patterns of mandibular morphological change and oral health differ between males and females within each sample, and over time between the Nubian samples?

A more detailed discussion of the research questions and associated hypotheses is provided in **Chapter 4**.

It is also important to address here the main limitation of this research, which primarily relate to the population samples included. Although the Northern Dongola Reach samples in this study represent time periods spanning the Sudanese Neolithic through to the Meroitic period, an earlier hunter-gatherer sample from the Northern Dongola Reach was not available for analysis. To compare the Northern Dongola Reach populations with a hunter-gatherer population, the Late Palaeolithic Jebel Sahaba sample was included. However, the relationship between the Jebel Sahaba and Upper Nubian populations is not fully understood, and previous research has provided evidence for genetic discontinuity between the Jebel Sahaba and later Nubian populations (e.g. Galland et al., 2016; Irish, 2000, 2005; Raxter, 2011). Therefore, it was not within the scope of this study to definitively determine if the observed morphological differences between the Jebel Sahaba population and later Upper Nubian populations were the result of population history and/or adaptive mechanisms. In addition, the primary Jebel Sahaba material was not available for analysis (only the 3D laser scans of the mandible). As such, the Jebel Sahaba sample was not included in the analyses of dental size change or oral health. A more detailed discussion of the limitations of this research is presented in Chapter 9. Despite these limitations, the bioarchaeological analyses presented here will contribute to the understanding of the craniofacial variation present between hunter-gatherers, agro-pastoralists and agriculturalists in ancient Nubia from the Late Palaeolithic to the Meroitic period.

1.4 Structure of the thesis

This thesis is organised into 8 further chapters, which explore the relationship between diet and craniofacial variation in ancient Nubia. **Chapter 2** provides a cultural and environmental history of ancient Nubia, and contextualises the populations used in this study. The cultural periods from the Late Palaeolithic through to the Meroitic are described, highlighting social structure, technological innovations, subsistence strategy characteristics and biological/cultural affinity with the preceding or more recent Nubian population. **Chapter 3** describes the anatomy of the mandible, including the masticatory muscles, and introduces the process of bone modelling and remodelling in response to biomechanical loading. Information regarding the skeletal samples included in this thesis (Jebel Sahaba, NDRS R12, NDRS P37, Kerma and NDRS Kawa) is presented in **Chapter 4**. The research objectives and hypotheses of this study are also presented in **Chapter 4**.

Chapters 5-8 are the results chapters, and each chapter is presented as an independent study. Chapter 5 presents the analyses of mandibular linear measurements to assess diachronic variation in mandibular size and shape associated with changes in diet. Chapter 6 focuses on the mandibular cross-sectional geometric properties calculated to infer how the strength and robusticity of the mandibular corpus was influenced by changes in dietary composition. In Chapter 7, the frequency and severity of dental pathology and wear in each population is presented to infer the overall oral health of each population. The observed patterns of oral health are compared to the archaeological and isotopic evidence for dietary composition in each population. Chapter 8 presents the analysis of mandibular dental crown size through linear measurements to compare concurrent modifications in mandibular and dental size. A summary of the hypotheses and main findings from each of the individual results chapters (Chapters 5–8) is presented in Chapter 9. These results are then considered together and contextualised within the cultural and dietary environment of each Nubian population. In addition, there is discussion of how these analyses contribute to the broader understanding of the mechanisms driving biological change in these populations. Chapter 9 concludes with a discussion of the limitations of the research and suggestions for future research.

2 Ancient Nubian Chronology

2.1 Introduction

This chapter explores the history of archaeological research in ancient Nubia, the geophysical context of the ancient Middle Nile Valley, and provides a brief cultural and historical summary of the ancient Nubian civilisation from the Late Palaeolithic through to the Meroitic period. There is a particular focus on the history of the Northern Dongola Reach in Upper Nubia, where the majority of the samples included in this research were located. The aim of this chapter is to provide the necessary cultural and environmental context to understand the biological change associated with subsistence strategy transitions in the Northern Dongola Reach populations.

2.2 History of archaeological research in Ancient Nubia

There is a debate over the origin of 'Nubia' to describe the peoples of the ancient Middle Nile Valley (Buzon, 2011; O'Connor, 1993). Ancient Egyptians referred to Nubia as 'Kush' (according to 12th Dynasty Egyptian texts), and the term 'Nubian' first appeared in Greek texts from the 3rd century BC (Wenig, 1980). Due to the importance of Nubia as a source of gold for ancient Egyptians, some researchers have argued that the name may derive from the ancient Egyptian word for gold, '*nebu*' (Adams, 1977; Bianchi, 2004). Regardless of the origin, 'Nubia' has long been used in relation to the ancient populations of southern Egypt and northern Sudan. It is important to note that throughout this thesis, the term 'Nubian' is used as a geographical designation and is not necessarily a reflection of ethnicity or language (Bianchi, 2004; Edwards, 2004; O'Connor, 1993).

The first recorded archaeological surveys of ancient Nubian sites began shortly after Egypt and Britain assumed joint control over Sudan in 1898. Early archaeological research in Sudan focused on pharaonic legacy (Edwards, 2007; Raue, 2019), and as such, many of the expeditions in the early 20th century targeted sites near the border of ancient Egypt and ancient Nubia (Edwards, 2004; Trigger, 1994). However, there were also excavations further south, near Meroe, in the early 1900s (Breasted, 1908; Garstang et al., 1911). Early 20th century researchers primarily reported their findings from ancient Nubian archaeological sites as a cultural and/or biological comparison for ancient Egyptians; many researchers did not report on Nubian archaeology at all (Adams, 1981b; Berry and Berry, 1972; Buzon, 2006; Carlson

and Van Gerven, 1979; Edwards, 2004; Geus, 1991; Godde, 2009; Irish, 2005; Smith, 2003c; Trigger, 1994; Williams, 1991). Without indigenous Nubian texts (and only partially deciphered Meroitic language texts available in later periods), early archaeologists in the Nile Valley tended to rely on information obtained from Egyptian written records (Adams, 1977; Arkell, 1961; Raue, 2019). These Egypto-centric records reinforced the commonly held view (in both ancient and modern times) that Egypt was the superior civilisation in the ancient Nile Valley, and that the Nubians were a poor, primitive people with limited cultural and technology advancements (Adams, 1977; Hafsaas-Tsakos, 2009; O'Connor, 1993; Smith, 2003c; Yamada and Kimmel, 1991).

The first large-scale Nubian excavation project was the First Archaeological Survey of Nubia (1907–1911), led by the American archaeologist George Reisner. The aim of this project was to recover archaeological artefacts from the Lower Nubia region that was due to be flooded with the construction of the original Aswan Dam (Edwards, 2004; Firth, 1912, 1915, 1927; Reisner, 1910). Following on from this project, Reisner led the 1913 Harvard-Boston expeditions to survey the area near Kerma, south of the Third Cataract. Reisner's expedition reports from this survey subsequently shaped the interpretation of the Kerma population, and ancient Nubian populations in general, for decades (Dunham, 1955; Edwards, 2004). Reisner, along with many other Nubian archaeologists at the time, was heavily influenced by the cultural diffusionism paradigm, in which observed cultural advancements and technological developments over time were attributed to population movement and racial differentiation (Raue, 2019; Trigger, 1990). It was argued that the 'emergence of civilisation' observed in Nubian archaeology resulted from an influx of 'whiter' populations, while the apparent gaps in the archaeological record were explained by shifts to populations with 'darker' skin (Reisner, 1923a,b; Trigger, 1994). In the context of this paradigm, Reisner hypothesised that the grand architectural remains and material wealth associated with Kerma could only be the result of Egyptian immigration and control of the area (Adams, 1981b; Bernal, 1987; Trigger, 1994). Early physical anthropologists were also influenced by the cultural diffusionist paradigm, with much of their research focused on the identification and classification of different 'types' of people present in the skeletal record of ancient Nubian archaeological sites (Binder, 2019).

Morton (1844) was the first to define the cranial morphological characteristics of an 'Egyptian'; a classification that was subsequently extremely influential to researchers interested in defining 'racial' types in Nile Valley populations. The early American and European archaeologists excavating sites in the Nile Valley were working during a period in

which racism was culturally widespread, and the existence of racial hierarchies was considered as the natural order for both modern and ancient populations (Raue, 2019). Racial hierarchies were used politically to justify colonialist practices, and for those working in the Nile Valley, the Nubians were considered culturally and technologically inferior to the Egyptian 'Dynastic' race (Raue, 2019; Roy, 2011). The physical anthropologist G. E. Smith was a strong proponent of the cultural diffusionism model, and his research aimed to identify racial groups based on the appearance of 'Negroid' cranial morphological traits (Smith and Wood-Jones, 1910). The discovery of 'racial' differences between Egyptian and Nubian cranial morphology further reinforced the presumed link between race and cultural/technological advances (Junker, 1921; Morant, 1925; Smith and Derry, 1910a,b). These paradigms influenced the analysis and interpretation of early archaeological research and had a long-lasting effect on how ancient Nubian populations were viewed and researched throughout the 20th century.

Three years after the Republic of Sudan became an independent nation, the Egyptian government announced plans in 1959 to construct a High Dam at Aswan, which would permanently flood the Nile Valley up to 200 km south of the modern Egypt/Sudan border (Trigger, 1994). In response to requests by both the Sudanese and Egyptian governments, the United Nations Education, Science and Culture Organization (UNESCO) led an effort to bring researchers from around the world to carry out archaeological research and salvage in the area due to be flooded. The resulting UNESCO campaign to 'Save the Monuments of Nubia' produced a vast amount of information about ancient settlement patterns in Lower Nubia, spanning the Neolithic through to the end of the Christian period (Säve-Söderbergh, 1987; Trigger, 1994). In addition, this global effort facilitated archaeological research that would finally recognise the leading role of Nubians in ancient Nile Valley politics, and as initiators of significant cultural and biological change in the region. Over the following decades, archaeological research in ancient Nubia steadily increased and spread further south, into regions of Upper Nubia and the Dongola Reach (Binder, 2019).

As discussed previously, most of the early physical anthropological research associated with ancient Nubia was focused on identifying racial differences between populations using skeletal morphology. A paradigm shift in bioarchaeology occurred with the publication of Carlson and Van Gerven's (1977) morphological study of a temporal series of crania from Nubia, which applied a biocultural approach to the study of human skeletal remains. A biocultural approach uses the cultural and behavioural framework of a population to contextualise observed human biological variation (Binder, 2019; Larsen, 2018). In their

research, Carlson and Van Gerven (1977) observed that Nubian farmers had more gracile faces and jaws, and shorter and rounder cranial vaults, compared with their hunter-gatherer predecessors. In the context of the cultural diffusionist paradigm, earlier researchers had attributed these morphological differences to population replacement; the agricultural populations with the rounder and more gracile crania had migrated and replaced the archaic, robust cranial groups. However, Carlson and Van Gerven (1977, 1979) questioned this racialised classification paradigm. Instead, they argued that the observed morphological differences between populations were reflective of the reduction in biomechanical demand on the masticatory complex associated with the shift from a tough hunter-gatherer diet to the soft and more processed agricultural diet. Importantly, subsequent testing of their masticatoryfunctional hypothesis offered a new way for other researchers to interpret craniofacial morphology in past human populations; the masticatory-functional hypothesis forms the framework for the current study.

Until recently, most of what was known about the prehistory of the Holocene period in ancient Nubia was based on research from Lower Nubia (e.g. Wendorf and Schild, 2001) and Central Sudan (Caneva et al., 1993; Haaland and Magrid, 1995; Reinold, 2007). Much of the research has been driven by salvage projects in areas of dam construction (such as the Aswan Dam and the Merowe Dam at the Fourth Cataract) (Adams, 1977; Paner, 1998; Welsby, 2003, 2008), expanding agriculture (Welsby, 2001b) and infrastructure projects (Mallinson et al., 1996). Only recently has systematic survey work and excavations in the Kerma area started to reveal hundreds of sites spanning several cultural periods (Honegger, 2007a, 2009). The research from the Northern Dongola Reach Survey (NDRS), conducted by the Sudan Archaeological Research Society (SARS), has begun to build a detailed chronological framework and cultural sequence in the area of Upper Nubia between the Third and Fourth Cataracts (e.g. Salvatori and Usai, 2008a; Welsby, 2001b). It is these populations from the Dongola Reach region of ancient Nubia that are the primary focus of the current research.

2.3 Geographical context and ecological perspective

The Nile River, with its unique environment and landscape, has heavily influenced the activities of both past and present human populations in Northeast Africa. Specifically, the Middle Nile Valley, the region between Aswan in Southern Egypt and the confluence of the Blue and White Niles in Khartoum in Southern Sudan, is the focus of this research (**Figure**)

2.1). Arable soil and a sufficient water supply are essential for sedentary populations (Klemm et al., 2019), and during periods of normal flow and adequate annual flooding, the Nile can provide a productive environment for crop growth and animal grazing up to 3 km from each riverbank (Butzer, 1959). Outside of this fertile area, the environment reverts to the barren, sandy deserts characteristic of most of northern Africa (Adams, 1977). Prehistoric populations relied heavily on the Nile River resources for sustenance, but also utilised the clay-rich Nile mud for architectural purposes; sun-dried mud-bricks were commonly used starting in the 3rd millennium BC (Klemm et al., 2019). Throughout the history of the Middle Nile region, fluctuations in the normal Nile River flow (both natural and anthropogenic) could dramatically change the local environment, alter patterns of population settlement, and ultimately influence the success of emerging nation states (Ball, 1939; Clark, 1980; Hafsaas-Tsakos, 2011; Hassan, 1997, 1998). In addition to the river, the desert also played a vital role in linking Nubian populations by providing communication and transport passages when the river was unnavigable (Auenmüller, 2019).

Along the Middle Nile are a series of six granite outcrops, the Cataracts, which span the Nile River from Aswan (in modern-day Egypt) to the Shabluka Gorge (in modern-day Sudan) (**Figure 2.1**). As major geological features, the Cataracts form dangerous rapids that narrow the navigable channel of the river outside of the annual flood season, and consequently impede travel and trade along the Nile. The location of the Cataracts is often used to delineate regions and populations in the ancient Nile Valley (Edwards, 2004). For much of the region's history, the First Cataract, just south of Aswan, marked the geographical border between ancient Egypt and Nubia (**Figure 2.1**) (Edwards, 2004).

The ancient Nubian civilisation is separated into two geographical sub-regions: Lower (northern) and Upper (southern) Nubia (Edwards, 2004). The region between the First and Second Cataracts (located near present-day Wadi Halfa) encompasses Lower Nubia (**Figure 2.1**). Today, much of the Lower Nubian region is submerged under Lake Nasser/Nubia following the construction of the Aswan Dam in the 1960s (Hafsaas-Tsakos, 2009). Upper Nubia, an area often referred to as "Kush" by the ancient Egyptians, extended south from the Second Cataract (Dixon, 1958; Kendall, 1997). Between the Second and Third Cataracts, the geographical boundary separating Lower from Upper Nubia is marked by an inhospitable region called the *Batn el-Hajar*, or 'Belly of the Rocks'. The *Batn el-Hajar* is a barren region with extremely limited arable soil due to a granite-rich bedrock (Van Gerven et al., 1995). The environmental barrier created by the *Batn el-Hajar* region is accentuated during the dry season,

when the Nile is often reduced to a narrow stream with rocky outcrops and islands, preventing movement along the river (Bard, 2015). Further south, between the Fifth and Sixth Cataracts, lies the ancient city of Meroe, the southern capital of Kush from c. 350 BC–AD 350 (Morkot, 2000). The Sixth Cataract of the Nile is approximately 100 km north of the modern-day city of Khartoum, and is often used to mark the southern boundary of the ancient Nubian civilisation (**Figure 2.1**) (Edwards, 2004). However, more recent research has shown that the influence of the ancient Nubian civilisation may have extended even further south of the Sixth Cataract, along the Blue and White Niles.





The region encompassing Ancient Nubia is outlined in orange. From Wikimedia Commons, adapted under the Creative Commons License: https://creativecommons.org/licenses/by-sa/3.0/deed.en.

The area between the Third and Fourth Cataracts is known as the Dongola Reach, named for the modern town of Dongola. This area was characterised in antiquity by a large and fertile alluvial plain that could support a dense population (Smith, 2003a; Trigger, 1976a). At the height of the flood season, the Kerma Basin could measure up to 15 km in width and 100 km in length, making it the largest span of fertile land between the First and Fourth Cataracts (Trigger, 1976a). The Dongola Reach has a long history of human occupation and was most notably the centre of major Nubian states at Kerma and Napata (**Figure 2.1**) (Arkell, 1961; O'Connor, 1991; Welsby, 2001b). It is worth noting that during the Pre-Kerma and Kerma periods, the Nile ran in multiple channels to the east of its current course, thereby influencing the location of the settlement sites that are found today (Honegger, 2005; Welsby, 2001b).

Many studies have demonstrated that the environment of today's Nile Valley differs greatly from that during the early Holocene (Ritchie et al., 1985; Williams and Adamson, 1980). The arid conditions that currently characterise northern Sudan and southern Egypt were not established until c. 1500 BC (Küper and Kröpelin, 2006). It is important to reconstruct the climate and environment of the ancient Nile Valley to understand how the river and the desert influenced patterns of human settlement (Auenmüller, 2019; Macklin and Lewin, 2015; Welsby et al., 2002; Woodward et al., 2015). Palaeoenvironmental and archaeological research has shown that within the Nile Valley, cultural changes were often concurrent with environmental fluctuations (DeMenocal and Tierney, 2012; Garcea et al., 2013; Hassan, 1997, 1998; Kröpelin et al., 2008; Küper and Kröpelin, 2006; Macklin and Lewin, 2015; Manning and Timpson, 2014; Mercuri et al., 2011). During periods of climatic fluctuation, the flexibility of the ancient Nile Valley populations to alter mobility patterns and subsistence strategy based on resource availability was crucial to their survival and prosperity (Armelagos, 2003).

2.4 Chronology of Ancient Nubian populations

The terminology used with reference to Sudanese Holocene prehistory is often criticised for reflecting European traditions rather than the unique history and local variation of the Middle Nile region (Sadig, 2013; Smith, 2013). In particular, the common chronological designations 'Mesolithic' and 'Neolithic' are almost universally used in archaeological literature to indicate the economic divide between hunting and gathering and food production. Arkell (1949) introduced the term 'Khartoum Mesolithic' to refer to populations in southern Sudan for which there was evidence of pottery vessels, but no evidence for plant or animal

domestication. However, the term Mesolithic, based on the European definition, does not fit well within a Sudanese context, and using the term Mesolithic to describe Nubian chronology and cultural sequences can be misleading (Sadig, 2013). Instead, the terms 'Epipalaeolithic' or 'Pre-pastoral phase' have been suggested to replace Mesolithic with reference to Sudanese archaeology (Garcea, 2004; Sadig, 2013). When used in a Sudanese context, the Epipalaeolithic reflects a period of fundamental socio-economic and technological changes across the Nile Valley. These changes vary by population, but may include a combination of pottery production, changes in resource exploitation and sedentism, and overall population growth (Haaland, 1995; Sadig, 2013). As such, the Epipalaeolithic terminology will be used throughout this thesis.

Similarly, Arkell (1953) defined the 'Khartoum Neolithic' based on an archaeological site with pottery, lithic artefacts and bones of domesticated animals, but with no evidence of cereal farming. However, in a European context the 'Neolithic' is associated almost exclusively with farming populations who have little to no evidence of hunting and gathering. Although the 'Neolithic' populations in North Africa were initially assumed to be culturally similar to the food-producing societies in the Levant and Europe, this is not the case. During this temporal period in Sudan, populations varied widely in their adoption of plant and animal cultivation, and still widely practiced hunting and gathering (Smith, 2013). Therefore, within Sudanese archaeology, the term 'Neolithic' is often used as chronological terminology rather than as a cultural definition (Sadig, 2013). Throughout this thesis, the term 'Sudanese Neolithic' will be used to differentiate these Nile Valley populations from the cultural traits associated with other Neolithic populations around the world (Edwards, 2007; Sadig, 2013).

The following section presents a broad chronological and cultural overview of ancient Nubia during the following periods: Late Palaeolithic, Epipalaeolithic, Sudanese Neolithic, Kerma, Napatan, and Meroitic (following the model from Edwards, 2007; Sadig, 2013). Particular attention is paid to populations within Upper Nubia and the Northern Dongola Reach, as these populations are the focus of this thesis research. However, these Upper Nubian populations will be described within the context of the larger cultural changes that were happening concurrently in Northeast Africa.

2.4.1 Late Palaeolithic (c. 15000–8500 BC)

During the Last Glacial Maximum (c. 18000 BC), most of Northern Africa was largely uninhabitable due to extreme aridity and a significantly reduced Nile River flow (10–20% of modern annual flow) (Close and Wendorf, 1990; Gasse, 2000; Godde and Jantz, 2017; Lamb et al., 2007; Pachur et al., 1987; Swezey, 2001; Williams, 2009). Around 12500 BC, there was a gradual improvement in climatic conditions that ultimately led to the Holocene Wet Phase (c. 9000–5000 cal BC); a period characterised by high Nile flows, the formation of freshwater lakes and the presence of an abundant, savannah-like vegetation across the Sahara (Williams et al., 2010). It was during the early stages of this climatic improvement that populations began to settle along the Nile, although Northeast Africa was still sparsely populated into the early Holocene. Archaeological sites from the Late Palaeolithic are rare due to low population density, high population mobility (Nicoll, 2004; Yeshurun, 2018) and the prevalence of destructive taphonomic processes such as erosion (Usai, 2019). Consequently, relatively little is known about the overall chronology, variation in settlement patterns, subsistence systems or symbolic behaviour of Late Palaeolithic Nubian populations (Usai, 2019).

Most of what is known about the cultural groups of the Late Palaeolithic derives from salvage projects necessitated by the construction of the Aswan Dam near the Second Cataract (Usai, 2019). Between c. 15000–8500 BC, the Nile Valley was populated by multiple cultural groups, each with a distinct combination of subsistence strategy and mobility patterns to exploit a range of local environments (Clark, 1971; Wendorf et al., 1976). Late Palaeolithic populations in southern Egypt/northern Sudan were largely nomadic and egalitarian, using a combination of opportunistic hunting of wild animals gathering near water sources, such as ungulates and hippopotami, and fishing in the Nile (Butzer and Hansen, 1968; Churcher, 1972; Gautier and Van Neer, 1989; Köhler, 2010; Peters, 1990; Yeshurun, 2018). The faunal remains from sites in Upper Egypt and Lower Nubia are similar, suggesting comparable environments with a narrow, watered corridor surrounded by hyper-arid desert (Schild and Wendorf, 2010; Vermeersch and Van Neer, 2015). South of the Second Cataract, the evidence from the Nubian sites around Wadi Halfa show a more diverse archaeofauna that includes monkeys, antelopes and other game animals characteristic of African wetland and riverine thickets (Gautier, 1968; Osypińska and Osypiński, 2016). However, there is little evidence (archaeological or skeletal) for Late Palaeolithic occupation south of the Second Cataract (Edwards, 2004).

Late Palaeolithic lithic industries were diverse, suggesting that there may have been seasonal and spatial variation in the hunting and fishing subsistence activities practiced by these populations (Clark, 1971, 1980; Gautier, 1968; Hassan, 1980; Osypińska and Osypiński, 2016; Van Peer et al., 2003; Wetterstrom, 1993, 1997; Yeshurun, 2018). The 'Qadan' lithic industries found at the Late Palaeolithic sites of Jebel Sahaba (c. 13000–9000 BC; near the Second Cataract) and at Toshka (just north of modern-day Wadi Halfa) suggest a more varied diet compared with earlier periods (**Figure 2.2**) (Irish, 2000; Kemp, 1989; Midant-Reynes, 2000; Phillipson, 2005; Shinnie, 1996; Trigger, 1976b; Wendorf, 1968). In addition, the widespread presence of grinding stones found in Late Palaeolithic sites suggest that as early as c. 15000 BC, the foraging and processing of wild grains and cereals was an important component of the overall diet (Clark, 1971; Shinnie, 1996; Wendorf and Schild, 1984).

The Late Palaeolithic cemeteries show evidence of mortuary ritual, including body placement and burial offerings, suggesting that these populations were composed of stable social groups with established territory (Clark, 1980; Wendorf, 1968). During this period, there may have been an expansion of populations and enhanced competition for resources increasing the risk of inter-group conflict. Resource competition has been traditionally used to explain the conflict inferred by the injuries and violent deaths of the Jebel Sahaba individuals (Anderson, 1968; Bard, 2015; Hassan, 1980). However, more recent analysis of the Jebel Sahaba individuals did not find skeletal evidence of systemic stress to support the narrative of widespread environmental pressure and resource depletion (Judd, 2006).

2.4.2 Epipalaeolithic (c. 8500–5700 BC)

A variety of floral, faunal and sedimentary evidence indicate that during the first half of the Holocene, environmental conditions across North Africa were much more hospitable compared with today's arid conditions (Alley et al., 1997; Cremaschi et al., 2014; Küper and Kröpelin, 2006; Watrin et al., 2009). This early Holocene climatic period in Northeast Africa is known as the African Humid Period (AHP) and was a period of high rainfall leading to an expansion of savannah vegetation (Cremaschi et al., 2014; DeMenocal et al., 2000; Nicoll, 2004; Sultan et al., 2013). As environmental conditions improved, populations moved away from the Nile alluvial plain and into desert areas that were suitable for at least short-term seasonal occupation (Edwards, 2004; Gatto, 2012; Gatto and Zerboni, 2015; Küper and Kröpelin, 2006; Wendorf and Schild, 2001). Populations also began moving north along the Nile. There is archaeological evidence that during this period, populations of pottery-using hunter-fisher-gatherers from the Sixth Cataract resettled in the Middle Nile Valley (Edwards, 2007; Küper and Kröpelin, 2006).





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The Nubian Epipalaeolithic (c. 8500–5700 BC) was first identified using archaeological evidence discovered near the modern-day city of Khartoum (**Figure 2.2**; **Table 2.1**) (Arkell, 1947, 1949; Haaland and Haaland, 2013; Salvatori and Usai, 2009; Salvatori et al., 2011). At the time of its discovery in 1944, this site provided evidence for the oldest pottery-bearing population known in the Middle Nile Valley, and became the type site for the 'Khartoum Mesolithic' or 'Wavy Line Culture' (Arkell, 1947, 1949). These pottery-using hunter-gatherers were established in the region by at least c. 8000 BC. Items defining the Epipalaeolithic at Khartoum have subsequently been found elsewhere in the Sahara, spanning a 2000–3000 year period along the Blue and White Niles, and as far north as the Dongola Reach (Arkell, 1949; Caneva, 1983; Edwards, 2004, 2007; Fernandez, 2003; Haaland, 1995; Manning and Timpson, 2014; Trigger, 1976b). The identification of pottery-using hunter-gatherers or other other of populations around the world, that a causal relationship exists between pottery development and agriculture (Edwards, 2004; Haaland, 1995; Haaland and Magrid, 1995; Khabir, 1987).

The extensive and dense spread of material found at early Holocene sites along the Nile reveal that Nubian Epipalaeolithic groups were semi-nomadic, occupied seasonal sites and used a combination of hunting, fishing and gathering for subsistence (Arkell, 1949; Caneva, 1983; Edwards, 2007; Fernandez, 2003; Haaland, 1995). Evidence from the large amounts of pottery and grinding stones found with these populations suggests that their diet included both wild wetland and savannah vegetation (Barich, 1998; Harlan, 1989; Hassan, 1980; Hillman, 1989; Wengrow, 2006). However, grinding stones can also be used for tool sharpening and pigment grinding, and therefore their presence in an archaeological assemblage is not definitive evidence of cereal consumption (Edwards, 2004). It is possible that the combination of a favourable climate and abundant natural resources, as a result of the AHP, allowed Epipalaeolithic populations to remain semi-sedentary without developing a reliance on domesticated plants or animals (Adams, 1977; Hassan, 1986; Holl, 2005). This level of sedentism among Epipalaeolithic Middle Nile Valley populations may have subsequently expedited the transition to food production, as compared with more mobile hunter-gatherers (Marshall and Hildebrand, 2002; Marshall and Weissbrod, 2011).

Despite overall favourable conditions during the AHP, there were still periods of aridity (Alley et al., 1997; Gasse, 2000; Gasse and Van Campo, 1994; Hoelzman et al., 2010; Nicholson and Flohn, 1980; Smith, 1998; Wendorf and Hassan, 1980). Therefore, populations in the Nile Valley had to remain relatively mobile to react to resource availability. The
increasing aridity that began during the Middle Holocene (c. 6500 BC) shifted the desert margin southwards and led to a major population resettlement from Lower Nubia and the hostile desert environments southwards to the Nile Basin and Kerma region, with its abundant resources (Gatto, 2012; Gatto and Zerboni, 2015; Honegger et al., 2012; Küper and Kröpelin, 2006; Macklin et al., 2015; Midant-Reynes, 2000; Nicoll, 2004; Pachur et al., 1987; Said, 1993). This population influx into the Kerma Basin led to the formation of several large settlements with associated cemeteries, most notably at El-Barga and Wadi El-Arab (**Figure 2.2**) (Brewer et al., 1994; Chaix and Honegger, 2015; Edwards et al., 2012; Honegger, 2004a, 2006a, 2010, 2011, 2014; Honegger et al., 2012; Welsby, 2001b).

The discovery of habitation structures and the presence of cemeteries indicates that the Epipalaeolithic populations in the Kerma Basin were sedentary, or at least that these populations organised their activities around a principal habitation site (Honegger, 2019). The faunal evidence from El-Barga is diverse and includes large quantities of animals both from aquatic/wet environments (such as molluscs, fish and turtles) and from the savannah and forested environments (such as giraffes and monkeys) (Chaix, 2019; Neumann, 1989). This provides further evidence to support the classification of Upper Nubian Epipalaeolithic populations as primarily hunter-fisher-gatherers, with associated pottery production (Linseele, 2012; Welsby, 2003). Middle Holocene presence outside of the Kerma Basin appears to have been limited, reflecting the reliance of populations on the resources in Upper Nubia during arid periods (Edwards, 2004).

It was around this time of mid-Holocene aridification and migration into the Kerma region that some populations along the Nile Valley began the shift from hunting-fishing-gathering (foraging) to farming (food production) (Barker, 2013; Honegger, 2019). Some researchers refer to the period between c. 7200–5000 BC as the 'proto-pastoral phase', in which the Nubian economy was still largely based on hunting and fishing, but evidence for food production (particularly herding) begins to appear (Honegger, 2014). There is growing evidence for the widespread adoption of herding in the centuries after c. 6000 BC, and herding became the defining characteristic of the following regional (i.e. the Kerma Basin) 'Neolithic' (Marshall and Hildebrand, 2002). Archaeological sites in the Kerma Basin provide particularly valuable information concerning the shifts from foraging to food production and the associated changes in population mobility (Barker, 2006).

Date B.C.	Egypt	Lower Nubia	Upper Nubia		
c. 8500–5700	Epipalaeolithic				
c. 5700–3500 BC		Sudanese Neolithic			
c. 3500–3050 BC	Predynastic Period	Sudanese Neolithic/A- Group	Sudanese Neolithic/Pre-Kerma		
c. 3050–2500	Early Dynastic Period (Dynasties 1–2)	A-Group Pre-Kerma			
c. 2500–2150	Old Kingdom Dynasties (3–6)				
c. 2150–2050	1 st Intermediate Period (Dynasties 7 – first half 11)	C Group	Kerma Ancien		
c. 2050–1750	Middle Kingdom (Second half of Dynasty 11–13)	Coloup	Kerma Moyen		
c. 1750–1500	2 nd Intermediate Period (Dynasties 14–17)		Kerma Classique		
c. 1500–1050	New Kingdom (Dynasties 18–20)	Kerma Recent/Eg	Kerma Recent/Egyptian Occupation		
c. 1050–750	3 rd Intermediate Period (Dynasties 21–24)	Pre-Napatan			
c. 750–350	Late Period (Dynasties 25–30)	Napatan			
c. 350–30 c. 30–AD 350	Ptolemaic Period Roman Period	Meroitic			

Table 2.1 Chronology of Egypt, Lower Nubia and Upper Nubia

Adapted from Edwards, 2004 and S.T. Smith, 1998

2.4.3 Sudanese Neolithic (c. 5700–3000 BC)

In contrast to the Late Palaeolithic and early Holocene periods, significantly more research has been carried out on the Sudanese Neolithic communities of the Middle Nile Valley. Systematic surveys and excavations have revealed a high density of Neolithic sites in the Kerma Basin, concentrated along the Nile palaeochannels (Edwards, 2004; Edwards et al., 2012; Honegger, 1999, 2004a,b, 2011, 2014; Honegger et al., 2013; Reinold, 1987, 2001; Salvatori and Usai, 2008a; Welsby, 2000, 2001b). The nature of these sites varies greatly (from permanent to seasonally habited sites), as populations began incorporating the domestication

of animals and cereals (of Near Eastern origin) alongside their hunting, fishing and gathering subsistence activities (Haaland, 1981, 1987; Salvatori and Usai, 2019).

The Sudanese Neolithic (c. 5700–3000 BC) is often divided into two sub-periods: the Early Neolithic (c. 5th millennium BC) and the Late Neolithic (from c. 4th to early 3rd millennium BC) (**Table 2.1**) (Edwards, 2004). The Sudanese Neolithic differs from the Neolithic period in other regions because a reliance on cereal-based agriculture was not the defining feature of the Sudanese Neolithic (Edwards, 2004; Sinclair et al., 1993). Currently, the earliest evidence of cereal domestication dates to the end of the Sudanese Neolithic (Madella et al., 2014; Out et al., 2016). Although the defining feature of the Sudanese Neolithic has traditionally been the development of, and increased reliance on, livestock herding, there was considerable variation in the balance of herding, hunting, fishing and eventual domesticated plant cultivation practiced by each population (Harlan, 1989; Holl, 1998a,b; Marshall and Hildebrand, 2002; Neumann, 2003, 2005; Salvatori and Usai, 2019).

The domestication of animals radically changed the lives of ancient Nubians during the Neolithic (Edwards, 2004; Haaland, 1991). The first definitive evidence of domestic livestock in the Kerma region originates from the Early Neolithic cemetery at El-Barga, where a single cattle skull (bucranium) was found associated with a grave dated to c. 5800 BC (Figure 2.2) (Gautier, 2001; Honegger, 2004a, 2005, 2007b; Linseele, 2013). Around the same time, domesticated sheep and goats (caprines) appeared in the region and became increasingly widespread during the sixth millennium BC (Close, 2002; Gautier, 2001; Vermeersch et al., 1994). DNA analyses have demonstrated that the domestic cattle, sheep and goats found in Northeast Africa were originally introduced by migrating populations from the Levant in the Near East (Brass, 2018; Gatto and Zerboni, 2015; Olivieri et al., 2015; Stock and Gifford-Gonzalez, 2013). This evidence refutes previous claims that North Africa was an independent centre of cattle domestication (e.g. Wendorf and Schild, 2001). Once introduced, reliance on cattle and caprines quickly spread throughout the region, alongside continued widespread desertification and expansion of population movement and trade (Bianchi, 2004; Gatto and Zerboni, 2015; Hassan, 2002; Honegger, 2014). With the ease of movement to resource-rich areas, domesticated herds were suited to desert environments (Di Lernia, 2002; Marshall and Hildebrand, 2002).

It can be difficult to identify levels of pastoralism in past populations because the presence of animal bones in an archaeological context can be an unreliable indicator of livestock use in day-to-day subsistence (Chang and Koster, 1986). Faunal remains in a funerary

context are more likely to represent animal death and/or consumption for symbolic practices, rather than reflect normal subsistence (Arioti and Oxby, 1997; Haaland, 1987; Pöllath, 2008). In many modern African pastoralist societies, cattle are a symbol of status and prestige used to reflect the owner's wealth and prosperity (Bender, 1978; Edwards, 2004). Cattle are often slaughtered during special feasts and for ritual purposes and cattle skulls (bucrania) are abundant in a funerary context (Pöllath, 2008). Therefore, the prevalence of livestock remains in grave goods is more likely to represent their symbolic value than the proportion and numbers of animals herded by the population (Pöllath, 2008). For example, sheep and goats are tradeable and can be easily converted into consumable goods (milk and meat), but they are often underrepresented in a funerary context (Pöllath, 2008). Furthermore, evidence from modern pastoral groups in East Africa indicates that secondary animal products, such as cattle milk and/or blood, are often more important for subsistence than the animal meat itself. Saharan rock art scenes dating from c. 4000–3000 BC, and even earlier, depict animal milking, indicating that it may have been practiced by ancient populations (Simoons, 1971).

It appears that there was a more widespread pastoral tradition in ancient Nubian populations compared with contemporaneous Egyptian populations (Linseele, 2013). However, for early Nubian herders, domesticated animals were just one way to acquire food, and these populations continued to hunt wild animals and fish (Pöllath, 2008). Petroglyphic evidence during this period depicts the hunting of pachyderms, giraffes, ostrich and other birds (Bakheit, 2014). Between the Second and Fourth Cataracts, archaeologists have found extensive networks of stone 'walls' that likely represent hunting drives or traps (Edwards, 2006b; Hester and Hobler, 1969; Riemer, 2004, 2009; Wolf and Nowotnick, 2006). These structures were used throughout the Neolithic and date to as late as the second millennium BC (Edwards et al., 2012). In addition, there is archaeological evidence that technological advances during this period fuelled an increase in open-water fishing and the exploitation of aquatic resources (Linseele et al., 2014; Van Neer, 2004).

The warmer and wetter conditions of the early Holocene meant that the gathering of wild grasses and fruits was common among North African populations (Hillman et al., 1989; Mercuri, 2008; Wendorf et al., 1993, 2001; Wendorf and Schild, 1980, 2001). Although direct evidence of wild plants in archaeological sites is rare, indirect evidence of plant subsistence, such as imprints of seeds and fruits and the presence of tools such as grinding stones, have supported the theory of extensive wild plant use in ancient Nubia (Barich, 1998; Clapham, 2019; Haaland, 1999; Magid, 1989). However, until recently there had been little direct

archaeobotanical evidence for the presence of domesticated cereals during the Nubian Neolithic. This lack of evidence was attributed to a combination of factors, including the types of archaeological site found, as well as the practical difficulties involved in recovering plant remains (Magid, 1995; Salvatori, 2012; Usai et al., 2014; Young and Thompson, 1999).

However, archaeobotanical evidence of *Hordeum* sp. phytoliths and starch grains, identified as domesticated emmer wheat and hulled barley, have recently been found in the Neolithic cemeteries of R12 in Upper Nubia and Ghaba in central Sudan, dating to c. 5000 BC (**Figure 2.2**) (Madella et al., 2014; Out et al., 2016; Ryan et al., 2016). These discoveries are the oldest evidence of Near Eastern domesticated crops in Africa, predating both the then-earliest evidence of cultivated barley from Nubia (at Kadruka, c. 4500–4000 BC) and the oldest cereal finds from the Fayum in Egypt (c. 4650–4350 cal BC) (**Figure 2.2**) (Caton-Thompson and Gardner, 1934; Madella et al., 2014; Out et al., 2016; Reinold, 2001, 2006; Wendrich et al., 2010). It is important to note that the R12 plant remains were found in a funerary context and therefore, might not reflect the use of domesticated crops in day-to-day subsistence. However, these discoveries support the growing body of evidence for the presence of domesticated emmer wheat and barley in the economy and diet of Neolithic Nubians (Madella et al., 2014).

Based on the current evidence, it is difficult to determine when cereal cultivation began during the Nubian Neolithic, or what proportion of the Nubian diet during this period consisted cultivated grains. The presence of domesticated cereals at R12 and Ghaba is not definitive evidence of local crop cultivation, as cultivated cereal products may have been traded into the area from another region. However, there are several factors that support the idea that the Nubians residing within the Dongola Reach were, to some degree, cultivating their own grains. The Neolithic Dongola Reach was particularly suitable for the cultivation of Near Eastern crops due to the fertile alluvial land along the river and the natural flood basins created by the Nile palaeochannels (Macklin et al., 2013; Welsby, 1996b). It is also possible that Neolithic populations could quickly adopt cultivated grains because they were already extensively exploiting wild grasses (Hillman et al., 1989; Mercuri, 2008; Wendorf and Schild, 1980, 2001). Since there is evidence that domesticated animals were introduced much earlier into the Nile Valley (c. 6000 BC) (Honegger, 2005, 2007b; Linseele et al., 2014), it may be that future excavations of ancient Nubian sites reveal even older evidence of domesticated cereals (Out et al., 2016). Although the recent archaeobotanical evidence suggests that cereal cultivation was present in these populations earlier than previously thought, Neolithic populations most likely still relied primarily on pastoralism and hunting/gathering for subsistence (Madella et al., 2014; Out et al., 2016). It is clear that within Nubian populations, there was a gradual shift from generalised to more specialised subsistence economies (Linseele, 2010). However, the development of food production in ancient Nubia was necessary to form and sustain the later, larger civilisations.

The transitions underway in the Sudanese Neolithic were not only about changing subsistence and technology, but also included shifts in ideology and social structure (Edwards, 2004; Haaland, 2012). By the middle of the 5th millennium BC, there was a shift from variability in pottery shapes and decorative motifs to a new standardised style, reflecting the presence of a strong regional identity between populations in Upper Nubia (Salvatori, 2008a; Salvatori and Usai, 2019). In addition, it was during the Sudanese Neolithic that large formal cemeteries began to appear and replace the smaller group burials of earlier periods. Domestic livestock bones, particularly cattle bucrania (horns and frontal bone), and plant remains have been found in Neolithic graves throughout the Middle Nile Valley (Chaix and Honegger, 2015; Lecointe, 1987; Madella et al., 2014; Reinold, 1991, 2001; Ryan et al., 2016; Salvatori and Usai, 2008a, 2019). In contrast to the evidence from the pottery design, there was much more regional variability in funerary rituals between populations. However, across all populations there was an increase in the disparity of grave goods between individuals, as levels of social hierarchy expanded and individuals were buried with objects reflecting their rank (Anderson, 1992; Edwards, 2004; Reinold, 2001; Salvatori and Usai, 2008a). In addition, the popularity of jewellery and other personal adornment items grew at this time, suggesting not only increasing craftsmanship, but greater social complexity and a growing importance of communicating individual status and identity (Edwards, 2004; Salvatori and Usai, 2019).

Despite the period of Neolithic prosperity during the 5th millennium BC, a gap in the archaeological record begins after c. 4000 BC (Sadig, 2013) and continues until c. 3400 BC; although in some regions of Upper Nubia this gap lasts until c. 2700–2500 BC (Honegger, 2019). Global cooling and rainfall decline from c. 4000–3000 BC marked the turn towards modern-day levels of aridity in Egypt and Sudan. Several major tributaries and palaeolakes of the Nile dried up, and the palaeochannels shifted westward (DeMenocal et al., 2000; Gatto and Zerboni, 2015; Haynes Jr., 1987; Kröpelin, 1987; Küper and Kröpelin, 2006; Lézine, 1989; Ritchie et al., 1985; Smith, 1998; Touzeau et al., 2013; Wendorf and Hassan, 1980; Williams, 2009). This climatic deterioration led to another major resettlement in the fertile Dongola Reach with a dense network of permanent agricultural settlements developing along the

margins of the Nile palaeochannels (Gratien, 1998; Gratien et al., 2003; Hoffman, 1991; Le Houérou, 1992; Malville et al., 1998; Nicoll, 2004; Welsby et al., 2002; Zerboni, 2013).

2.4.4 Pre-Kerma (c. 3500–2500 BC)

Traces of settlements begin to reappear in the Dongola Reach dating to c. 3400–3200 BC (Honegger, 2019). These sites represent the Pre-Kerma population, who existed concurrently with the A-Group population in Lower Nubia (c. 3700–2800 BC) (Table 2.1) (Bonnet, 1997; Edwards, 2004). The A-Group was an agro-pastoral polity primarily centred around the First Cataract in Lower Nubia, although A-Group sites have been found as far south as the Second Cataract (Gatto, 2000; Nordström, 1972). Evidence from archaeological sites demonstrates that there was variation in mobility patterns and subsistence practices between different A-Group populations, with a clear distinction between sites along the Nile and those in the desert. Sites adjacent to the Nile show evidence of fishing and cultivation, whereas desert sites have evidence of domesticated animals and herding (Gatto 2006, Nordström, 1972). The value of herding to the A-Group population is further emphasised by the presence of ritual animal remains in elite burial grounds (Gatto, 2020). The A-Group population also established extensive trade networks with Predynastic Egypt to the north (O'Connor; Shinnie, 1996). However, a combination of increasingly arid conditions in the region and the unification of Egypt under the First Dynasty (c. 3050 BC) led to the decline of the A-Group population, with sites disappearing by c. 2800 BC (Edwards, 2004; Gatto, 2020; O'Connor, 1993).

As compared with the A-Group population in Lower Nubia, little is known about the Pre-Kerma period. The primary Pre-Kerma settlement was located near the city of Kerma (Honegger, 2004b; Marcolongo and Surian, 1993, 1997), but the population's influence spread as far south as the Fourth Cataract (Bonnet, 1997; Edwards and Osman, 2000; Geus, 1998; Honegger, 2006b, 2019). Although the A-Group and Pre-Kerma were distinct populations, there is increasing evidence for cultural similarities between the two groups, particularly with regards to pottery (Edwards, 2004; Honegger, 2020). However, additional research comparing the archaeological and skeletal evidence is needed to better understand the nature of the relationship between the A-Group and Pre-Kerma material; a result of historically low interest in Upper Nubia and poor archaeological preservation (Edwards, 2004). Almost all the current archaeological evidence for Pre-Kerma populations is restricted to the northern part of Upper Nubia.

The Pre-Kerma culture was first identified in the 1980s based on ceramic evidence from a site beneath Kerma's Eastern Cemetery (Emberling, 2014; Honegger, 2004b). This initial pottery analysis led to the chronological definitions of a Pre-Kerma Middle Phase c. 3000 BC and a Late Phase dating from c. 2900–2500 BC (Honegger, 2004b). The Early Phase is assumed to begin c. 3500 BC, but there is currently little to no archaeological evidence from this period (Table 2.1) (Honegger, 2019). Both the A-Group and Pre-Kerma populations had a primarily agro-pastoral economy, but fishing, hunting and gathering remained economically important (Beckett and Lovell, 1994; Nordström, 1972; Phillipson, 2005; Trigger, 1976a). Pre-Kerma sites provide evidence for a sedentary lifestyle, with the remains of storage pits and surrounding palisades, habitation huts and animal enclosures (Edwards et al., 2012; Honegger, 1999, 2004b,c, 2014). At Saï Island in Upper Nubia (c. 2900-2600 BC), the storage pits predominately contain caprine remains, with limited evidence of cattle (Figure 2.2) (Chaix and Honegger, 2015; Geus, 2004). However, closer to Kerma, cattle dominate the Pre-Kerma faunal assemblages (Honegger, 2004b). Pottery from the storage pits at Saï Island that date from c. 2700 BC have traces of cultivated cereals and fruit stones, suggesting that there was significant agricultural production in the Kerma Basin during this period (Bonnet, 1990; Geus, 2000, 2004; Hildebrand, 2007; Honegger, 1999, 2004c; Privati, 1988). In addition, the discovery of a substantial Pre-Kerma fortification (c. 3000 BC) indicates that the area was beginning to develop into a regional military power (Honegger, 2014).

With access to luxury goods and slaves from the interior of Africa, the expanding Kerma civilisation was a more valuable trading partner for Egypt than the A-Group (Bard, 2015; Bonnet, 1990, 1991, 1994, 1997; Gratien 1078; Shaw 2000a). Egypt, in part motivated to intensify trade with Kerma, led a military intervention during the First Dynasty (c. 3000–2890 BC) that resulted in the demise of the A-Group culture in Lower Nubia (Adams, 1977; Edwards, 2004; Morkot, 2000; O'Connor, 1993; Smith, 1991a; Smith and Horwitz, 2007; Vagn Nielsen, 1970). It is possible that some A-Group Nubians moved south to Upper Nubia and were assimilated into the Kerma culture. Other members of the A-Group may have remained in the Second Cataract area, eventually developing into the C-Group (c. 2500–1500 BC; **Table 2.1**). The lack of archaeological evidence from Lower Nubia suggests that the region may have been uninhabited for the next two centuries. In contrast, the high density of archaeological sites in the Northern Dongola Reach indicates a sustained occupation of the Kerma region between the Pre-Kerma and Kerma periods (Welsby, 2000). The continuity between Pre-Kerma and Kerma Ancien populations is also demonstrated through the discovery of earlier, Pre-Kerma

burials (c. 2550–2450 BC) west of the main burials from the Eastern Cemetery of Kerma (Honegger, 2004a, 2007b, 2013). The older burial pits and pottery are characteristic of the Pre-Kerma culture and, therefore, suggest a continuity into the formation of the Kerma state (Honegger, 2019; O'Connor, 1993). By the second half of the third millennium BC, the Pre-Kerma communities had transformed into an emergent political power that would eventually become the first Nubian state (Edwards, 2004).

2.4.5 Kerma (c. 2500–1500 BC)

The Kerma civilisation developed and prospered from c. 2500–1500 BC, and at the height of its political power controlled over 1,000 km of the Nile Valley and its hinterlands (Bonnet, 1990; Edwards, 2004, 2007; Gratien, 1978; Reisner, 1923b). The name Kerma has become synonymous with both the first Nubian State and the Nubian 'Bronze' Age. The primary settlement and religious centre of the emerging Nubian state was near the modern-day town of Kerma, just south of the Third Cataract (**Figure 2.2**). The geographical position of Kerma, on the Nile connecting Egypt, central Africa and the Red Sea, reflects its position as an important trading centre (Buzon and Judd, 2008; Edwards, 2004; Hafsaas-Tsakos, 2009; Kendall, 1997). The Kerma period is typically divided into three temporal periods: Ancien or Early (c. 2500–2050 BC), Moyen or Middle (c. 2050–1750 BC) and Classique or Classic (c. 1750–1500 BC) (**Table 2.1**) (Adams, 1977; Bonnet, 1992; Reisner, 1923a,b; Smith, 1998; Welsby, 2001b).

2.4.5.1 Kerma Ancien (c. 2500–2050 BC)

Ancient Egyptian texts suggest that, during the Kerma Ancien period, the Nubian population consolidated power under a unified ruler and faciliated trade between Egypt and central Africa (Breasted, 1962; Shinnie, 1996). This period also saw important developments in other populations living in the Nile Valley. The formation of the Old Kingdom (c. 2500–2150 BC) created political and religious unity in Egypt (**Table 2.1**). By c. 2500 BC, an indigenous Nubian population, the C-Group (c. 2500–1500 BC), had also re-established themselves in what was previously A-Group territory in Lower Nubia (between the First and Second Cataracts) (Bietak, 1986; Buzon, 2011; Gratien, 1995; Raue, 2002; Reisner, 1909; Trigger, 1976a; Vagn Nielsen, 1970).

Early Kerma settlements in the Northern Dongola Reach were more numerous and densely distributed compared with the distribution of sites during the Pre-Kerma period (Emberling, 2014). The Kerma sites were located both on the alluvial plain and along the desert edge, possibly reflecting a differentiation between predominately agricultural and pastoral populations (Chaix and Honegger, 2015). Further inland, areas were used for relatively short-term (perhaps seasonal) herding and/or hunting (Edwards et al., 2012; Wolf and Nowotnick, 2005). However, the discovery of occasional clusters of graves inland suggests that some communities may have lived more permanently away from the river (Edwards et al., 2012). The location of habitation sites may also reflect social distinctions between populations (Welsby, 2018).

Over time, the Kerma civilisation needed to expand its agricultural output to support its growing population. The Nile palaeochannels were essential to facilitate this agricultural expansion through the utilisation of the annually flooded, or *seluka*, land (Bonnet, 1992; Welsby et al., 2002). By growing cereal crops, herding and periodically hunting, the Kerma population was able to produce a resource surplus to support a hierarchical social structure, as evidenced by an increase in the differentiation of burial goods during this period (Adams, 1977; Buzon, 2011; Chaix, 1984, 1988; Chaix and Grant, 1993; Edwards, 2004; Emberling, 2014; Gratien, 1985; O'Connor, 1993; Trigger, 1976a). Compared with the modest burials of the Late Neolithic/Pre-Kerma period, the Kerma Ancien burials were characterised by an increasing abundance of grave goods and surface deposits. The symbolic and ritualistic importance of domesticated animals is clear from the remains of complete caprines and dogs found within graves and the placement of bucrania in front of the *tumuli*¹ (Chaix, 1986; Chaix and Grant, 1987; Honegger, 2019; Ryder, 1984a,b, 1987).

By c. 2150 BC, a combination of socio-political fragmentation alongside increasing aridity and reduced Nile flow led to a destabilisation of centralised power in Egypt, marking the beginning of the First Intermediate Period (Bell, 1970; Butzer, 2012; Krom et al., 2002; Stanley et al., 2003). During this period, Kerma continued to build its authority and establish itself as a substantial threat to Egypt's territory (Gatto and Zerboni, 2015).

¹*Tumuli* are mounds of earth and/or stones raised over a grave(s). In many cases, these mounds are covered with small rings of upright stones.

2.4.5.2 Kerma Moyen (c. 2050–1750 BC)

During the Kerma Moyen period (c. 2050–1750 BC; **Table 2.1**), Kerma became increasingly politically centralised, further developed trade route connections and expanded resource reserves (Gatto and Zerboni, 2015). As the Kerma Moyen population in Upper Nubia was growing rapidly in size and political power, the Egyptian state reunified under the Middle Kingdom (c. 2050–1750 BC) and established a southern capital at Thebes. In response to Kerma's growing political and military power, from c. 1943–1843 BC Egypt attacked and conquered Lower Nubia, and subsequently built military fortresses near the Second Cataract (Adams, 1977, 1984; Smith, 1997; Trigger, 1976a; Watterson, 1997). These mud-brick fortifications were occupied by Egyptian administrators and military personnel (Edwards, 2004; Smith, 1995, 1998), and were primarily used as a visual deterrent to Kerma encroachment into Lower Nubia and southern Egypt (Bard, 2015; Smith, 1995; Trigger, 1976a). However, the Egyptian fortifications were also used to control trade and population movement along the Nile (Bourriau, 1991; O'Connor, 1993; Smith, 1991b, 2003b). Egyptian influence over Lower Nubia altered the relationship between Upper and Lower Nubia, and as such, divergent Nubian cultures began to develop in both regions.

While Egypt was establishing its military presence further north, population and settlement density during the Kerma Moyen in Upper Nubia increased significantly. During this period, Kerma effectively controlled the entire region south of the Second Cataract, expanding its cultural and political influence along the Middle Nile and serving as the major intermediary for trade with southern Africa (Emberling, 2014; Trigger, 1976a). The city of Kerma became more powerful by expanding the city limits, developing its infrastructure and intensifying fortifications. Increased urbanisation of the city included the construction of permanent mud-brick houses, temples and a large royal palace (Bonnet, 1992). However, most of the Kerma population continued to live in communities outside of the city walls (Bonnet, 1990, 1992, 1994). By this time, agriculture and domesticated herd animals had become essential to the Kerma economy and diet, and on a much larger scale compared with earlier periods (Bianchi, 2004).

The city of Kerma was the religious centre of the Kerma civilisation, and as such, is associated with a cemetery that was in use for over 1,000 years and contains more than 20,000 graves (Bonnet, 1990; Edwards, 2004, 2007). The construction of large and elaborate temples, unique to Nubian architecture, known as *deffufas*, suggests an increase in the formalisation of

religious rituals during this period (Ambridge, 2007; Bard, 2015; Bonnet, 1992; Trigger, 1976a). Although construction began in the Kerma Moyen, the western *deffufa* was not completed until the Kerma Classique (Bonnet, 1984). The eastern *deffufas* were built later during the Kerma Classique period (Ambridge, 2007; Bard, 2015).

During the Kerma Moyen period, the differences between burials increased, with the appearance of larger *tumuli* surrounded by graves of associated individuals (Bonnet, 1990, 1992; Edwards, 2004; Schrader, 2015). Anthropological studies have shown that the individuals surrounding the central inhumations were biologically similar to each other, and to individuals buried throughout the cemetery (Buzon and Judd, 2008; Judd, 2004; Judd and Irish, 2009). Therefore, it is likely that the larger *tumuli* with a central inhumation were used for rulers, whereas the surrounding smaller *tumuli* may represent the willing sacrifices of high-status individuals or other free men/women from the Kerma community, rather than slaves or prisoners from other populations (Hafsaas-Tsakos, 2013). Some of the largest *tumuli* are also associated with hundreds of animal bones, particularly bucrania, reflecting the importance of cattle within Kerma ideology (Edwards, 2007). The evidence from the Kerma Moyen burials indicates an ever increasing powerful and socially stratified society. However, it would be during the following Kerma Classique period that the Nubian state would reach the height of political power and overall influence.

2.4.5.3 Kerma Classique (c. 1750–1500 BC)

During the Kerma Classique Period (c. 1750–1500 BC), Kerma reached the height of its power, both economically and territorially, regaining control of all of Nubia as far north as modern-day Aswan, from Egyptian control (Adams, 1977; Aldred, 1998; Bonnet, 1990, 1994; Edwards, 2007; Morkot, 2000; O'Connor, 1993; Török, 2009). The rising power of Kerma, supported by political and military alliances with the Hyksos (a Near Eastern population) contributed to the decline of the Egyptian Middle Kingdom, and Egypt entered the Second Intermediate Period (c. 1750–1500 BC; **Table 2.1**) (Bietak, 1996, 1997; Callender, 2000; Morkot, 2000; Smith, 1997). Kerma experienced rapid growth and expansion via trade with the C-Group population, the remaining Egyptians at the Second Cataract, and the Hyksos (Kendall, 1997; Smith, 1995).

During the Kerma Classique period, the Kerma capital itself more than quadrupled in size, growing from 6 to 25 hectares (Bonnet, 1994). The Eastern Cemetery continued to be

used, and it was during this period that some of the largest 'royal' *tumuli* were built, and the number of subsidiary graves and accompanying individuals increased considerably (Honegger, 2019). These elaborate burials demonstrated the political power of the Kerma rulers (Kendall, 1997; Reisner, 1923a,b). The grave goods associated with the Kerma Classique royal burials displayed vast wealth, and included ivory hooks, alabaster vessels, cattle hides, mica insets for clothing, bronze knives and 'tulipiform' beakers (Bonnet, 1994; Edwards, 2004). Over time, the animal offerings (particularly bucrania) in the graves became less numerous compared with earlier periods (Honegger, 2019). Instead, there was a shift towards the use of caprines in a funerary context (Chaix, 1994). It is likely that the decline in cattle funerary offerings was linked to increasing aridity which limited the land available for pastures and led to a reduction in cattle herding sizes (Chaix, 1994, 2019). Caprines were better suited for an arid environment, and as such became more abundant and important in the local economy (Chaix, 2019).

The revival of Egyptian military power during the New Kingdom (c. 1500–1050 BC; Dynasties 18-20), threatened Nubia's prosperity (Edwards, 2007; Shaw, 2000b). Around c. 1502 BC, the Egyptian Pharaoh Thutmose I captured both Lower and Upper Nubia. This act marked the end of Kerma as a regional power and began a period of Egyptian control over Nubia that would last c. 5 centuries (Morkot, 2001).

2.4.6 Kerma Recent and Egyptian Occupation (c. 1500–1050 BC)

The Egyptian New Kingdom conquest of Lower and Upper Nubia marked the end of the Kerma Classique period and the beginning of a 'Late' phase during which the Kerma region remained under Egyptian control. The Egyptians built stelae and monuments throughout the Kerma region to celebrate and reinforce their victory over the 'Wretched Kush' (Smith, 2003c). Primarily interested in the extraction of gold, the Egyptians established a colonial administration north of the Third Cataract (Emery, 1965; Kemp, 1989; Morkot, 1991; Säve-Söderbergh, 1991; Smith, 1995, 2003c). However, Egypt had less control further south, and it appears that within the Dongola Reach, local Nubian officials were able to maintain positions of leadership within the local colonial government (Edwards, 2004; Morkot, 1991).

Ever-increasing aridity and desiccation of land away from the river forced many permanent settlements to relocate along the main banks of the Nile. By the middle of the first millennium BC, the Nile palaeochannels, which had been crucial to the prosperity of the Kerma population, were significantly reduced and the flood waters of the Nile were largely restricted to the main channel of the Nile (Welsby et al., 2002). This climatic deterioration greatly reduced the agricultural output and carrying capacity of the region (Welsby et al., 2002).

It is around this time that the Kerma capital, Eastern Cemetery and central temple were abandoned (Breasted, 1962; Emberling, 2014). Kerma material culture also disappears from the major urban centres (Morkot, 2000; Nikita et al., 2014). Recent surveys and excavations indicate that there was a complex and multidirectional exchange of cultural practices between Nubians and Egyptians, with no evidence to suggest that Nubians uniformly assimilated to Egyptian traditions (Edwards and Osman, 1994, 2001; Schrader, 2015; Smith, 2003c; Welsby, 2001b). However, in urban centres, individuals may have been pressured to adopt Egyptian cultural traditions to maintain their status under colonial rule (Ward, 1994).

Outside of the urban centres, the fate of local Nubian traditions within rural Kerma communities during Egyptian occupation remains largely unknown. During this period, many communities migrated away from the old capital city and established new settlements to the southwest (Edwards, 2004). However, there is no evidence for population movement out of Nubia, or a return to a semi-nomadic lifestyle (Welsby, 2001b). It is likely that many Kerma period settlements continued to be occupied by indigenous populations throughout this period, with the addition of new settlements established along the Nile as its course gradually shifted west. In addition, although some cemeteries exhibit a general shift toward Egyptian mortuary tradition, local communities seem to have incorporated elements of indigenous tradition alongside Egyptian practices and objects (Säve-Söderbergh, 1991; Smith, 1998, 2003c). These burial patterns suggest that the Egyptian control allowed for the development of new Nubian cultural traditions (at least in rural populations), rather than necessitating a rejection of local cultural practices.

Egypt's colonial presence in Nubia continued until foreign invasion and environmental degradation led to another period of decentralised power in Egypt (Third Intermediate Period; c. 1050–750 BC) (Wilkinson, 2007). During this period, Egypt lost its power over Nubia and local Nubian leaders regained power. By c. 850 BC, the Nubians in Upper Nubia had successfully restored their own state system (Bard, 2015).

2.4.7 The Kushite Period (c. 750 BC–AD 350)

By the eighth century BC, the Dongola Reach was the site of the formation of the Second Kingdom of Kush, centred at Napata (located upstream of the Fourth Cataract) (Vincentelli, 2006; Welsby, 2019). There is a debate over the origins of the Napatan kingdom,

with no clear evidence to explain how the Napatan state regained control of the region (Edwards, 2007). Over time, the Kushite state would exceed the Kerma state in both size and influence, and at its peak extend southwards from Lower Nubia to modern-day Khartoum and along the Blue and White Niles (Edwards, 2004; Iliffe, 1997; Phillipson, 2005; Trigger, 1976b). In addition to Napata, there were major urban centres at Kerma and Kawa (Bonnet and Valbelle, 2006; Edwards, 2004). The Kushite Period has traditionally been divided into the Napatan (c. 750–350 BC) and Meroitic (c. 350 BC–AD 350) periods (**Table 2.1**) (Welsby, 1996a).

2.4.7.1 The Napatan Period (c. 750–350 BC)

By c. 760 BC, Napata had conquered Egypt and ruled for almost a century through a succession of rulers known as the 25th Dynasty (Aldred, 1998; Bard, 2015; Morkot, 2000; Smith, 1998). The Nubian Pharaohs combined aspects of Egyptian ideology, such as cosmology and mortuary rituals, with Nubian traditions to create a new and distinctive Kushite culture (Edwards, 2007). Increasing Assyrian aggression throughout the c. 650s BC led to the end of Nubian rule in Egypt. However, Napata maintained control over large regions of Upper and Lower Nubia, particularly in the region of the Second Cataract (Adams, 1977; Kirwan, 2002; Morkot, 2000; O'Connor, 1993; Shinnie, 1996).

Although Napata was the major economic and religious centre of the Napatan kingdom (Bard, 2015), there were major cities and associated cemeteries in other areas of the Dongola Reach such as el-Kurru, Nuri and Jebel Barkal, and additional settlements in the vicinity of Kerma and Wadi el-Khowi (**Figure 2.2**) (Edwards, 2004; Macadam, 1949, 1955). Many towns in Upper Nubia, such as Kawa, were important urban centres during the Egyptian New Kingdom and, following colonial withdrawal, remained influential during the Kushite period. However, it is unclear whether these sites experienced a continuity in occupation from the Egyptian colonial period, or were new urban complexes built on the sites of abandoned towns (Welsby, 2019). At Kawa, Kushite occupation precedes the period of Taharqo's building programme from c. 690–664 BC, so if there was any abandonment of the town after Egyptian rule, it was short lived (Welsby, 2017). It has been suggested that Kawa was one of the capitals of the independent Nubian states whose unification led to the formation of the Kushite state (Török, 2004).

Despite regional variability, Napatan populations were predominately agricultural (relying on barley and wheat) and used simple irrigation methods reliant on the annual Nile floods to keep numerous 'basins' (low-lying depressions away from the river, but still subject to flooding) agriculturally productive (O'Connor, 1993). In addition, fishing continued to be important, as evidenced by the discovery of fish in jars in a Napatan building in Kerma (Edwards, 2004). Napatan pottery and other objects have been found across the entire geographical range of the Napatan state (Buzon et al., 2016; Edwards, 2004; Edwards et al., 2012; Wolf, 2004).

Until recently, most archaeological work had focused on the monumental remains (temples, palaces and tombs) from this period in both Egypt and Sudan (Dunham, 1955; Macadam, 1949; Török, 1997a). Consequently, relatively little is known about wider social or economic conditions, or indeed the wider settlement patterns of the period. The relocation of the royal cemeteries from the Napata region to Meroe c. 350 BC defined a new and distinct era for the Kushite Kingdom.

2.4.7.2 The Meroitic Period (c. 350 BC–AD 350)

The act by the Nubian King Arkamani to move the royal cemetery from Napata to the town of Meroe marked the beginning of the Meroitic period (c. 350 BC–AD 350). Meroe, in the fertile Shendi reach area between the Fifth and Sixth Cataracts, 200 km northeast of Khartoum, replaced Napata as the capital of the Kushite state (**Figure 2.2**). Although the boundaries of the Meroitic state are difficult to define, it is widely accepted that Meroe established control of an expansive region stretching from south of modern Khartoum as far north as the Second Cataract (Edwards, 2004; Török, 2009). In the Dongola Reach, major Meroitic settlements have been identified at Jebel Barkal, Kawa and Kerma (Welsby, 2001a).

Although there was general cultural and political continuity between the Napatan and Meroitic periods, there were important differences in settlement distribution, economy and literacy. A locally developed, indigenous Meroitic writing system replaced the Egyptian hieroglyphics previously used for royal monuments (from the 3rd century BCE; Török, 1997b). Although the written annals of the Meroitic rulers have survived, the Meroitic language remains poorly understood and these accounts have remained largely undeciphered (see Rilly and de Voogt, 2012). Consequently, the translated historical records from this period are often from a Greek or, later, Roman perspective (as the Ptolemaic and Roman periods in Egyptian

history were contemporaneous with the Meroitic period in Nubia) (Adams, 1977; Edwards, 2004).

Moving the Kushite capital south to Meroe most likely also corresponded with dynastic/political changes. Many of the Napatan era urban centres were abandoned in favour of newer, larger settlements in central Sudan. A series of temples, shrines and palaces were built in the Meroe region (Edwards, 2004; Iliffe, 1997; Phillipson, 2005; Shinnie, 1996; Trigger, 1976b; Welsby, 1996a; Wolf et al., 2009), many using Egyptian styles of monumental architecture (Dunham, 1970; Török, 2002). Meroitic wealth was derived from a significant iron industry and expanding trade routes, particularly with China and India (Adams, 1977; Edwards, 2004; Humphris et al., 2018; Newman, 1995; Phillipson, 2005). Excavations at Meroe have suggested that iron production may have begun as early as c. 500 BC in the late Napatan period (Humphris et al., 2018; Rehren, 2001; Tylecote, 1982). Due to increasing wealth and population size, the Meroitic period was characterised by the development of a powerful elite social class.

The mortuary architecture, artefacts and iconography of the capital of Meroe and surrounding areas were characterised by mainly Egyptian traditions, typified by the Meroitic pyramids and practice of interring royal individuals in wooden coffins (Edwards, 2004; Francigny, 2012; Kendall, 1997). Further north around the Fourth cataract, the traditional tumulus structures that had been characteristic of the Nubian mortuary tradition for centuries were common (Francigny, 2012). However, Egyptian traditions were not just reserved for royal individuals. Meroitic pyramids have been found associated with non-royal individuals, and painted cartonnage coffins have also been associated with non-royal individuals at Kawa (Francigny, 2012; Welsby 2002). In addition, new Meroitic funerary traditions, such as the importance of grave goods reflecting the prosperous copper-alloy and iron industries, indicate that the Meroitic funerary culture was a mixture of traditional and novel, Egyptian and Nubian practices (Francigny, 2012).

In both Upper and Lower Nubia, the Meroitic subsistence economy was dependent almost entirely on agriculture. During this period, changes to agricultural practices led to an increase crop yields (Adams, 1981a; Edwards, 1989; Fuller, 2004a; Madella et al., 2014; Out et al., 2016; Shinnie, 1984). Traditional riverine agriculture in the Nile basin was dependent on a form of flood recession farming, exploiting the alluvium and seasonal islands exposed after the annual flood and within low-lying basins. Since this method of cultivation was reliant on natural flooding, it limited the geographical areas, time of year and variety of crops that could be grown (Clapham, 2019). The introduction of Egyptian methods of irrigation, such as the labour intensive *shaduf*, would have expanded the areas suitable for cultivation (Trigger, 1976b). However, the continued reliance on floodplain cultivation restricted the types of crops that could be grown to the winter crops of wheat and barley (Chowdhury and Buth, 2005; Fuller, 2004a, 2013; Hildebrand, 2007; Shinnie and Anderson, 2004).

It was during the Meroitic period that savannah crops with summer seasonality, particularly sorghum and millet, appeared in the archaeological record and indicate that agriculture had become sustainable throughout the year in Upper Nubia (Clapham and Rowley-Conwy, 2007; Fuller, 2004a; Wetterstrom, 1993). The introduction of the summer crops has often been linked to the introduction of the animal-driven waterwheel, known as the *saqia*, into Lower Nubia (Adams, 1977). However, the presence of domesticated sorghum and millet in the archaeological record predates the introduction of the saqia, and it may be that the successful cultivation of the new summer crops provided the incentive to adopt new irrigation technology (Fuller, 2004a, 2013). These summer crops were of African origin and droughtresistant, so they could be cultivated in areas with limited water supply (Clapham, 2019). Therefore, the introduction of the *saqia* led to an expansion of crop cultivation, rather than initiating the adoption of summer crops (Clapham, 2019). The addition of the summer crops to the winter cereals and pulses diversified the dietary base of the population, which improved health and led to further population growth (Clapham, 2019). Once fully introduced, the saqia vastly increased agricultural output and helped to sustain the ever-increasing Nubian population (Fuller, 2004a, 2013, 2015). Additional evidence indicates that alongside wild fruit consumption, there was cultivation of several fruit crops, such as dates and doum palm (Fuller, 2004a; Trigger, 1976b). There is also archaeobotanical evidence for the presence of grapes at Kawa (Fuller, 2004a).

Around AD 350, the Ethiopian/Axumite kings claimed sovereignty over the city of Meroe, and this led to the decline of the Meroitic population in this region (Edwards, 2004, 2007). Further north, the Romans took control of Lower Nubia and established a Roman fort at Qasr Ibrim, north of Abu Simbel (**Figure 2.2**). From this base, the Romans moved upstream and eventually captured the religious centre of Napata (Bard, 2015; Wilkins et al., 2006). The end of the Meroitic period was characterised by decentralisation and population fission, with several autonomous centres appearing under the X-Group (AD 350–550). There was a gap of 150–200 years between the decline of the Meroitic Kingdom and the arrival of Christian missionaries from Egypt into Nubia (AD 500) (Edwards, 2007). It is possible that

environmental changes, such as extreme fluctuations in Nile floods and droughts caused by low rainfall during the first millennium AD, contributed to cultural and political change alongside the influx of new religions and traditions (Hummert and Van Gerven, 1983; Van Gerven et al., 1995).

2.5 Summary

This chapter examined the cultural history of the Middle Nile Valley from the Late Palaeolithic (c. 15000–9000 BC) to the Meroitic (c. 350 BC–AD 350). As the specific focus of this research is on populations from the Dongola Reach of Upper Nubia, the history of this region was specifically highlighted.

The majority of Late Palaeolithic (c. 15000–9000 BC) sites in the Nile valley have been found in the vicinity of the First Cataract, although occupation has been identified as far south as the Second Cataract (Edwards, 2004). There was variation between populations in the mobility and subsistence patterns, but each population relied on a combination of hunting, fishing and gathering (Clark, 1971; Yeshurun, 2018). Grinding stones have also been found in some sites, indicating that the gathering and processing of wild cereals was practiced by these Late Palaeolithic populations (Clark, 1971). As climatic conditions improved at the beginning of the Epipalaeolithic (c. 8500–5700 BC), populations spread throughout the Middle Nile Valley and away from the resources of the Nile (Edwards, 2004; Gatto and Zerboni, 2015; Küper and Kröpelin, 2006). Evidence from Khartoum indicates that these populations were pottery-producing hunter-fisher-gatherers (Arkell, 1947, 1949).

Increasing aridity c. 6500 BC initiated population movement towards the Nile valley and increased settlement in the fertile Kerma Basin (Gatto and Zerboni, 2015; Küper and Kröpelin, 2006). The Sudanese Neolithic (c. 5700–3000 BC) marked the adoption of animal domestication and cereal cultivation alongside hunting, fishing and gathering (Madella et al., 2014; Out et al., 2016; Salvatori and Usai, 2019). This was also a period marked by significant cultural shifts with the appearance of large cemeteries, standardised pottery styles and differentiation in grave goods indicative of increasing social hierarchies (Edwards, 2004; Salvatori and Usai, 2019).

Although current knowledge of the Pre-Kerma period (c. 3500–2500 BC) is limited, it is apparent that these populations were primarily agro-pastoral, increasingly sedentary and were expanding defensive fortifications (Edwards et al., 2012; Honegger, 2014). The

subsequent Kerma period (c. 2500–1500 BC) witnessed the first Nubian state: a period of increasing military power, expanding trade networks, and the development of monumental architecture (Edwards, 2004). Expansion of agricultural output was necessary to support a hierarchical social structure, evidenced by the increasing abundance and differentiation in grave goods (Edwards, 2004; O'Connor, 1993; Trigger, 1976a). There appeared to be a social and subsistence differentiation between habitation sites close to the river and further inland, reflective of agricultural and pastoral populations, respectively (Chaix and Honegger, 2015; Welsby, 2018).

The Kerma period ended with the Egyptian New Kingdom conquest of Lower and Upper Nubia c. 1500 BC (Edwards, 2007). This was followed by a Nubian revival in the Kushite period (c. 750 BC–AD 350). The Meroitic period (c. 350 BC–AD 350) was a time of agricultural intensification facilitated by the adoption of new technologies such as the *shaduf* (irrigation method) and the *saqia* (animal-driven waterwheel), as well as the introduction of domesticated sorghum, millet and fruit crops (Fuller, 2004a). The Meroitic period ended with encroachment from the Ethiopian/Axumite kings and the Romans (Bard, 2015).

The archaeological evidence from the Northern Dongola Reach illustrates a process of cultural adaptation over time, alongside changes in regional political power and climate. In particular, the populations exhibit a gradual shift from generalised hunter-gatherer economies to more specialised subsistence strategies based on pastoralism and agriculture. The following chapters will discuss the influence of such subsistence strategy transitions in Upper Nubia on skeletal biology, particularly mandibular and dental morphology.

3 Mandibular Anatomy

3.1 Introduction

With high levels of preservation in an archaeological context, the mandible and teeth are important resources to reconstruct both the biology and behaviour of past human populations. The first half of this chapter describes the anatomy of the mandible, dentition and the major muscles of mastication, which are important to understand how bone remodelling is stimulated by muscle activity. Then, the biomechanics of chewing are explained, as well as the biological and osteological response to masticatory loadings. This background information is information necessary to understand how mandibular shape variation can be used to study subsistence strategy transitions in past human populations.

3.2 The human masticatory complex

The human skull is a complex, highly integrated structure that performs a wide range of functions, including housing and protecting the brain, respiration, vocalisation and mastication (Ackermann, 2005; Bastir and Rosas, 2005; Lieberman, 2008, 2011; Lieberman et al., 2000). In particular, the highly derived modern human masticatory apparatus is a formed by a complex functional unit between the cranium and the mandible (Lieberman, 2011). Overall, primates display significant diversity in masticatory apparatus form and function (e.g. Bouvier, 1986b; Daegling, 1989, 1992; Vinyard and Ravosa, 1998). Compared with other primates, humans have a gracile masticatory apparatus relative to overall body size (Lahr, 1996; Ledogar et al., 2016; Lieberman, 2011; Lieberman et al., 2002; Zink and Lieberman, 2016).

The human masticatory complex consists of the maxilla, mandible, dentition, temporomandibular joints (TMJ) and the masticatory muscles. The mandible forms the movable bony part of the masticatory complex, housing the lower dentition and providing attachment sites for the major masticatory muscles. The mandible is made up of two main parts that join at the gonial angle: the body (corpus) and the ascending ramus (**Figure 3.1**). The mandibular condyles articulate with the cranium within the glenoid (mandibular) fossa of the temporal bone, to form the temporomandibular joint (TMJ). Within each TMJ, a mobile and fibrous articular disc separates the mandibular condyle from the temporal bone (Hylander, 2006). The human mandible is involved in two specific types of chewing: incising with the

anterior teeth and masticating with the postcanine dentition. The primary function of chewing is to mechanically break down food to produce a soft food ball (a bolus) that can be more efficiently digested in the gut.



Figure 3.1 Mandible (lower jaw) anatomy

The mandible forms the lower jaw and holds the lower teeth (top left, shaded region). The **mandibular condyle** articulates with the glenoid fossa of the temporal bone to form the TMJ. The mandible is composed of a horizontally oriented body (or **corpus**) and two vertical **rami**, which meet at the **gonial angle**. The body of the mandible is curved, and at the most anterior portion is a triangular eminence called the **mental protuberance**, or chin. The superior portion of the body is the **alveolar process**, which contains the sockets for the 16 lower teeth. The **mental foramen** is located below the premolar teeth and is the location for the passage of the mental nerve and blood vessels. Many masticatory muscles attached to the **ramus**, particularly the masseter. The **coronoid process** is the site of attachment for the temporalis muscle. The **mandibular notch** is the semilunar depression that separates the coronoid process and the condyle.

Tooth size, shape and internal composition are all adapted to maximise the efficiency of mastication. There are three defined regions of the tooth: the crown, the root and the neck. The crown is covered with a layer of hard, brittle material known as enamel. The roots anchor the teeth in the sockets (alveoli) of the mandible using periodontal ligaments. The neck (cervix) of the tooth connects the crown with the root (White and Folkens, 2005). Internally, each tooth is composed of dentine: a dense, bone-like tissue. In individuals with excessive occlusal wear, the underlying dentine may be revealed underneath the worn dental enamel. In such cases, the dentine often becomes concave over time because dentine is softer than enamel (White and Folkens, 2005). In modern humans, deciduous (primary or milk) teeth are the first to erupt, and throughout development these teeth are lost and replaced by the permanent (secondary) dentition (White and Folkens, 2005).

Photo of mandible removed for copyright reasons. Copyright holder is Elsevier-Academic Press.

Figure 3.2 Left mandibular dentition with identifying labels

The capital letters I, C, P and M represent the permanent incisors, canines, premolars and molars, respectively. Right and left teeth are designated by the letters R and L, respectively (only left teeth are labelled in this figure). Upper and lower teeth are indicated by subscripting or superscripting their position numbers. LI₁: central incisor; LI₂: lateral incisor; LC₁: canine; LP₃ and LP₄ are premolars; and LM₁, LM₂ and LM₃ are molars (adapted from White and Folkens 2005)

Although tooth form is variable among mammals (Jernvall, 1995), most teeth are a combination of three morphological elements: blades, which are sharp and narrow; cusps (or wedges), which are rounded and blunt; and basins (fossae) found between cusps and blades (Hiiemae and Crompton, 1985; White and Folkens, 2005). In adult humans, the mandibular incisors are the four anterior teeth (two on the right and two on the left), and are flat and blade-like with thin cutting edges. Modern human canines function primarily as an extension of the incisor row, but canines are more conical in shape than incisors. In humans there are two pairs of 'bicuspid' (two-cusp) premolars in the mandible. Molars are the largest teeth and there are typically six (two sets of three teeth) in the mandible (**Figure 3.2**). Both the premolars and molars consist of low, blunt cusps ('bunodont') to crush and grind food (White and Folkens, 2005).

Photo of mandible removed for copyright reasons. Copyright holder is Elsevier-Academic Press.

Figure 3.3 Superior view of the mandible with directional terms for dentition

Mesial (red) is the anterior portion of the tooth, closest to the central incisors; distal (blue) is the opposite of mesial and refers to the posterior of tooth; lingual (orange) is the part of the tooth crown adjacent to the tongue; labial (purple) is the opposite of lingual for the incisors and canines and is the side of the dental crown closest to the lips; and buccal (green) is the opposite of lingual for the premolars and molars and is the side of the tooth crown closest to the cheek (adapted from White and Folkens 2005)

When referring to dental morphology, there are specific directional terms that are used to indicate orientation in the mouth (**Figure 3.3**). The anterior morphology of a tooth closest to the central incisors is referred to as mesial, whereas the posterior tooth morphology towards the back of the mouth is called distal. The lingual surface of a tooth is closest to the tongue. The opposite of lingual is either labial, for the incisors and canines, or buccal, for the premolars and molars. The interproximal surfaces of the teeth are those that are in contact with the adjacent dentition. The chewing surface of a tooth is called the occlusal surface (White and Folkens, 2005).

Variation in dental crown size and enamel thickness between species is not only reflective of allometric scaling (i.e. larger animals have larger teeth), but can also reflect species-specific adaptations (Lieberman, 2011). This is because both the total surface area of the dental crown and the thickness of the enamel can influence the rate of food breakdown. For example, among New World monkeys, folivores typically have larger teeth than frugivores; for folivores, a larger occlusal area is more efficient at breaking or grinding small items, such as seeds (Kay, 1975; Lucas, 2004). For modern humans with relatively short jaws, having small

teeth compared with body size prevents dental overcrowding and malocclusion (Brace, 1963; Brace et al., 1987; Dahlberg, 1963; Gómez-Robles et al., 2017; Lieberman, 2011; Lucas, 2004; Wolpoff, 1971). However, research has shown that the trade-off for the reduction in postcanine tooth size observed in humans may be reduced chewing efficiency and a slower rate of food breakdown (Laird et al., 2016; Lucas, 2004). The relationship between the size of the mandible and of the mandibular dentition will be discussed further in **Chapter 8**.

3.3 Masticatory muscles

Mastication requires the movement of the mandible in several apposable directions: elevation (adduction) and depression (abduction); anteroposterior translation (protrusion and retraction); and medial/lateral translation (side-to-side movements) (Hylander 2006; Lucas 2004). These movements are controlled by the TMJ and the four main muscles of mastication: the temporalis, masseter, medial and lateral pterygoids (**Figure 3.4**) (Hylander, 2006; Lieberman, 2011). However, it is important to note that these four muscles do not work in isolation during mastication, but act alongside many other facial muscles, including the digastric, mylohyoid, geniohyoid, stylohyoid and infrahyoid muscles (Hylander, 2006).

The temporalis muscle stretches from the lateral surface of the cranial vault, behind the zygomatic arch, to attach on the coronoid process and mandibular notch (**Figure 3.4a**; **Figure 3.5a,b**) (Hylander, 2006; Lieberman, 2011). The temporalis is the largest masticatory muscle and mainly controls the elevation/adduction of the mandible during mastication. However, the fan-shaped morphology of the temporalis allows for multi-directional movement, and as such, can also move the mandible anteriorly and posteriorly (Hylander, 2006; Lieberman, 2011). In some apes and fossil hominins, the temporalis muscle is so large that it requires extra surface area on the cranium for its attachment, and this is accomplished through the presence of the protruding sagittal/nuchal crest (Ashton and Zuckerman, 1956).

The masseter muscle is rectangular in shape and attaches onto both the zygomatic arch and the lateral surface of the ramus (from the gonial angle to the coronoid process) (**Figure 3.4b**; **Figure 3.5a**) (Hylander, 2006). The masseter primarily elevates/adducts the mandible during mastication (i.e. closes the jaw), but can also move the mandible laterally and anteriorly (Hylander, 2006; Hylander and Johnson, 1994; Lieberman, 2011).

Photo of muscles of mastication removed for copyright reasons. Copyright holder is Belknap Press of Harvard University.

Figure 3.4 Muscles of mastication

By inserting onto the medial side of the ramus (in the gonial angle region), the medial pterygoid muscle forms a V-shaped sling around the ramus with the masseter muscle. The other portion of the medial pterygoid inserts onto the maxilla/sphenoid (**Figure 3.4c**; **Figure 3.5b**) (Hylander, 2006; Lieberman, 2011). The medial pterygoid works with the masseter to elevate/adduct the mandible during mastication, but whereas the masseter can pull the mandible laterally, the medial pterygoid works in opposition to pull the mandible medially (Hylander, 2006). The lateral pterygoid muscle has two heads (one of which originates on the sphenoid and the other on the temporal fossa), both of which insert onto the mandibular condyle (**Figure 3.4c**; **Figure 3.5b**). During mastication, the lateral pterygoid stabilises the condyle within the TMJ and pulls the condyle anteriorly (Lieberman, 2011).

Arrows show approximate direction of the vector of force for (a) temporalis (green); (b) masseter (orange); (c) lateral pterygoid (blue), medial pterygoid (red). The medial pterygoid inserts onto the medial side of the ramus and therefore is shown by removing a section of the ramus (adapted from Lieberman, 2011).



Figure 3.5 Muscle insertion sites on the mandible (a) lateral view and (b) medial view The temporalis (green) inserts on the medial and lateral sides of the coronoid process and mandibular notch; the masseter (orange) inserts onto the lateral side of the ramus from the gonial angle to the temporalis on the coronoid process; the medial pterygoid (red) inserts on the medial side of the ramus around the gonial angle; the lateral

pterygoid (blue) inserts onto the medial side of the condylar neck.

3.4 Incision and mastication

Although there is a general pattern to the overall movement of the mandible during chewing, the actual movements vary both within and between individuals. Masticatory movements are dependent on the shape of the individual's jaw and dentition, as well as the material properties of the food (Hylander, 2006). Jaw movements during food consumption fall into two general categories: incision, which is a cutting movement to produce smaller pieces of food; and mastication, a repetitive crushing and grinding movement that breaks down food before ingestion. Incision is mainly carried out by the incisors (with some involvement of canines and premolars), while mastication is driven by the postcanine dentition (Hylander, 2006).

From a resting position, incision consists of the following three functional phases: the opening phase, the closing phase and the power stroke. During the opening phase, the mandible opens (abducts) from gravity and the contractions of muscles attached to the hyoid (including the digastric muscle) (Lieberman, 2011). The degree of jaw opening is primarily dependent on food size (Hylander, 2006). During the closing phase, muscles on both sides of the skull contract and elevate/adduct the mandible, while the lateral pterygoids on the condyles pull the mandible anteriorly. The closing phase ends with the power stroke, during which the maxillary and mandibular incisors apply force to the food as the jaw closes (Hylander, 2006; Miller, 1991). The lateral pterygoids stabilise the mandibular condyles during the power stroke of

incision (Hylander, 2006). Incision is a bilateral process during which the muscles that elevate the mandible contract with equal force, so there is overall little lateral movement (Hylander, 1984; Lieberman, 2011).

Mastication also has three functional phases: the opening phase, the closing phase and the power stroke (Hylander, 2006). The completion of these three functional phases constitutes one chewing cycle; the combination of all the chewing cycles used to masticate a single piece of food is a chewing sequence (Hylander, 2006). In mammals, mastication is almost always unilateral (as opposed to bilateral incision) to generate a more powerful and efficient bite force. During mastication, the chewing side of the mandible that directly exerts the maximum bite force is called the 'working-side', while the other side of the mandible is called the 'balancing-side' (Lieberman, 2011). During each chewing cycle, the masticatory muscles can change their functional roles depending on whether they are located on the balancing- or working-side of the masticatory complex (Weijs, 1994).

During the opening phase, both condyles are pulled forward as the jaw opens and shifts between the balancing-side and the working-side (Figure 3.6) (Hylander, 2006). Similar to incision, the degree of jaw opening depends on the size and consistency of the food. The closing phase includes both a fast- and slow-close stage. During the fast-close stage, the condyles slide posteriorly as the mandible adducts (due to a combination of the balancing-side medial pterygoid and the working-side masseter), and shifts towards the working-side (Lieberman, 2011). This movement aims to place the mandibular postcanine teeth on the working-side just lateral to those of the maxilla (Figure 3.6). During the slow-close stage (commonly called occlusion), all the elevator muscles (the medial pterygoid, masseter and temporalis) contract and concentrate their force on the working-side. The working-side is pulled medially as the balancing-side condyle retracts into the glenoid fossa (due to a combination of contractions from the balancing-side masseter, the working-side medial pterygoid and the working-side temporalis; Figure 3.6) (Hylander, 2006; Hylander et al., 1987; Weijs, 1994). Completion of the closing phase leads to the power stroke, which is the forceful contact of the food with the occlusal surfaces of the working-side mandibular and maxillary postcanine dentition. During this process, the balancing-side mandibular and maxillary dentition do not occlude, because the mandibular arch is slightly narrower than the maxillary arch. After the power stroke, muscle activity and bone strain quickly decrease as the mandible opens to begin another chewing cycle (Hylander and Johnson, 1997; Wall et al., 2006).

Photo of movements of the mandible during mastication removed for copyright reasons. Copyright holder is Belknap Press of Harvard University.

Figure 3.6 Movements of the mandible during the closing stage of mastication

Inferior view of the crania with the mandible in grey and the glenoid fossae highlighted by red circles (A) During the opening phase, both condyles are pulled forward as the jaw abducts; (B) During the fast-close stage, the working-side condyle is pulled posteriorly while the jaw elevates; (C) During the slow-close stage (occlusion) the working-side condyle remains in place while the balancing-side condyle is retracted, initiating the power stroke during which the mandibular and maxillary postcanine dentition make forceful contact with the food (adapted from Lieberman, 2011).

The above description is a generalised representation of the movement of the muscles and the jaw during mastication. In reality, the movement of the mandible during mastication varies and is largely dependent on the mechanical properties of the food (Foster et al., 2006; Hylander, 2006; Hylander et al., 1987; Koç et al., 2014). When tough, mechanically resistant foods are consumed, the power stroke often ends before the occlusal surfaces of the workingside maxillary and mandibular teeth make contact. This type of power stroke primarily consists of a series of up-and-down movements known as puncture-crushing (Hylander, 2006). Conversely, a power stroke that ends with direct contact between the occlusal surfaces of the working-side maxillary and mandibular teeth is called tooth-tooth contact. Generally, more transverse movement of the mandible occurs during a tooth-tooth contact power stroke than during a puncture-crushing power stroke (Hylander, 2006).

Chewing is a repetitive process, which means that the mandible is subject to sustained and cumulative strain from high bite force magnitudes. Typical peak bite forces in adult humans can be as high as 200-450 Newtons (N) at the premolars or first molar (Ellis et al., 1996; Hylander, 1977; Jenkins 1978; Sasaki et al., 1989). Accordingly, human skull design reflects adaptations to generate and resist such large, repetitive chewing forces (Lieberman, 2011).

3.5 Mandibular growth and development

Studying the development and growth of the human mandible has been vital to interpreting morphological change within the human masticatory complex (Carlson and Van Gerven, 1977; Holmes and Ruff, 2011; Holton et al., 2014; Karup et al., 2005; Lee et al., 2001; Moss and Rankow, 1968; Radlanski et al., 2003; Remy et al., 2019). A substantial shift in understanding craniofacial growth started with Moss' (1960) proposal of the 'functional matrix hypothesis' (Moss and Salentijn, 1969); this model was in direct contrast to the predominant genetics-based framework used to explain cranial growth at that time. According to the functional matrix hypothesis, craniofacial growth is not just a result of genetic predetermination, but adapts during development to the surrounding, non-genetic environment (i.e. the adjacent soft tissues) (Carlson, 2005; Moss, 1960, 1962). Within Moss' framework, cranial components are categorised as either a functional matrix or a skeletal unit (Carlson, 2005; Moss, 1960, 1962). A functional matrix includes all the soft tissues and associated spaces that perform a given function. A skeletal unit is any bony structure that provides support and

facilitates the performance of the associated functional unit. Within the context of craniofacial growth, the mandible is viewed as a skeletal unit that supports the functional matrix of the oral cavity, particularly the masticatory apparatus. Moss (1962) was the first to describe the mandible as a combination of six functional growth units: the symphysis, alveolar process, condylar process, coronoid process, gonial angle and the mandibular body (Moss and Rankow, 1968). The soft tissues of the oral cavity functional matrix (primarily the muscles) influence the overall growth of the mandible by directly affecting the development of each individual mandibular functional growth unit (Moss, 1962; Precious and Delaire, 1987).

Other important studies investigating mandibular development have identified the rotational pattern of mandibular growth (Björk, 1955, 1969) and the principle of arcial growth (Ricketts, 1972).² The inferences from the functional matrix hypothesis and the mandibular growth studies form the basis upon which researchers can consider variation in mandibular shape and size partly as a result of differences in masticatory force magnitudes experienced during development, rather than just the result of genetic differences (Atchley and Hall, 1991; Carlson and Van Gerven, 1977; Fukase and Suwa, 2008; Hatch et al., 2000; Holmes and Ruff, 2011; Lepley et al., 2011).

The morphology of the human mandible and phenotypic plasticity during life ensure that the mandible can withstand the biomechanical strains experienced during mastication (Hylander, 1979b; Lieberman, 2011). Excessive bone strains from mechanical loading, or conversely diminished strains, can change bone morphology by inducing or reducing, respectively, the amount and direction of bone formation (Barak et al., 2011; Frost, 1987; Lieberman et al., 2004b; Rubin and Lanyon, 1985). The frequency and magnitude of masticatory muscle activity and biomechanical loading during mastication is an important determiner of mandibular shape (e.g. Beecher et al., 1983; Ciochon et al., 1997; Kiliaridis et al., 1985; Larsen, 2015; Lieberman, 2011; Lieberman et al., 2004a). Providing mandibular shape is at least partly dependent on biomechanical stimulus, the individuals and/or populations that are subjected to greater masticatory loads may be expected to have more biomechanically robust mandibles and/or denser cortical bone (e.g. Bouvier and Hylander, 1981; Corruccini and Beecher, 1982; Ravosa et al., 2007).

² Björk (1955, 1969) studied mandibular growth in adolescents and discovered that the mandible grew in relation to a centre of rotation, rather than linearly. The principle of arcial growth further classified mandibular growth as bone apposition at the ramus on an arc-like trajectory (from the mental protuberance through the ramus) rather than posterior growth (Ricketts 1972). Therefore, the increase in mandibular size during growth is a vertical rather than horizontal process (Ricketts 1972).

3.6 Summary

This chapter presented the biological and biomechanical framework necessary to understand how masticatory muscles induce strain on the mandible during mastication, and how this can initiate morphological adaptation in the mandible. In addition, the anatomy of the dentition and its functional role was described to highlight the important relationship between the mandible and the dentition during mastication. The following chapters aim to investigate the relationship between diachronic oral health and morphological changes in the mandible and dentition in ancient Nubian populations alongside changes in subsistence strategy and dietary composition. The samples that are included in this study, along with the specific research objectives and hypotheses, will be discussed in the following chapter.

4 Sample populations and research objectives

4.1 Introduction

This chapter describes the history, archaeological context and skeletal material for each sample population included in this research. The populations were chosen due to their geographic proximity and the accompanying archaeological evidence of subsistence practices. Chronologically, the populations range from the Late Palaeolithic (c. 13000–9000 BC) to the Meroitic Period (c. 350 BC–AD 350). This study utilised populations from the Northern Dongola Reach in Upper Nubia, as well as a Late Palaeolithic hunter-gatherer population from Jebel Sahaba in Lower Nubia, in order to address the research questions outlined in the second half of this chapter.

4.2 Ancient Nubian populations

Many of the samples used in this study were discovered as part of the Sudan Archaeological Research Society's (SARS) systematic survey of the Northern Dongola Reach. Beginning in 1993, the survey covered 80 km along the east bank of the Nile and up to 18 km into the desert hinterlands (Welsby, 1997a). The purpose of the Northern Dongola Reach Survey (NDRS) was to learn more about the archaeology of the largely unknown area surrounding the well-researched ancient city of Kerma and to assess the threat to ancient sites from modern development and natural processes (Welsby, 1997a). The R12, KAW, KER and KUS samples were selected for inclusion in this study due to their geographic proximity and the evidence available regarding their subsistence strategy and diet. The geographic proximity of these populations presents an opportunity to partially account for environmental and genetic variation, while evaluating diachronic changes in mandibular morphology and oral health associated with shifts in subsistence strategy (Judd, 2008). However, as discussed in Chapter 2, there have been few archaeological habitation sites and cemeteries found in Upper Nubia dating to before the Neolithic, and even fewer have adequate skeletal remains for analysis. Therefore, the Jebel Sahaba sample from Lower Nubia was included in this study to represent a Late Palaeolithic hunter-gatherer population.

Region	Site Name	Time Period	Date	Abbreviation ¹	Location
Lower	Jebel Sahaba	Late	c. 13000–9000 BC	JSA	BM
Nubia		Palaeolithic			
Upper Nubia	NDRS R12	Neolithic	c. 5000–4000 cal BC	R12	BM
	NDRS P37	Kerma Ancien	c. 2500–2050 BC	KAW	BM
	Kerma	Kerma Classique	c. 1750–1500 BC	KER	CAM
	Kawa (R18)	Meroitic	c. 350 BC–AD 350	KUS	BM

Table 4.1 Information for the Nubian sample populations

¹Population sample three-letter abbreviation used in all subsequent text, tables and figures NDRS: Northern Dongola Reach Survey; Collections curated at: BM: British Museum; CAM: University of Cambridge Duckworth Collection.

Adult individuals were selected for inclusion in the study based primarily on the availability and level of preservation of the mandible. If the associated mandible was too fragmented or had severe surface damage that would prevent an accurate 3D laser scan, that individual was excluded from the study. Preferentially, individuals with associated postcrania were included to allow for more accurate age and sex determination. Due to poor levels of mandibular preservation in these samples, it was unfortunately not possible to select individuals to ensure a balanced age and sex distribution within each sample. Further information regarding selection criteria for each analyses (such as limitations imposed by severe oral pathology) can be found in the relevant results chapters. Although there are different methodologies used throughout this research, the processes for sex and age determination, stature and body mass estimation, as well as a broad overview of the 3D laser scanning methodology apply to the entire research study (a description of these methodologies can be found in Appendix A). Each results chapter includes a description of the specific methodology applied for that analysis. Further information about the laser scanning methodology as it relates to mandibular metric and cross-sectional geometric analysis will be included in the Methods sections of Chapters 5 and 6.

The following section provides contextual information for each of the Nubian samples included in this study. First, the population from Jebel Sahaba will be discussed, followed by the samples from the NDRS Neolithic site R12, the NDRS Kerma Ancien site P37, the Kerma Classique sample from Kerma and finally the Meroitic sample from Kawa (**Figure 4.1**; **Table 4.1**). The three-letter abbreviations for the samples will be used extensively throughout the remainder of the thesis.



Figure 4.1 Map of the sample population sites included in this study

4.2.1 Jebel Sahaba (JSA) – Late Palaeolithic (c. 13000–9000 BC)

The Late Palaeolithic burial site 117, located in northern modern-day Sudan (Lower Nubia), is named for the nearby exposed rock hill of Jebel Sahaba (JSA) (Wendorf, 1968). The JSA site is located 1 km from the east bank of the Nile and about 3 km north of the modernday town of Wadi Halfa (**Figure 4.1**) (Wendorf, 1968). Based on the presence of the diagnostic Qadan microliths and overall site geology, the site has been dated to between c. 13000 and 9000 BC (Antoine et al., 2013; Wendorf, 1968). The site was first discovered in 1962 by Roland Paepe and Jean Guichard during an archaeological survey of the areas to be flooded by the construction of the Aswan High Dam (Holliday, 2015; Wendorf, 1968). Under the guidance of Fred Wendorf, the excavation of the JSA cemetery revealed a total of 58 individuals (Wendorf, 1968). The JSA sample is curated at the British Museum in London.

The JSA sample represents a hunter-gatherer population associated with the Qadan lithic industry (Shiner, 1968; Wendorf, 1968). The JSA burials consisted of both single and multiple interments in shallow, oval pits that were often covered with sandstone slabs

(Wendorf, 1968). This site is particularly well-known because it provides some of the earliest evidence for inter-populational violence in the region. Of the 58 individuals recovered, at least 23 have signs of violence, evidenced by cut-marks, parry fractures and fragments of lithic tools found embedded in the skeleton (Anderson, 1968; Bard, 2015; Midant-Reynes, 2000; Wendorf, 1968). It was initially hypothesised that worsening environmental conditions and a depletion of food resources during this period increased competition and led to violence between populations (Antoine et al., 2013; Wendorf, 1968, 1980a). However, a re-analysis of the human remains has shown little to no evidence of infection or metabolic disease in the JSA individuals, indicating that they were a relatively healthy, non-stressed population (Judd, 2006). In addition, the frequency of parry fractures within the JSA populations is similar to that found within the Kerma Ancien sample included in this study (Judd, 2001b, 2006). Therefore, the cause of the inter-populational violence displayed within the JSA sample is not yet known.

Based on archaeological evidence from other Qadan sites along the Nile, the subsistence of Late Palaeolithic populations was based primarily on the hunting of large game and fishing (Clark, 1971, 1980; Hassan, 1980; Yeshurun, 2018). Faunal collections from Late Palaeolithic sites are dominated by remains of large land animals that would congregate around permanent water sources, such as ungulates and hippopotami (Churcher, 1972; Clark, 1980; Gautier and Van Neer, 1989; Hassan, 1980; Peters, 1990; Yeshurun, 2018). Grinding stones have also been found at Qadan sites, often with a 'sickle sheen': a silica residue thought to be produced during the grinding of soft, fibrous material, such as the stems of cereal plants and starchy vegetables (Wetterstrom, 1993).

In this study a total of 12 individuals from JSA (8 males and 4 females) were examined. The JSA sample was used in the analysis of mandibular metrics and mandibular cross-sectional geometry.

4.2.2 NDRS R12 (R12) – Neolithic (c. 5000–4000 cal BC)

The Sudanese Neolithic cemetery R12 was discovered during the SARS systematic survey of the Northern Dongola Reach, and is located on the east bank of the Nile c. 2 km north/north-east of Kawa (**Figure 4.1**). The cemetery covers an area of about 650 m² on the south-eastern end of the Seleim basin (**Figure 4.2**) and dates from c. 5000–4000 cal BC (Judd, 2008; Macklin et al., 2013; Salvatori and Usai, 2002, 2008a,b). The R12 site was excavated under the direction of S. Salvatori and D. Usai from 2000–2003, in a joint effort by the *Centro*
Veneto di Studi Classici e Orientali and SARS (Salvatori and Usai, 2001, 2002; Welsby, 1995, 1997b, 2001b). Over three seasons a total of 166 graves were excavated, yielding the remains of 198 individuals including men, women and children (Judd, 2008). Unfortunately, a combination of strong salinification processes, termite action and erosion, have meant that the overall state of the human bone preservation from the R12 cemetery is poor. The R12 sample is curated at the British Museum in London.

Photo of Seleim Basin removed for copyright reasons. Copyright holder is Archaeopress.

The surface of the R12 site was covered by small quartzite and flint pebbles, which had originally formed small mounds on the surface of each grave (Salvatori and Usai, 2001). The burials were predominantly single deposition pit graves with individuals mainly lying flexed on their left side, oriented west-east and facing north (Salvatori and Usai, 2001, 2002, 2004). The individuals were buried alongside a diverse range of grave goods, including pottery bowls and jars, ovicaprine or gazelle bone spatulas and perforators, tools and jewellery (Salvatori and Usai, 2001, 2002). The distribution of grave goods was relatively homogeneous, with no overt indicators of rank between individuals; nor is there evidence of gender-specific funerary symbolism (Salvatori, 2008b). The burial practices and ceramic style at R12 fit within the overall Sudanese Neolithic tradition observed throughout northern and central Sudan (Reinold, 1994, 2001; Salvatori and Usai, 2001, 2002).

Figure 4.2 Location of R12 Neolithic cemetery at the edge of the Seleim Basin (adapted from Welsby 2001)

The isotopic analysis (Iacumin, 2008) and data from faunal collections (Pöllath, 2008) indicate that environmental conditions of the Seleim Basin (c. 5900–5600 BP) were less arid than during the subsequent Kerma period. The population represented by the R12 cemetery had a diverse economy that utilised the rich resources of the Seleim Basin. Due to the abundance of resources in the region, it is likely that the R12 population was more sedentary than other contemporary Sudanese Neolithic populations. However, evidence based on burial position suggests that part or most of the group spent the winter in another location; possibly devoting the winter period to animal grazing and/or hunting outside the basin (Salvatori and Usai, 2002, 2004). Archaeozoological research indicates that domesticated animals such as cattle and caprines represent almost half of the faunal sample found at this site, confirming that pastoralism was an important part of the R12 subsistence strategy (Salvatori and Usai, 2002, 2004). The presence of bucrania in the funerary ritual also highlights the important symbolic role of cattle in the R12 population (Salvatori and Usai, 2002). However, hunting was still a significant part of the R12 economy, evidenced by the remains of many wild animals in the faunal sample, such as gazelles, hippopotami and elephants (Pöllath, 2008).

Although Sudanese Neolithic populations have traditionally been viewed as pastoral populations, the R12 cemetery provides the earliest evidence of Near Eastern wheat/barley in Northeast Africa (Madella et al., 2014; Out et al., 2016). Based on direct evidence from phytoliths and dental calculus (starch), the R12 population diet most likely also included domesticated grains (emmer wheat/hulled barley and legumes) (Madella et al., 2014; Zohary et al., 2012). In addition, grinding stones were present in many of the R12 graves, and these tools may be linked to the processing of wild and/or cultivated grains (Salvatori and Usai, 2002; Salvatori et al., 2008; Usai, 2008). Isotopic studies on the R12 skeletal remains have confirmed the presence of a mixed isotope signature, containing both C3 and C4 grasses (Iacumin, 2008). However, the isotopic signature of the R12 individuals may represent either direct consumption of plants or ingestion via the grazing animals consumed for meat (Iacumin, 2008). The evidence of domesticated plants at the R12 site does not necessarily indicate that grains were being actively cultivated, since the cereals could have been traded into the area from another farming population. Much of the evidence from this and other cemeteries of the time period points to R12 as primarily a pastoral population, but one that also consumed wild or domesticated crops obtained through seasonal gathering or small-scale cultivation (Usai, 2008).

For this study, a total of 25 individuals from the R12 cemetery (10 males and 15 females) were studied. The R12 sample was included in the analysis of oral health, dental metrics, mandibular metrics and mandibular cross-sectional geometry.

4.2.3 NDRS P37 (KAW) – Kerma Ancien (c. 2500–2050 BC)

Discovered during the NDRS project, SARS surveyed and excavated the two Kerma period sites of O16 and P37 during the 1995/6 and 1996/7 excavation seasons (Judd, 2001a; Welsby, 2001b). The O16 and P37 sites are located near the modern-day town of Kawa and are situated within 3 km of each other (**Figure 4.1**). Chronologically the sites overlap, with the O16 site dated to the Kerma Ancien (c. 2500–2050 BC) and the P37 site containing material dating from both the Kerma Ancien and Moyen periods (c. 2050–1750 BC) (Judd, 2001a). The O16/P37 cemeteries are thought to represent rural populations of lower socioeconomic status compared with the urban individuals from the Eastern Cemetery at Kerma 70 km north (Adams, 1977; Welsby, 1996a,b, 1997a). In previous bioarchaeological research, the O16 and P37 sites have been analysed together due to their temporal and spatial proximity (see Judd, 2002). However, due to the poor mandibular preservation of the O16 sample, only individuals from P37 were used in this study. The O16 and P37 samples are curated at the British Museum in London.

The P37 cemetery site consists of two mounds with several well-preserved *tumuli* (Welsby, 1997a,b). The abundance of bone (both human and animal) and pottery scattered across the sides of the mounds, particularly the southern mound, suggests that this site was disturbed by grave robbing (Welsby, 1997a,b). The pottery from the P37 mounds are similar to pottery associated with both the Lower Nubian A-Group and the later Kerma Classique period (Welsby, 2001b). The pottery from the northern mound dates to the Kerma Ancien period (c. 2500–2050 BC) and was very fragmentary, which may reflect that the ceramics were placed on the surface of the grave rather than within the grave itself (Gratien, 1978; Sjöström, 1997). The southern mound pottery dates to the Kerma Moyen period (c. 2050–1750 BC) (Welsby, 1997b) and is mostly complete due to its placement within each grave (Sjöström, 1997). For both periods, there appears to be no distinction in grave goods between men and women (Welsby, 2001b). A total of 56 graves were excavated from the northern mound (the excavation areas were labelled as J3, K3 and K4) and most graves contained a single skeleton (Welsby, 1997a) (**Figure 4.3**).

Photo of NDRS site P37 removed for copyright reasons. Copyright holder is The Sudan Archaeological Research Society.

Figure 4.3 NDRS site P37 – Kerma Ancien graves visible after the removal of the surface sand (From Welsby, 1997)

The reliance on pastoralism characteristic of the Sudanese Neolithic and Pre-Kerma periods (Krzyżaniak, 2004; Wendorf and Schild, 1998; Wengrow et al., 2014) was likely to have continued into the early Kerma period. Isotopic evidence indicates that during the Kerma Ancien period, there was a dominant C4 plant signature in the diet (Iacumin et al., 1998). This may reflect that individuals were consuming animals who had on C4 plants (Iacumin et al., 1998) and/or that wild sorghum and millet grasses were part of the diet; the remains of wild sorghum and millet grasses have been found at a similar rural, Kerma Ancien cemetery H29 (Ryan, 2018). The faunal remains within the P37 graves were limited to a few domesticated animals, such as caprines and dogs. Although no cattle remains were found within the graves, a number of bucrania were arranged in a crescent shape around a single P37 Kerma Moyen grave. The absence of wild animal remains at the P37 site suggests that their economy was based primarily on animal domestication (Welsby, 2001b). These findings fit within the overall pattern of domesticated animal burial traditions that is well known from other Kerma cemeteries (Chaix, 1993; Welsby, 2018).

For this study, 17 individuals (13 males and 4 females) from the P37 northern mound were studied, representing the Kerma Ancien period (c. 2500–2050 BC). The KAW sample was included in analysis of oral health, dental metrics, mandibular metrics and mandibular cross-sectional geometry.

4.2.4 Kerma (KER) – Kerma Classique (c. 1750–1500 BC)

The ancient city of Kerma was located on the east bank of the Nile about 30 km south of the Third Cataract (**Figure 4.1**). With a broad floodplain, this area was one of the most fertile and productive regions in ancient Nubia and provided a large cultivation area suitable for irrigation (Adams, 1977). Kerma was the centre of the first Nubian State that ruled within the Nile Valley from c. 2500–1500 BC (Edwards, 2004). Between 1913 and 1916, George Reisner led the excavations at Kerma through the joint effort of the Archaeological Mission of Harvard University and the Museum of Fine Arts Boston (Reisner, 1923a,b). Beginning in the 1970s, Charles Bonnet led excavations to further explore the city and cemetery and helped to establish a more accurate chronology of the Kerma period (Bonnet, 1992, 2000; Emberling, 2014). Since 1998, excavations have focused on the oldest parts of the cemetery to understand the early stages and emergence of the powerful Kerma nation-state (Honegger, 2013; Honegger and Fallet, 2015). The skeletal sample is curated in the Duckworth Collection at the University of Cambridge.

The Kerma skeletal sample is from the Eastern Cemetery located about 3 km east of the main city and dates to the Kerma Classique period (Reisner, 1923a,b). Organised into multiple *tumuli* of various sizes and individual graves surrounding the *tumuli*, the cemetery todate covers an area of 70 hectares, and is estimated to have contained around 40,000 tombs (Honegger, 2019; Reisner, 1923a,b)

Figure 4.4). The variation in the size of the tombs and distribution of grave goods reflects the highly hierarchical Kerma society (Chaix and Grant, 1993). The landscape of the site is dominated by two examples of monumental architecture: the *deffufas*, or mud brick temples (Adams, 1984). Developing from north to south, the cemetery was used during the entire duration of the Kerma period (Honegger, 2019).

Photo of the Eastern Cemetery at Kerma removed for copyright reasons. Copyright holder is Harvard University Press.

Figure 4.4 Excavation plot of the Eastern Cemetery at Kerma. Roman numerals correspond to major tumuli (adapted from Reisner 1923a: Plan II; Judd and Irish 2009)

Individuals were discovered both within the central chambers of the *tumuli* (thought to be the 'royal' individuals/families) and the main corridors bisecting each of the large *tumuli*. The number and position of the latter burials has led to speculation that these 'corridor' individuals were sacrifices (Bonnet, 1990; Kendall, 1997; Reisner, 1923a,b). However, it is unclear whether these individuals were forcibly sacrificed (Davies, 2003) or members of the king's entourage who willingly sacrificed themselves (Adams, 1977; Edwards, 2004; Kendall, 1997; O'Connor, 1993; Reisner, 1923a,b). The 'corridor' individuals do not show any signs of violent perimortem trauma. In addition, craniometric analyses has demonstrated biological similarity between the two burial groups, suggesting that the 'corridor' individuals were not foreign slaves or prisoners (Judd and Irish, 2009). There is speculation that strong narcotics may have been used to assist their willing sacrifice (Judd and Irish, 2009; Kendall, 1997; Reisner, 1923b). The sample in this study includes both 'corridor' and 'non-corridor' individuals, a grouping that has been used in previous bioarchaeological studies (e.g. Buzon and Judd, 2008).

The Kerma population used flood and basin irrigation to increase the productivity of cereal agriculture and animal husbandry, resulting in a food surplus that could support a hierarchical social structure (Adams, 1977; Buzon, 2011; Chaix and Grant, 1993; Trigger, 1976a). Similar to earlier periods, domesticated animals, specifically cattle, remained

important in both the subsistence strategy and symbolic culture of the Kerma population. This is evident through the abundance of animal remains, particularly bucrania, that are found associated with the Kerma burials (Bonnet, 2000; Reisner, 1923b). Pottery is more commonly found on the surface of the burials than within the graves, indicating that the pottery was primarily used as an offering to the dead (Bonnet, 2012). Kerma pottery is very characteristic with black-topped, red-polished hand-made bowls, decorated with geometric motifs that have been finely incised or impressed onto the surface (Bonnet, 2012).

In this study, 49 individuals from Kerma (24 males and 25 females) all dating from the Kerma Classique period (c. 1750–1500 BC) were examined. The KER population was included in analysis of oral health, dental metrics, mandibular metrics and mandibular cross-sectional geometry.

4.2.5 Kawa R18 (KUS) – Meroitic (c. 350 BC–AD 350)

Kawa is one of the largest and most significant sites in the Dongola Reach (covering 40 hectares) and lies on the eastern bank of the Nile at the southern end of the Kerma basin, around 50 km south of Kerma (**Figure 4.1**) (Morkot, 2012). Kawa's historical significance as a religious centre is evident from its ancient name *Gem Aten* ('the Sun Disc is Found'), suggesting an origin for the religious cult in the reign of Amenhotep III or Akhenaten (Morkot, 2012). A team from the University of Oxford completed the first excavations at Kawa under the direction of Francis Griffith (1921–1931) and later under M.F.L. Macadam and Laurence Kirwan (1935–1936) (Macadam, 1949, 1955; Morkot, 2012). The original excavations focused on the monumental structures, such as the stone temples and palace complex at the centre of the settlement mound, rather than the associated town and cemetery (Fuller, 2004a; Macadam, 1949, 1955; Morkot, 2012). In 1993, a team from SARS and the British Museum began a systematic excavation of the town and associated cemeteries (Welsby, 1998, 2000, 2001a, 2002).

The eastern cemetery, site R18, is located 1 km east of the town and was most likely used throughout the Meroitic period. There is no evidence for its use into the post-Meroitic period. Most of the graves have long descendaries and are arranged roughly in north to south rows (**Figure 4.5**). In addition, two dressed stone pyramids were discovered at the north-eastern end of the Kushite cemetery (Welsby, 2009, 2010). Burials were often accompanied by an abundance of grave goods including pottery, but the full extent of grave goods is unknown due

to extensive grave robbing. Mud-brick blocking walls are visible in the doorways of the grave chambers, and this may suggest that the tombs were used more than once (Welsby, 2000). The skeletal sample from the R18 cemetery is curated at the British Museum in London.

Photos of Kawa site R18 removed for copyright reasons. Copyright holder is The Sudan Archaeological Research Society.

Figure 4.5 Kawa site R18 (a) Site R18, the eastern cemetery: descendaries of tombs arranged in north-south rows and (b) Tumuli (45) and (46) after removal of surface sand, looking south-west towards the town (Welsby, 2001a)

The Meroitic population at Kawa were intensive agriculturalists. Within the R18 site there is abundant evidence of plant remains including emmer wheat, barley, sorghum, dates and watermelon (Fuller, 2004a, 2013; Martin et al., 1984; Wetterstrom, 1993). The herding of cattle, sheep and goats was also an important economic activity for Meroitic populations, as was the case for their Nubian predecessors (Martin et al., 1984).

In this study 10 individuals from the KUS population (6 males and 4 females) were examined. The KUS population was included in the analysis of oral health, dental metrics, mandibular metrics and mandibular cross-sectional geometry.

4.3 Research objectives and hypotheses

Nubian cultural history is marked by a gradual transition from a primarily hunting, fishing and gathering lifestyle to a period of pastoralism with limited plant cultivation, before eventually progressing to intensive agricultural production. This study will use several methods to assess the changes in mandibular and dental anatomy associated with subsistence strategy transitions in ancient Nubian populations. Analyses will include mandibular osteometrics,

mandibular cross-sectional geometry, dental wear and pathology (i.e. caries, calculus, linear enamel hypoplasia [LEH] and periodontal disease) and dental metrics. This study will add to the bioarchaeological understanding of the transition to agriculture in ancient Nubia by examining diachronic changes in the morphology of the mandible and dentition alongside changing oral health associated with dietary practices. Understanding the temporal trends associated with craniofacial variability in the ancient Nile Valley will help to expand our knowledge of the complex relationship between human biological variation and culture. The following section outlines the overall thesis objectives, as well as the research questions specific to each sub-section of the study. In addition, hypotheses are included for each research question. The research questions and hypotheses as they relate to the results will be discussed directly in each of the relevant results chapters (**Chapters 5–8**) and in the overall Discussion Chapter (**Chapter 9**).

4.3.1 Mandibular osteometrics (Chapter 5)

Previous research has demonstrated that differences in subsistence strategy and the associated changes in masticatory behaviours and jaw loading patterns can significantly influence overall skull morphology (e.g. Carlson, 1976; Carlson and Van Gerven, 1977; von Cramon-Taubadel, 2011; González-José et al., 2005; Noback and Harvati, 2015; Paschetta et al., 2010; Sardi et al., 2006). The gracilisation of the skull, and particularly the mandible, that accompanied the transition to agriculture in many areas of the world has been linked to a concomitant decrease in masticatory biomechanical stress, due to a combination of an increase in soft food consumption and advances in food processing (Carlson and Van Gerven, 1977; von Cramon-Taubadel, 2011; Galland et al., 2016; Katz et al., Weaver 2017; May et al., 2018; Paschetta et al., 2010). Analysis of mandibular morphology can provide valuable information about the dietary composition and subsistence strategy of past human populations.

Chapter 5 will assess diachronic patterns of mandibular morphological variation across subsistence strategy transitions in ancient Nubia. Mandibular linear measurements were analysed to quantify differences in mandibular size and shape between the Nubian populations in this study. In particular, the analyses focused on the mandibular functional units associated with masticatory musculature (May et al., 2018; Pepicelli et al., 2005; Weijs and Hillen, 1986). The following research questions and hypotheses are addressed:

- 1. Does mandibular size and shape (assessed through linear measurements) change over time between sample populations? Are diachronic changes related to overall mandibular size or specific to certain functional regions of the mandible, such as the mandibular body and/or the ramus?
 - Over time, there will be a reduction in the overall size of the mandible both in breadth (dental arch and overall breadth as quantified by bigonial and bicondylar measurements) and length. On average, the individuals from Jebel Sahaba (JSA) will have the largest mandibles and those from the Meroitic sample (KUS) will have the smallest.
 - The most significant difference in overall mandibular morphology and size will be observed between the JSA and Upper Nubian samples, rather than between the Upper Nubian samples.
 - The mandibles of the more recent farming populations will not just be size-reduced versions of the earlier populations, but will display specific changes in morphology associated with smaller incremental dietary and cultural changes associated with an increasing reliance on agricultural products. Changes in mandibular shape will be concentrated in areas of major masticatory muscle attachment, such as the ramus.
- 2. Are there differences in mandibular size and shape between males and females within the same sample? Over time, how do mandibular size and shape trends differ between males and females from different sample populations?
 - In general, males will have larger mandibles than females within each sample, and this is expected to relate to overall differences in body size.
 - It is expected that there will be differences in the diachronic mandibular size and shape trends observed between males and females. Observed variation may be the result of differences in biology (sex-based genetic/hormonal bone functional adaptation) or behavioural (sexual division of labour). However, identifying the cause of any observed sex-specific trends is likely beyond the scope of the current research.

4.3.2 Mandibular cross-sectional geometry (Chapter 6)

Although the relationship is complex (Daegling, 2002, 2007), global patterns of recent human mandibular morphology are thought to reflect differences in biomechanical loading associated with dietary variation (Antón et al., 2011; Carlson and Van Gerven, 1977; Hinton and Carlson, 1979; Holmes and Ruff, 2011; Kaifu, 1997; Lieberman et al., 2004a; Paschetta et al., 2010). The seminal work of Carlson and Van Gerven (1977) first introduced the masticatory-functional hypothesis following the observation that measurements directly related to masticatory robusticity (ramal width, symphyseal thickness, corpus length and masseter length) decreased through time from Nubian Mesolithic to Christian populations. The decrease in craniofacial robusticity was attributed by Carlson and Van Gerven (1977) to changes in subsistence strategy between the populations, which resulted in reduced biomechanical strain, smaller masticatory muscles and an overall gracilisation of features associated with masticatory function. Following on from this work, differences in mandibular size and robusticity between populations have often been used to infer divergent dietary patterns in past populations (Carlson and Van Gerven, 1979; Daegling and Grine, 1991; Dobson and Trinkaus, 2002; Fukase, 2007; Holmes and Ruff, 2011; Hylander, 1988; Ravosa, 1996a). Analysing the cross-sectional geometry (CSG) of the human mandibular corpus facilitates the understanding of its biomechanical behaviour during mastication and how that has changed over time between populations.

In Chapter 6, the mandibular CSG properties at the symphysis and within the molar region are estimated to assess the mechanical variation of the human mandible in Nubian samples from the Late Palaeolithic through to the Meroitic Period. The results from this study will help to elucidate the effect of dietary transitions on mandibular strength and robusticity in these ancient Nubian samples. The following research questions and related hypotheses are addressed:

- Do mandibular indicators of robusticity (based on CSG properties) change over time between samples? Do trends differ when raw or standardised (to overall mandibular length) values are analysed?
 - It is predicted that on average the older samples (JSA and R12) will have the largest CSG properties (both raw and standardised) compared with the later Holocene samples. Relatively larger CSG values indicate greater strength and robusticity, and the reduction in CSG over time will be particularly strong with regards to vertical bending at the symphysis (I_x and I_{max}), parasagittal bending in the molar region (I_x and I_{max}) and torsional rigidity at the symphysis and in the molar region (J).
 - The most significant decrease in cross-sectional strength will be between the JSA and later Holocene samples, but mandibular robusticity will continue to decline throughout the later samples. This pattern of change was observed in the results

from Carlson and Van Gerven (1977), in which the largest magnitude of morphological change was observed between the Mesolithic and A-/C-Group populations, but reductions in robusticity continued between the A-/C-Group and later Meroitic/X-Group-Christian populations.

- 2. How do CSG trends differ between the symphyseal and molar regions?
 - Since mastication mainly affects the molar region of the mandible, the reduction in mandibular strength will be more prominent in the molar region.
- 3. When males and females are analysed separately, how does this affect the CSG trends observed over time?
 - Although the males will tend to have larger raw CSG values compared with females, the overall trend for a diachronic reduction in robusticity for the size-standardised values is expected to be similar between the two groups. However, the magnitude of such a reduction may be different between males and females.

4.3.3 Oral health (Chapter 7)

The study of oral health is often used to provide insight into the dietary habits and subsistence strategies of past human populations, because both dental wear and oral pathologies are strongly correlated with diet. In particular, oral health has been used to biologically characterise the transition to agriculture in many populations around the world (e.g. Eshed et al., 2006; De Groote et al., 2018; Hillson, 1996; Larsen, 2015; Larsen et al., 1991; Lukacs, 1989, 1992; Munoz, 2017; Powell, 1985; Starling and Stock, 2007; Turner II, 1979; Walker et al., 1986). Many of the above studies observed an overall decline in oral health following the adoption of agriculture, largely attributed by the researchers to an increase in softer and more processed carbohydrates in the diet. Many studies show that the frequency of carious lesions, abscesses and ante-mortem tooth loss are higher in farming populations than among huntergatherers (Cohen and Armelagos, 1984; Larsen, 1995, 2006). In addition to dental pathology, many studies have also used rates of linear enamel hypoplasia (LEH) within a sample population, to reflect levels of physiological stress experienced during development. Although the relationship between LEH frequency and health is not fully understood, the frequency of LEH has been shown to increase in early farming populations, with a subsequent decrease in later more advanced agricultural populations with greater dietary heterogeneity (Goodman et al., 1984; Hutchinson and Larsen, 1988; Starling and Stock, 2007). However, recent studies have shown that the relationship between food production and oral health varies is complicated

and can often be different for males and females within the same population. In addition, the local environmental and cultural factors, such as variation in the nature of the cultivated crops and diversity of food processing practices, can all influence oral health (Eshed et al., 2006; Tayles et al., 2000). Therefore, studies need to focus on comparisons between local populations instead of assuming a common trend across global populations.

The research presented in Chapter 7 explores the oral health consequences associated with shifts in subsistence strategies for the Upper Nubian samples studied. The frequency and severity of dental wear, dental caries, dental calculus, LEH and periodontal disease in the mandibular dentition were assessed to understand the effects of diet on the oral health of ancient Nubian samples. The following research questions and hypotheses are addressed:

- 1. Does the frequency and/or severity of mandibular dental wear and pathology change over time between samples? How do such changes in dental pathology relate to each other?
 - As observed in other areas of the world, an increased reliance on cereal cultivation in the KER (Kerma Classique) sample will be associated with an increase in dental caries, LEH frequency and periodontal disease.
 - Despite an expected rise in the prevalence of LEH with agricultural intensification and dietary homogeneity in the KAW and KER sample, the Meroitic sample will have lower levels of LEH due to improving health following urbanisation, expanded social complexity and greater dietary heterogeneity.
 - Dental wear is expected to decrease with agricultural intensification in the Nubian samples due to greater access to softer foods and improvements in food processing technology that reduce levels of wear.
- 2. Do trends in oral health vary by sex and age categories? What conclusions can be drawn based on such observed differences?
 - Based on previous research, it is expected that there will be differences in the frequency and severity of dental pathology between sexes. Specifically, with the adoption of agriculture females will have higher prevalence of dental caries and periodontal disease than their male counterparts.
 - Since oral pathologies are age-progressive processes, older individuals will have a higher prevalence of the oral pathologies analysed in this study.

4.3.4 Dental metrics (Chapter 8)

Pronounced reductions in human dental dimensions have been reported for Early Holocene populations across the world (e.g. Brace, 1966; Brace et al., 1987; Brose and Wolpoff, 1971; Calcagno, 1989; Calcagno and Gibson, 1988; Christensen, 1998; Hill, 2004; Lieberman, 2011; Pinhasi et al., 2008; Y'Edynak and Fleisch, 1983). Many of the post-Pleistocene dental changes are observed over a relatively short period of time in evolutionary terms (Hillson, 2005). Most commonly, dental size reduction is related to an overall increase in the proportion of softer food in the diet, initiated by a combination of advances in food preparation technology and the introduction of new foods into the diet following subsistence strategy changes. However, the causal relationship between dental reduction and subsistence strategy (particularly at the agricultural transition) is complex and varies by population.

This study explores diachronic dental size change in ancient Nubian populations within the context of changes in subsistence strategy and food preparation techniques. The mesiodistal and buccolingual measurements of the mandibular dentition were analysed to assess changes in dental size over time in these samples. The following research questions and hypotheses are addressed:

- 1. Are there significant changes in mandibular dental dimensions (based on mesiodistal and buccolingual measurements) between samples?
 - It is expected that there will be a long-term reduction in dental size, with the smallest dentition observed in the Meroitic farming sample (KUS).
- 2. Are there different trends present for the anterior/posterior dentition or buccolingual/mesiodistal measurements?
 - Based on the observations from previous studies, any observed dental reduction trend will be most pronounced in the posterior teeth and in the buccolingual dimension.
- 3. How do the dental size trends in this study fit within previously proposed mechanisms for dental reduction, such as the Probable Mutation Effect (PME), Increasing Population Density Effect (IPDE) and/or Selective Compromise Effect (SCE)?
 - If trends are observed, they will most likely fit under the Selective Compromise Effect (SCE), which incorporates aspects of selection related to caries resistance and the masticatory-functional demand model into its mechanism of dental size change.

4.3.5 Discussion (Chapter 9)

The overall objective of this study is to identify the biological implications of subsistence strategy transitions and the associated dietary changes on the mandible and dentition in Upper Nubian populations. Although other studies have used the methodologies in this study independently, this study aims to combine the insights from mandibular metric analysis, oral health, mandibular CSG and dental metrics to create a comprehensive picture of how the mandible and dentition adapt alongside changes in dietary consumption. Each methodology, when used in isolation, has limitations. However, by combining the results from each individual analysis, it will be possible to identify how the functional components of the mandible and dentition change in relation to each other. In addition, this study focuses on the influence of small changes in diet, rather than the large dietary changes that are typically studied.

An important part of the overall synthesis and analysis of the individual methodologies will be to assess how the trends from each data set relate to each other. For example, how do the mandibular linear measurements and CSG properties change in relation to each other? Can differences in the observed trends answer different questions about size/shape versus robusticity/strength? In addition, how does the size and shape of the mandible change in relation to size changes in the dentition? Finally, are the results from the oral health analysis congruent with what is inferred about the dietary consumption of the populations based on evidence from previous archaeological, isotopic and palaeobotanical research?

The populations in this study were chosen to be representative of their subsistence strategy, rather than as exceptions or outliers. In addition, the populations were chosen due to their geographic proximity with limited evidence for immigration, limiting the influence of genetic factors on the observed morphology. Therefore, it is expected that the results from this study will be able to provide insight into how mandibular and dental morphology can reflect semi-nomadic agropastoral and sedentary agricultural subsistence strategies in these populations.

4.4 Summary

Across the world, the shift to agriculture significantly changed human culture, but also dramatically impacted human biology. Previous studies have indicated that softer agricultural diets may have resulted in a less robust masticatory complex in early farmers as compared with their hunter-gatherer ancestors. This thesis attempts to quantify changes in human mandibular shape and robusticity, and link such changes with oral health and dental metrics. The incremental dietary changes and geographic proximity of the Northern Dongola Reach populations used in this study provides a unique opportunity to identify diachronic changes in mandibular size and shape and dental pathology over time, while controlling for significant genetic variation. The results of this study will help to elucidate the changes in craniofacial morphology that accompanied shifts in subsistence strategy and demonstrate the degree of plasticity of the mandible in adapting to changes in dietary composition. The following chapters will present the results from the individual analyses of the mandibular osteometrics, mandibular cross-sectional geometry, oral health and dental metrics.

5 Mandibular Osteometrics

5.1 Introduction

The early Holocene transition from hunting and gathering to pastoralism and agriculture initiated major biological and cultural change in human populations worldwide (Bellwood, 2004; Pinhasi and Stock, 2011). Patterns of food consumption changed dramatically and included a decrease in overall dietary diversity and changes to dietary texture. A combination of the types of food consumed and advances in food preparation technology led to a softer and more processed diet, that reduced the biomechanical load on the masticatory complex in agricultural populations (Carlson and Van Gerven, 1977; Hannam and Wood, 1989; Kiliaridis, 1995; Larsen, 2015; Lieberman, 2008, 2011; van Spronsen et al., 1991). This reduction in masticatory biomechanical stress has been linked to gracilisation of the skull, particularly the mandible (Galland et al., 2016; Katz et al., 2017; May et al., 2018; Paschetta et al., 2010; Pinhasi et al., 2015; von Cramon-Taubadel, 2011). As such, analysis of mandibular morphology (particularly the functional regions directly involved with masticatory muscle forces) can provide valuable information about the dietary composition and subsistence strategy of past human populations.

This portion of the overall study assessed diachronic patterns of mandibular morphological variation alongside shifts in masticatory function that were associated with changes in subsistence strategy in ancient Nubia. Using linear measurements, variations in mandibular size and shape were quantified both between and within the samples studied. The main objective was to elucidate the patterns and magnitude of the plastic response of the mandible to changes in masticatory loading. In addition, males and females were analysed separately to reveal sex-specific patterns of mandibular morphological change. This research will ultimately add to the understanding of the effect that agriculture has had on global patterns of human mandibular variation.

5.2 Mandibular osteometric research

5.2.1 Animal studies

There is a significant body of experimental work that has explored the relationship between diet and mandibular morphology in animals. This research is based on the hypothesis that individuals exposed to greater masticatory loads during development will have biomechanically more robust mandibles and/or denser cortical bone than individuals subjected to reduced masticatory loads. Studies have found that rats and mice fed a hard diet have larger craniofacial dimensions than soft diet groups (Abed et al., 2007; Bouvier and Hylander, 1984; Enomoto et al., 2010; Kiliaridis, 1989; Maki et al., 2002; Mavropoulos et al., 2004; McFadden et al., 1986; Ödman et al., 2008; Sato et al., 2005; Spassov et al., 2017; Sugimoto et al., 1997), particularly in terms of maxillary breadth (Beecher and Corruccini, 1981; Yamamoto, 1996) and within the mandibular ramus/angular region (Moore, 1965; Watt and Williams, 1951). Similarly, pigs fed a soft diet have reduced craniofacial musculature (Ciochon et al., 1997), but wider dental arches (Larsson et al., 2005) than hard-diet groups. In both rats and rabbits, soft diets slowed the rate of bone growth and reduced overall bone mineral density (particularly around muscle attachment sites in the ramus) (Bresin et al., 1999; Grunheid et al., 2011; Kiliaridis et al., 1985, 1999; Yamada and Kimmel, 1991; Yamamoto, 1996). Another study found that inducing masseter muscle paralysis in adult mice led to both a reduction in bone tissue mass and trabecular thickness within the mandibular condylar head (Balanta-Melo et al., 2018). Hyraxes are a valuable experimental animal because they have a retrograthic face similar to humans and, therefore, experience a comparable mandibular strain gradient (Lieberman et al., 2004a).³ In an experimental study, hyraxes fed a soft diet had reduced growth throughout the facial region compared with their hard-diet counterparts and, specifically, had narrower and shorter faces, as well as shorter and thinner mandibular bodies (Lieberman et al., 2004a).

Experimental work on non-human primates has shown that durophagy (i.e. ingesting hard and tough food) generates the highest strains in the lower face (i.e. the mandibular corpus, the maxilla and the zygomatic arch) (Hylander and Johnson, 1992; Hylander et al., 1991, 1992; Hylander and Ravosa, 1992; Ravosa et al., 2000; Ross and Hylander, 1996; Ross et al., 2012). Compared with animals fed a naturally tough diet, non-human primates raised on artificially softened foods demonstrated narrowing of the maxillary arch, palate arching, rotated and displaced teeth, crowded premolars, reduced cranial bone mineralisation and reduced height of the mandibular corpus in the molar region (Bouvier and Hylander, 1981; Corruccini and

³ Some researchers believe that the human retrognathic face is an adaptation that results in higher bite force due to the proximity of the dental occlusal plane with the temporomandibular joint (TMJ) which creates a shorter loading arm for the masticatory muscles (Demes and Creel 1988; Lieberman 2011; Wroe et al., 2010).

Beecher, 1982). However, the relationship between diet and facial shape is not straightforward, and a study using colobus monkeys failed to show the predicted correlation. For the colobus monkeys, the unexpected results may have been due to the influence of the large canine on biomechanical strain patterns within the masticatory region (Daegling and McGraw, 2001).

Experimental studies using animal models to investigate the relationship between mandibular morphology and dietary toughness are important because they can largely control for sources of environmental and genetic variation. It is clear from the research that the most consistent differences between animals fed diets of varying toughness are found in the mandibular corpus (e.g. Bouvier and Hylander, 1981, 1996; Lieberman et al., 2004) and in areas of masticatory muscle attachment, such as the gonial angle region and the ramus (e.g. Hylander and Johnson, 1992; Hylander et al., 1991; Lieberman et al., 2004). However, experimental conditions do not reflect the natural feeding environment of an animal, and there are differences between what is observed in a controlled laboratory setting and what occurs in a natural population. In addition, inter-species variation in anatomy and feeding behaviour can make it difficult to compare the results from experiments using different animals (Meloro and O'Higgins, 2011; Raia et al., 2010). Particularly, important functional characteristics of the modern human face, such as its relatively small size and retraction under the braincase, are not observed in other modern primates and mammals (Lacruz et al. 2019; Lieberman, 2011). Therefore, conclusions from animal studies may have limited value when aiming to interpret observed human morphological variation.

5.2.2 Clinical evidence

Due to obvious methodological difficulties, there is limited clinical research on the relationship between mandibular shape, bite force and the development of the masticatory muscles in living humans (e.g. Bakke et al., 1992; Raadsheer et al., 1999; Sasaki et al., 1989). Consequently, the way that the human face is loaded during mastication is only partially understood (Wroe et al., 2010). Using medical data from modern populations, it has been observed that although muscle force is weakly correlated to cranial shape (Toro-Ibacache et al., 2016), it is more closely related to the shape of the mandible (Sella-Tunis et al., 2018). Multiple clinical studies have shown that increased bite force is positively correlated with increased ramus height (Ingervall and Helkimo, 1978; Raadsheer et al., 1999; Ringqvist, 1973), the length of the mandibular corpus (Hannam and Wood, 1989; Raadsheer et al., 1999; Ringqvist, 1973; Sondang et al., 2003) and a smaller gonial angle (Ingervall and Bitsanis, 1987;

Ingervall and Helkimo, 1978; Ingervall and Minder, 1997; Kiliaridis et al., 1995; Raadsheer et al., 1999; Ringqvist, 1973; Sondang et al., 2003; Throckmorton et al., 2000; Tuxen et al., 1999). In addition, masticatory muscle development is inversely correlated with the magnitude of the gonial angle (Benington et al., 1999; Bloem and van Hoof, 1971; Gionhaku and Lowe, 1989; Kasai et al., 1994, 1997; Kubota et al., 1998) and positively correlated with bigonial/bicondylar width (Castelo et al., 2008; Raadsheer et al., 1996; van Spronsen et al., 1991; Weijs and Hillen, 1986), ramus height (Benington et al., 1999; Gionhaku and Lowe, 1989; Kasai et al., 1994; Kubota et al., 1999; Gionhaku and Lowe, 1989; Kasai et al., 1994; Kubota et al., 1999; Gionhaku and Lowe, 1989; Kasai et al., 1994; Kubota et al., 1999) and mandibular length (Weijs and Hillen, 1986). However, some studies have failed to identify a relationship between bite force, craniofacial dimensions and masticatory muscle size (Charalampidou et al., 2008; Ingervall and Thilander, 1974; Kitai et al., 2002; van Spronsen et al., 1991; Watanabe and Watanabe, 2001).

Much of the recent research in living humans has been conducted within the field of dentistry and, therefore, focuses primarily on the effect of jaw morphology (particularly mandibular shape deformities) on malocclusions and maxilla-mandibular functionality (Corruccini, 1984; Howe et al., 1983; Park et al., 2010; Toro-Ibacache et al., 2014, 2019). A study comparing anatomically correct mandibles with prognathic and retrognathic mandibles found that shape differences were concentrated within the functional units of the mandibular body and ramus associated with masticatory muscles (i.e. the coronoid and condyle), rather than throughout the entire mandible (Park et al., 2010).⁴ Despite the inference that low masticatory loads may cause malocclusion (Corruccini, 1984), a recent study found no evidence to support the relationship between malocclusion and mechanically weak mandibles in modern populations (Toro-Ibacache et al., 2019). In modern populations with relatively low masticatory strains and reduced functional constraints, other factors such as genetics, nutrition or basal metabolism may be driving the observed mandibular morphology (Toro-Ibacache et al., 2019). This finding suggests that the factors influencing mandibular shape in past human populations may be different to those shaping modern human mandibles (Toro-Ibacache et al., 2019), and therefore caution is needed when comparing results between modern and ancient populations.

⁴ Prognathism and retrognathism are both types of malocclusions caused by differential growth of the facial bones that result in the misalignment of the mandibular and maxillary dentition. Prognathism results in an anterior extension (protrusion) of the mandible beyond the maxilla, whereas retrognathism is characterised by a posterior positioning of the mandible with the maxilla overhanging the mandible (commonly referred to as an 'overbite') (Chang et al., 2006).

5.2.3 Archaeological evidence

Several bioarchaeological studies have compared craniofacial morphology between hunter-gatherers and agriculturalists, based on the hypothesis that changes observed in the facial growth patterns of farmers are due to a softer diet and reduced masticatory strain (Larsen, 1995, 1997). These studies have shown the presence of craniofacial gracilisation, particularly of the mandible, in agricultural populations (Brace et al., 1987, 1991; Carlson and Van Gerven, 1977; Galland et al., 2016; Goodman et al., 1984; Hannam and Wood, 1989; Hinton and Carlson, 1979; Holmes and Ruff, 2011; Kaifu, 1997; Kiliaridis, 1995; Larsen, 1982, 1995, 1997, 2015; Pinhasi et al., 2008; Sardi et al., 2006; Smith, 1984; van Spronsen et al., 1991; Y'Edynak and Fleisch, 1983). In general, these studies have found that hunter-gatherer mandibles were larger and more robust than those of later agriculturalists (e.g. Carlson and Van Gerven, 1977; Galland et al., 2016; Kaifu, 1997; Larsen, 1982; von Cramon-Taubadel, 2011; Y'Edynak and Fleisch, 1983), but there are regional differences in the degree of variation and the areas of the mandible that are most affected (Paschetta et al., 2010; Pinhasi et al., 2008).

Research comparing archaeological and modern populations has also shown a general reduction in the size of the mandible in recent times in Europe (Goose, 1962; Humphrey et al., 1999; Lavelle, 1972; Lysell, 1958; Mohlin et al., 1978; Moore et al., 1968; Rando et al., 2014), North America (Martin and Danforth, 2009), Japan (Kaifu, 1995, 1997, 2000; Maeda, 2002) and China (Li et al., 2012; Wu et al., 2007). However, the results for specific mandibular dimensions can be inconsistent. Some studies reported reduced corpus length in archaeological populations compared with modern populations (Ingervall et al., 1972; Luther, 1993), while others found greater corpus length in the archaeological populations (Martin and Danforth, 2009) or found no difference between the two groups (Seddon, 1984; Varrela, 1992). In addition, some research has shown that archaeological groups had smaller gonial angles (Ingervall et al., 1972; Kaifu, 1997; Li et al., 2012; Luther, 1993; Martin and Danforth, 2009; Seddon, 1984) and greater ramus height (Ingervall et al., 1972; Varrela, 1990, 1992) than more recent populations. However, some researchers found no difference in ramus height between European archaeological and modern populations (Luther, 1993; Seddon, 1984). The larger ramus and smaller gonial angle observed in some archaeological samples may reflect greater biomechanical force required for their respective diet, whereas the smaller dimensions in other areas of the mandible may be an allometric effect of overall smaller body size in these past populations compared with modern populations (Ingervall et al., 1972).

The evidence from experimental animal studies, clinical research and archaeological evidence supports the notion that changes in mechanical stress due to variation in dietary composition is an important factor influencing human craniofacial growth, particularly in relation to the mandible. However, the trends observed in past human populations are not universally applicable and are affected by specific cultural and biological factors in each region. In addition, it is important to understand how the craniofacial region is influenced by incremental dietary changes. Further study by region is, therefore, required to elucidate the relationship between mandibular morphology and the diets and subsistence strategies of past human populations.

5.3 Materials and methods

5.3.1 Materials

The data included in this study were collected from populations representing the Late Palaeolithic (JSA; c. 13000–9000 BC), Sudanese Neolithic (**R12**; c. 5000–4000 cal BC), Kerma Ancien (**KAW**; c. 2500–2050 BC), Kerma Classique (**KER**; c. 1750–1500 BC) and Meroitic (**KUS**; c. 350 BC–AD 350) cultural periods from Upper Nubia. Background information on the populations used in this study can be found in **Chapter 4**. Age and sex were assessed using standard osteological techniques (White and Folkens, 2005; **Appendix A.1**).

Mandibles from adult individuals were included in the study if they were complete or near complete. Due to poor preservation, there were many incomplete/damaged mandibles in the sampled populations. Where possible, the fragmented mandibles were reconstructed using the 3D laser scanning software (**Appendix A.3**). Adults displaying poor preservation (affecting the surface of the mandible) or oral pathologies influencing mandibular shape (such as dental abscesses) were excluded from analysis. It has been demonstrated that within an individual, severe ante-mortem tooth loss (AMTL) can influence the chewing cycle, patterns of masticatory muscle force, and may ultimately influence mandibular morphology (Mays, 2013). Therefore, individuals were excluded from the analysis if the associated mandible displayed two instances of AMTL on one side of the mandibular body.

It may also be the case that the differential age distribution of the individuals within each sample population may limit the interpretation of the results, as the human mandible can continue to adapt and grow into adult life (e.g. Behrents, 1990). However, the influence of agerelated factors in this study was minimised due to the selection criteria regarding adult status, severe oral pathologies and AMTL. The sex and age distribution of the samples analysed here can be found in **Table 5.1**. The only sample with a higher proportion of older individuals was the R12 population.

	•		*			•
Sample		Sex			Age	
	Male	Female	Indeterminate	Younger	Older	Indeterminate
JSA	8	4	1	_*	_*	_*
R12	8	15	-	5	17	1
KAW	13	4	-	12	5	-
KER	21	18	-	24	13	2
KUS	6	1	_	6	4	_

Table 5.1 Sex and age distribution for each sample included in the mandibular osteometric analysis

*Access to JSA material was not available, and the age of these individuals was not recorded when the original scans were taken. JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Younger adults \leq 35 years old; Older adults >35 years old.

5.3.2 Methods

Each mandible was digitised using a 3D surface scanner (NextEngine HD device; **Appendix A.3**). Mandibular metric analysis was performed on each specimen according to standard osteological definitions (Buikstra and Ubelaker, 1994). The definitions of the measurements used in the present study and their abbreviations are provided in **Table 5.2**. Measurements corresponding to mandibular length are shown in **Figure 5.1**, mandibular breadth are in **Figure 5.2**, measurements of the ramus are in **Figure 5.3** and mandibular corpus measurements are shown in **Figure 5.4**. The measurements that were included in this study were specifically chosen to facilitate comparison with previous studies on mandibular osteometrics. Measurements were taken to the nearest 0.1 mm using the Rapidform software. Where possible, measurements were taken preferentially on the left side. If the left side was damaged, the right-side measurement was substituted.

Abbreviation	Measurement	Definition	Source
ML1	Mandibular length	Gnathion to the midsagittal point of the condyle-condyle chord (Gn to Co-Co)	Buikstra and Ubelaker 1994
ML2	Mandibular length	Direct distance between the gnathion and the condyle (Gn to Co)	Buikstra and Ubelaker 1994
ML3	Mandibular length	Infradentale to the midsagittal point of the gonion-gonion chord (Id to Go-Go)	Daegling and McGraw 2007
BGoB	Bigonial breadth	Direct distance between right and left gonion	Buikstra and Ubelaker 1994
ВСоВ	Bicondylar breadth	Direct distance between the most lateral points on the right and left condyle	Buikstra and Ubelaker 1994
LRB	Minimum ramus breadth	Least breadth on the mandibular ramus measured perpendicular to the height of the ramus	Buikstra and Ubelaker 1994
MRB	Maximum ramus breadth	Distance between the most anterior point on the mandibular ramus and a line connecting the most posterior point on the condyle and angle of the jaw	Buikstra and Ubelaker 1994
RH	Ramus height	Direct distance from the highest point on the mandibular condyle to the gonion	Buikstra and Ubelaker 1994
СгН	Coronoid height	Direct distance from highest point on the mandibular coronoid to the inferior point on the mandibular ramus	Buikstra and Ubelaker 1994
GA	Gonial angle	Angle formed by the inferior border of the corpus and the posterior border of the ramus	Buikstra and Ubelaker 1994
UML	Upper mandibular length	Infradentale to the midsagittal point of BCoB (Id to Co-Co)	Kaifu 1995
LML	Lower mandibular length	Gnathion to the midsagittal point of BGoB (Gn to Go-Go)	Kaifu 1995
GML	Gn to M ₃	Measured distance from gnathion to posterior alveoli of M ₃	Buikstra and Ubelaker 1994
DAL	Dental arch length	Measured from the infradentale to the midsagittal point of BM2B	Kaifu 1995
BCP3B	Dental arch breadth (C/P ₃ - C/P ₃)	Measured at the most lateral point of the alveolar ridge	Kaifu 1995
BM1B	Dental arch breadth (M1- M1)	Measured at the intersection point of the lateral tangent line of the proximal and distal M ₁ alveoli and the midline between the alveoli	Kaifu 1995
BM2B	Dental arch breadth (M ₂ - M ₂)	Measured at the intersection point of the lateral tangent line of the proximal and distal M ₂ alveoli and the midline between the alveoli	Kaifu 1995

 Table 5.2 Definitions of mandibular linear measurements

Co: condyle; Gn: gnathion; Go: gonion; Id: infradentale.



Figure 5.1 Mandibular length linear measurements

ML1: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal gonion-gonion chord; **UML**: upper mandibular length, infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **GML**: mandibular length, gnathion to M₃.



Figure 5.2 Mandibular and dental arcade breadth linear measurements

BGoB: bigonial breadth; **BCoB**: bicondylar breadth; **BCP3B**: dental arch breadth at C_1/P_3 ; **BM1B**: dental arch breadth at M_1 ; **BM2B**: dental arch breadth at M_2 ; **DAL**: dental arch length, infradentale to midsagittal BM2B.





LRB: least ramus breadth; MRB: maximum ramus breadth; RH: ramus height; CrH: coronoid height; GA: gonial angle.





SH: symphyseal height; **SB**: symphyseal breadth; **MH**: mental foramen height; **MB**: mental foramen breadth; **LH**: left M_1/M_2 height; **LB**: left M_1/M_2 breadth; **RH**: right M_1/M_2 height; **RB**: right M_1/M_2 breadth.

The height and the width of the mandibular corpus at the symphysis, mental foramen and between M_1 and M_2 on both sides of the corpus (where available) were also measured (**Table 5.3**; **Figure 5.4**). In addition, the height and width measurements were used to calculate a robusticity index (breadth/height), along with a mathematical correlate for overall corpus cross-sectional area at the symphysis, mental foramen and both molar regions (Antón et al., 2011; Daegling and McGraw, 2007).

Abbreviation	Measurements	Definition	Source
SH	Symphyseal height	The maximum linear distance between the midline crest of the mandibular incisor alveolus (infradentale) and the most inferior portion of the mandibular symphysis	Hylander 1985
SB	Symphyseal breadth	The maximum linear (anteroposterior) dimension of the symphysis in the sagittal plane taken perpendicular to the symphyseal length	Hylander 1985
SR	Symphyseal robusticity index	Symphyseal breadth/height	Antón et al. 2011
SS	Symphyseal size	Symphysis height x breadth x $\pi/4$	Daegling and McGraw 2007
MH	Mental foramen height	The maximum distance from the midpoint of the alveolus superior to the mental foramen to the distal margin of the corpus	Buikstra and Ubelaker 1994
MB	Mental foramen breadth	The maximum buccolingual distance at the mental foramen	Buikstra and Ubelaker 1994
MR	Mental foramen robusticity index	Mental foramen breadth/mental foramen height	Antón et al. 2011
MS	Mental foramen size	Mental foramen height x breadth x $\pi/4$	Daegling and McGraw 2007
LH	Left M ₁ /M ₂ height	The maximum distance from the midpoint of the alveolus between left M ₁ and M ₂ to the distal margin of the corpus	Taylor 2006; Daegling and McGraw 2007
LB	Left M ₁ /M ₂ breadth	The maximum buccolingual distance at the midpoint of left M ₁ and M ₂	Taylor 2006; Daegling and McGraw 2007
LR	Left M ₁ /M ₂ robusticity index	Left M_1/M_2 breadth/left M_1/M_2 height	Antón et al. 2011
LS	Left M ₁ /M ₂ size	Left M_1/M_2 height x breadth x $\pi/4$	Daegling and McGraw 2007
RH	Right M ₁ /M ₂ height	The maximum distance from the midpoint of the alveolus between right M_1 and M_2 to the distal margin of the corpus	Taylor 2006; Daegling and McGraw 2007
RB	Right M ₁ /M ₂ breadth	The maximum buccolingual distance at the midpoint of right M_1 and M_2	Taylor 2006; Daegling and McGraw 2007
RR	Right M ₁ /M ₂ robusticity index	Right M_1/M_2 breadth/right M_1/M_2 height	Antón et al. 2011
RS	Right M_1/M_2 size	Right M_1/M_2 height x breadth x $\pi/4$	Daegling and McGraw 2007

Table 5.3 Definitions of mandibular corpus measurements and cross-sectional calculated values

5.3.3 Statistical analysis

Linear measurements quantifying dimensions of mandibular length, width, ramus and the mandibular body were analysed to identify diachronic changes in size and shape between Nubian populations. Additionally, to examine how mandibular dimensions changed over time in relation to each other, a series of mandibular measurement ratios were analysed. Summary statistics of the linear metric data by sample were generated in SPSS (a full set of the ratios that were analysed and the descriptive statistics can be found in **Appendix B**). Data were tested for normality using the Shapiro-Wilk Test. ANOVAs were used to evaluate statistically significant differences in mandibular linear measurements (significance level: $p \le 0.05$). Hochberg's GT2 *post-hoc* tests (significance level: $p \le 0.05$) were used following significant ANOVAs to test for differences between groups, because this *post-hoc* test is robust for small and unequal sample sizes (Field, 2013). For measurements with a non-normal distribution and for the measurement ratios, the non-parametric Kruskal-Wallis test was used. Significant Kruskal-Wallis tests (significance level: $p \le 0.05$) were followed by Mann-Whitney tests to analyse differences between populations (significance level: $p \le 0.005$ following Bonferroni correction) (Hoel et al., 1971).⁵ In addition, independent sample *t*-tests were used to identify significant sexual dimorphism in mandibular dimensions within each sample (significance level: $p \le 0.05$). The full results of the *t*-tests between males and females can be found in **Appendix B**. Dependent sample *t*-tests were used to analyse differences between the left and right linear measurements of the mandible within the same individual (significance level: $p \le 0.05$) (Appendix B). All mandibular measurements were analysed as a pooled-sex sample and separately for males and females.

5.4 Results

The descriptive statistics for the mandibular linear measurements for the pooled-sex samples by population can be found in **Table 5.4**. The descriptive statistics for the male and female samples can be found in **Table 5.6**.

⁵ The Bonferroni correction is an adjustment made to *p*-values to limit the likelihood of a Type I error when several dependent or independent statistical tests are being performed simultaneously on a single data set. A Bonferroni correction is calculated by dividing the critical *p*-value (α) by the number of comparisons made (Hoel et al., 1971).

		1	ML1			1	ML2		_	M	L3		BGoB				
Population	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	
JSA	11	110.36	6.67	6.04	11	127.86	6.36	4.97	11	80.02	4.77	5.96	10	102.89	6.58	6.40	
R12	13	100.33	3.93	3.92	13	115.50	3.70	3.20	13	72.14	4.60	6.38	7	86.99	5.54	6.37	
KAW	15	101.28	4.86	4.80	14	116.71	3.64	3.12	16	71.31	4.76	6.68	15	89.92	7.85	8.73	
KER	39	100.16	6.10	6.09	39	116.39	6.46	5.55	39	67.57	5.69	8.42	37	88.99	6.48	7.28	
KUS	9	96.59	3.48	3.60	9	113.32	4.95	4.37	9	67.82	5.01	7.39	8	89.90	6.34	7.05	
	_	E	BCoB]	LRB			M	RB		_	F	RH		
Population	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	
JSA	10	118.22	9.89	8.37	13	41.46	2.74	6.61	13	53.71	2.59	4.82	13	64.55	6.57	10.18	
R12	7	104.80	9.22	8.80	19	32.78	2.29	6.99	17	41.95	2.52	6.01	18	59.26	4.46	7.53	
KAW	11	104.54	3.71	3.55	17	35.17	2.57	7.31	15	43.92	3.32	7.56	15	56.94	5.41	9.50	
KER	39	107.24	7.10	6.62	39	32.83	2.58	7.86	39	44.80	3.25	7.25	39	60.72	6.74	11.10	
KUS	6	105.83	6.52	6.16	9	31.98 2.98		9.32	9	43.19	3.99	9.24	9	57.14	5.45	9.54	
		<u> (</u>	<u>CrH</u>				<u>GA</u>			U	<u>ML</u>			\mathbf{L}	ML		
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	
JSA	13	61.99	7.52	12.13	13	117.26	4.15	3.54	11	108.95	4.27	3.92	11	88.24	5.69	6.45	
R12	18	57.23	3.20	5.59	21	118.63	5.78	4.87	13	94.33	4.43	4.70	14	81.76	4.31	5.27	
KAW	16	57.53	5.87	10.20	16	119.64	7.76	6.49	15	97.17	3.90	4.01	16	79.87	4.58	5.73	
KER	38	60.97	6.42	10.53	38	122.80	6.79	5.53	38	95.89	5.18	5.40	39	76.35	4.54	5.95	
KUS	9	55.85	5.19	9.29	9	123.62	5.20	4.21	9	94.66	3.88	4.10	9	73.99	3.92	5.30	
		<u>(</u>	<u>GML</u>			<u>]</u>	DAL			<u>BC</u>	<u>P3B</u>		<u>BM1B</u>				
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	
JSA	11	56.18	2.74	4.88	11	38.04	2.07	5.44	10	34.28	1.73	5.05	10	56.13	1.88	3.35	
R12	13	56.13	3.56	6.34	14	32.10	3.01	9.38	10	30.23	2.74	9.06	8	50.46	1.52	3.01	
KAW	17	55.86	4.52	8.09	17	33.12	4.96	14.98	17	31.99	2.40	7.50	15	51.98	2.82	5.43	
KER	37	55.01	4.00	7.27	37	33.81	3.19	9.44	38	31.34	2.43	7.75	37	51.99	2.94	5.65	
KUS	9	54.56	2.19	4.01	9	31.52	2.91	9.23	8	31.42	2.36	7.51	8	51.53	2.86	5.55	
		<u>B</u>	<u>M2B</u>														
Population	п	Mean	SD	CV	_												
JSA	10	61.23	1.95	3.18													
R12	8	55.47	1.98	3.57	_												
KAW	15	57.96	3.35	5.78													
KER	36	57.84	3.73	6.45													
KUS	8	57.65	2.65	4.60													

 Table 5.4 Descriptive statistics for mandibular linear measurements

Mean is reported in mm except for GA which is reported in degrees (°). JSA: Jebel Sahaba (c. 13000–9000 BC); **R12**: NDRS R12 (c. 5000–4000 cal BC); **KAW**: NDRS P37 (c. 2500–2050 BC); **KER**: Kerma (c. 1750–1500 BC); **KUS**: Kawa (R18) (c. 350 BC–AD 350). **ML1**: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bigonial breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length, infradentale to midsagittal gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch length from infradentale to midsagittal BM2B; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *n*: sample size; SD: standard deviation; CV: coefficient of variation.⁶

⁶ The Coefficient of Variation (CV) provides a standardised way to compare the magnitude of morphological variation in the mandible (Sokal and Braumann, 1980): CV=100 x (SD/X); where SD=standard deviation and X=mean.

5.4.1 Mandibular length

Of the seven measurements relating to the length of the mandible, differences between samples for six measurements were statistically significant following the ANOVA (ML2, ML3, UML, LML: all p<0.001) and Kruskal-Wallis tests (ML1, DAL: all p<0.001) (**Table 5.5**; **Figure 5.5**). *Post-hoc* analyses identified that for all the significant length measurements, the JSA sample was significantly larger than the other Nubian samples. Although there were fewer significant trends amongst the Holocene samples, there was a clear trend for the length measurements ML3 and LML to continue to decrease over time from the Sudanese Neolithic (R12) through to the Meroitic sample (KUS) (**Table 5.5**; **Figure 5.5**). The ML3 and LML measurements record the length of the mandible from the infradentale (ML3) or the gnathion (LML) of the symphysis to the midsagittal point of the gonion-gonion chord (BGoB). The mean LML measurement for the R12 sample was significantly larger than KER and KUS (**Table 5.5**; **Figure 5.5**). For most of the measurements, the largest reduction in mandibular length occurred between the JSA and R12 samples, particularly within males.

There were significant differences between males for all of the dimensions of mandibular length except for GML (ML1, ML2, ML3, UML, LML: all $p \le 0.001$; DAL: p=0.005) (**Table 5.6**; **Figure 5.6**). *Post-hoc* analyses showed that the only significant differences in male mandibular length were between JSA and the later samples. For ML1, ML2 and UML males from JSA were significantly larger than males from all the other samples. For ML3, LML and DAL, males from JSA were significantly larger than males from KAW and KER (**Table 5.6**; **Figure 5.6**). There were reduction trends within the males of the Holocene samples for ML1, ML3, LML and DAL, but these trends were not statistically significant.

When females from different populations were compared using ANOVAs, there were fewer statistically significant differences in mandibular length measurements compared with males (**Table 5.6**). Females were significantly different in the following dimensions: ML1 (p=0.011), ML2 (p=0.002), ML3 (p=0.001), LML (p<0.001) and DAL (p=0.016) (**Figure 5.6**). *Post-hoc* analyses showed that there were no significant pairwise comparisons for ML1 or DAL. For ML2 and LML, females from JSA were significantly larger than females from the later samples, KER and KUS. In addition, females from JSA had significantly larger mean ML3 than females from KER. Females from R12 had significantly larger mean LML than females from KER or KUS (**Table 5.6**). Non-significant reduction trends amongst females in

the Holocene samples were observed for ML1, ML2 and LML (**Figure 5.6**). However, it is important to note that small sample sizes may limit the interpretation of these results.

Measurement	F (df1, df2)	р	ω	Hochberg's GT2 post-hoc
				tests
ML2	8.50 (4, 28.28) ^a	<0.001	N/A	JSA>R12, KAW, KER, KUS ^b
ML3	13.28 (4, 83)	<0.001	.60	JSA>R12, KAW, KER, KUS
UML	20.28 (4, 81)	<0.001	.69	JSA>R12, KAW, KER, KUS
LML	18.31 (4, 84)	<0.001	.66	JSA>R12, KAW, KER, KUS R12>KER, KUS
GML	0.51 (4, 82)	0.73	N/A	N/A
BGoB	9.47 (4, 72)	<0.001	.55	JSA>R12, KAW, KER, KUS
ВСоВ	6.04 (4, 68)	<0.001	.47	JSA>R12, KAW, KER, KUS
BCP3B	4.18 (4, 78)	0.004	.36	JSA>R12, KER
BM1B	6.34 (4, 73)	<0.001	.46	JSA>R12, KAW, KER, KUS
BM2B	3.76 (4, 72)	0.008	.35	JSA>R12, KER
RH	3.53 (4, 89)	0.01	.31	JSA>KAW
CrH	3.27 (4, 30.85) ^a	0.024	N/A	KER>R12 ^b
GA	3.15 (4, 92)	0.018	.29	No sig. results
Kruskal-Wallis	п	Hc	р	Mann-Whitney tests
ML1	86	22.26	<0.001	JSA>R12, KAW, KER, KUS
LRB	96	41.16	<0.001	JSA>R12, KAW, KER, KUS
MRB	92	38.21	<0.001	JSA>R12, KAW, KER, KUS KER>R12
DAL	86	24.33	<0.001	JSA>R12, KAW, KER, KUS

Table 5.5 ANOVAs and *post-hoc* tests for mandibular measurements (pooled sex)

^aWelch statistic; ^bGames Howell *post-hoc* test; ^cdegrees of freedom=4. ANOVA level of significance $p \le 0.05$; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; K-W level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.005$. **JSA**: Jebel Sahaba (c. 13000–9000 BC); **R12**: NDRS R12 (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18) (c. 350 BC–AD 350); **ML1**: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length, infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch length from infradentale to midsagittal BM2B; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *F*: ANOVA test statistic; df1: degrees of freedom 1; df2: degrees of freedom 2; ω : effect size;⁷ *n*: sample size; *H*: K-W test statistic.

⁷ Omega (ω) is a measure of effect size: $\omega = \sqrt{\frac{SS_M \cdot (df_M)MS_R}{SS_T + MS_R}}$ where $SS_M = Sum$ of squares between groups, $df_M =$ degrees of freedom between groups; $MS_R =$ Mean square within groups; $SS_T =$ Sum of squares total (Field 2009). $\omega^2 = .01$, small effect; $\omega^2 = .06$, medium effect; $\omega^2 = .14$, large effect (Kirk, 1996)











Figure 5.5 Mandibular length measurements by population (pooled sex) for (a) ML1, (b) ML2, (c) ML3, (d) UML, (e) LML, (f) GML, and (g) DAL

Error bars 95% confidence interval. * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$ or Mann-Whitney test $p \le 0.005$). **ML1**: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal gonion-gonion chord; **UML**: upper mandibular length, infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **CML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **CML**: length from gnathion to M₃; **DAL**: dental arch length; **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

				M	L1							M	L2					<u>ML3</u>								
		Ma	ale			Fer	nale			Μ	lale			Fei	male			Ν	Iale			Fe	male			
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV		
JSA	7	113.12	5.92	5.23	4	105.52	5.43	5.15	7	130.57	4.89	3.75	4	121.56	4.08	3.36	7	82.82	1.87	2.26	4	75.12	4.28	5.70		
R12	4	101.28	4.35	4.30	9	99.91	3.93	3.93	4	115.99	3.31	2.85	9	115.28	4.03	3.50	4	74.12	5.27	7.11	9	71.26	4.30	6.03		
KAW	11	102.73	4.51	4.39	4	97.28	3.66	3.76	10	117.72	3.17	2.69	4	114.17	3.91	3.42	11	71.64	5.67	7.91	4	70.12	1.88	2.68		
KER	21	103.39	5.39	5.21	18	96.39	4.58	4.75	21	120.73	5.26	4.36	18	111.90	4.44	3.97	21	69.98	4.52	6.46	18	64.75	5.73	8.85		
KUS	3	99.04	3.30	3.33	6	95.37	3.11	3.26	3	117.03	5.70	4.87	6	111.46	3.71	3.33	3	69.43	7.82	11.26	6	67.01	3.68	5.49		
	BGoB										BCoB									L	RB					
	Male					Fer	nale			Μ	lale		Female			Male				Female						
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV		
JSA	6	105.76	4.15	3.92	4	98.57	7.74	7.85	6	121.04	7.47	6.17	4	114.00	12.68	11.12	8	42.71	2.81	6.58	4	39.28	0.85	2.16		
R12	1	85.36	N/A	N/A	6	87.26	6.01	6.89	1	92.75	N/A	N/A	6	106.81	8.26	7.73	8	32.63	2.67	8.18	11	32.89	2.20	6.69		
KAW	11	92.46	7.46	8.07	4	82.93	3.70	4.46	9	105.13	3.80	3.61	2	101.87	2.15	2.11	12	35.60	2.86	8.03	5	34.15	1.39	4.07		
KER	21	92.63	5.05	5.45	16	84.22	4.90	5.82	21	111.45	4.49	4.03	18	102.32	6.43	6.28	21	33.55	2.71	8.08	18	32.00	2.22	6.94		
KUS	3	89.87	2.59	2.88	5	89.91	8.19	9.11	2	106.64	11.43	10.72	4	105.42	5.15	4.89	3	34.33	3.38	9.85	6	30.80	2.16	7.01		
				M	<u>RB</u>					RH										<u>C</u>	·Н					
		Ma	ale			Fer	nale			Μ	lale			Fei	male			Ν	Iale			Fe	male			
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV		
JSA	8	54.81	2.67	4.87	4	51.69	1.12	2.17	8	66.01	5.26	7.97	4	58.87	4.35	7.39	8	64.53	4.85	7.52	4	54.32	6.36	11.71		
R12	6	41.12	3.33	8.10	11	42.40	2.00	4.72	7	62.85	3.99	6.35	11	56.97	3.08	5.41	6	58.13	2.37	4.08	12	56.79	3.56	6.27		
KAW	11	44.50	3.59	8.07	4	42.30	1.98	4.68	10	58.45	5.02	8.59	5	53.92	5.34	9.90	11	58.93	6.48	11.00	5	54.45	2.64	4.85		
KER	21	46.11	3.39	7.35	18	43.28	2.36	5.45	21	64.58	6.38	9.88	18	56.22	3.71	6.60	20	64.77	6.12	9.45	18	56.74	3.47	6.12		
KUS	3	45.73	3.00	6.56	6	41.92	4.02	9.59	3	62.19	6.12	9.84	6	54.62	3.09	5.66	3	59.50	7.20	12.10	6	54.02	3.21	5.94		

Table 5.6 Descriptive statistics for mandibular measurements by sex and sample	
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Table 5.6	continued
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				G	A					$\underline{\mathbf{UML}}$								LML							
		Ma	ıle			Fen	nale			Ν	Iale			Fe	male			Ν	Iale			Fe	male		
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	
JSA	8	115.53	3.29	2.85	4	121.77	1.57	1.29	7	111.00	2.66	2.40	4	105.37	4.42	4.19	7	91.55	2.61	2.85	4	82.46	4.92	5.97	
R12	9	115.70	4.99	4.31	12	120.83	5.51	4.56	4	94.17	5.43	5.77	9	94.40	4.28	4.53	6	85.19	4.41	5.18	12	79.86	3.01	3.76	
KAW	11	117.62	8.08	6.87	5	124.08	5.15	4.15	11	98.46	3.73	3.79	4	93.61	1.35	1.44	11	80.60	5.26	6.53	5	78.24	2.20	2.81	
KER	20	120.71	5.91	4.90	18	125.13	7.09	5.67	20	98.56	4.26	4.32	18	92.93	4.52	4.86	20	78.78	3.44	4.37	18	73.51	4.05	5.51	
KUS	3	123.08	5.11	4.15	6	123.90	5.71	4.61	3	96.25	2.58	2.68	6	93.87	4.37	4.66	3	75.08	6.60	8.79	6	73.44	2.46	3.35	
	GML											DA	L							BC	CP3B				
	Male Female						Ν	Iale		Female			Male				Female								
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	
JSA	7	57.52	2.18	3.79	4	53.85	2.01	3.73	7	38.83	2.01	5.18	4	36.64	1.45	3.96	6	33.99	1.55	4.56	4	34.71	2.14	6.17	
R12	4	58.51	2.11	3.61	9	55.07	3.65	6.63	4	34.11	2.20	6.45	9	31.20	2.98	9.55	2	32.01	2.14	6.69	8	29.78	2.81	9.44	
KAW	12	55.72	5.18	9.30	5	56.21	2.78	4.95	12	32.90	5.14	15.62	5	33.66	5.00	14.85	12	31.97	2.83	8.85	5	32.02	0.95	2.97	
KER	21	55.94	4.28	7.65	16	53.79	3.35	6.23	20	33.49	2.41	7.20	17	34.18	3.96	11.59	20	32.40	2.24	6.91	18	30.16	2.10	6.96	
KUS	3	55.33	2.88	5.21	6	54.17	1.96	3.62	3	32.38	3.81	11.77	6	31.09	2.66	8.56	3	30.46	1.35	4.43	5	31.99	2.79	8.72	
				BN	[<u>1B</u>							BM	2 <u>B</u>												
		Ma	ıle			Fen	nale			Ν	Iale			Fe	male										
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV									
JSA	6	56.45	1.25	2.21	4	55.66	2.75	4.94	6	61.73	1.64	2.66	4	60.48	2.38	3.94									
R12	1	52.88	N/A	N/A	7	50.11	1.26	2.51	1	55.85	N/A	N/A	7	55.41	2.13	3.84									
KAW	11	52.53	3.12	5.94	4	50.48	0.86	1.70	11	58.98	3.33	5.65	4	55.16	1.00	1.81									
KER	20	53.65	1.93	3.60	17	50.05	2.76	5.51	20	59.88	3.29	5.49	16	55.3	2.51	4.54									
KUS	3	51.54	3.10	6.01	5	51.52	3.09	6.00	3	58.74	2.48	4.22	5	57.00	2.80	4.91									

Mean is reported in mm except for GA which is reported in degrees (°). JSA: Jebel Sahaba (c. 13000–9000 BC); **R12**: NDRS R12 (c. 5000–4000 cal BC); **KAW**: NDRS P37 c. (2500–2050 BC); **KER**: Kerma (c. 1750–1500 BC); **KUS**: Kawa (R18) (c. 350 BC–AD 350). **ML1**: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length, infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *n*: sample size; SD: standard deviation; CV: coefficient of variation.










Figure 5.6 Mean mandibular length measurements by sex and sample for (a) ML1, (b) ML2, (c) ML3, (d) UML, (e) LML, (f) DAL and (g) GML

Error bars 95% confidence interval. * = significant sexual dimorphism (independent samples *t*-test $p \le 0.05$). **ML1**: mandibular length, gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length, gnathion to condyle; **ML3**: mandibular length, infradentale to midsagittal goniongonion chord; **UML**: upper mandibular length, infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length, gnathion to midsagittal gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch length; **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000– 9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

5.4.2 Mandibular breadth

Two measurements of overall mandibular breadth (BGoB and BCoB) and three measurements of dental arch breadth (BCP3B, BM1B and BM2B) were significantly different between samples following ANOVA and Kruskal-Wallis tests (**Table 5.4**; **Table 5.5**; **Figure 5.7**). *Post-hoc* analyses revealed that the majority of the significant pairwise differences were between the hunter-gatherer JSA sample and the more recent samples (for pooled sex and when males and females were analysed separately). For measurements of overall mandibular breadth (BGoB and BCoB) and the breadth of the mandible at M₁ (BM1B), the JSA sample was significantly larger than all of the later Nubian samples (**Table 5.5**; **Figure 5.7**). For the breadth of the dental arch at C₁/P₃ and M₂, JSA was significantly larger than R12 and KER (**Table 5.5**; **Figure 5.7**). The main decrease in mandibular breadth occurred between the JSA and later Holocene samples. There were no clear trends among the Upper Nubian samples for either mandibular breadth or dental arch breadth.

For comparisons of mandibular width between males, R12 was excluded from the analysis because width measurements were only available for one male mandible. Among males, there were significant differences between samples in BGoB (p<0.001), BCoB (p<0.001) and BM1B (p=0.008) (**Table 5.6**; **Figure 5.8**). For the BGoB and BCoB width dimensions, males from JSA were significantly larger than KAW, KER and KUS. In addition, males from KER had significantly greater BCoB than males from KAW. For BM1B, males from JSA were significantly larger than KAW and KUS. Males were not significantly different in BM2B dimension (p=0.34). When females were compared, there were significant differences between samples in BGoB (p=0.002), BM1B (p=0.005) and BM2B (p=0.041). For BGoB, females from JSA were significantly larger than females from KAW and KER. For the breadth of the dental arch at M₁ (BM1B), females from JSA were significantly larger than females from JSA were significantly larger than females from KAW and KER. For the breadth of the dental arch at M₁ (BM1B), females from JSA were significantly larger than females from KAW and KER. For the breadth of the dental arch at M₁ (BM1B), females from JSA were significantly larger than females from R12 and KER (**Table 5.6**; **Figure 5.8**). There were no significantly larger than females from R12 and KER (**Table 5.6**; **Figure 5.8**). There were not significantly different between the samples in breadth at C₁/P₃ (BCP3B: males: p=0.17; females: p=0.059).





Figure 5.7 Mean mandibular breadth measurements by population (pooled sex) for (a) BGoB, (b) BCoB, (c) BCP3B, (d) BM1B, and (e) BM2B

Error bars 95% confidence interval. * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$ or Mann-Whitney test $p \le 0.005$). **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).





Figure 5.8 Mean mandibular width measurements by sex and population for (a) BGoB, (b) BCoB, (c) BCP3B, (d) BM1B, and (e) BM2B

Error bars 95% confidence interval. * = significant sexual dimorphism (independent samples *t*-test $p \le 0.05$). **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

5.4.3 Ramus

For the combined analysis, JSA had the largest value for all the ramus measurements. Two measures of ramus breadth (LRB and MRB) were significantly different between the samples (all p < 0.001) (**Table 5.5**; **Figure 5.9**). For both LRB and MRB, the hunter-gatherer JSA was significantly larger than the other samples (and KUS had the smallest mean) (**Table 5.5**; **Figure 5.9**). In addition, for the MRB dimension, KER was significantly larger than R12 (**Table 5.5**; **Figure 5.9**). There was a non-significant trend for ramus breadth measurements (LRB and MRB) to decrease over time within females, but this was not observed between males.

The measures of ramal height at the coronoid process (CrH) and along the posterior border of the ramus between the condyle and the gonion (RH) were significantly different between samples (CrH: p=0.024; RH: p=0.01; **Table 5.5**). For the CrH measurement, KER was significantly larger than R12; for RH, JSA was significantly larger than KAW. There were significant differences in the gonial angle (GA) between Nubian samples (p=0.018) but *posthoc* tests did not show any significant pairwise comparisons. Although not statistically significant, there was a clear increase in gonial angle over time: the older samples JSA and R12 had more acute gonial angles, whereas the more recent agricultural populations, KER and KUS, had more obtuse gonial angles (**Table 5.5**; **Figure 5.9**).

Trends for males and females were similar to those observed for the pooled-sex data (**Table 5.6**; **Figure 5.10**). Both males and females were significantly different between samples in LRB and MRB (all p<0.001), and *post-hoc* analyses showed that males and females from JSA were significantly larger than all the other samples in both ramal width dimensions (LRB and MRB). In addition, males from KER had significantly larger MRB measurement than males from R12. Females were not significantly different in the other ramus dimensions (CrH: p=0.34; RH: p=0.27; GA: p=0.42). Males were significantly different in CrH (p=0.024) and RH (p=0.049), but there were no significant pairwise comparisons. Males were not significantly different in GA (p=0.088), but there was a strong trend (albeit not statistically significant) for an increase in GA over time, particularly between the KAW and KUS samples (**Table 5.6**; **Figure 5.10**). The increase in GA was also seen over time in females, and this trend seemed to be particularly pronounced following the Sudanese Neolithic R12 sample.



Population



Figure 5.9 Mean mandibular ramal measurements by population (pooled sex) for (a) LRB, (b) MRB, (c) CrH, (d) RH, and (e) GA

Error bars 95% confidence interval. * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$ or Mann-Whitney test $p \le 0.005$). **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).





Figure 5.10 Mean mandibular ramus measurements by sex and sample for (a) LRB, (b) MRB, (c) CrH, (d) RH, and (e) GA

Error bars 95% confidence interval. * = significant sexual dimorphism (independent samples *t*-test $p \le 0.05$). **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

5.4.4 Mandibular corpus

There were significant differences between samples in the height of the mandibular corpus at the symphysis (p<0.001), mental foramen (p<0.001), left M₁/M₂ (p<0.001) and right M₁/M₂ (p<0.001) (**Table 5.7**). *Post-hoc* analyses showed that at the symphysis, mental foramen, left and right M₁/M₂, JSA was significantly larger than all the other samples (**Figure 5.11**). While there was no clear trend within the Holocene populations in the height of the mandibular body at the symphysis or mental foramen, there was a decrease over time in the Holocene populations in the molar region, a trend that was more pronounced for males.

Among males, there were significant differences between samples in mandibular height at the symphysis, mental foramen, left M_1/M_2 and right M_1/M_2 (all p<0.001) (**Table 5.8**). For each region of the mandibular body, JSA was significantly larger in mean height than all the other samples (**Figure 5.12**). The height of the mandibular body for females was significantly different between samples at the symphysis (p<0.001), left M_1/M_2 (p=0.009) and right M_1/M_2 (p=0.043) (**Table 5.8**). At the symphysis, females from JSA had significantly larger mean height than all the other samples. Height at left M_1/M_2 was significantly larger for females from JSA compared with females from KER. There were no significant pairwise comparisons between females at right M_1/M_2 (**Table 5.8**; **Figure 5.12**). Females were not significantly different in mandibular body height at the mental foramen (p=0.12).

The breadth of the mandibular corpus at the symphysis, mental foramen, left M_1/M_2 and right M_1/M_2 were not significantly different between samples (symphysis: *p*=0.99; mental foramen: *p*=0.54, left M_1/M_2 : *p*=0.29; right M_1/M_2 : *p*=0.79) (**Table 5.7**; **Figure 5.11**). Within the Holocene samples, the breadth of the mandibular body at the symphysis and mental foramen slightly decreased over time, although this trend was not statistically significant. There was no clear trend within Holocene samples in mandibular molar breadth. When the breadth of the mandibular body was compared between samples, males were not significantly different at the symphysis (*p*=0.98), mental foramen (*p*=0.42), left M_1/M_2 (*p*=0.62) or right M_1/M_2 (*p*=0.46) (**Table 5.8**; **Figure 5.12**). Similarly, there were no significant differences in breadth between females at the symphysis (*p*=0.87), mental foramen (*p*=0.42), left M_1/M_2 (*p*=0.15) or right M_1/M_2 (*p*=0.49) (**Table 5.8**; **Figure 5.12**). Among males, the main difference in breadth at the symphysis and mental foramen was between the JSA and Holocene samples. For breadth of the molar region, there was a decrease in males after R12. For females, there were no major differences between JSA and later samples for any of the breadth measurements.

			SH				<u>SB</u>				SR				SS	
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	11	37.40	3.19	8.53	11	15.44	1.90	12.31	11	0.41	0.053	12.93	11	454.75	75.54	16.61
R12	13	26.68	1.72	6.45	14	15.30	1.67	10.92	13	0.53	0.061	11.51	13	344.45	48.15	13.98
KAW	15	28.57	2.04	7.14	16	15.33	1.01	6.59	15	0.54	0.048	8.89	15	343.67	38.34	11.16
KER	35	30.43	2.73	8.97	38	15.34	1.73	11.28	35	0.51	0.069	13.53	35	368.99	57.31	15.53
KUS	8	28.62	2.03	7.09	8	15.26	1.48	9.70	8	0.53	0.042	7.92	8	344.39	52.67	15.29
			MH				MB				MR				<u>MS</u>	
Population	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV
JSA	13	34.76	4.03	11.59	12	13.54	6.07	44.83	12	0.35	0.060	17.14	12	322.98	59.43	18.40
R12	21	28.90	2.05	7.09	21	12.75	1.40	10.98	21	0.44	0.050	11.36	21	289.88	40.84	14.09
KAW	17	27.82	2.75	9.88	17	12.98	1.84	14.18	17	0.47	0.066	14.04	17	285.22	58.54	20.52
KER	39	28.37	2.37	8.35	39	12.43	1.53	12.31	39	0.44	0.059	13.41	39	277.32	43.12	15.55
KUS	9	27.18	2.07	7.62	9	11.73	2.06	17.56	9	0.43	0.062	14.42	9	252.19	57.70	22.88
			<u>LH</u>				<u>LB</u>				<u>LR</u>				<u>LS</u>	
Population	n	Mean	LH SD	CV	n	Mean	LB SD	CV	n	Mean	LR SD	CV	n	Mean	LS SD	CV
Population JSA	<i>n</i> 10	Mean 31.94	<u>LH</u> SD 3.70	CV 11.58	<i>n</i> 10	Mean 14.48	<u>LB</u> SD 1.55	CV 10.70	<i>n</i> 10	Mean 0.46	<u>LR</u> SD 0.096	CV 20.87	<i>n</i> 10	Mean 363.25	LS SD 77.67	CV 21.38
Population JSA R12	n 10 19	Mean 31.94 27.15	LH SD 3.70 2.29	CV 11.58 8.43	<i>n</i> 10 19	Mean 14.48 14.88	<u>LB</u> SD 1.55 1.55	CV 10.70 10.42	<i>n</i> 10 19	Mean 0.46 0.55	<u>LR</u> SD 0.096 0.083	CV 20.87 15.09	<i>n</i> 10 19	Mean 363.25 316.51	<u>LS</u> SD 77.67 34.75	CV 21.38 10.98
Population JSA R12 KAW	<i>n</i> 10 19 16	Mean 31.94 27.15 26.23	LH SD 3.70 2.29 2.28	CV 11.58 8.43 8.69	<i>n</i> 10 19 16	Mean 14.48 14.88 13.77	<u>LB</u> SD 1.55 1.55 1.76	CV 10.70 10.42 12.78	<i>n</i> 10 19 16	Mean 0.46 0.55 0.53	<u>LR</u> SD 0.096 0.083 0.070	CV 20.87 15.09 13.21	<i>n</i> 10 19 16	Mean 363.25 316.51 284.47	LS SD 77.67 34.75 48.81	CV 21.38 10.98 17.16
Population JSA R12 KAW KER	<i>n</i> 10 19 16 35	Mean 31.94 27.15 26.23 26.19	LH SD 3.70 2.29 2.28 2.40	CV 11.58 8.43 8.69 9.16	<i>n</i> 10 19 16 36	Mean 14.48 14.88 13.77 13.93	<u>LB</u> SD 1.55 1.55 1.76 1.74	CV 10.70 10.42 12.78 12.49	n 10 19 16 35	Mean 0.46 0.55 0.53 0.54	LR SD 0.096 0.083 0.070 0.084	CV 20.87 15.09 13.21 15.56	n 10 19 16 35	Mean 363.25 316.51 284.47 288.08	LS SD 77.67 34.75 48.81 42.49	CV 21.38 10.98 17.16 14.75
Population JSA R12 KAW KER KUS	n 10 19 16 35 8	Mean 31.94 27.15 26.23 26.19 24.87	LH SD 3.70 2.29 2.28 2.40 1.53	CV 11.58 8.43 8.69 9.16 6.15	n 10 19 16 36 8	Mean 14.48 14.88 13.77 13.93 13.79	<u>LB</u> SD 1.55 1.55 1.76 1.74 1.28	CV 10.70 10.42 12.78 12.49 9.28	n 10 19 16 35 8	Mean 0.46 0.55 0.53 0.54 0.56	LR SD 0.096 0.083 0.070 0.084 0.055	CV 20.87 15.09 13.21 15.56 9.82	n 10 19 16 35 8	Mean 363.25 316.51 284.47 288.08 269.47	LS SD 77.67 34.75 48.81 42.49 31.15	CV 21.38 10.98 17.16 14.75 11.56
Population JSA R12 KAW KER KUS	<i>n</i> 10 19 16 35 8	Mean 31.94 27.15 26.23 26.19 24.87	LH SD 3.70 2.29 2.28 2.40 1.53 RH	CV 11.58 8.43 8.69 9.16 6.15	n 10 19 16 36 8	Mean 14.48 14.88 13.77 13.93 13.79	LB SD 1.55 1.55 1.76 1.74 1.28 RB	CV 10.70 10.42 12.78 12.49 9.28	<i>n</i> 10 19 16 35 8	Mean 0.46 0.55 0.53 0.54 0.56	LR SD 0.096 0.083 0.070 0.084 0.055 RR	CV 20.87 15.09 13.21 15.56 9.82	<i>n</i> 10 19 16 35 8	Mean 363.25 316.51 284.47 288.08 269.47	LS SD 77.67 34.75 48.81 42.49 31.15 RS	CV 21.38 10.98 17.16 14.75 11.56
Population JSA R12 KAW KER KUS Population	n 10 19 16 35 8 <i>n</i>	Mean 31.94 27.15 26.23 26.19 24.87 Mean	LH SD 3.70 2.29 2.28 2.40 1.53 RH SD	CV 11.58 8.43 8.69 9.16 6.15 CV	n 10 19 16 36 8 n	Mean 14.48 14.88 13.77 13.93 13.79 Mean	<u>LB</u> SD 1.55 1.55 1.76 1.74 1.28 <u>RB</u> SD	CV 10.70 10.42 12.78 12.49 9.28 CV	n 10 19 16 35 8 n	Mean 0.46 0.55 0.53 0.54 0.56 Mean	LR SD 0.096 0.083 0.070 0.084 0.055 RR SD	CV 20.87 15.09 13.21 15.56 9.82 CV	n 10 19 16 35 8 n	Mean 363.25 316.51 284.47 288.08 269.47 Mean	LS SD 77.67 34.75 48.81 42.49 31.15 RS SD	CV 21.38 10.98 17.16 14.75 11.56 CV
Population JSA R12 KAW KER KUS Population JSA	n 10 19 16 35 8 n 10	Mean 31.94 27.15 26.23 26.19 24.87 Mean 32.93	LH SD 3.70 2.29 2.28 2.40 1.53 RH SD 2.95	CV 11.58 8.43 8.69 9.16 6.15 CV 8.96	n 10 19 16 36 8 n 10	Mean 14.48 14.88 13.77 13.93 13.79 Mean 14.39	LB SD 1.55 1.55 1.76 1.74 1.28 RB SD 2.03	CV 10.70 10.42 12.78 12.49 9.28 CV 14.11	n 10 19 16 35 8 n 10	Mean 0.46 0.55 0.53 0.54 0.56 Mean 0.44	LR SD 0.096 0.083 0.070 0.084 0.055 RR SD 0.061	CV 20.87 15.09 13.21 15.56 9.82 CV 13.86	n 10 19 16 35 8 n 10	Mean 363.25 316.51 284.47 288.08 269.47 Mean 373.25	LS SD 77.67 34.75 48.81 42.49 31.15 RS SD 70.17	CV 21.38 10.98 17.16 14.75 11.56 CV 18.80
Population JSA R12 KAW KER KUS Population JSA R12	n 10 19 16 35 8 n 10 16	Mean 31.94 27.15 26.23 26.19 24.87 Mean 32.93 27.18	LH SD 3.70 2.29 2.28 2.40 1.53 RH SD 2.95 2.09	CV 11.58 8.43 8.69 9.16 6.15 CV 8.96 7.69	n 10 19 16 36 8 n 10 17	Mean 14.48 14.88 13.77 13.93 13.79 Mean 14.39 11.76	LB SD 1.55 1.55 1.76 1.74 1.28 RB SD 2.03 1.82	CV 10.70 10.42 12.78 12.49 9.28 CV 14.11 15.48	n 10 19 16 35 8 n 10 15	Mean 0.46 0.55 0.53 0.54 0.56 Mean 0.44 0.53	LR SD 0.096 0.083 0.070 0.084 0.055 RR SD 0.061 0.081	CV 20.87 15.09 13.21 15.56 9.82 CV 13.86 15.28	n 10 19 16 35 8 n 10 16	Mean 363.25 316.51 284.47 288.08 269.47 Mean 373.25 308.51	LS SD 77.67 34.75 48.81 42.49 31.15 RS SD 70.17 48.02	CV 21.38 10.98 17.16 14.75 11.56 CV 18.80 15.57
Population JSA R12 KAW KER KUS Population JSA R12 KAW	n 10 19 16 35 8 n 10 16 15	Mean 31.94 27.15 26.23 26.19 24.87 Mean 32.93 27.18 26.19	LH SD 3.70 2.29 2.28 2.40 1.53 RH SD 2.95 2.09 2.47	CV 11.58 8.43 8.69 9.16 6.15 CV 8.96 7.69 9.43	n 10 19 16 36 8 n 10 17 15	Mean 14.48 14.88 13.77 13.93 13.79 Mean 14.39 11.76 14.18	LB SD 1.55 1.55 1.76 1.74 1.28 RB SD 2.03 1.82 1.71	CV 10.70 10.42 12.78 12.49 9.28 CV 14.11 15.48 12.06	n 10 19 16 35 8 n 10 16 15	Mean 0.46 0.55 0.53 0.54 0.56 Mean 0.44 0.53 0.54	LR SD 0.096 0.083 0.070 0.084 0.055 RR SD 0.061 0.081 0.063	CV 20.87 15.09 13.21 15.56 9.82 CV 13.86 15.28 11.67	n 10 19 16 35 8 n 10 16 15	Mean 363.25 316.51 284.47 288.08 269.47 Mean 373.25 308.51 293.12	LS SD 77.67 34.75 48.81 42.49 31.15 RS SD 70.17 48.02 52.92	CV 21.38 10.98 17.16 14.75 11.56 CV 18.80 15.57 18.05
Population JSA R12 KAW KER KUS Population JSA R12 KAW KER	n 10 19 16 35 8 <i>n</i> 10 16 15 33	Mean 31.94 27.15 26.23 26.19 24.87 Mean 32.93 27.18 26.19 26.46	LH SD 3.70 2.29 2.28 2.40 1.53 RH SD 2.95 2.09 2.47 1.97	CV 11.58 8.43 8.69 9.16 6.15 CV 8.96 7.69 9.43 7.45	n 10 19 16 36 8 n 10 17 15 36	Mean 14.48 14.88 13.77 13.93 13.79 Mean 14.39 11.76 14.18 13.86	LB SD 1.55 1.76 1.74 1.28 RB SD 2.03 1.82 1.71 1.87	CV 10.70 10.42 12.78 12.49 9.28 CV 14.11 15.48 12.06 13.46	n 10 19 16 35 8 n 10 16 33	Mean 0.46 0.55 0.53 0.54 0.56 Mean 0.44 0.53 0.54 0.53	LR SD 0.096 0.083 0.070 0.084 0.055 RR SD 0.061 0.081 0.063 0.087	CV 20.87 15.09 13.21 15.56 9.82 CV 13.86 15.28 11.67 16.42	n 10 19 16 35 8 n 10 16 33	Mean 363.25 316.51 284.47 288.08 269.47 Mean 373.25 308.51 293.12 288.49	LS SD 77.67 34.75 48.81 42.49 31.15 RS SD 70.17 48.02 52.92 43.17	CV 21.38 10.98 17.16 14.75 11.56 CV 18.80 15.57 18.05 14.96

Table 5.7 Descriptive statistics for cross-sectional linear measurements and calculated values (pooled sex)

Mean is reported in mm except for the calculated size which is reported in mm². **JSA**: Jebel Sahaba (c. 13000–9000 BC); **R12**: NDRS R12 (c. 5000–4000 cal BC); **KAW**: NDRS P37 (c. 2500–2050 BC); **KER**: Kerma (c.1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **SH**: symphyseal height; **SB**: symphyseal breadth; **SR**: symphyseal robusticity index; **SS**: symphyseal size; **MH**: mental foramen height; **MB**: mental foramen breadth; **MR**: mental foramen robusticity index; **MS**: mental foramen size; **LH**: left M₁/M₂ height; **LB**: left M₁/M₂ breadth; **RH**: right M₁/M₂ breadth; **RB**: right M₁/M₂ breadth; **RR**: right M₁/M₂ robusticity index; **RS**: right M₁/M₂ size; robusticity index: breadth x $\pi/4$; *n*: sample size; SD: standard deviation; CV: coefficient of variation.



Population

104







Figure 5.11 Mean cross-sectional linear measurements by population (pooled sex) for (a) SH, (b) MH, (c) LH, (d) RH, (e) SB, (f) MB, (g) LB, (h) RB, (i) SR, (j) MR, (k) LR, (l) RR, (m) SS, (n) MS, (o) LS, and (p) RS

Error bars 95% confidence interval. * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$ or Mann-Whitney test $p \le 0.005$). SH: symphyseal height; SB: symphyseal breadth; SR: symphyseal robusticity index; SS: symphyseal size; MH: mental foramen height; MB: mental foramen breadth; MR: mental foramen robusticity index; MS: mental foramen size; LH: left M₁/M₂ height; LB: left M₁/M₂ breadth; LR: left M₁/M₂ robusticity index; LS: left M₁/M₂ size; RH: right M₁/M₂ height; RB: right M₁/M₂ breadth; RR: right M₁/M₂ robusticity index; RS: right M₁/M₂ size; robusticity index: breadth/height; size: height x breadth x $\pi/4$; JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); KAW: NDRS P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350).

The ratio of breadth to height at each point along the mandibular corpus was used to calculate the robusticity index, which was used to assess shape changes over time. For each point along the mandibular body, the JSA sample had the lowest index, likely driven largely by the significant differences in mandibular body height between the JSA and later samples. There were significant differences at the symphysis (p<0.001), mental foramen (p=0.001) and right M₁/M₂ (p=0.008), but not left M₁/M₂ (p=0.14). At the symphysis, JSA had a significantly smaller ratio of breadth/height than all the other samples. At the mental foramen, JSA was significantly smaller than R12, KAW and KER. At right M₁/M₂ JSA was significantly smaller than KAW and KUS (**Table 5.7**; **Figure 5.11**). Within the Holocene samples, there was no clear trend in the robusticity index at the symphysis or mental foramen. In the molar regions (both left and right) the KUS sample had the highest value, indicating a more circular cross-section.

When males and females were analysed separately, the results for the robusticity index mirrored the pooled-sex data, and JSA had the smallest index for both males and females. Females were significantly different at the symphysis (p=0.037), but there were no significant pairwise comparisons. Females were not significantly different at the mental foramen (p=0.30), left M₁/M₂ (p=0.23), or right M₁/M₂ (p=0.31). Males were significantly different at the symphysis (p=0.014), mental foramen (p=0.003), and right M₁/M₂ (p=0.026). *Post-hoc* tests showed that at the mental foramen and right M₁/M₂, JSA had a significantly smaller ratio than KAW and KER. At the symphysis, JSA had a significantly smaller index than KAW (**Table 5.8; Figure 5.12**).

The calculated size of each cross-section (linear height x breadth x $\pi/4$; Daegling and McGraw, 2007), was the largest in the JSA sample, and was significantly different between samples at the symphysis (*p*=0.001), left M₁/M₂ (*p*=0.002) and right M₁/M₂ (*p*=0.003), but not at the mental foramen (*p*=0.056). At the symphysis, JSA had a significantly larger calculated area than all the other samples (**Figure 5.11**). However, JSA only had a significantly larger calculated area at both molar regions compared with KER and KUS. Although there were no clear trends in symphyseal size over time, for the mental foramen and both molar cross-sections the calculated size decreased over time in the Holocene samples. The reduction trends were stronger in males than females, but that may be reflective of the small sample size of female JSA.

The calculated size of the mandibular body was not significantly different for females along the mandibular body: symphysis (p=0.16), mental foramen (p=0.16), left M₁/M₂

(p=0.074) or right M₁/M₂ (p=0.36). Males were significantly different in symphyseal size (p=.006) and right M₁/M₂ (p=0.002), but not at the mental foramen (p=0.14) or left M₁/M₂ (p=0.84). For both calculated sizes, the JSA sample was larger than both KAW and KER. In addition, JSA was significantly larger in right M₁/M₂ size than R12 (**Table 5.8**; **Figure 5.12**). For full statistical results of the mandibular body analyses for the pooled-sex, male and female data, see **Appendix B**.

					SH							<u>S</u>	B			
			Male				Female				Male			F	emale	
Population	п	Mean	SD	CV	п	Mean	SD	CV	n	Mean	SD	CV	п	Mean	SD	CV
JSA	7	39.05	1.86	4.76	4	34.52	3.10	8.98	7	16.08	1.98	12.31	4	14.33	1.23	8.58
R12	4	28.51	2.14	7.51	9	28.75	1.64	5.70	4	15.16	1.76	11.61	10	15.36	1.72	11.20
KAW	10	29.50	1.40	4.75	5	26.70	1.90	7.12	11	15.51	0.97	6.25	5	14.92	1.07	7.17
KER	19	31.32	2.73	8.72	16	29.37	2.39	8.14	20	15.65	1.59	10.16	18	15.18	1.88	12.38
KUS	3	30.76	1.27	4.13	5	27.34	0.93	3.40	3	15.74	1.98	12.58	5	14.98	1.28	8.54
					<u>SR</u>				-			<u>S</u>	S			
			Male				Female				Male			F	emale	
Population	п	Mean	SD	CV	п	Mean	SD	CV	n	Mean	SD	CV	п	Mean	SD	CV
JSA	7	0.41	0.054	13.17	4	0.42	0.060	14.29	7	493.27	64.44	13.06	4	387.34	34.54	8.92
R12	4	0.53	0.065	12.26	9	0.53	0.063	11.89	4	339.86	51.47	15.14	9	346.48	49.69	14.34
KAW	10	0.53	0.033	6.23	5	0.56	0.067	11.96	10	359.30	34.78	9.68	5	312.40	24.32	7.78
KER	19	0.51	0.072	14.12	16	0.51	0.066	12.94	19	385.70	50.75	13.18	16	349.14	59.84	17.14
KUS	3	0.51	0.045	8.82	5	0.55	0.037	6.73	3	381.57	62.37	16.35	5	322.08	35.37	10.98
				1	MH							\mathbf{M}	<u>1B</u>			
			Male				Female				Male			F	emale	
Population	n	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	8	36.07	2.27	6.29	4	30.92	4.57	14.78	7	12.14	1.96	16.14	4	11.86	0.83	7.00
R12	8	29.63	2.93	9.89	13	28.46	1.21	4.25	8	12.34	1.20	9.72	13	13.00	1.49	11.46
KAW	12	27.99	3.09	11.04	5	27.41	1.92	7.00	12	13.25	1.87	14.11	5	12.33	1.77	14.36
KER	21	29.65	1.93	6.51	18	26.87	1.95	7.26	21	12.75	1.64	12.86	18	12.05	1.32	10.95
KUS	3	27.82	0.78	2.80	6	26.86	2.49	9.27	3	11.43	2.12	18.55	6	11.88	2.22	18.69
				<u>I</u>	MR							N	<u>1S</u>			
			Male				Female				Male			F	emale	
Population	n	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	7	0.34	0.055	16.18	4	0.39	0.051	13.08	7	342.02	62.19	18.18	4	288.85	53.02	18.36
R12	8	0.42	0.050	11.90	13	0.46	0.045	9.78	8	287.68	43.07	14.97	13	291.24	41.14	14.13
KAW	12	0.48	0.053	11.04	5	0.45	0.096	21.33	12	294.02	66.48	22.61	5	264.12	27.72	10.50
KER	21	0.43	0.065	15.12	18	0.45	0.052	11.56	21	296.58	39.18	13.21	18	254.86	36.95	14.50
KUS	3	0.41	0.067	16.34	6	0.44	0.063	14.32	3	250.44	51.85	20.70	6	253.06	65.18	25.76

 Table 5.8 Descriptive statistics for cross-sectional linear measurements and calculated values by sex and sample

Table 5.8 continued

	LH															
	Male Female					Male				Female						
Population	n	Mean	n SD	CV	n	Mean	SD	CV	n	Mean	SD	CV	n	Mean	SD	CV
JSA	6	32.17	1.83	5.69	3	29.22	4.32	14.78	6	15.09	3.32	22.00	3	13.32	0.17	1.28
R12	7	27.37	3.32	12.13	12	27.03	1.59	5.88	7	14.75	2.09	14.17	12	14.96	1.24	8.29
KAW	11	26.48	2.44	9.21	5	25.70	2.05	7.98	11	13.69	1.96	14.32	5	13.95	1.39	9.96
KER	19	27.50	1.57	5.71	16	24.64	2.32	9.42	19	13.87	1.69	12.18	17	14.00	1.84	13.14
KUS	3	24.73	0.80	3.23	5	24.95	1.94	7.78	3	14.25	1.93	13.54	5	13.51	0.88	6.51
					LR				_			L	<u>'S</u>			
]	Male			Fei	male			Μ	ale			Fe	male	
Population	n	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	n	Mean	SD	CV
JSA	6	0.47	0.11	23.40	3	0.46	0.073	15.87	6	379.93	81.49	21.45	3	305.81	46.34	15.15
R12	7	0.55	0.13	23.64	12	0.55	0.046	8.36	7	313.74	30.07	9.58	12	318.12	38.41	12.07
KAW	11	0.52	0.067	12.88	5	0.55	0.08	14.55	11	285.90	55.92	19.56	5	281.32	33.14	11.78
KER	19	0.51	0.072	14.12	16	0.58	0.082	14.14	19	299.24	36.84	12.31	16	274.81	46.03	16.75
KUS	3	0.58	0.068	11.72	5	0.54	0.050	9.26	3	277.35	43.25	15.59	5	264.74	26.24	9.91
	-	0.000							-				-		= = = :	
	-				RH							R	B			
]	Male]	<u>RH</u>	Fei	male			М	ale	<u>R</u>	B	Fe	male	
Population	n	Mean	Male SD	CV	RH n	Fea	male SD	CV	n	Mean	ale SD	<u>R</u> CV	<u>В</u> п	Fe Mean	male SD	CV
Population JSA	<i>n</i> 8	Mean 33.96	Male SD 2.11	CV 6.21	n 2	Fen Mean 28.80	male SD 2.04	CV 7.08	n 8	Mean 14.69	ale SD 2.14	<u>R</u> CV 14.57	B <i>n</i> 2	Fean Mean 13.17	male SD 1.07	CV 8.12
Population JSA R12	n 8 6	Mean 33.96 27.95	Male SD 2.11 2.73	CV 6.21 9.77	n 2 10	Fen Mean 28.80 26.71	male SD 2.04 1.59	CV 7.08 5.95	n 8 6	Mean 14.69 14.05	ale SD 2.14 2.40	<u>R</u> CV 14.57 17.08	n 2 11	Fean Mean 13.17 14.79	male SD 1.07 1.68	CV 8.12 11.36
Population JSA R12 KAW	n 8 6 11	Mean 33.96 27.95 26.46	Male SD 2.11 2.73 2.36	CV 6.21 9.77 8.92	n 2 10 4	Fer Mean 28.80 26.71 25.46	male SD 2.04 1.59 2.97	CV 7.08 5.95 11.67	n 8 6 11	Mean 14.69 14.05 13.86	SD 2.14 2.40 1.33	<u>R</u> CV 14.57 17.08 9.60	B <i>n</i> 2 11 4	Fea Mean 13.17 14.79 15.09	male SD 1.07 1.68 2.49	CV 8.12 11.36 16.50
Population JSA R12 KAW KER	n 8 6 11 16	Mean 33.96 27.95 26.46 27.63	Male SD 2.11 2.73 2.36 1.44	CV 6.21 9.77 8.92 5.21	n 2 10 4 17	Fer Mean 28.80 26.71 25.46 25.35	male SD 2.04 1.59 2.97 1.77	CV 7.08 5.95 11.67 6.98	n 8 6 11 18	Mean 14.69 14.05 13.86 13.57	SD 2.14 2.40 1.33 1.86	R CV 14.57 17.08 9.60 13.71	n 2 11 4 18	Fe: Mean 13.17 14.79 15.09 14.16	male SD 1.07 1.68 2.49 1.88	CV 8.12 11.36 16.50 13.28
Population JSA R12 KAW KER KUS	n 8 6 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19	Male SD 2.11 2.73 2.36 1.44 0.87	CV 6.21 9.77 8.92 5.21 3.45	n 2 10 4 17 6	Fer Mean 28.80 26.71 25.46 25.35 24.25	male SD 2.04 1.59 2.97 1.77 2.21	CV 7.08 5.95 11.67 6.98 9.11	<i>n</i> 8 6 11 18 2	Mean 14.69 14.05 13.86 13.57 15.64	SD 2.14 2.40 1.33 1.86 1.26	R CV 14.57 17.08 9.60 13.71 8.06	n 2 11 4 18 6	Fe Mean 13.17 14.79 15.09 14.16 13.49	male SD 1.07 1.68 2.49 1.88 1.74	CV 8.12 11.36 16.50 13.28 12.90
Population JSA R12 KAW KER KUS	n 8 6 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19	Male SD 2.11 2.73 2.36 1.44 0.87	CV 6.21 9.77 8.92 5.21 3.45	n 2 10 4 17 6 RR	Mean Fer 28.80 26.71 25.46 25.35 24.25 24.25	male SD 2.04 1.59 2.97 1.77 2.21	CV 7.08 5.95 11.67 6.98 9.11	n 8 6 11 18 2	Mean 14.69 14.05 13.86 13.57 15.64	SD 2.14 2.40 1.33 1.86 1.26	<u>CV</u> 14.57 17.08 9.60 13.71 8.06 <u>R</u>	n 2 11 4 18 6 SS 5	Fe. <u>Mean</u> 13.17 14.79 15.09 14.16 13.49	male SD 1.07 1.68 2.49 1.88 1.74	CV 8.12 11.36 16.50 13.28 12.90
Population JSA R12 KAW KER KUS	n 8 6 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19	Male SD 2.11 2.73 2.36 1.44 0.87 Male	CV 6.21 9.77 8.92 5.21 3.45	n 2 10 4 17 6 RR	Fer Mean 28.80 26.71 25.46 25.35 24.25 Fer	male SD 2.04 1.59 2.97 1.77 2.21 male	CV 7.08 5.95 11.67 6.98 9.11	n 8 6 11 18 2	Mean 14.69 14.05 13.86 13.57 15.64 M	SD 2.14 2.40 1.33 1.86 1.26	R CV 14.57 17.08 9.60 13.71 8.06 R	n 2 11 4 18 6 S 1	Fe: <u>Mean</u> 13.17 14.79 15.09 14.16 13.49 Fe:	male SD 1.07 1.68 2.49 1.88 1.74 male	CV 8.12 11.36 16.50 13.28 12.90
Population JSA R12 KAW KER KUS Population	n 8 6 11 16 2 <i>n</i>	Mean 33.96 27.95 26.46 27.63 25.19	Male SD 2.11 2.73 2.36 1.44 0.87 Male SD	CV 6.21 9.77 8.92 5.21 3.45 CV	n 2 10 4 17 6 RR n	Fer Mean 28.80 26.71 25.46 25.35 24.25 Fer Mean	male SD 2.04 1.59 2.97 1.77 2.21 male SD	CV 7.08 5.95 11.67 6.98 9.11 CV	n 8 6 11 18 2 <i>n</i>	Mean 14.69 14.05 13.86 13.57 15.64 Mean	fale SD 2.14 2.40 1.33 1.86 1.26 fale SD	R CV 14.57 17.08 9.60 13.71 8.06 R CV	B 2 11 4 18 6 S n	Fer Mean 13.17 14.79 15.09 14.16 13.49 Fer Mean	male SD 1.07 1.68 2.49 1.88 1.74 male SD	CV 8.12 11.36 16.50 13.28 12.90 CV
Population JSA R12 KAW KER KUS Population JSA	n 8 6 11 16 2 8	Mean 33.96 27.95 26.46 27.63 25.19 Mean 0.43	Male <u>SD</u> 2.11 2.73 2.36 1.44 0.87 Male <u>SD</u> 0.069	CV 6.21 9.77 8.92 5.21 3.45 CV 16.05	n 2 10 4 17 6 RR 2	Mean Fer 28.80 26.71 25.46 25.35 24.25 Fer Mean 0.46	male SD 2.04 1.59 2.97 1.77 2.21 male SD 0.005	CV 7.08 5.95 11.67 6.98 9.11 CV 1.09	n 8 6 11 18 2 n 8	Mean 14.69 14.05 13.86 13.57 15.64 Mean 391.88	SD 2.14 2.40 1.33 1.86 1.26 fale SD 63.65	CV 14.57 17.08 9.60 13.71 8.06 CV CV 16.24	n 2 11 4 18 6 S n 2 2	Fe: <u>Mean</u> 13.17 14.79 15.09 14.16 13.49 Fe: <u>Mean</u> 298.71	male SD 1.07 1.68 2.49 1.88 1.74 male SD 45.44	CV 8.12 11.36 16.50 13.28 12.90 CV 15.21
Population JSA R12 KAW KER KUS Population JSA R12	n 8 6 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19 Mean 0.43 0.51	Male <u>SD</u> 2.11 2.73 2.36 1.44 0.87 Male <u>SD</u> 0.069 0.11	CV 6.21 9.77 8.92 5.21 3.45 CV 16.05 21.57	n 2 10 4 17 6 RR 10 110 110 110 110 110 110 110	Fer Mean 28.80 26.71 25.46 25.35 24.25 Fer Mean 0.46 0.55	male SD 2.04 1.59 2.97 1.77 2.21 male SD 0.005 0.058	CV 7.08 5.95 11.67 6.98 9.11 CV 1.09 10.55	n 8 6 11 18 2 n 8 6	Mean 14.69 14.05 13.86 13.57 15.64 M Mean 391.88 307.20	SD 2.14 2.40 1.33 1.86 1.26 ale SD 63.65 50.67	CV 14.57 17.08 9.60 13.71 8.06 CV 16.24 16.49	n 2 11 4 18 6 S n 2 10	Fe: <u>Mean</u> 13.17 14.79 15.09 14.16 13.49 Fe: <u>Mean</u> 298.71 309.29	male SD 1.07 1.68 2.49 1.88 1.74 male SD 45.44 49.14	CV 8.12 11.36 16.50 13.28 12.90 CV 15.21 15.89
Population JSA R12 KAW KER KUS Population JSA R12 KAW	n 8 6 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19 Mean 0.43 0.51 0.52	Male SD 2.11 2.73 2.36 1.44 0.87 Male SD 0.069 0.11 0.026	CV 6.21 9.77 8.92 5.21 3.45 CV 16.05 21.57 5.00	n 2 10 4 17 6 RR 10 4 17 6 4 17 6 4 10 4 10 4	Fer Mean 28.80 26.71 25.46 25.35 24.25 Fer Mean 0.46 0.55 0.60	male SD 2.04 1.59 2.97 1.77 2.21 male SD 0.005 0.058 0.11	CV 7.08 5.95 11.67 6.98 9.11 CV 1.09 10.55 18.33	n 8 6 11 18 2 n 8 6 11	Mean 14.69 14.05 13.86 13.57 15.64 M Mean 391.88 307.20 289.85	sp 2.14 2.40 1.33 1.86 1.26 ale SD 63.65 50.67 50.59	CV 14.57 17.08 9.60 13.71 8.06 CV 16.24 16.49 17.45	n 2 11 4 18 6 S 10 4	Fe: <u>Mean</u> 13.17 14.79 15.09 14.16 13.49 Fe: <u>Mean</u> 298.71 309.29 302.10	male SD 1.07 1.68 2.49 1.88 1.74 male SD 45.44 49.14 66.26	CV 8.12 11.36 16.50 13.28 12.90 CV 15.21 15.89 21.93
Population JSA R12 KAW KER KUS Population JSA R12 KAW KER	n 8 6 11 16 2 n 8 6 11 11 16 2	Mean 33.96 27.95 26.46 27.63 25.19 Mean 0.43 0.51 0.52 0.49	Male SD 2.11 2.73 2.36 1.44 0.87 Male SD 0.069 0.11 0.026 0.076	CV 6.21 9.77 8.92 5.21 3.45 CV 16.05 21.57 5.00 15.51	n 2 10 4 17 6 RR 10 4 17 6 10 4 17 10 4 17	Fer Mean 28.80 26.71 25.46 25.35 24.25 Fer Mean 0.46 0.55 0.60 0.57	male SD 2.04 1.59 2.97 1.77 2.21 male SD 0.005 0.058 0.11 0.082	CV 7.08 5.95 11.67 6.98 9.11 CV 1.09 10.55 18.33 14.39	n 8 6 11 18 2 n 8 6 11 16	Mean 14.69 14.05 13.86 13.57 15.64 Mean 391.88 307.20 289.85 292.71	SD 2.14 2.40 1.33 1.86 1.26 ale SD 63.65 50.67 50.59 44.08	CV 14.57 17.08 9.60 13.71 8.06 CV 16.24 16.49 17.45 15.06	n 2 11 4 18 6 S 10 4 17	Fe: <u>Mean</u> 13.17 14.79 15.09 14.16 13.49 Fe: <u>Mean</u> 298.71 309.29 302.10 284.53	male SD 1.07 1.68 2.49 1.88 1.74 male SD 45.44 49.14 66.26 43.25	CV 8.12 11.36 16.50 13.28 12.90 CV 15.21 15.89 21.93 15.20

Mean is reported in mm except for the calculated size which is reported in mm². **JSA**: Jebel Sahaba (c. 13000–9000 BC); **R12**: NDRS R12 (c. 5000–4000 cal BC); **KAW**: NDRS P37 (c. 2500–2050 BC); **KER**: Kerma (c.1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **SH**: symphyseal height; **SB**: symphyseal breadth; **SR**: symphyseal robusticity index; **SS**: symphyseal size; **MH**: mental foramen height; **MB**: mental foramen breadth; **MR**: mental foramen robusticity index; **MS**: mental foramen size; **LH**: left M₁/M₂ height; **LB**: left M₁/M₂ breadth; **RB**: right M₁/M₂ breadth; **RR**: right M₁/M₂ robusticity index; **RS**: right M₁/M₂ size; robusticity index: breadth x $\pi/4$; *n*: sample size; SD: standard deviation; CV: coefficient of variation.





Figure 5.12 Mean mandibular body by sex and sample for (a) SH, (b) MH, (c) LH, (d) RH, (e) SB, (f) MB, (g) LB, (h) RB

Error bars 95% confidence interval. * = significant sexual dimorphism (independent samples *t*-test $p \le 0.05$). SH: symphyseal height; SB: symphyseal breadth; MH: mental foramen height; MB: mental foramen breadth; LH: left M₁/M₂ height; LB: left M₁/M₂ breadth; RH: right M₁/M₂ height; RB: right M₁/M₂ breadth. JSA (c. 13000–9000 BC); R12 (c. 5000–4000 cal BC); KAW (c. 2500–2050 BC); KER (c. 1750–1500 BC); KUS:(c. 350 BC–AD 350).

5.5 Discussion

The results from this study showed that there were significant differences in overall mandibular size and shape between the Late Palaeolithic Nubians from Jebel Sahaba (JSA) and the later Holocene samples from Upper Nubia. JSA mandibles were characterised by greater overall size, and of the 17 mandibular linear measurements that were compared between the samples, JSA had the largest mean value for 14 measurements. The mandibles from the JSA sample were longer, wider and had a more upright and larger ramus (both in width and height) than the subsequent samples from Upper Nubia. The mandibular body of the JSA sample was taller than the other samples at the symphysis, mental foramen and in the molar region. Patterns of between-group variation amongst the four Holocene Upper Nubian samples (the Sudanese Neolithic R12 [c. 5000–4000 cal BC], the Kerma Ancien KAW [c. 2500–2050 BC], the Kerma Classique KER [1750–1500 BC] and the Meroitic KUS [c. 350 BC–AD 350]) were complex and varied by mandibular region and sex. However, clear trends were present that showed a reduction of overall mandibular length, mandibular body height within the molar region, width of the ramus and increase in the magnitude of the gonial angle over time. The results of this study support the trends observed in previous studies demonstrating mandibular gracilisation associated with the adoption of agricultural practices in Lower Nubia (Carlson and Van Gerven, 1977, 1979; Galland et al., 2016; Martin et al., 1984; Small, 1981) and around the world (Galland et al., 2016; Goodman et al., 1984; Kaifu, 1997; Katz et al., 2017; Larsen, 1982; May et al., 2018; Noback and Harvati, 2015; Pinhasi et al., 2008; Sardi et al., 2006; Smith et al., 1984; von Cramon-Taubadel, 2011; Y'Edynak and Fleisch, 1983).

The majority of the statistically significant results observed in this study were between the JSA sample and the later Upper Nubian samples; for almost every linear dimension, the JSA population had the largest mean value. The Late Palaeolithic Nubian (JSA) subsistence was based on hunting and gathering, and their diet primarily consisted of mechanically tough food items, such as tubers and wild animal meat (Churcher, 1972; Clark, 1976; Hassan, 1988; Wendorf, 2001; Wenke et al., 1988). This mechanically tough diet may be reflected in the greater overall size of the JSA mandibles compared with the later samples. However, it is important to note that there is some evidence for genetic discontinuity between the JSA population and later Nubian populations (Galland et al., 2016; Irish, 2000, 2005; Raxter, 2011). Therefore, the morphological differences observed in this study may be a result of genetic differences between populations, rather than representative of dietary change. However, the mandibles from the later Upper Nubian samples were not just simply smaller versions of the JSA hunter-gatherers, but there was a mosaic pattern of morphological change that continued to be observed throughout the Upper Nubian samples. Valuable insight can be derived from these findings, since the regions of the mandible which continued to change throughout the Holocene periods are areas of masticatory muscle attachment and therefore, most heavily influenced by alterations in masticatory behaviour.



Figure 5.13 Mandibular length results for the pooled-sex sample and by sex

Hochberg's GT2 *post-hoc* test level of significance *p*≤0.05; arrows indicate direction of the significant relationship. **ML1**: mandibular length gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length gnathion to condyle; **ML3**: mandibular length infradentale to midsagittal condyle-condyle chord; **LML**: upper mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length gnathion to gonion-gonion chord; **GML**: length from gnathion to M₃. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

The mandibular length measurements ML3 and LML, measuring the length of the mandible from the infradentale and gnathion of the symphysis to the midsagittal point of the gonion-gonion chord (BGoB), respectively, decreased over time in the Upper Nubian samples (**Figure 5.13**). These measurements encompass aspects of symphyseal breadth, dental arch length, and the antero-posterior width of the ramus. Since the dental arch length (DAL) and symphyseal breadth (SB) did not show significant reduction trends amongst the Upper Nubian

samples, it is likely that the mandibular length reduction trends in ML3 and LML were driven by changes in the gonial region. The masticatory muscles play a key role in shaping adult mandibular form (Hunt, 1998) and large cross-sectional areas of the medial pterygoid and masseter muscles (which insert on the medial and lateral surface of the gonial angle region respectively), have been shown to be positively correlated with mandibular length (Weijs and Hillen, 1984). An overall softer diet may limit the development of the masseter and medial pterygoid muscles (Hylander, 2006; Lieberman, 2011) and, as such, reduce the biomechanical strain induced on the gonial region.

The overall width of the mandible (quantified as the bigonial, BGoB, and bicondylar, BCoB, breadth) did not change significantly between the Upper Nubian samples (Figure 5.14). Although the cross-sectional area of masticatory muscles, such as the medial pterygoid and masseter, have been shown to be positively correlated to bigonial (Castelo et al., 2008; Raadsheer et al., 1996; van Spronsen et al., 1991; Weijs and Hillen, 1986) and bicondylar breadth (van Spronsen et al., 1991), results from archaeological studies have failed to identify a consistent relationship between mandibular width and dietary consistency. Some studies have found wider mandibles in hunter-gatherers than farmers (Galland et al., 2016), while others have found the reverse trend (Pinhasi et al., 2015; von Cramon-Taubadel, 2011). Although studies have shown that the absolute size of the temporomandibular joint (TMJ) has reduced across the agricultural transition (Hinton and Carlson, 1979; Paschetta et al., 2010), maintaining alignment between the mandibular and cranial widths is crucial to form the TMJ. In this study, the ratios of dental arch breadth to overall mandibular breadth (particularly at the condyles, BCoB) remained consistent within the Holocene samples (Appendix B). Consistency in mandibular breadth amongst agricultural populations has been observed in other studies (Galland et al., 2016; Katz et al., 2017; Li et al., 2012). While the relative size of the cranium has been shown to correlate with diet (Carlson and Van Gerven, 1977; González-José et al., 2005; Perez et al., 2011; Sardi et al., 2006), it may be that variation in mandibular width observed in other studies was driven by differences in the overall size of the cranium that were due to factors other than diet (e.g. population history).



Figure 5.14 Mandibular breadth results for the pooled-sex sample and by sex

Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; arrows indicate direction of the significant relationship. **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; **DAL**: dental arch length from infradentale to midsagittal BM2B. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

In addition to biomechanical stresses, the dental arch region of the face can be affected by factors such as age, disease and paramasticatory behaviours (Carlsson, 1967; Hylander, 1977; Klemetti et al., 1996; Lysell, 1958; Noback and Harvati, 2015). Despite a significant reduction from the JSA sample, the size and shape of the dental arch did not change over time within the Holocene samples (**Figure 5.14**). Studies in humans and animals have shown that softer diets associated with reduced masticatory strain can result in shorter (Corruccini, 1991; Enlow and Hans, 1996) and narrower dental arches (Beecher and Corruccini, 1981; Ciochon et al., 1997; Corruccini and Beecher, 1982; Corruccini et al., 1983; Frake and Goose, 1977; Goose, 1962, 1981; Harper, 1994; Lavelle, 1973; Luther, 1993; Rock et al., 2006; Varrela, 1990, 1992). Within the Upper Nubian samples, the ratios of dental arch breadth measured at C_1/P_3 (BCP3B), M₁ (BM1B) and M₂ (BM2B) remained consistent over time, which corroborates the results from Noback and Harvarti (2015) who did not find a relationship between dental arch shape and subsistence strategy. However, in contrast to Noback and Harvati (2015), this study did not find a correlation between the overall size of the dental arch region and diet. The results for this study indicate that for the Upper Nubian samples, the size and shape of the dental arch was fairly constrained over time, despite concurrent changes in dietary consumption. Precise occlusal alignment between the mandibular and maxillary dental arches during the power stroke of mastication is crucial for chewing efficiency (Hylander, 2006; Lieberman, 2011). Therefore, for the samples in this study, there may be a functional constraint on the shape and size of the mandibular dental arch to maintain proper occlusion with the maxilla.



	Combined	Male	Female
SH	JSA > all	JSA > all	JSA > all
MH	JSA > all	JSA > all	N/A
LH	JSA > all	JSA > all	N/A
RH	JSA > all	JSA > all	N/A

Figure 5.15 Corpus height results for the pooled-sex sample and by sex

Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; arrows indicate direction of the significant relationship. SH: symphyseal height; MH: mental foramen height; LH: left M₁/M₂ height; RH: right M₁/M₂ height. JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); KAW: NDRS P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350).

Linear measurements at the symphysis, mental foramen and molar region were used to assess how morphological changes affect different areas of the mandibular corpus. Symphyseal height has been shown to be correlated with resistance to bending in the coronal plane (Hylander, 1984), whereas symphyseal width (anterior-posterior breadth) provides rigidity against lateral transverse bending (Daegling and McGraw, 2007). This study found that although the JSA sample had the largest symphyseal height, there was no further change within the Upper Nubian samples (Figure 5.15). In addition, the symphyseal breadth was not significantly different between any of the samples (Figure 5.16). These trends were observed in both males and females. Although Carlson and Van Gerven (1977) documented a decrease in symphyseal breadth in agriculturalists, other studies have failed to find a similar relationship (Varrela, 1992; Y'Edynak and Fleisch, 1983). The results from the archaeological literature generally suggest that the size and shape of the symphysis may be more reflective of genetics and population history than variation in masticatory stress (Carlson and Van Gerven, 1977; Fukase and Suwa, 2008; Kaifu, 1997; Martin and Danforth, 2009; Mays, 2015; Moore et al., 1968; Pinhasi et al., 2008; Rando et al., 2014; Smith et al., 1984). Functional demands on the symphysis have been shown to influence both internal and external morphology (Fukase, 2007). For example, increasing the labio-lingual width of the inferior symphysis can reduce tensile strains caused by coronal bending (Daegling, 1993a; Gröning et al., 2011). Therefore, the shape of the symphysis captured by external linear height and breadth dimensions may not be an informative measure of masticatory stress.

In contrast, the height of the mandibular body in the molar regions decreased over time between the Upper Nubian samples, particularly on the left side and in males (**Figure 5.15**). Although some animal studies have observed a decrease in mandibular body height within the molar region in response to a softer diet (Bouvier and Hylander, 1981; Lieberman et al., 2004), the results are less clear from the archaeological literature. Some researchers have observed a decrease in mandibular body height (Galland et al., 2016; Mays, 2015), particularly in the molar region (Kaifu, 1997; Li et al., 2012; May et al., 2018) in populations with a softer diet. However, other studies have found no association between mandibular body height and diet (Pinhasi et al., 2008; Y'Edynak and Fleisch, 1983). Maximum bite forces are normally generated in the molar region of the adult mandible (Helkimo et al., 1977; Linderholm and Wennström, 1970) and it is, therefore, not surprising that this study found the strongest morphological trends in the molar region of these samples.



Figure 5.16 Corpus breadth results for the pooled-sex sample and by sex

Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; arrows indicate direction of the significant relationship. **SB**: symphyseal breadth; **MB**: mental foramen breadth; **LB**: left M₁/M₂ breadth; **RB**: right M₁/M₂ breadth. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

The width of the mandibular corpus can provide an estimate of resistance to transverse bending, and the 'robusticity' index (breadth/height) provides a general measure of resistance to masticatory stress (Hylander, 1985; Ravosa, 1991). This study found that at the symphysis, mental foramen and molar region, the breadth of the mandibular body did not change significantly over time, even between the JSA and later samples (**Figure 5.16**). However, the related robusticity index (breadth/height) did increase over time, particularly in the molar region. An index approaching 1.0 reflects increasing circularity of the mandibular body over time. Based on the separate trends from the height and breadth measurements, it is likely that the robusticity index observed in this study was largely driven by a decrease in mandibular body height over time. Studies have indicated that a rectangular mandibular body may be stronger mechanically (Toro-Ibacache et al., 2019; Sella-Tunis et al., 2018), and previous studies have shown that hunter-gatherers had more rectangular mandibular bodies than more

modern populations (Pokhojaev et al., 2019). The observation that the trends were much clearer in the molar region than at the mental foramen may reflect the role of the molar region in mastication (Helkimo et al., 1977; van Eijden, 1991).

For the populations in this study, the morphological trends were more pronounced in the left molar region as compared with the right side. Even though many of the mandibles were fragmentary, the sample sizes between right and left sides were similar. Therefore, the observed differences in molar regions were not just due to unequal samples sizes. Mild asymmetry in mandibular body morphology has also been recorded in the literature (Pierrakou, 1990; Remy et al., 2019). Asymmetry can result from genetic factors, masticatory behaviours, or may be due to partial/complete tooth loss (Hylander, 2006; Martinez-Gomis et al., 2009; Molnar et al., 1983; Puişoru et al., 2006; Smith et al., 1984). Research from humans and nonhuman primates has shown that muscle force during mastication can differ between the left and right sides of the mandible due to the mechanical properties of food, the magnitude of bite force and/or the location of the bite point (Blanksma and van Eijden, 1995; Herring, 1993; Hylander et al., 1992, 2000; Remy et al., 2019; Spencer, 1998, 1999; Vinyard et al., 2005). The loading of the working-side versus balancing-side masseter has been shown to be up to 1.5 times different for tough food and about 3.0 times different for soft food (Hylander, 1983; Hylander et al., 1987, 1992). Based on this evidence, the mechanical properties of food can cause asymmetrical loading of the mandible, and this may result in the morphological differences observed between the left and right sides of the mandibular corpus.

Animal experiments have shown that the ramus, and particularly the gonial angle region, is often the area of the mandible that demonstrates the most significant morphological differences between hard- and soft-diet groups (Anderson et al., 2014; Ito et al., 1982; Kikuta, 1985; Moore, 1965; Watt and Williams, 1951; Yamada and Kimmel, 1991). Studies of human populations have also shown that the most consistent differences in mandibular morphology associated with diet relate to the gonial angle and the width of the ramus (corresponding to the attachment area for the masseter and medial pterygoid muscles) (Galland et al., 2016; Kaifu, 1997; Katz et al., 2017; Li et al., 2012; Moore et al., 1968; Rando et al., 2014; von Cramon-Taubadel, 2011; Y'Edynak and Fleisch, 1983). This study found that the JSA hunter-gatherer sample had a more upright and larger ramus (in both width and height) than later samples (**Figure 5.17**). Hunter-gatherers have been shown to use their anterior dentition more than agriculturalists, which involves greater loading of the temporalis and masseter muscles inserted into the ramus (Hinton and Carlson, 1979). Intensive anterior dental loading has been

associated with increases in the size of the ascending ramus, mandibular condyle and coronoid process of the mandible (Hinton and Carlson, 1979); patterns that were observed in this study.

Among the Upper Nubian samples, the least ramus width (LRB) decreased and the gonial angle increased, but the height of the ramus and coronoid process did not show any clear trends (**Figure 5.17**). A narrower mandibular ramus (represented by LRB) indirectly suggests a reduced attachment area for (and overall smaller) masseter and medial pterygoid muscles, the primary elevators of the jaw during mastication (Bastir et al., 2004). Reduction in the size of the muscles of mastication may result in the masticatory complex's reduced capacity to generate high or repetitive bite forces.



	Combined	Male	Female
LRB	JSA > all	JSA > all	JSA > all
MRB	JSA > all; KER > R12	JSA > all	JSA > all
CrH	KER > R12	N/A	N/A
RH	JSA > KAW	N/A	N/A
GA	N/A	N/A	N/A

Figure 5.17 Ramus linear measurement results for the pooled-sex sample and by sex

Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; arrows indicate direction of the significant relationship. **LRB:** least ramus breadth; **MRB:** maximum ramus breadth; **RH:** ramus height; **CrH:** coronoid height; **GA:** gonial angle. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

In this study, there was a clear trend observed in both males and females for an increase in the magnitude of the gonial angle over time. The relationship between gonial angle and diet has been recorded in previous studies comparing hunter-gatherer and agricultural groups (Galland et al., 2016; von Cramon-Taubadel, 2011), and in comparisons of more recent archaeological populations (Frake and Goose, 1977; Goose, 1962, 1981; Ingervall et al., 1972; Luther, 1993; Mays, 2015; Rando et al., 2014; Rock et al., 2006; Seddon, 1984). Results from animal and clinical studies have found that bite force (Ingervall and Helkimo, 1978; Ingervall and Minder, 1997; Kiliaridis et al., 1995; Raadsheer et al., 1999; Ringqvist, 1973; Sondang et al., 2003; Throckmorton et al., 2000; Tuxen et al., 1999) and masticatory musculature development (Benington et al., 1999; Bloem and van Hoof, 1971; Gionhaku and Lowe, 1989; Kasai et al., 1997, 1994) are inversely correlated with gonial angle, such that more acute gonial angles correlate with larger muscles and bite forces.

Although there is a clear trend in the literature for a decrease in ramus width and an increase in gonial angle, the results pertaining to ramus and coronoid height are less clear. Some studies have found a decrease in ramus height over time (Carlson and Van Gerven, 1977; Y'Edynak and Fleisch, 1983), while other studies have found that hunter-gatherers had relatively shorter rami compared with agricultural populations (Galland et al., 2016; Katz et al., 2017; May et al., 2018; Pinhasi et al., 2015; von Cramon-Taubadel, 2011). The results from the experimental and clinical literature are also inconclusive on the relationship between mandibular ramus height, masticatory muscle development and maximum bite force (Benington et al., 1999; Gionhaku and Lowe, 1989; Hannam and Wood, 1989; Ingervall and Helkimo, 1978; Ingervall and Thilander, 1974; Kasai et al., 1994; Kubota et al., 1998; Raadsheer et al., 1999; Ringqvist, 1973; van Spronsen et al., 1991; Watanabe and Watanabe, 2001). For example, a relatively taller coronoid process may reflect a smaller (shorter) temporalis muscle, but the absolute size of the muscle may not necessarily reflect bite force magnitude (Katz et al., 2017; Sella-Tunis et al., 2018). The apparent discrepancy between studies may reflect methodological differences, since the height of the ramus can either be measured as the direct distance between the condyle and the gonion, or as the distance from the condyle perpendicular to the occlusal plane. In addition, the height of the ramus and coronoid process may result from secondary changes to the ramus caused by biomechanical stress, such as posterior rotation of the mandible that occurs due to a more obtuse gonial angle (Rando et al., 2014).

Although much of the existing literature predicts that global patterns of mandibular variation may reflect the intensity and duration of mastication (von Cramon-Taubadel, 2011), it is possible that the mandibular size reductions observed in this study were a result of a concurrent reduction in body size due to poor nutrition and dietary homogeneity introduced with agriculture (Larsen, 2006; Tanner, 1989). Experimental work with animals confirms that reduced body size due to poor nutrition also affects mandibular growth (Alippi et al., 2002). Agricultural diets are characteristically low in protein (Larsen, 2006), which tends to limit overall growth (Frayer, 1984) and may result in allometric cranial size changes (Perez and Monteiro, 2009). However, there were no significant differences in stature or body mass between the Nubian samples in this study (Appendix A.2). In addition, the mandibles of the later samples were not just smaller versions of those in the hunter-gatherer sample, and morphological changes were concentrated in functional areas of the mandible directly involved in mastication. If differences in mandibular morphology were a result of overall body size changes, then a uniform reduction in mandibular dimensions would be expected. Although body size may contribute to certain aspects of mandibular size, it is unlikely that the diachronic mandibular size and shape trends observed in this study are due to associated changes in stature.

This study found trends for reduced mandibular length, body height, width of the ramus and a more obtuse gonial angle over time. This morphological evidence corresponds to the archaeological and isotopic evidence for agricultural intensification and an increased reliance on softer foods throughout the Nubian Holocene period. Although there is archaeobotanical evidence for some level of cereal domestication within the R12 population (Out et al., 2016), the R12 population still relied heavily on hunting and wild plant collection and/or cultivation (Salvatori and Usai 2019). Isotopic evidence shows the predominance of animal protein (particularly cattle) in the diets of the R12 and subsequent KAW population, indicating that these populations continued to primarily rely on tough animal meat (Caneva, 1988; Caneva et al., 1993; Caneva and Gautier, 1994; Iacumin et al., 1998). The intensification of agriculture in the KER population (Fuller, 2004b; Iacumin et al., 1998; O'Connor, 1993) is supported by isotopic evidence that demonstrates a shift to C3 plant consumption (wheat and barley) during this period (Iacumin et al., 1998). The KER population also practised animal domestication (cattle and caprine) alongside limited hunting (Chaix, 1993). Finally, the Meroitic (KUS) populations in ancient Nubia further increased carbohydrate consumption through the adoption of new technology for irrigation, such as the water wheel (Edwards, 1998; Fuller, 2004a; Martin et al., 1984). Over time, the ever-increasing reliance on agricultural food products

resulted in an overall softer diet, which led to functionally-relevant morphological change within the mandibles of these populations.

5.6 Conclusions

Due to a combination of food material properties and advances in food preparation, agricultural food products, such as cereal and dairy, were likely to have been easier to chew than foods typically consumed by hunter-gatherers. The results from this study support the predictions of the masticatory-functional hypothesis (Carlson and Van Gerven, 1977), revealing a trend towards decreasing mandibular size throughout the transition from hunter-gathering to agro-pastoral and later farming groups.

The results presented also indicate that changes in mandibular morphology continued to reflect cultural and subsistence variation from c. 5000 cal BC–AD 350 in the Upper Nubian samples, which is consistent with the hypothesis of continued reduced biomechanical demands in mixed-subsistence strategy and agricultural populations (Armelagos et al., 1989; Carlson and Van Gerven, 1977; Galland et al., 2016; Martin et al., 1984; Pinhasi et al., 2008; Sardi et al., 2006). It is important to note that mandibular shape is ultimately determined by multiple factors, and that some of the observed shape variation may be a result of genetic differences, or reflective of other environmental variables (Atchley and Hall, 1991; Harvati and Weaver, 2006; Hubbe et al., 2009; Nicholson and Harvati, 2006). Although there is some data suggesting genetic discontinuity between the JSA and later Nubian populations (Galland et al., 2016; Irish, 2000, 2005; Raxter, 2011), there is little evidence for major population movement within the Upper Nubian populations. The relative genetic continuity of the Upper Nubian populations is important to be able to support the assertion that the morphological trends observed in this study are, in part, the result of dietary transitions, rather than simply reflective of population history.

The morphological trends observed in this research are consistent with evidence that the mandible is a highly plastic bone, capable of substantial shape change throughout development in direct response to biomechanical stress (Carlson and Van Gerven, 1977; Galland et al., 2016; Larsen, 2015; Lieberman, 2011; Noback and Harvati, 2015; Paschetta et al., 2010; Pinhasi et al., 2015; von Cramon-Taubadel, 2011). Most of the reduction trends over time from the hunter-gatherers to the Meroitic populations were concentrated in the overall length of the mandibular body, the mandibular body in the molar region, ramus width and an increase in the gonial angle. The variation in morphological trends observed in the mandibles of the Nubian samples indicate that the influence of biomechanical stress due to mastication on the mandible is specific, and manifests as localised shape changes, rather than systemic changes throughout the mandible.
6 Mandibular Cross-Sectional Geometry

6.1 Introduction

Although there is a complex relationship between mandibular morphology and masticatory stress (Daegling, 2002, 2007), research has shown that differences in biomechanical loading due to variation in dietary composition and texture influence morphological patterns in the human mandible (Antón et al., 2011; Carlson and Van Gerven, 1977; Hinton and Carlson, 1979; Holmes and Ruff, 2011; Kaifu, 1997; Lieberman et al., 2004a; Paschetta et al., 2010). Comparative studies of human populations have documented a predictable relationship between dietary variation and measures of overall mandibular size and robusticity (Carlson and Van Gerven, 1977; Fukase and Suwa, 2008; Hinton and Carlson, 1979; Holmes and Ruff, 2011; Kaifu, 1997; Nicholson and Harvati, 2006; Paschetta et al., 2010; Pinhasi et al., 2008; Smith, 2009, 2011; von Cramon-Taubadel, 2011). Therefore, variation in mandibular size and robusticity observed between past human populations can be used to infer differences in masticatory function caused by temporal changes in diet and culture (Carlson and Van Gerven, 1979; Daegling and Grine, 1991; Dobson and Trinkaus, 2002; Fukase, 2007; Holmes and Ruff, 2011; Hylander, 1988; Ravosa, 1996a). Analysing the cross-sectional geometry (CSG) of the human mandibular corpus facilitates the understanding of its biomechanical behaviour during mastication.

This portion of the study used mandibular CSG properties to analyse diachronic variation in mandibular strength and robusticity in relation to changes in subsistence strategy in ancient Nubia. Five ancient Nubian samples were compared, spanning a temporal range of c. 13000 BC to AD 350, a period which included the initial adoption and intensification of pastoralism and agriculture. Biomechanical properties were analysed at the symphysis and within the molar region to determine how trends in mandibular robusticity may differ across the mandibular corpus. In addition, trends in mandibular strength and robusticity were analysed separately for males and females in order to identify sex-specific trends. The results from this study will help to elucidate the long-term effect of dietary transitions on mandibular strength and robusticity in these ancient Nubian populations.

6.2 Mandibular stress and strain

Functional studies of the human mandibular corpus operate under the premise that bone is responsive to stress, and can respond by changing its mass and shape to efficiently disperse biomechanical loads (sensu Wolff's law or 'bone functional demand') (Enlow, 1968; Ruff et al., 2006). In the context of bone morphology, stress is defined as an internal force exerted by either of two adjacent parts upon the other, and strain is a bone's deformation under stress. Resistance to biomechanical stress and strain depends on the material properties of bone (collagen fibre orientation, bone mineral density), the type of bone (cortical versus trabecular bone) and the cross-sectional geometric shape of the bone (Roark and Young, 1975). To mitigate the stress caused by increased biomechanical loading, bone may respond by changing its overall size, shape and/or distribution of compact or trabecular bone. In the absence of stress, bone will often be resorbed.

Analysing in vivo loading regimes in humans is difficult (Pampush and Daegling, 2016a), and studies of human mandibular biomechanics, therefore, rely on inferences from nonhuman primates with similar morphology and masticatory behaviour. In vivo bone strain research and in vitro bone structural analyses in primates have been used to identify the functional environment of the mandible and to understand the biomechanical significance of mandibular cross-sectional morphology (Bouvier, 1986a,b; Bouvier and Hylander, 1981; Daegling, 1992; Daegling and Hylander, 1997, 1998, 2000; Daegling et al., 1992; Herring and Teng, 2000; Hylander, 1977, 1979a, 1984, 1986; Hylander and Johnson, 1997; Hylander et al., 1987, 1998; Marinescu et al., 2005; Ravosa et al., 2000; Ross et al., 2005). Results from experimental dietary studies using animal models have shown that variation in dietary consistency, feeding behaviour and masticatory stress loading patterns are significantly correlated with differences in the morphology of the mandibular corpus (Bouvier, 1986a,b; Bouvier and Hylander, 1981; Cole, 1992; Hylander, 1979a, 1985, 1988; Jablonski, 1993; Organ et al., 2006; Ravosa, 1991, 1996, 2000; Ravosa et al., 2007; Smith, 1983; Taylor, 2002, 2003, 2006). In general, the results have shown that animals fed harder diets during growth develop thicker and stronger mandibular corpora (reflected in both the external and internal anatomy of the mandibular corpus), as compared with animals fed a softer diet (Biknevicius and Ruff, 1992; Bouvier and Hylander, 1981; Coiner-Collier et al., 2018; Hylander, 1979a, 1988; Lieberman et al., 2004; Organ et al., 2006). Hence, the mandibular corpus exhibits plasticity in response to changes in dietary consistency, and behaves in a way that is analogous to the adaptation in long bones resulting from changes in activity patterns during an individual's life

(Coiner-Collier et al., 2018; Ruff et al., 2006). Stress and strain patterns in the mandible can be infered by studying mandibular cross-sectional size, shape and bone distribution (Daegling, 1989; Daegling and Hylander, 2000; Holmes and Ruff, 2011). Based on the current evidence, the populations and/or individuals with diets that induce greater masticatory load are expected to have biomechanically more robust mandibles than those consumming softer diets (Bouvier and Hylander, 1981; Corruccini and Beecher, 1982; Ravosa et al., 2007).

There are alternative approaches to assess mandibular biomechanics in humans that do not directly involve living material. External linear measurements of the mandible can be useful to assess overall size and shape changes (see **Chapter 5**), but are limited in use when trying to identify subtle strength differences between populations (Biknevicius and Ruff 1992; Daegling 1989; Humphrey et al., 1999). Mathematical modeling (both static and dynamic), based on mandibular morphometric and functional data analysis, can provide insight into the biomechanics of the mandible under conditions of stress and strain (Curtis et al., 1999; Hannam, 1994; Hannam et al., 1997; Koolstra and van Eijden, 1995, 1997a,b; Korioth and Hannam, 1994; Korioth et al., 1992; Peck et al., 2000; Rohrle and Pullan, 2007). The magnitude of stress and strain patterns can also be inferred through the biomechanical analysis of mandibular cross-sectional size, shape and bone distribution (Antón et al., 2011; Daegling, 1989, 1993a; Daegling and Grine, 1991; Daegling and Hylander, 1998, 2000; Daegling and Jungers, 2000; Daegling et al., 1992; Holmes and Ruff, 2011; Hylander, 1985; Vinyard and Ravosa, 1998).

6.2.1 Symphyseal morphology

The potential underlying biomechanical and/or genetic influences on variation in the mandibular symphysis have received considerable attention both across primates (Beecher, 1977, 1979; Daegling, 1992, 1993c, 2001, 2004, 2007; Hylander, 1984, 1985, 1988; Lieberman and Crompton, 2000; Panagiotopoulou and Cobb, 2009, 2011; Ravosa, 1991, 1996b; Ravosa and Hylander, 1994; Vinyard and Ravosa, 1998), and within the genus *Homo* (Antón et al., 2011; Bastir and Rosas, 2004; Daegling, 1993a; Dobson and Trinkaus, 2002; DuBrul and Sicher, 1954; Fukase and Suwa, 2008; Kaifu, 1997; Marshall et al., 2011; Scott et al., 2009, 2010). Some researchers believe that variation in biomechanical stress generated by mastication is the cause of interspecific differences in anthropoid symphyseal shape (Beecher, 1977, 1979; Daegling, 1992, 2001, 2007; Daegling and McGraw, 2009; Enlow, 1966; Fukase, 2007; Fukase and Suwa, 2008; Gröning et al., 2011; Hylander, 1984, 1985, 1988; Johnson et

al., 1976; Koyabu and Endo, 2009; Lieberman and Crompton, 2000; Panagiotopoulou and Cobb, 2011; Ravosa, 1991; Ravosa and Hylander, 1994; Vinyard and Ravosa, 1998; Vinyard and Ryan, 2006). However, there is a debate over the influence of masticatory strain on intraspecific symphyseal shape, particularly within *Homo sapiens*.

The mental eminence (chin) is a unique and integral part of human symphyseal morphology (Schwartz and Tattersall, 2000). The chin is a relatively recent morphological trait in modern human history, first appearing in the fossil record between the Middle and Late Pleistocene (Dobson and Trinkaus, 2002). However, the evolutionary origin of the human chin is debated (Pampush and Daegling, 2016b). Hypotheses proposed to explain the presence of the human chin either classify it as an evolutionary by-product (known as a spandrel; Gould and Lewontin 1979) or as an adaptation. An example of a spandrel hypothesis is the hypofunction hypothesis, which argues that the chin is a by-product of a reduction in dental size resulting from reduced masticatory loads (Biggerstaff, 1977; Gould, 1977; Gould and Lewontin, 1979; Riesenfeld, 1969; Waterman, 1916; Weidenreich, 1936). Another spandrel hypothesis, the airway impingement hypothesis, proposes that following increased bipedalism and the development of a prognathic jaw in human ancestors, the chin structure evolved to provide more space within the facial complex to counteract constriction of the pharyngeal viscera (Coquerelle et al., 2013a,b; DuBrul and Sicher, 1954). Finally, the self-domestication hypothesis suggests that the chin formed as a result of facial reduction and a drop in androgen levels following an increase in social cohesion (Cieri et al., 2014; Franciscus et al., 2013).

However, most research views the chin as an adaptation in its own right, and not a byproduct of other selective forces. Early researchers who proposed a speech hypothesis argued that the chin provided an important structure to counteract the stresses caused by tongue movement during speech (Coon, 1962; Hooton, 1942; Robinson, 1914). More recently, researchers hypothesised that sexual selection may have driven the development of the chin (Hershkovitz, 1970; Thayer and Dobson, 2010). Finally, supporters of the masticatory stress hypothesis argue that the shape and size of the chin structurally reinforces the symphysis against the biomechanical loading strains produced during mastication (Daegling, 1993a; Gröning et al., 2011; Hylander, 1985). Although some studies have shown that variation in masticatory loading alters the severity and patterns of stress and strain experienced by the symphysis (Antón et al., 2011; Daegling, 1993c; Dobson and Trinkaus, 2002; Fukase and Suwa, 2008; Hylander, 1984, 1985), others have found that chin morphology (or lack thereof) does not influence patterns of symphyseal strain and is, therefore, unlikely to be influenced by the functional demands of mastication (Daegling, 2012; Holton et al., 2015; Ichim et al., 2006). Therefore, considerable attention has been devoted towards understanding the functional relationship between mandibular symphyseal form and biomechanical stress.

6.2.2 Patterns of symphyseal stress and strain

Electromyographic analyses have shown that human and macaque symphyses experience a similar strain pattern during mastication, prompting the frequent use of macaques as an experimental model to understand human mastication (Hylander and Johnson, 1994; Van Eijden et al., 1993). Mastication induces three primary stresses at the symphysis: dorsoventral shear in the sagittal plane, vertical bending in the coronal plane and lateral bending in the transverse plane (more commonly referred to as 'wishboning'; Figure 6.1) (e.g. Hylander, 1984, 1985). During unilateral mastication, the parasagittal bending stress on the balancing-side corpus induces dorsoventral shear strain within the symphysis, particularly on the inferior surface of the midline (Figure 6.1a) (Hylander, 1979a,b, 1984, 1988; Hylander et al., 1987; Ravosa, 1996a). The ability of bone to resist shearing strain is largely a function of the total amount of cortical bone in the plane of stress, regardless of symphyseal cross-sectional shape (Hylander, 1984, 1985). Since shearing strain does not appear to greatly influence symphyseal shape (Daegling and Grine, 1991; Hylander, 1984, 1985), researchers have largely focused on the influence of wishboning and coronal bending on symphyseal shape. Results from three-dimensional finite element analyses (3D FEA) have shown that resistance to wishboning and vertical bending is correlated with symphyseal shape dimensions (Daegling, 1993a; Demes et al., 1984; Gröning et al., 2011; Hylander, 1984, 1985; Umetani and Inoue, 1988; Weijs, 1989).

During mastication, both sides of the mandibular corpus twist about their anteroposterior axis, generating vertical bending stress in the coronal plane at the symphysis. Vertical bending stress causes tensile strain in the inferior region of the symphysis, and compressive strain in the superior alveolar region (**Figure 6.1b**) (Daegling, 1989, 1993a). Due to its material properties, bone is weaker against tensile strain than compressive strain (Daegling, 1993a, 2007). Therefore, the most efficient structural way to counter vertical bending and tensile strain is to stimulate bone growth along the inferior border of the symphysis, increasing symphyseal height (Daegling, 1993c, 2001; Hylander, 1985; Pearson and Lieberman, 2004). Similarly, the prominent inferior transverse torus (simian shelf)

observed in some anthropoids is viewed as a structure to resist the tensile strain caused by vertical bending stress (Daegling, 2001; Hylander, 1985).





White arrows indicate the direction of stresses induced by mastication on the mandible and the black arrows show the corresponding type of strain at the symphysis. a) dorsoventral shear in the sagittal plane places parallel shear strain on the symphysis. b) vertical bending stress in the coronal plane places compressive strain in the alveolar region and tensile strain at the symphyseal base. c) lateral bending in the transverse plane (wishboning) places compressive strain on the labial surface of the symphysis and tensile strain on the lingual side of the symphysis.

Within the anthropoid symphysis, the largest magnitude strains are produced by lateral bending in the transverse plane, or wishboning (Hylander, 1984, 1985; Hylander and Johnson, 1994; Hylander et al., 1987). Research on macaques and in humans using 3D FEA have shown

that within the symphysis, wishboning induces compressive strain along the labial side of the mandibular midline, but generates a relatively greater tensile strain along the lingual surface of the symphyseal midline (**Figure 6.1c**) (Hart et al., 1992; Hylander, 1984, 1985; Hylander and Johnson, 1994; Korioth et al., 1992). An efficient way to counter wishboning stress at the symphysis is to increase anteroposterior thickness by depositing bone on the lingual surface (Daegling, 1992, 1993a, 2001; Daegling and McGraw, 2009; Fukase, 2007; Gröning et al., 2011; Hylander, 1984, 1985; Hylander and Johnson, 1994; Lieberman, 2008; Panagiotopoulou and Cobb, 2011; Ravosa, 1991). Previous research has supported this predicted osseous response to wishboning in the human mandible (Fukase, 2007; Fukase and Suwa, 2008; Schwartz-Dabney and Dechow, 2003). It is important to note that the magnitude of wishboning stress is not only influenced by the overall size and bone distribution of the symphysis, but also by the curvature of the symphysis and the overall length of the mandible (Daegling, 1993a, 2001; Hylander, 1984, 1985; Hylander and Johnson, 1994; Ravosa, 1996a, 2000; Vinyard and Ravosa, 1998).

6.2.3 Patterns of mandibular corpus stress and strain

During mastication, the postcanine mandibular corpus is subjected to biomechanical stress generated by a combination of forces produced by the masticatory muscles, the temporomandibular joints (TMJ) and the dentition (Hylander, 1984, 1985). However, to identify how differences in mandibular corpus morphology between individuals and populations reflect dietary practices, it is important to understand the forces that are generated during mastication in the mandibular postcanine corpus.

Mastication induces three main stresses in the postcanine corpus: parasagittal bending, torsion, and lateral bending in the transverse plane. During unilateral mastication, parasagittal bending stress induces shearing strain along the entire length of the mandible. The shearing strains are highest in the region between the bite location and the muscle force on the working-side corpus (ramus), and between the muscle and joint force (TMJ) on the balancing-side corpus (van Eijden, 2000; Weijs, 1989). Shearing strain is largely counteracted by the total amount of bone in a cross-section, and therefore is not easily inferred through analysis of cross-sectional shape (Daegling and Grine, 1991; Hylander, 1984, 1985). On the working-side corpus, sagittal bending stress also causes tensile strain along the inferior border and compressive strain along the superior border. The opposite strain pattern is experienced on the balancing-side corpus, where sagittal bending causes compressive strain along the inferior

border of the corpus and tensile strain along the alveolar border (Hylander, 1979b; Korioth et al., 1992; van Eijden, 2000; Weijs, 1989). The ideal mandibular shape to resist parasagittal bending in the molar region is a tall corpus (vertically), which acts to increase the cross-sectional second moment of areas with respect to the transverse axis of the corpus (I_x and I_{max} ; Daegling and Grine 1991).

During mastication, torsion of the mandibular corpus occurs on both the working- and balancing-side (Hylander, 1979a,b), and is highest in the molar region (Daegling and Grine, 1991; Hylander, 1979a,b). The most effective cross-sectional shape and bone distribution to counter torsional stress is a circular hollow section with the maximum possible external transverse dimension (I_y and I_{min} ; Daegling and Grine 1991). This observation has led to the hypothesis that large transverse dimensions in primate mandibular corpora represent a structural response to countering large torsional stresses (Bouvier, 1986a,b; Cole, 1992; Daegling, 1989, 1992; Daegling and Grine, 1991; Hylander, 1979a, 1988; Ravosa, 1991; Smith, 1983).

Lateral bending in the transverse plane, or 'wishboning' of the mandibular corpus results from activation of the masseter muscle on the balancing-side corpus (Daegling and Grine, 1991; Hylander et al., 1987). Medial transverse bending occurs throughout the corpus during the jaw opening phase, while lateral transverse bending occurs during the jaw closing phase (Hylander, 1985; Hylander and Johnson, 1994). Both medial and lateral transverse bending induce relatively low patterns of stress within the mandibular molar region but these stresses increase anteriorly and are the highest at the symphyseal midline (Daegling and Grine, 1991). Therefore, transverse bending is unlikely to have a substantial impact on mandibular morphology in the molar region, compared with the effects of sagittal bending and torsion.

6.3 Solid vs. open cross-sectional models

To infer mandibular biomechanics from CSG properties, both open- and solid-section models have been used (Dobson and Trinkaus, 2002; Holton et al., 2015; Hylander, 1979a; Smith, 1983). Open-section models, often creating using CT-scanned images, allow for detailed analysis of the relationship between cortical thickness, the internal distribution of bone and biomechanical properties (Daegling, 1989, 2001; Fukase and Suwa, 2008; Holmes and Ruff, 2011). This is particularly important if there is variation in how cortical bone at the endosteal border responds to biomechanical stress (Daegling, 1989, 2007; Daegling and Grine,

1991; Smith, 1983). For example, populations that have different external mandibular dimensions may have the same absolute amount of cortical bone (which may reflect resistance to shearing strain), or conversely mandibles of similar external shape may vary significantly in the quantity and distribution of cortical bone in a cross-section (and thus vary in strength) (Daegling, 2007; Daegling and Grine, 1991). In addition, some research indicates that modelling of the endosteal contour is important due to the bone loss that may occur within the medullary cavity as individuals age (Cooper et al., 2008; Perreard Lopreno, 2016).

Although the mandibular corpus appears to be anatomically 'hollow' (in that the cortical bone is distributed predominately at the periphery of a cross-section), the corpus does not necessarily behave as a hollow beam during mastication. Within the interior of the mandibular corpus are extensive networks of trabecular bone. Although the apparent density of trabecular bone is less than that of cortical bone, studies have shown that both types of bone can have similar biomechanical properties (Hylander, 1985). In addition, the distribution of bite forces within the mandibular corpus can be affected by the presence of teeth, tooth roots and periodontal ligaments (Daegling et al., 1992). Experimental data seem to support the hypothesis that corpus behaviour is more compatible with a closed-section interpretation (Daegling and Hylander, 1998, 2000; Daegling et al., 1992).

Previous research has also demonstrated that in postcranial elements, there is a strong correlation between the cross-sectional values calculated from solid-section models and from those that include the endosteal border (Macintosh et al., 2013; Stock and Shaw, 2007). Furthermore, between-population variation in the relative cortical thickness of postcranial elements has been shown to be limited, and therefore does not significantly affect the biomechanical inferences from open- versus closed-section models (Sparacello and Pearson, 2010). Similarly, within the mandibular symphysis, researchers have found significant correlations between CSG calculated from CT-scanned images versus solid-section models (Bonner, 2013; Holton et al., 2015). The periosteal bone is more mechanically relevant than the bone at the endosteal border, and unless there are significant differences in medullary dimensions, the data calculated from the periosteal cross-sectional shape will capture the primary mechanical differences between populations. Therefore, in most cases the periosteal contour alone can provide an accurate estimation of biomechanical properties (Sparacello and Pearson, 2010; Stock and Shaw, 2007).

For this study, CT-scanning of the mandibles was not possible and consequently, solid-section models were used to calculate mandibular cross-sectional geometry (Dobson and

Trinkaus, 2002; Holton et al., 2015). While the use of external mandibular corpus contours does not allow for the assessment of population-level variation in the internal morphology of the cross-section, it does facilitate the study of longitudinal trends for other important biomechanical parameters. Based on previous research on postcrania and mandibles, the use of solid-section models is not thought to significantly affect the comparative biomechanical inferences within this study (Bonner, 2013; Holton et al., 2015; Macintosh et al., 2013; Sparacello and Pearson, 2010; Stock and Shaw, 2007). However, it is important to note that by using a solid-section model, this study was unable to examine differences between populations in mandibular corpus cortical or trabecular cross-sectional area, thickness and distribution.

6.4 Materials and methods

6.4.1 Materials

The current study examined mandibular strength and robusticity across subsistence strategy transitions in ancient Nubia through the analysis of mandibular cross-sectional geometry. Five samples were compared: a Late Palaeolithic sample from Lower Nubia (JSA; c. 13000–9000 BC); and samples across the agricultural intensification in Upper Nubia, representing cultural groups from the Sudanese Neolithic (**R12**; c. 5000–4000 cal BC), Kerma Ancien (**KAW**; c. 2500–2050 BC), Kerma Classique (**KER**; c. 1750–1500 BC) and Meroitic (**KUS**; c. 350 BC–AD 350). For background information on these samples, see **Chapter 4**. Only skeletally mature adults were used in the following analyses. Age and sex were assessed using standard osteological techniques (**Appendix A.1**) (Buikstra and Ubelaker, 1994; White and Folkens, 2005). The sex and age distribution of the samples used in the cross-sectional analysis by population can be found in **Table 6.1**.

Complete mandibles were preferentially included in this analysis, although fragmented mandibles were included if reconstruction in ScanStudio was possible (see Section 6.4.2). However, if there was damage to the symphyseal or molar region, the relevant cross-section was not included in this analysis. Due to the potential effect of severe ante-mortem tooth loss (AMTL) on mastication patterns and mandibular morphology (Mays, 2015), individuals with more than two AMTL on one side of the mandible were excluded from analysis. It was important to ensure the integrity of the symphyseal/molar cross-sectional shape and, therefore, if there was any clear damage in those regions (due to taphonomic processes and/or post-mortem damage), the relevant cross-section was excluded from the final analysis.

Similarly, for individuals with AMTL affecting I_1 , M_1 or M_2 , the relevant symphyseal or molar cross-section was not included in the analysis. In addition, any severe oral pathology that resulted in alteration of the surface of the mandible in the symphyseal or molar region, such as a dental abscess, was excluded from the analysis.

Population		Se	X		Age				
	Male	Female	Indeterminate	Younger	Older	Indeterminate			
JSA	8	4	-	_*	-*	_*			
R12	6	13	-	4	14	1			
KAW	13	4	-	12	5	-			
KER	20	18	-	24	12	2			
KUS	6	4	_	6	4	_			

Table 6.1 Sex and age distribution for each sample by population for cross-sectional geometry analysis

*Access to JSA material was not available, and the age of these individuals was not recorded when original scans were taken. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Younger adults \leq 35 years old; Older adults >35 years old.

6.4.2 Methods

Each mandible was digitised using a NextEngine 3D laser scanner and preliminary digital models were created using ScanStudio software (**Appendix A.3**). When possible, fragmented mandibles were reconstructed using the ScanStudio software (**Appendix A.3.1**). Following initial modelling in ScanStudio, the mandibular 3D models were exported into Rapidform (a 3D scanning software program) for further analysis.

Using the Rapidform software, each fused mandibular model was aligned to ensure that the mandibular cross-sections examined were comparable between individuals. Each mandible was oriented by placing a virtual plane parallel to the inferior border of the mandibular corpus (**Figure 6.2a**). Another plane was positioned perpendicular to the inferior plane that bisected the midline (between LI₁ and RI₁) and the midsagittal point of the bicondylar chord (**Figure 6.2b**). In this study, the cross-sections of interest were at the midline of the symphysis (between LI₁ and RI₁) and in the molar region of the left and right corpus (between M₁ and M₂). Previous research has shown that, in the primate mandible, the most severe bending and torsional stresses in the postcanine corpus occur in the molar region, while in the anterior corpus the most severe stresses occur in and around the midsagittal plane (Hylander, 1979b, 1985; Ravosa and Hylander, 1994). Therefore, analysing cross-sections in both the incisor and the molar regions allows for the comparison of mechanical loading along the mandibular corpus.

In each of the targeted cross-sectional areas, a plane was drawn perpendicular to both the occlusal and inferior surface of the mandibular body (**Figure 6.2c**). Where each plane representing a targeted cross-section intersected the mandibular corpus, a digital polyline was created to represent the external contour of the fused 3D model. Therefore, the digital polyline represents the external outline of the corpus cross-section (**Figure 6.2d**). In order to expose the polyline and cross-section of interest, the rest of the mandible was digitally removed (**Figure 6.3a,c**). Once the polyline was anatomically oriented correctly, the image of the cross-section was exported from Rapidform into Adobe Photoshop to create solid cross-sectional models (**Figure 6.3b,d**). Due to poor preservation, fragmentation and dental pathologies, not all scanned mandibles produced three usable cross-sections. Therefore, sample sizes vary by the cross-section analysed and are specified in the data tables.



Figure 6.2 3D mandibular models and alignment planes in Rapidform (a) Inferior plane parallel to the inferior border of the mandibular body; (b) midline plane perpendicular to the inferior plane and bisecting the midline at LI_1/RI_1 and the bicondylar chord; (c) right molar M_1/M_2 cross-sectional plane perpendicular to the inferior and occlusal plane; (d) digital polyline highlighting the outline of the symphyseal cross-section.



Figure 6.3 Mandibular cross-sections in Photoshop (a) symphyseal raw cross-section; (b) symphyseal closed-section model; (c) right molar raw cross-section; (d) right molar closed-section model.

6.4.3 Cross-sectional properties

All cross-sectional images were uploaded into ImageJ and scaled to pixels/mm based on the known height of the cross-section (measured in Rapidform). Second moments of area were calculated for each cross-section using Moment Macro for ImageJ. The biomechanical properties of the mandibular corpus were assessed using second moments of area which measure resistance, within a given cross-section, to bending about a defined axis (e.g. Antón et al., 2011; Daegling and Grine, 1991; Dobson and Trinkaus, 2002; Fukase and Suwa, 2008; Holmes and Ruff, 2011; Holton et al., 2014, 2015; Organ et al., 2006; van Eijden, 2000). All cross-sectional properties assessed in this analysis and their biomechanical significance are shown in **Table 6.2**.

Cross-sectional properties that were calculated included TA, I_x , I_y , I_{max} , I_{min} and J (**Table 6.2**). Total subperiosteal area (TA) measures the area of a mandibular cross-section, and includes both the cortical bone and medullary cavity (Daegling and Grine, 1991). Total cross-sectional area, regardless of the distribution of the bone, is an important factor in countering strain due to shearing stress (Daegling and Grine, 1991; Hylander, 1984, 1985).

Abbreviation	Measurement (units)	Biomechanical significance			
ТА	Total subperiosteal area (mm ²)	The total area of the mandibular cross-section including the cortical bone and medullary cavity			
I_x and I_y	Second moment of area (mm ⁴); the distribution of bone around a particular neutral axis: the x-axis is either the mediolateral (molar region) or antero-posterior axis (symphysis); the y-axis is the supero-inferior axis	Resistance to bending: I_x is bending about the x-axis: vertical bending (symphysis), parasagittal bending (molar); I_y is bending about the y-axis: wishboning (symphysis) or torsion (molar)			
I _{max} and I _{min}	Second moment of area (mm ⁴); distribution of bone around a particular neutral axis, in this case the maximum and minimum values for the cross- section	Maximum and minimum resistance to bending around a given principal axis; <i>I_{max}</i> represents maximum bending about the x-axis and <i>I_{min}</i> represents bending about the y-axis			
J	Polar second moment of area (mm ⁴)	Sum of <i>I_{max}</i> and <i>I_{min}</i> , represents torsional rigidity of a cross-section			
I_y/I_x and I_{min}/I_{max}	Bending index	I_y/I_x is analogous to standard robusticity index; I_{min}/I_{max} : circularity of the cross-section and reflects torsional rigidity (low values should be inefficient for torsion but favourable for sagittal bending)			

Table 6.2 Mandibular cross-sectional properties and biomechanical significance

Definitions based on Daegling and Grine, 1991; van Eijden, 2000; Organ et al., 2006; Antón et al., 2011

Second moments of area are measures of the distribution of bone in a cross-section and are calculated based on the total mass of bone and its distribution about a particular axis. Depositing bone as far as possible from the neutral axis of a cross-section can efficiently increase the second moment of area without increasing the absolute quantity of bony material

(van Eijden, 2000). Second moments of area are sometimes referred to as moments of inertia, and are expressed as *I* (Ruff, 2000). The second moments of area I_x and I_y are measurements of bending rigidity about the x- and y-axis respectively (defined with respect to the alveolar plane). Similarly, I_{max} and I_{min} represent the maximum and minimum bending rigidity about the x- and y-axis respectively. The polar second moment of area (*J*) is the sum of I_{max} and I_{min} , and represents the torsional rigidity of a cross-section; rigidity is defined as the ability to resist deformation (Ruff, 2008; Stock et al., 2011). Biomechanical 'shape' indices were also calculated from cross-sectional parameters (I_y/I_x and I_{min}/I_{max}), and these describe the circularity of a cross-section; they are analogous to traditional mandibular 'robusticity' indices based on linear measurements (Chamberlain and Wood, 1985; Daegling and Grine, 1991). In this study, the second moments of area reflect rigidity to specific biomechanical strain patterns (Stock et al., 2011).

6.4.4 Statistical analysis

Statistical analyses on the mandibular CSG properties were performed using IBM SPSS Statistics for Mac, version 22 (IBM Corp. Armonk, N.Y., USA). The data were tested for normality using the Shapiro-Wilk test. Due to some deviations from normality, prior to statistical analysis, all cross-sectional parameters (except biomechanical indices) were natural log-transformed (Sokal and Rohlf, 1995). Dependent samples *t*-tests were used to identify significant differences within an individual between the cross-sectional properties of the left and right M_1/M_2 cross-sections (**Appendix C**). In addition, independent samples *t*-tests were used to identify significant sexual dimorphism in cross-sectional properties within each Nubian sample (**Appendix C**). Differences between populations for each of the six cross-sectional properties (TA, I_x , I_y , I_{max} , I_{min} and J) were identified using one-way ANOVAs. Following significant ANOVAs, the Hochberg's GT2 *post-hoc* test was used to identify significant pairwise differences between samples. In addition to the pooled cross-sectional data, males and females were analysed separately to identify sex-specific trends by using ANOVAs and Hochberg's GT2 *post-hoc* tests.

Although overall body size may not greatly influence the size of the mandible (Daegling, 1992; Daegling and McGraw, 2001), size standardisation can be important when comparing pooled-sex samples to limit the influence of sexual dimorphism in mandibular size on the interpretation of the results (Daegling, 1989). Size-standardising the cross-sectional properties to mandibular length has been used in other studies to compare CSG values between

populations (Biknevicius and Ruff, 1992; Bouvier, 1986a,b; Cole, 1992; Daegling, 2007; Holmes and Ruff, 2011; Hylander, 1979b, 1988). Mandibular length was measured to the nearest 0.1 mm using Rapidform (**ML1**; **Figure 6.4**; **Table 6.4**). Size-standardised cross-sectional values were compared between samples by the same method as the raw cross-sectional values: using ANOVAs and follow-up Hochberg's GT2 *post-hoc* tests.



Figure 6.4 Mandibular length measurement 1 (ML1)

Distance from the gnathion to the midsagittal point on the condyle-condyle chord (BCoB). Co, condyle; Gn, gnathion.

		Combined			Male		ī	Female	
Population	n	Mean (mm)	SD	n	Mean (mm)	SD	n	Mean (mm)	SD
JSA	11	110.36	6.67	7	113.12	5.92	4	105.52	5.43
R12	13	100.33	3.93	4	101.28	4.57	9	99.91	3.93
KAW	15	101.28	4.86	11	102.73	4.51	4	97.28	3.66
KER	39	100.16	6.10	21	103.39	5.39	18	96.39	4.58
KUS	9	96.59	3.48	3	99.04	3.30	6	95.37	3.11

Table 6.3 Descriptive statistics for ML1 (mm) by population and sex

ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB); *n*: sample size; SD: standard deviation.

Analysis of the cross-sectional properties was also completed separately for males and females because the effect of sexual dimorphism on shape in the mandible is not fully understood. Although it is unlikely that mandibular shape variation reflects sexual dimorphism alone (Reno et al., 2003), there are subtle levels of sexual dimorphism in the mandible that need to be accounted for (Coquerelle et al., 2011). In addition, the appearance of sexually

dimorphic traits can be altered by systemic factors such as malnutrition (Galdames et al., 2008), which may be relevant to the study of these early farming populations.

In addition to standardising mandibular cross-sectional properties for overall size variation, adjusting these values to estimated moment arm and beam length can provide additional insight into biomechanical differences between populations (Antón et al., 2011; Daegling, 2007; Hylander, 1985; Organ et al., 2006; Smith, 1983). The appropriate approximation of moment arm varies by location along the mandibular corpus and is dependent upon the specific second moment of area of interest (**Table 6.4**). Standardisation methods using CSG value and location along the mandible are described below and were first described in the relevant cited papers.

Cross-sectional property	Linear Measurement	Biomechanical Relevance	References
Symphysis I_x and I_{max}	BGoB BM2B	Vertical bending moment arm	BGoB : Daegling 1992; Daegling and McGraw 2001; Fukase and Suwa 2008; Holton et al. 2014, 2015; Organ et al. 2006 BM2B : Daegling 2001a; Dobson and Trinkaus 2002
I_y and I_{min}	ML3	Wishboning moment arm	Daegling 1993; Holton et al. 2014, 2015
M_1/M_2 I_x and I_{max}	ML2 ML3 LML	Parasagittal bending moment arm	ML2/LML: Antón et al. 2011 ML3: Daegling 2007
I_y and I_{min}	BGoB BM2B	Wishboning moment arm	BGoB/BM2B: Antón et al. 2011

Table 6.4 Cross-sectional property and linear measurement indices

BGoB: direct distance between the right and left gonion; **BM1B**: dental arch breadth at M_1 ; **BM2B**: dental arch breadth at M_2 ; **LML**: mandibular length from gnathion to midsagittal point of the BGoB; **ML2**: mandibular length from gnathion to the condyle; **ML3**: mandibular length from infradentale to the midsagittal point of the gonion-gonion chord; **UML**: mandibular length from infradentale to the midsagittal point of the condyle-condyle chord.

Within the symphysis, the second moments of area I_x and I_{max} were scaled to bigonial breadth (**BGoB**; Daegling, 1992; Daegling and McGraw, 2001; Fukase and Suwa, 2008; Holton et al., 2014, 2015; Organ et al., 2006) and dental arcade breadth at M₂ (**BM2B**; Daegling, 2001; Dobson and Trinkaus, 2002), which approximate the beam length associated

with vertical bending stress at the symphysis. The symphyseal second moments of area I_y and I_{min} were scaled to a wishboning moment arm proxy that was most closely approximated by the mandibular length measured from the infradentale to the midsagittal point of the bigonial chord, **ML3** (**Table 6.4**) (Daegling, 1993a; Holton et al., 2014, 2015).

To create indices of relative biomechanical strength within the molar region, researchers have used a variety of linear measurements to approximate moment arms. Here, the mandibular length measurement **ML3** (infradentale to BGoB) was used to approximate the moment arm for parasagittal bending (I_x and I_{max}) (Daegling, 2007). In addition, **ML2** (gnathion to condyle) and **LML** (gnathion to BGoB) have also been used to approximate the moment arm for parasagittal bending (I_x and I_{max}) (Antón et al., 2011). Measures of mandibular width (**BGoB** and **BM2B**) have been used to represent moment arms in wishboning (I_y and I_{min} ; **Table 6.4**) (Antón et al., 2011). All indices were rendered dimensionless by transformation of variables to the units of length, mm. Kruskal-Wallis tests were used to identify significant differences between populations in the above ratios, and *post-hoc* Mann-Whitney tests (with a Bonferroni correction; $p \le 0.005$) were used to identify significant pairwise relationships between populations (**Appendix 3**).

6.5 Results

6.5.1 Symphysis

The descriptive statistics for the pooled-sex raw and standardised symphyseal CSG can be found in **Table 6.5**. There were significant differences between samples for mean symphyseal TA, I_x , I_y , I_{max} and J (all p<0.001; **Table 6.6**, **Figure 6.6**), and for each measurement the JSA sample had significant larger means than the other samples. In addition, raw I_{min} was significantly different between samples (p=0.018), but JSA was only significantly larger than R12 (**Table 6.6**). There were fewer significant relationships and trends when the standardised symphyseal data were analysed (**Table 6.5**, **Table 6.6**), and only for I_x , I_{max} and Jdid JSA remain significantly larger than some of the other samples (**Table 6.6**). For standardised I_x and J, JSA was significantly larger than R12 and KAW. For I_{max} , JSA was significantly larger than R12, KAW and KER (**Table 6.6**).

Symphyseal I_x and I_{max} was also scaled to the dental arcade breadth at M₂ (BM2B), because the magnitude of vertical bending stress experienced at the symphysis is influenced by how much of the symphysis lies within the coronal plane (Antón et al., 2011; Daegling, 1992,

2001; Dobson and Trinkaus, 2002; Hylander, 1985; Ravosa, 2000). At the symphysis, I_{max} /BM2B was significantly different between samples (p=0.033), and individuals from JSA had a significantly larger ratio than individuals from KAW and KUS (**Appendix C**). In addition, the ratio of I_{min}/I_{max} was significantly different between samples (p=0.001), and JSA had a significantly smaller value than all of the other samples (**Figure 6.5a**; **Appendix C**).



Figure 6.5 Cross-sectional I_{min}/I_{max} index (pooled-sex sample) for (a) symphysis, (b) left M_1/M_2 , and (c) right M_1/M_2

Error bars 95% confidence interval; * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$). **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

When standardised symphyseal data were compared by sex, males were significantly different in symphyseal I_x (p=0.005), I_{max} (p=0.002) and J (p=0.008) (**Table 6.8**). Males from JSA were significantly larger than: R12 and KER for I_x ; R12, KAW and KER for I_{max} ; and R12 for J (**Table 6.8**). When standardised symphyseal data were compared between females, there were no significant differences between samples (**Table 6.9**). For the raw and standardised symphyseal data for males, the highest values for I_x , I_{max} and J were in the JSA sample and the lowest were in the R12 sample (**Table 6.7**). The values continued to increase in the more recent samples after R12, with the highest value in the KUS sample. For females, the highest I_x , I_{max} and J raw and standardised values were found in the JSA sample. However, the lowest I_x , I_{max} and J values for females were found in the KAW and KUS samples. (**Table 6.7**).

<u> </u>	I.						8	J - J F - F	The second se	,			
<u>Symphysis</u>			T 4										
		מ	IA	G / 1	1. 1	מ	I_x	C.	, ,, ,	م ا	I_y	C.	1 1. 1
Demulation		Rav	V CD	Stana	araisea	Kaw	, CD	Stana	laraisea	Kaw	, CD	Stana Maar	araisea
Population	<u>n</u>	Mean (mm ⁻)	<u>SD</u>	Mean	SD	Mean (mm ⁺)	<u>SD</u>	Mean	SD	Mean (mm ⁺)	SD 2702.00	Mean	SD
JSA	11	390.40	59.47	3.21	0.44	36219.42	9988.30	0.24	0.063	6594.83	2792.38	0.045	0.018
R12	14	284.73	47.29	2.83	0.54	16299.89	4770.53	0.16	0.056	3331.05	1269.50	0.033	0.014
KAW	15	303.15	31.88	2.97	0.30	18306.41	5239.63	0.18	0.049	3692.49	121.19	0.036	0.0072
KER	33	310.03	41.07	3.09	0.47	19151.70	5202.44	0.19	0.052	4116.82	1275.67	0.041	0.014
KUS	8	285.18	59.21	3.04	0.51	16776.07	6263.12	0.19	0.051	3338.60	1467.10	0.038	0.013
		I –	I _{max}			I –	Imin	_		I –	J	_	
		Rav	v	Stand	ardised	Raw		Stand	lardised	Raw	,	Stana	ardised
Population	n	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD
JSA	11	37913.49	10752.24	0.26	0.069	4900.75	1997.15	0.033	0.012	42814.24	12306.29	0.29	0.077
R12	14	16413.27	4798.20	0.16	0.056	3217.67	1237.85	0.032	0.014	19630.94	5859.39	0.20	0.068
KAW	15	18404.32	5219.22	0.18	0.049	3594.58	740.20	0.035	0.0072	21998.90	5695.50	0.21	0.054
KER	33	19444.07	5268.95	0.19	0.052	3824.45	1139.44	0.038	0.014	23268.51	6007.72	0.23	0.062
KUS	8	16882.42	6274.70	0.19	0.051	3232.25	1447.14	0.036	0.013	20114.67	7535.63	0.23	0.062
Left M ₁ /M ₂													
		1	ТА				I_x				I_y		
		Rav	V	Stand	ardised	Raw	,	Stana	lardised	Raw	,	Stand	ardised
Population	n	Mean (mm ²)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD
JSA	10	379.07	75.95	2.99	0.49	28888.18	10762.76	0.17	0.035	6831.02	3803.80	0.044	0.022
R12	13	322.75	37.48	3.22	0.46	16078.06	4842.21	0.16	0.052	5944.43	1853.71	0.059	0.020
KAW	14	305.77	41.03	2.97	0.33	14880.24	4331.59	0.14	0.042	5066.46	1166.24	0.049	0.012
KER	36	281.80	41.60	2.83	0.44	12899.15	3770.39	0.13	0.036	4450.38	1534.46	0.045	0.017
KUS	8	281.39	32.65	2.99	0.45	11329.35	2344.98	0.13	0.038	4582.44	1025.67	0.052	0.014
			I max				Imin				J		
		Rav	V	Stand	ardised	Raw	,	Stand	lardised	Raw	,	Stand	lardised
Population	n	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD
JSA	10	30628.54	10898.53	0.18	0.038	5090.66	843.80	0.032	0.016	35719.20	12738.02	0.21	0.051
R12	14	18069.05	5143.25	0.18	0.056	3953.43	315.94	0.039	0.013	22022.49	5695.23	0.22	0.064
KAW	15	15997.75	4400.41	0.15	0.042	3948.95	1086.62	0.039	0.012	19946.69	5311.59	0.19	0.052
KER	36	14226.80	4055.86	0.14	0.038	3122.74	1069.85	0.032	0.012	17349.53	4768.80	0.17	0.047
KUS	8	12555.02	2278.64	0.14	0.039	3356.77	939.26	0.038	0.012	15911.79	3060.52	0.18	0.049

Table 6.5 Descriptive statistics of raw and standardised mandibular cross-sectional geometry by population (pooled sex)

Table 6.5 conti	inued												
Right M ₁ /M ₂													
			ТА				I_x				I_y		
		Raw	,	Stande	ardised	Raw	,	Stand	ardised	Raw	,	Stand	ardised
Population	n	Mean (mm ²)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD
JSA	10	353.04	62.20	2.90	0.43	23459.78	7200.15	0.16	0.044	6158.16	2516.05	0.041	0.013
R12	15	309.78	37.80	3.09	0.47	15024.73	4148.31	0.15	0.045	5435.13	1679.73	0.055	0.020
KAW	15	303.04	46.64	2.99	0.55	14079.97	4338.09	0.14	0.045	5003.47	1744.06	0.050	0.022
KER	35	279.33	38.09	2.84	0.47	12961.83	3487.94	0.13	0.041	4424.61	1451.67	0.046	0.017
KUS	8	284.71	34.99	3.07	0.31	11596.03	2589.76	0.14	0.031	4839.27	1580.29	0.056	0.015
			I _{max}				I_{min}				J		
		Raw	,	Stande	ardised	Raw	,	Stand	ardised	Raw	,	Stand	ardised
Population	n	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD	Mean (mm ⁴)	SD	Mean	SD
JSA	10	25140.89	7752.62	0.17	0.046	4477.05	1855.02	0.030	0.01	29617.94	9262.73	0.20	0.053
R12	15	16657.82	4160.21	0.17	0.047	3802.04	1213.79	0.038	0.014	20459.86	4834.27	0.20	0.057
KAW	15	15227.80	4584.23	0.15	0.048	3855.64	1428.44	0.038	0.018	19083.44	5807.68	0.19	0.065
KER	35	14450.68	3686.67	0.15	0.042	2935.75	944.64	0.031	0.011	17386.43	4391.78	0.18	0.052
KUS	8	12993.28	2634.36	0.15	0.030	3442.02	1234.42	0.040	0.012	16435.29	3537.42	0.19	0.036

149

Values standardised to ML1. JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB); *n*: sample size; SD: standard deviation.



Figure 6.6 Mean standardised symphyseal cross-sectional values for pooled-sex data by sample for (a) TA, (b) I_x, (c) I_y, (d) I_{max}, (e) I_{min} and (f) J

Values standardised to ML1; error bars 95% confidence interval; * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$). **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350); ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB).



Figure 6.7 Mean standardised left M₁/M₂ cross-sectional values for pooled-sex data by sample for (a) TA, (b) I_x, (c) I_y, (d) I_{max}, (e) I_{min} and (f) J

Values standardised to ML1; error bars 95% confidence interval; * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$). **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350); ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB).



Figure 6.8 Mean standardised right M_1/M_2 cross-sectional values (error bars 95% confidence interval) for pooled-sex data by sample for (a) TA, (b) I_x , (c) I_y , (d) I_{max} , (e) I_{min} , and (f) J

Values standardised to ML1; error bars 95% confidence interval; * = significant *post-hoc* tests (Hochberg's GT2 $p \le 0.05$). **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350); ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB).

			Raw	S	tandardised ^a
Cross-section	Measurement	p^{b}	Post-hoc ^c	p^{b}	Post-hoc ^c
	ТА	<0.001	JSA>R12, KAW, KER, KUS	0.28	-
	I_x	<0.001	JSA>R12, KAW, KER, KUS	0.006	JSA>R12, KAW
Symphysis	I_y	<0.001	JSA>R12, KAW, KER, KUS	0.23 ^d	-
Symphysis	Imax	<0.001	JSA>R12, KAW, KER, KUS	0.001	JSA>R12, KAW, KER
	Imin	0.018	JSA R12	0.51	-
	J	<0.001	JSA>R12, KAW, KER, KUS	0.01	JSA>R12, KAW
	ТА	<0.001	JSA>KAW, KER, KUS	0.12	-
	I_x	<0.001	JSA>R12, KAW, KER, KUS	0.027	No sig. results
Left M./Ma	I_y	0.011	JSA>KER	0.12	-
	Imax	<0.001	JSA>R12, KAW, KER, KUS	0.022	No sig. results
	Imin	0.003	JSA>KER	0.21	-
	J	<0.001	JSA>R12, KAW, KER, KUS	0.050	No sig. results
	TA	<0.001	JSA>KER, KUS	0.41	-
	I_x	<0.001	JSA>R12, KAW, KER, KUS	0.49	-
Dickt M /M	I_y	0.068	-	0.26	-
Kigiit W11/W12	Imax	<0.001	JSA>R12, KAW, KER, KUS	0.57	-
	Imin	0.004	JSA>KER	0.12	-
	J	<0.001	JSA>R12, KAW, KER, KUS	0.65	-

Table 6.6 ANOVAs and *post-hoc* tests for raw and standardised cross-sectional geometry (pooled sex)

^aStandardised to ML1; ^bANOVA level of significance $p \le 0.05$; ^cHochberg's GT2 *post-hoc* test level of significance $p \le 0.05$, arrows indicate direction of significance relationship between the samples; ^dWelch's ANOVA level of significance $p \le 0.05$. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350); ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB).

Descriptive statistics for the raw and standardised symphyseal CSG by sex are shown in **Table 6.7**. When the raw symphyseal properties were compared between males from different samples, there were significant differences observed for all of the properties (**Table 6.8**). The majority of the significant differences between samples were between JSA and the rest of the samples (TA, I_x , I_y , I_{max} and J) (**Table 6.8**). In addition, males from R12 were significantly smaller than those from KAW and KER for raw symphyseal I_x , I_{max} and J (**Table 6.8**). There were fewer significant relationships between females from different samples, and the raw cross-sectional values that were significantly different were I_x (p=0.014), I_{max} (p=0.009) and J (p=0.016). Females from JSA were significantly larger than KAW and KUS in raw values for symphyseal I_x , I_{max} and J (**Table 6.9**).

<u>Symphysis</u>										
ТА				Raw ((mm ²)			Standa	ardised	
	Sampl	e size (n)	Ма	ıle	Fen	nale	М	ale	Fei	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	7	4	415.62	56.64	346.27	35.95	3.27	0.53	3.11	0.21
R12	4	10	261.82	35.41	293.90	49.85	2.48	0.23	2.98	0.57
KAW	10	5	319.69	24.37	270.07	13.02	3.03	0.35	2.86	0.17
KER	18	15	324.65	38.64	292.48	37.91	3.04	0.55	3.16	0.37
KUS	3	5	314.30	53.05	267.70	60.91	3.21	0.58	2.94	0.49
I_x	1		1	Raw ((mm ⁴)		1	Standa	ardised	
	Sampl	e size (n)	Ма	ıle	Fen	nale	М	ale	Fei	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	7	4	41711.59	6720.30	26608.11	6976.81	0.26	0.071	0.21	0.027
R12	4	10	13833.90	4139.39	17286.28	4835.01	0.12	0.024	0.18	0.058
KAW	10	5	20542.93	4865.14	13833.36	2305.65	0.19	0.056	0.15	0.026
KER	18	15	20691.48	4597.21	17303.96	5430.87	0.18	0.058	0.20	0.043
KUS	3	5	21392.17	2198.00	14006.41	6376.61	0.22	0.030	0.17	0.051
I_y	I		I	Raw ((mm ⁴)		1	Stand	ardised	
	Sampl	e size (n)	Ма	ıle	Fen	nale	М	ale	Fei	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	7	4	7637.92	3061.49	4769.42	514.17	0.048	0.021	0.040	0.011
R12	4	10	2817.51	872.62	3536.05	1382.03	0.025	0.006	0.037	0.015
KAW	10	5	3992.09	682.82	3093.31	362.79	0.036	0.0086	0.035	0.0039
KER	18	15	4538.31	1360.71	3611.03	984.29	0.041	0.016	0.042	0.012
KUS	3	5	3878.17	1745.67	3014.86	1376.10	0.040	0.018	0.036	0.012
Imax		•		Raw ((mm ⁴)	1		Stand	ardised	1
	Sampl	$e \ size \ (n)$	Ma	ile	Fen	ale		ale	Fei	male
Population	Male	Female	Mean	SD	Mean	SD (520.02	Mean	SD	Mean	SD
JSA	/	4	43895.39	/521.08	27445.17	6528.93	0.28	0.079	0.22	0.028
K12	4	10	13922.23	4186.62	1/409.68	4852.98	0.12	0.024	0.18	0.058
KAW	10) 15	20622.22	4817.01	13968.51	2497.91 5415.70	0.19	0.050	0.16	0.027
KUS	3	5	21000.30	2103.28	1/304.27	6437.04	0.18	0.039	0.20	0.043
	5	5	21431.20	2175.20 Dow ((mm^4)	0437.94	0.22	Stand	ordicod	0.032
1 min	Sampl	e size (n)	M	naw ((IIIIII) Fon	nale	м	Jale	ai uiscu Fa	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
ISA	7	4	5454.11	2328.67	3932.36	696.43	0.034	0.014	0.032	0.0058
R12	4	10	2729.18	794 33	3413.07	1361 79	0.024	0.0053	0.035	0.0050
KAW	10	5	3912.80	706.63	2958.15	186.17	0.035	0.0084	0.033	0.0043
KER	18	15	4169.22	1112.36	3410.71	1062.48	0.037	0.014	0.040	0.013
KUS	3	5	3819.14	1766.36	2880.12	1300.59	0.040	0.019	0.034	0.011
 J	-			Raw	(mm ⁴)			Stand	ardised	
-	Sampl	e size (n)	Ма	ale	Fen	nale	М	ale	Fei	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	7	4	49349.51	9529.94	31377.53	7008.77	0.31	0.090	0.25	0.030
R12	4	10	16651.41	4842.33	20822.75	6020.92	0.15	0.028	0.22	0.071
KAW	10	5	24535.02	5094.75	16926.66	2625.69	0.22	0.062	0.19	0.030
KER	18	15	25229.79	5422.12	20914.99	5993.17	0.22	0.072	0.24	0.049
KUS	3	5	25270.34	3929.15	17021.27	7730.39	0.26	0.045	0.20	0.062

Table 6.7 Descriptive statistics for raw and standardised cross-sectional properties by sample and sex

Left M ₁ /M ₂										
ТА	1		I	Raw	(mm ²)		I	Stand	ardised	
	Sampl	le size (n)	Ма	le	Fen	ıale	М	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	6	3	399.10	70.72	312.62	49.96	3.10	0.58	2.77	0.14
R12	3	10	328.97	26.32	320.88	41.26	3.10	0.24	3.25	0.52
KAW	10	4	309.30	46.97	296.94	23.02	2.90	0.36	3.14	0.16
KER	18	18	297.03	33.33	266.58	44.28	2.79	0.39	2.88	0.49
KUS	3	5	278.48	34.02	283.14	35.73	2.86	0.51	3.07	0.45
I_x				Raw	(mm ⁴)		I	Stand	ardised	
D	Sampl	le size (n)	Ма	le	Fen	iale	M	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	6	3	29916.14	6898.14	19935.97	8056.57	0.18	0.036	0.15	0.029
R12	3	10	18187.89	6949.92	15234.13	3872.69	0.17	0.070	0.16	0.048
KAW	10	4	15572.81	4393.39	12975.65	4077.26	0.14	0.046	0.14	0.032
KER	18	18	14993.72	2730.36	10804.59	3538.72	0.13	0.032	0.13	0.040
KUS	3	5	10945.07	1464.14	11559.91	2893.79	0.12	0.026	0.14	0.044
I_y				Raw	(mm ⁴)			Stand	ardised	
	Sampl	le size (n)	Ма	le	Fen	nale		ale		male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	6	3	7976.76	4528.20	4580.25	1517.91	0.049	0.027	0.036	0.0048
R12	4	10	5516.30	1870.01	6115.68	1919.31	0.049	0.011	0.063	0.022
KAW	10	4	5128.94	1352.11	4894.62	446.58	0.047	0.014	0.055	0.0075
KER	18	18	4648.93	1537.55	4251.83	1025.00	0.041	0.014	0.050	0.018
KUS I	3	5	42/3.4/	1102.12 Dow	(mm^4)	1023.99	0.040	Stand	ordicod	0.012
1 max	Sampl	$l_{\rho} siz_{\rho}(n)$	Ma	Naw	(IIIIII) Fon	nale	м	Stanu	ai uiseu Fa	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
ISA	6	3	32055.04	7195.62	21298 32	8920.71	0.19	0.039	0.16	0.034
R12	4	10	20311 72	7016.98	17167 59	4317.06	0.19	0.032	0.10	0.054
KAW	11	4	16683.86	4443.60	14110.94	4251.14	0.15	0.045	0.16	0.034
KER	18	18	16332.53	3172.31	12121.06	3796.61	0.14	0.035	0.14	0.043
KUS	3	5	11830.28	1476.49	12989.86	2714.04	0.12	0.027	0.15	0.043
Imin	-			Raw	(mm ⁴)		0.02	Stand	ardised	
	Sampl	le size (n)	Ма	le	Fen	ıale	М	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	6	3	5837.87	3098.41	3217.91	677.69	0.036	0.019	0.025	0.00098
R12	4	10	3381.47	812.87	4182.22	1262.82	0.030	0.0041	0.043	0.014
KAW	11	4	4017.90	1276.91	3759.33	98.81	0.037	0.014	0.042	0.0059
KER	18	18	3310.11	1086.87	2935.36	1049.21	0.029	0.01	0.035	0.013
KUS	3	5	3390.26	1145.81	3336.68	941.31	0.037	0.016	0.039	0.012
J				Raw	(mm ⁴)			Stand	ardised	
	Sampl	le size (n)	Ма	le	Fen	ıale	М	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	6	3	37892.90	9478.91	24516.23	9570.96	0.23	0.055	0.19	0.034
R12	4	10	23704.19	7141.06	21349.80	5300.33	0.21	0.070	0.22	0.066
KAW	11	4	20701.76	5635.08	17870.27	4239.63	0.19	0.059	0.20	0.032
KER	18	18	19642.65	3737.11	15056.42	4660.40	0.17	0.041	0.18	0.053
KUS	3	5	15220.54	2552.88	16326.54	3543.99	0.16	0.043	0.19	0.054

Table 6.7 continued

	<u>2</u>			Dom	(2)			Ctore J.		
IA	G	(Kaw	(mm-) E			Standa	araisea	
Population	Sampi Male	Eemale	Mean	ue SD	ren Mean	sD	Mean	aie SD	Ге. Mean	sD
	o	2	270.59	52.80	282.80	46.82	2.06	0.46	2 64	0.10
J5A R12	0 1	2 11	310.28	33.11	202.09	40.82	2.90	0.40	2.04	0.10
K12 KAW	11	11	207 50	/1 95	318.05	62.24	2.95	0.33	3.13	0.73
KER	18	17	257.55	35.92	269.86	39.08	2.05	0.42	2.93	0.44
KUS	2	6	310.85	50.96	276.00	28.81	3.27	0.39	3.01	0.29
Ir	_	Ŭ	010100	Raw	(\mathbf{mm}^4)	20101	0.27	Standa	ardised	0.27
-*	Sampl	e size (n)	Ма	ale	Fen	ıale	М	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	8	2	25640.08	5963.70	14738.60	5241.40	0.17	0.046	0.13	0.014
R12	4	11	17944.38	5515.00	13963.04	3212.1	0.17	0.060	0.14	0.041
KAW	11	4	13855.60	4174.95	14696.99	5387.90	0.13	0.037	0.16	0.061
KER	18	17	14740.19	2795.05	11078.85	3197.89	0.14	0.040	0.13	0.043
KUS	2	6	12504.57	3003.18	11293.18	2673.11	0.14	0.021	0.13	0.036
I_y	1		1	Raw	(mm ⁴)		1	Standa	ardised	
	Sampl	e size (n)	Ма	ale	Fen	ıale	М	ale	Fe	male
Population	Male	Female	Mean	SD	Mean	SD	Mean	SD	Mean	SD
JSA	8	2	6708.60	2526.93	3956.40	396.89	0.043	0.014	0.036	0.00054
R12	4	11	4949.77	1841.73	5611.62	1674.51	0.044	0.013	0.058	0.021
KAW	11	4	4690.92	1296.32	5862.97	2692.60	0.043	0.013	0.067	0.034
KER	18	17	4429.88	1514.99	4419.02	1428.07	0.041	0.016	0.052	0.016
KUS	2	6	5524.20	2162.65	4607 50	151762	0.061	0.010	0.054	0.015
i i i i i i i i i i i i i i i i i i i	2	0	5554.29	2102.05	4007.39	1317.03	0.001	0.017	0.034	0.015
			5554.29	Raw ((mm ⁴)	1317.03	0.001	Standa	ardised	0.015
I max Population	Sampl	le size (n) Female		Raw ((mm⁴) <i>Fen</i>	nale	Mean	Stand:	ardised Fe	male
I max Population	Sampl Male	le size (n) Female	Mean 27480 16	2102.05 Raw (ale SD 6566.74	(mm⁴) <i>Fen</i> <u>Mean</u>	1317.05 nale SD	Mean	Standa SD	ardised Fe Mean	male SD
Imax Population JSA R12	Sampl Male 8	le size (n) Female 2	<i>Mean</i> 27480.16	Raw (ale 56566.74 5459.62	(mm⁴) <i>Fen</i> 15783.82	1317.03 nale SD 4492.96 3254.63	0.001 Mean 0.18 0.18	Standa <i>ale</i> 0.048 0.059	0.034 ardised Fe Mean 0.14 0.16	male SD 0.0045
Imax Population JSA R12 KAW	Sampl Male 8 4	<i>le size (n)</i> Female 2 11 4	<i>Mean</i> 27480.16 19591.82 14925.35	Raw (ale 5459.62 4413.07	(mm ⁴) Fen Mean 15783.82 15590.91 16059.56	1317.03 nale SD 4492.96 3254.63 5647.61	<i>M</i> ean 0.18 0.18 0.14	Stand: ale SD 0.048 0.059 0.038	0.034 ardised Fe Mean 0.14 0.16 0.18	0.013 male SD 0.0045 0.044 0.065
Imax Population JSA R12 KAW KER	2 Sampl Male 8 4 11 18	le size (n) Female 2 11 4 17	Mean 27480.16 19591.82 14925.35 16206.73	Raw (ale 5566.74 5459.62 4413.07 3191.84	(mm ⁴) Fen 15783.82 15590.91 16059.56 12591.33	1317.03 nale SD 4492.96 3254.63 5647.61 3303.78	<i>M</i> ean 0.18 0.18 0.14 0.15	Stand: <i>Slaw</i> 0.048 0.059 0.038 0.043	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15	0.013 male SD 0.0045 0.044 0.065 0.043
Imax Population JSA R12 KAW KER KUS	<i>Sampl</i> Male 8 4 11 18 2	<i>le size (n)</i> Female 2 11 4 17 6	Mean 27480.16 19591.82 14925.35 16206.73 13389.09	SD 6566.74 5459.62 4413.07 3191.84 3284.39	(mm ⁴) Fen 15783.82 15590.91 16059.56 12591.33 12861.34	SD 4492.96 3254.63 5647.61 3303.78 2734.01	Mean 0.18 0.18 0.14 0.15 0.15	Stand: ale SD 0.048 0.059 0.038 0.043 0.023	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15	sp 0.0045 0.0045 0.044 0.065 0.043 0.034
Imax Population JSA R12 KAW KER KUS Imin	Sampl Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6	Mean 27480.16 19591.82 14925.35 16206.73 13389.09	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw	(mm ⁴) Fen 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴)	1317.03 male SD 4492.96 3254.63 5647.61 3303.78 2734.01	Mean 0.18 0.14 0.15	Stands SD 0.048 0.059 0.038 0.043 0.023 Stands	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 ardised	sb sb 0.0045 0.044 0.065 0.043 0.034
Imax Population JSA R12 KAW KER KUS Imin	Sampl Male 8 4 11 18 2 Sampl	le size (n) Female 2 11 4 17 6	Ma Mean 27480.16 19591.82 14925.35 16206.73 13389.09	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ((mm ⁴) <i>Fen</i> Mean 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i>	ale SD 4492.96 3254.63 5647.61 3303.78 2734.01 male	M Mean 0.18 0.18 0.14 0.15 0.15	Stand: <i>slae</i> SD 0.048 0.059 0.038 0.043 0.023 Stand:	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.15	sp 0.0045 0.0045 0.044 0.065 0.043 0.034
Imax Population JSA R12 KAW KER KUS Imin Population	Sampl Male 8 4 11 18 2 Sampl Male	le size (n) Female 2 11 4 17 6 le size (n) Female	Man 27480.16 19591.82 14925.35 16206.73 13389.09 Man Man	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw Raw	(mm ⁴) Fen 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) Fen Mean	SD 4492.96 3254.63 5647.61 3303.78 2734.01 vale SD	M Mean 0.18 0.14 0.15 0.15 M Mean	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 ardised Fe Mean	0.013 male SD 0.0045 0.044 0.065 0.043 0.034
Imax Population JSA R12 KAW KER KUS Imin Population JSA	Sampl Male 8 4 11 18 2 Sampl Male 8	le size (n) Female 2 11 4 17 6 le size (n) Female 2	Mean 27480.16 19591.82 14925.35 16206.73 13389.09 Mean 4868.52	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18	ale SD 4492.96 3254.63 5647.61 3303.78 2734.01 ale SD 1145.33	M Mean 0.18 0.18 0.14 0.15 0.15 M Mean 0.031	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 ardised Fe Mean 0.025	male SD 0.0045 0.044 0.065 0.043 0.034
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12	Sampl Male 8 4 11 18 2 Sampl Male 8 4	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11	Ma Mean 27480.16 19591.82 14925.35 16206.73 13389.09 Ma Mean 4868.52 3302.34	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw Raw ale SD 1833.35 841.73	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> <u>Mean</u> 2911.18 3983.75	SD 4492.96 3254.63 5647.61 3303.78 2734.01 male SD 1145.33 1309.14	M Mean 0.18 0.18 0.14 0.15 M Mean 0.031 0.030	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD 0.011 0.0061	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.25 0.025 0.041	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12 KAW	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> <u>Mean</u> 2911.18 3983.75 4500.41	SD 4492.96 3254.63 5647.61 3303.78 2734.01 male SD 1145.33 1309.14 2278.76	Mean 0.18 0.18 0.14 0.15 0.15 Mean 0.031 0.030 0.034	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD 0.011 0.0061 0.011	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 ardised Fe Mean 0.025 0.041 0.052	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12 KAW KER	Sample Male 8 4 11 18 2 Sample Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17	Mage 27480.16 19591.82 14925.35 16206.73 13389.09 Mage 4868.52 3302.34 3621.18 2963.34	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55	SD 4492.96 3254.63 5647.61 3303.78 2734.01 aale SD 1145.33 1309.14 2278.76 925.31	Mean 0.18 0.18 0.14 0.15 0.15 M 0.031 0.034 0.028	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.012	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.25 0.041 0.052 0.034	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011
ImaxPopulationJSAR12KAWKERKUSIminPopulationJSAR12KAWKERKUS	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18 2963.34 4649.77	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw alle SD 1833.35 841.73 1035.40 988.54 1881.44	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> <u>Mean</u> 2911.18 3983.75 4500.41 2906.55 3039.43	ale SD 4492.96 3254.63 5647.61 3303.78 2734.01 ale SD 1145.33 1309.14 2278.76 925.31 804.60	M Mean 0.18 0.18 0.18 0.17 0.15 M Mean 0.031 0.032 0.034 0.051	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.012 0.016	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.25 0.041 0.025 0.041 0.052 0.034 0.036	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082
ImaxPopulationJSAR12KAWKERKUSIminPopulationJSAR12KAWKERKUSJ	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18 2963.34 4649.77	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54 1881.44	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> <u>Mean</u> 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴)	SD 4492.96 3254.63 5647.61 3303.78 2734.01 nale SD 1145.33 1309.14 2278.76 925.31 804.60	M Mean 0.18 0.18 0.14 0.15 0.15 Mean 0.031 0.034 0.028 0.051	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD 0.011 0.0061 0.011 0.0012 0.016 Stand:	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 ardised Fe Mean 0.025 0.041 0.052 0.034 0.036 ardised	o.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12 KAW KER KUS JSA R12 KAW KER KUS J Denote intervent	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6 le size (n)	3334.29 Maan 27480.16 19591.82 14925.35 16206.73 13389.09 Maan 4868.52 3302.34 3621.18 2963.34 4649.77	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54 1881.44 Raw	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i>	ale SD 4492.96 3254.63 5647.61 3303.78 2734.01 ale SD 1145.33 1309.14 2278.76 925.31 804.60 ale	M Mean 0.18 0.18 0.18 0.15 0.15 M Mean 0.031 0.032 0.034 0.051	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.0012 0.016 Stands	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.25 0.041 0.025 0.034 0.036 0.056 0.	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12 KAW KER KUS J Population	Sampl Male 8 4 11 18 2 Sampl Male Sampl Male	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6 le size (n) Female	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18 2963.34 4649.77 Main	Raw (ale 50 6566.74 5459.62 4413.07 3191.84 3284.39 Raw (ale 5D 1833.35 841.73 1035.40 988.54 1881.44 Raw (ale 5D	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i> Mean	SD 4492.96 3254.63 5647.61 3303.78 2734.01 nale SD 1145.33 1309.14 2278.76 925.31 804.60 nale SD	M Mean 0.18 0.18 0.18 0.17 0.15 M Mean 0.031 0.032 0.034 0.051 M Mean	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.012 0.016 Stands ale	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.15 0.25 0.041 0.025 0.041 0.052 0.034 0.036 ardised Fe Mean	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082 male SD
Imax Population JSA R12 KAW KER KUS Imin Population JSA R12 KAW KER KUS J Population JSA	Sample Sample 8 4 11 18 2 Sample	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 5 17 6	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18 2963.34 4649.77 Main 32348.68	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw (ale SD 1833.35 841.73 1035.40 988.54 1881.44 Raw (ale SD	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i> Mean 18695.00	SD 4492.96 3254.63 5647.61 3303.78 2734.01 male SD 1145.33 1309.14 2278.76 925.31 804.60 male SD 5638.29	M Mean 0.18 0.18 0.18 0.17 0.15 0.15 0.15 0.15 0.15 0.031 0.034 0.028 0.051 M Mean 0.21 0.21	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD 0.011 0.0061 0.011 0.012 0.016 Stand: ale SD 0.016 Stand: ale SD	0.034 ardised Fe Mean 0.14 0.16 0.18 0.15 0.15 ardised Fe Mean 0.025 0.041 0.052 0.034 0.036 ardised Fe Mean	0.013 male SD 0.0045 0.044 0.065 0.043 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082 male SD
ImaxPopulationJSAR12KAWKERKUSIminPopulationJSAR12KAWKERKUSJPopulationJSAR12KAWKERKUSJPopulationJSAR12KAW	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 17 17 17 17 17 17 17 17 17	3334.29 Maan 27480.16 19591.82 14925.35 16206.73 13389.09 Maan 4868.52 3302.34 3621.18 2963.34 4649.77 Maan 32348.68 22894.16 1854.52	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54 1881.44 Raw ale SD 7947.30 5678.30	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i> Mean 18695.00 19574.66 20550.25	ale SD 4492.96 3254.63 5647.61 3303.78 2734.01 ale SD 1145.33 1309.14 2278.76 925.31 804.60 ale SD 5638.29 4451.19 759.100	M Mean 0.18 0.18 0.18 0.17 0.15 M 0.031 0.032 0.034 0.051 M Mean 0.028 0.051 M 0.21 0.21	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.012 0.016 Stands ale SD 0.016 Stands ale SD 0.056 0.061 0.054	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.052 0.041 0.025 0.041 0.052 0.034 0.036 ardised Fe Mean 0.16 0.12 0.034 0.025 0.041 0.036 ardised Fe Mean 0.16 0.20 0.22	0.013 male SD 0.0045 0.044 0.065 0.043 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082 male SD 0.082 0.058 0.058 0.022
ImaxPopulationJSAR12KAWKERKUSIminPopulationJSAR12KAWKERKUSJPopulationJSAR12KAWKERKUSJPopulationJSAR12KAWKEPKAW	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18	le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6 le size (n) Female 2 11 4 17 6	Main 27480.16 19591.82 14925.35 16206.73 13389.09 Main 4868.52 3302.34 3621.18 2963.34 4649.77 Main 32348.68 22894.16 18546.52 10170.07	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54 1881.44 Raw ale SD 7947.30 5678.30 5364.35 2042.82	(mm ⁴) <i>Fen</i> Mean 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i> Mean 18695.00 19574.66 20559.96 15407.87	ISIT.03 nale SD 4492.96 3254.63 5647.61 3303.78 2734.01 nale SD 1145.33 1309.14 2278.76 925.31 804.60 nale SD 5638.29 4451.19 7584.08	M Mean 0.18 0.18 0.18 0.11 0.15 M 0.031 0.030 0.034 0.028 0.051 M Mean 0.21 0.17 0.18	Stands ale SD 0.048 0.059 0.038 0.043 0.023 Stands ale SD 0.011 0.0061 0.011 0.012 0.016 Stands ale SD 0.016 Stands ale SD 0.056 0.061 0.049	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.052 0.041 0.025 0.041 0.052 0.034 0.036 ardised Fe Mean 0.16 0.19 0.25 0.041 0.036 0.13 0.15 0.025 0.041 0.034 0.036 0.034 0.036 0.034 0.036 0.034 0.036 0.034 0.036 0.034 0.036 0.034 0.036 0.036 0.034 0.036 0.036 0.036 0.036 0.036 0.036 0.034 0.036 0.025 0.034 0.036 0.16 0.025 0.034 0.036 0.025 0.034 0.036 0.16 0.025 0.034 0.036 0.16 0.20 0.16 0.20 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.12 0.23 0.12 0.12 0.23 0.12 0.23 0.12 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.12 0.23 0.23 0.25 0.25 0.25 0.23 0.25 0.55	0.013 male SD 0.0045 0.044 0.065 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082 male SD 0.082 0.058 0.092 0.053 0.092 0.05 0.092 0.05 0.092 0.05 0.05 0.092 0.05 0.05 0.05 0.05 0.05 0.05 0.05 0.0
ImaxPopulationJSAR12KAWKERKUSIminPopulationJSAR12KAWKERKUSJPopulationJSAR12KAWKERKUSJPopulationJSAR12KAWKERKLS	Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2 Sampl Male 8 4 11 18 2	le size (n) Female 2 11 4 17 6 le size (n) 17 17 17 17 17 17 17 17 17 17	3334.29 Maan 27480.16 19591.82 14925.35 16206.73 13389.09 Maan 4868.52 3302.34 3621.18 2963.34 4649.77 Maan 32348.68 22894.16 18546.52 19170.07 18028.86	SD 6566.74 5459.62 4413.07 3191.84 3284.39 Raw ale SD 1833.35 841.73 1035.40 988.54 1881.44 Raw ale SD 7947.30 5678.30 5364.35 3943.82 5165.82	(mm ⁴) <i>Fen</i> 15783.82 15590.91 16059.56 12591.33 12861.34 (mm ⁴) <i>Fen</i> Mean 2911.18 3983.75 4500.41 2906.55 3039.43 (mm ⁴) <i>Fen</i> Mean 18695.00 19574.66 20559.96 15497.87 15000.77	SD 4492.96 3254.63 5647.61 3303.78 2734.01 male SD 1145.33 1309.14 2278.76 925.31 804.60 male SD 5638.29 4451.19 7584.08 4134.25 2287.86	M Mean 0.18 0.18 0.13 0.14 0.15 0.15 M 0.031 0.034 0.028 0.051 M Mean 0.121 0.17 0.18 0.20	Stand: ale SD 0.048 0.059 0.038 0.043 0.023 Stand: ale SD 0.011 0.0061 0.011 0.016 Stand: ale SD 0.016 Stand: ale SD 0.056 0.061 0.049 0.053	0.034 Fe Mean 0.14 0.16 0.18 0.15 0.15 0.15 0.15 0.15 0.15 0.041 0.025 0.041 0.052 0.041 0.052 0.041 0.052 0.034 0.036 ardised Fe Mean 0.16 0.20 0.23 0.18 0.19 0.025 0.041 0.036 0.041 0.036 0.036 0.041 0.036 0.036 0.041 0.036 0.036 0.041 0.036 0.036 0.041 0.036 0.036 0.041 0.036 0.025 0.034 0.036 0.025 0.034 0.036 0.025 0.036 0.020 0.036 0.020 0.020 0.036 0.020 0.036 0.020 0.02	0.013 male SD 0.0045 0.044 0.065 0.043 0.043 0.034 male SD 0.0037 0.015 0.029 0.011 0.0082 male SD 0.082 0.058 0.092 0.052

Table 6.7 continued

Values standardised to ML1. JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); KAW: NDRS P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350). ML1: distance from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB); SD: standard deviation.

6.5.2 Molar region

The descriptive statistics for the pooled-sex raw and standardised molar CSG can be found in **Table 6.5**. Dependent *t*-tests were used to analyse significant differences in cross-sectional properties between the left and right molar cross-sections for each individual (**Appendix C**). The JSA sample had significant differences between left and right molar regions for TA, I_x , I_{max} and J, while the KER sample had significant differences for I_{min} (for full results see the **Appendix C**). As significant differences were observed between left and right molar cross-sectional properties, left and right CSG values were considered separately during all subsequent analyses.

For raw CSG there were significant differences between samples in mean TA, I_x , I_{max} and J for both the left and right molar cross-sections (all p<0.001; **Table 6.6**). Most of these differences were between JSA and later samples, with JSA having a significantly larger mean for left and right molar I_x , I_{max} and J (**Table 6.6**). Although not all differences between samples were significant, there was an overall trend of reduction in TA, I_x , I_{max} and J values over time for both the left and right molar cross-sections (**Table 6.5**). In addition, for the molar sections JSA was significantly larger than KER for I_y (only the left side) and I_{min} (**Table 6.6**).

When the standardised molar cross-sectional properties were compared between samples, there were no significant results for the right molar region (**Table 6.6**; **Figure 6.8**). In contrast, within the left molar region, there were significant differences in I_x (p=0.027), I_{max} (p=0.022) and J (p=0.050) between samples, but there were no significant pairwise relationships (**Table 6.6**; **Figure 6.7**). Despite the lack of statistically significant relationships, there were still reduction trends in molar I_x and I_{max} , particularly in the left molar region, and these trends mirrored the results from the raw CSG data (**Table 6.5**).

Within the left molar cross-section, ratios of I_x and I_{max} to ML2 were significantly different between samples (I_x /ML2: p=0.005; I_{max} /ML2: p=0.017) (**Appendix C**). These ratios have been used by other researchers to approximate the moment arm for parasagittal bending within the molar region (Antón et al., 2011). For both ratios, JSA was significantly larger than KER. For both the left and right molar cross-sections, I_y /BGoB was significantly different between samples (left: p=0.041; right: p=0.015). Although within the left cross-section there were no significant pairwise comparisons, within the right cross-section JSA was significantly smaller than R12. Measures of mandibular width (including BGoB) have been used by other researchers to represent moment arms in lateral transverse bending (Antón et al., 2011). In addition, the ratio of I_y/I_x was significantly different between samples in both the left and right molar cross-section (left: p=0.029; right: p=0.022), but there were no significant pairwise results for either cross-section. There were significant differences in I_{min}/I_{max} between samples for both molar regions (left: p=0.01; right: p=0.001). For the left region, KAW and KUS were significantly larger than JSA and for the right region KAW was significantly larger than JSA and KER (**Figure 6.5b,c**; **Appendix C**).

			Raw	S	tandardised ^a
Cross-section	Measurement	p^{b}	Post-hoc ^c	p^{b}	Post-hoc ^c
	ТА	<0.001	JSA>R12, KAW, KER, KUS; R12 <ker< th=""><th>0.14</th><th>-</th></ker<>	0.14	-
	I_x	<0.001	JSA>R12, KAW, KER, KUS; R12 <kaw, ker<="" td=""><td>0.005</td><td>JSA>R12, KER</td></kaw,>	0.005	JSA>R12, KER
Symphysis	I_y	<0.001	JSA>R12, KAW, KER, KUS	0.061 ^d	-
	Imax	<0.001	JSA>R12, KAW, KER, KUS; R12 <kaw, ker<="" th=""><th>0.002</th><th>JSA>R12, KAW, KER</th></kaw,>	0.002	JSA>R12, KAW, KER
	Imin	0.036	JSA>R12	0.45	-
	J	<0.001	JSA>R12, KAW, KER, KUS; R12 <kaw, ker<="" th=""><th>0.008</th><th>JSA>R12</th></kaw,>	0.008	JSA>R12
	ТА	0.001	JSA>KAW, KER, KUS	0.50	-
	I_x	<0.001	JSA>R12, KAW, KER, KUS	0.10	-
Left M ₁ /M ₂	I_y	0.088	-	0.75	-
	Imax	<0.001	JSA>R12, KAW, KER, KUS	0.074	-
	Imin	0.041	JSA>KER	0.51	-
	J	<0.001	JSA>R12, KAW, KER, KUS	0.17	-
	ТА	0.002	JSA>KER, KAW	0.53	-
	I_x	<0.001	JSA>KAW, KER, KUS	0.26	-
Right M ₁ /M ₂	I_y	0.071	-	0.53	-
	Imax	<0.001	JSA>KAW, KER, KUS	0.27	
	Imin	0.009	JSA>KER	0.09	-
	J	<0.001	JSA>KAW, KER, KUS	0.45	-

Table 6.8 Male ANOVAs and *post-hoc* tests for raw and standardised cross-sectional geometry

^aStandardised to ML1; ^bANOVA level of significance $p \le 0.05$; ^cHochberg's GT2 *post-hoc* test level of significance $p \le 0.05$, arrows indicate direction of significance relationship between the samples; ^dWelch's ANOVA level of significance $p \le 0.05$. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

Following independent *t*-tests to test for sexual dimorphism of cross-sectional properties (see **Appendix C** for complete sexual dimorphism results), both the raw and standardised molar cross-sectional data were analysed by sex. Descriptive statistics for the raw and standardised cross-sectional geometry data by sex are shown in **Table 6.7**. For males, the only raw molar properties that was not significantly different between samples was I_y (left:

p=0.088; right: p=0.071) (**Table 6.8**). For left molar raw I_x , I_{max} and J, males from JSA were significantly larger than males from all of the other samples. For left molar raw TA, males from JSA were significantly larger than those from KAW, KER and KUS; for I_{min} males from JSA were significantly larger than males from KER. For the right molar section, there were fewer significant differences between JSA and later samples (I_x and I_{max} , JSA>KAW, KER and KUS; TA, JSA>KAW, KER; I_{min} , JSA>KER). For both the left and right molar section there were non-significant reduction trends over time for the majority of the CSG properties (**Table 6.7**). When the standardised molar CSG properties were compared, there were no significant differences between males from different samples for either the left or right molar region (**Table 6.8**). However, there were reduction trends that were particularly strong for I_x , I_{max} and J (**Table 6.7**).

			Raw	Standa	ardised ^a
Cross-section	Measurement	p^{b}	Post-hoc ^c	p^{b}	Post-hoc ^c
	ТА	0.81	-	0.23 ^d	-
	I_x	0.014	JSA>KAW, KUS	0.23	-
Symphysis	I_y	0.15	-	0.69	-
	Imax	0.009	JSA>KAW, KUS	0.18	-
	Imin	0.53	-	0.68	-
	J	0.016	JSA>KAW, KUS	0.083 ^d	-
	ТА	0.032	R12>KER	0.28	-
	I_x	0.012	JSA>KER	0.39	-
Left M ₁ /M ₂	I_y	0.11	-	0.15	-
	Imax	0.015	JSA>KER	0.36	-
	Imin	0.064	-	0.16	-
	J	0.017	R12>KER	0.35	-
	ТА	0.081	-	0.32	-
	I_x	0.089	-	0.69	-
Right M ₁ /M ₂	I_y	0.29	-	0.36	-
	Imax	0.12	-	0.72	-
	Imin	0.077	-	0.81	-
	J	0.097	-	0.52	-

Table 6.9 Female ANOVAs and post-hoc tests for raw and standardised cross-sectional geometry

^aStandardised to ML1; ^bANOVA level of significance $p \le 0.05$; ^cHochberg's GT2 *post-hoc* test level of significance $p \le 0.05$, arrows indicate direction of significance relationship between the samples; ^dWelch's ANOVA level of significance $p \le 0.05$. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

For females, there were only significant differences in raw molar CSG properties for the left side of the mandible: TA (p=0.032), I_x (p=0.012), I_{max} (p=0.015) and J (p=0.017) (**Table**

6.9). For TA and *J*, females from R12 had significantly higher values than females from KER. For I_x and I_{max} , females from JSA has significantly higher values than females from KER. Trends for raw molar CSG properties within females were not as pronounced as those in males, but in general, the oldest three samples (JSA, R12 and KAW) had higher values than the more recent samples (KER and KUS). Similar to the findings for the males, there were no significant differences in standardised CSG molar properties between females from different samples. Within females, the clearest reduction trends were in standardised I_x and I_{max} over time, with a reduction between the oldest three samples (JSA, R12, KAW) and the more recent KER and KUS samples (**Table 6.7**).

6.6 Discussion

In this study, the long-term effect of dietary transitions on mandibular strength and robusticity in ancient Nubian populations was assessed using cross-sectional geometry (CSG). The populations selected span a period including the initial adoption of pastoralism through agricultural intensification and increasing social complexity. Previous studies have found that populations with contrasting dietary regimes exhibit differences in mandibular morphology and robusticity (Antón et al., 2011; Carlson and Van Gerven, 1977; Holmes and Ruff, 2011; Spencer and Demes, 1993). The results of this study support the hypothesis that changes in dietary composition spanning subsistence transitions in ancient Nubia significantly affected mandibular strength in the symphyseal and molar regions, as indicated by CSG properties. Overall measures of mandibular robusticity decreased through time from the hunter-gatherers to the more recent agricultural samples, particularly regarding vertical/parasagittal bending of the mandibular molar region (I_x and I_{max}). However, not all biomechanical properties were significantly different between samples, suggesting that the human mandible reacts in specific ways to the reduction of biomechanical stress associated with a softer diet. Although the results from males and females largely mirrored the results from the combined analyses, males demonstrated a clearer trend of biomechanical reduction than their female counterparts, particularly within the molar region.

Although many researchers have argued for the importance of vertical bending resistance on adult symphyseal form (i.e. Daegling, 1993a; Dobson and Trinkaus, 2002; Gröning et al., 2011), others have failed to find a relationship between symphyseal I_x and I_{max} values and estimated measures of vertical bending stress within the mandible (Holton et al., 2014). In this study, the significantly higher values for raw and standardised symphyseal I_x

 I_{max} and J in the hunter-gatherer Jebel Sahaba (JSA) sample suggest that when compared with later samples, JSA had greater symphyseal rigidity to vertical bending in the coronal plane (Daegling, 1989). This trend was observed for the combined data, as well as separately for males and females. The main decrease in symphyseal biomechanical strength was observed between the JSA and Sudanese Neolithic R12 sample, a reduction that was particularly prominent in males. However, symphyseal I_x , I_{max} and J did not change significantly between the Upper Nubian samples, which suggests that these CSG properties were not affected by smaller dietary changes.

Previous studies have shown that symphyseal I_y and I_{min} are positively correlated with the estimated magnitude of lateral bending stress in the transverse plane (or 'wishboning') (Fukase, 2007; Fukase and Suwa, 2008; Holton et al., 2014; Schwartz-Dabney and Dechow, 2003). In this study, although the raw absolute values for symphyseal TA, I_y and I_{min} were highest in the JSA sample, there were no significant differences between samples in the standardised values. The results from this study suggest either that wishboning of the mandible did not differ significantly between samples, and/or that wishboning stress did not influence symphyseal shape within these samples. Although wishboning has been shown to be a significant cause of biomechanical stress in the nonhuman primate mandible (Daegling, 2001; Hylander and Johnson, 1994; Ravosa, 2000), changes in modern human facial morphology, such as shorter mandibular length and parabolic dental arches, have been shown to adequately reduce wishboning stress within the symphysis without the need for changes in symphyseal shape (Daegling, 1993a; Holton et al., 2015; Hylander and Johnson, 1994).

In fact, there was a slight, non-statistically significant increase in I_y and I_{min} values over time in the Holocene samples; a trend that was observed in males, but not females. The I_y and I_{min} CSG properties are influenced by the anterior-posterior width of the symphysis and, therefore, these values may be influenced by changes in chin morphology. Chin morphology has long been used by researchers as part of a set of cranial characteristics used for sex classification in skeletal samples (Buikstra and Ubelaker, 1994). It may be that an increase in the prominence of the male chin over time, possibly related to improvements in diet and nutrition in later agricultural populations (Galdames et al., 2008; Oettlé et al., 2009), in part explains the slight increase in male symphyseal I_y and I_{min} values over time.

The relative stability of standardised symphyseal CSG properties throughout the Holocene samples (in comparison with the reduction observed in the molar region), may indicate that although the morphology of the mandibular symphysis affects the mechanical environment of the anterior corpus and impacts on bite force magnitude, the symphysis may not be directly shaped by biomechanical loading (Chan et al., 2008; Holton et al., 2014; Ingervall and Bitsanis, 1987; Pepicelli et al., 2005; Throckmorton et al., 1980). A previous study found that measures of vertical bending resistance were correlated with patterns of lower facial dimensions. A dolichofacial (i.e. long-faced) pattern was associated with an increase in vertical bending resistance, whereas a brachyfacial (i.e. short-faced) pattern was associated with a reduction in vertical bending resistance (Holton et al., 2014). Additional research has also supported the hypothesis that differences in symphyseal shape may be more reflective of variation in lower facial morphology between individuals than biomechanical loading during mastication (Bastir and Rosas, 2004; Bishara and Jakobsen, 1985; Fukase and Suwa, 2008; Mangla et al., 2011). In addition, variation in chin size, mandibular curvature and symphyseal inclination can all influence the biomechanical properties of the symphysis (Daegling, 2001; Fukase and Suwa, 2008; Hylander, 1984, 1988). The molar region of the mandibular corpus is more vertically shaped and, therefore, more accurately modelled by standard beam theory (Holmes and Ruff, 2011).

Within the molar region, there was an overall decrease in raw and standardised I_x , I_{max} and J (particularly on the left side), which continued throughout the Holocene samples. The CSG properties I_x and I_{max} in the molar region are reflective of parasagittal bending rigidity (Weijs, 1989). Therefore, this result suggests that agricultural intensification in these Upper Nubian samples was accompanied by a decrease in overall robusticity and resistance to sagittal bending in the molar region. In contrast, standardised I_y and I_{min} , indicators of resistance to lateral transverse bending within the molar region, did not change significantly between samples. In fact, although the JSA sample had the largest raw values of I_y and I_{min} , when standardised, JSA had relatively smaller values for I_y and I_{min} compared with the other samples.

The bending indices I_y/I_x and I_{min}/I_{max} reflect mandibular corpus shape and resistance to torsional strain (Daegling, 1989; Daegling and Grine, 1991; Hylander, 1988; van Eijden, 2000). In this study, these indices were found to increase over time in the molar region, and JSA had the lowest value of all the samples. An increasing index approaching the value of 1 reflects a cross-section becoming more circular over time. Some researchers have found that hard-diet groups have a rounder, more buccolingually buttressed posterior mandibular corpus, which may be an adaptation to resist torsional stress (Holmes and Ruff, 2011; Toro-Ibacache et al., 2019). However, in this study, the CSG properties used to calculate the bending indices were not changing at the same rate. Transverse bending (represented by I_y and I_{min}) has been shown
to cause very low stress in the molar region (Daegling and Grine, 1991), and within this study the values of I_y and I_{min} did not change significantly over time within these samples. In contrast, I_x and I_{max} (representative of sagittal bending stress) declined significantly across the samples. Therefore, in this study it is unlikely that the changes in I_y/I_x and I_{min}/I_{max} were driven by an increase in resistance to torsional and transverse bending strain. Instead, the overall increase in both bending indices is more likely reflective of a significant decrease in sagittal bending stress as represented by I_x and I_{max} .

Within the molar region, raw values of I_x and I_{max} declined for both males and females, although the trend was stronger for males. However, there was no reduction in standardised molar I_x or I_{max} during the initial transition to agriculture from JSA to R12 for males or females. The earliest grinding stones in Sudan date from c. 9500 BP, predating the current evidence of domesticated cereals from around c. 7000 BP in the R12 population (Out et al., 2016). Therefore, grinding stones were likely used to process wild grasses for an extended period before domesticated cereals were present in the Nile Valley (Brass, 2009; Brass and Schwenniger, 2013; Wendorf and Said, 1967). Processing of wild grasses or agricultural cereals, by milling and/or grinding, breaks down the outer shell of the plant, reducing toughness before consumption (Wrangham and Conklin-Brittain, 2003). The introduction of food processing technology, such as grinding stones, may have been one of the first significant innovations to reduce biomechanical stress in early hunter-gatherer populations. Despite the presence of domesticated cereals in the R12 population (Out et al., 2016), the archaeological and isotopic evidence indicates that animal protein was a large component of the R12 diet (Iacumin et al., 1998; Salvatori and Usai, 2019). A tough, meat-based diet may explain why there was no substantial decrease in standardised molar I_x and I_{max} from the JSA to the R12 sample.

With agricultural intensification in the Kerma period and into the Meroitic, the proportion of soft, cereal products in the diet was increasing over time (Iacumin et al., 1998). Changes in the proportion and types of domesticated cereals starting in the Kerma period may be behind the patterns of change in mandibular robusticity that were observed in this study in the KAW, KER and KUS samples. Within these samples, the standardised values declined overall for both males and females, but both sexes had the same value for standardised molar I_x and I_{max} in the KER sample. Furthermore, in the most recent sample (KUS), although females had lower values for raw molar I_x and I_{max} , the standardised molar CSG values were higher in females than males.

If the assumption is that males and females have comparable osseous responses to similar loading environments, then in this study, the sex-specific trends of mandibular CSG properties over time indicate variation in masticatory loading, such as paramasticatory behaviour or dietary consumption. The results from this study showed that, in general, the main reduction in symphyseal CSG properties for males occurred between the JSA and R12 samples, whereas for females the main reduction in symphyseal CSG properties occurred within the later agricultural samples. For this study, differences in paramasticatory behaviours between sexes may have influenced the nature and timing of changes in CSG properties between males and females. For the R12 population, the presence of lingual surface attrition of the maxillary anterior teeth (LSAMAT) has been identified in two adult males, and possibly reflects paramasticatory behaviour (Crivellaro, 2001; Judd, 2012). In addition, the adoption of agriculture in many populations was accompanied by increasing social complexity and sexual division of labour, which may have resulted in significant differences in dietary consumption between the sexes (Hill and Hurtado, 1989; Temple and Larsen, 2007; Thompson et al., 2008; Walker and Hewlett, 1990). Therefore, differences in diet between males and females due to cultural factors may explain the observed patterns of morphological change in the current study.

However, the relationship between the sex of an individual and how bone responds to mechanical loading is poorly understood. Many archaeological studies using biomechanical methods to assess postcranial strength and robusticity over time have found that trends among women are often less pronounced, or follow different patterns, to those of their male counterparts (Macintosh et al., 2014, 2015; Ruff, 1987; Sparacello et al., 2011; Stock et al., 2011). Differences in sex and growth hormone levels (particularly during puberty) mean that in general, females build bone and muscle at a slower rate than males and, as a result, have less bone and muscle mass (Callewaert et al., 2010; Gosman et al., 2011). In addition, pregnancy and reproductive life history may affect the magnitude of bone remodelling in the women included in these Nubian samples, even if both sexes had similar dietary consumption (Cohen and Armelagos, 1984; Järvinen et al., 2003a,b; Lukacs, 2008). Therefore, differences between males and females in mandibular bending strength and robusticity do not necessarily indicate that there were actual differences in dietary consumption.

The central assumption of this and other comparative studies is that based on the principles of bone remodelling, there is a predictable relationship between levels of biomechanical stress and mandibular morphology (Daegling and McGraw, 2007). However,

the relationship between dietary properties and mandibular morphology is not always straightforward or predictable (e.g. Daegling, 2007; Daegling and McGraw, 2001, 2007; Ross et al., 2012). In addition to the magnitude of masticatory loading, there are other variables that may have a significant influence on the relationship between mandibular strength and robusticity. For example, jaw loading patterns (e.g. the magnitude, frequency, number of cycles and seasonal variation in diet/loading patterns), can vary between populations who have similar diets. Therefore, mandibular morphology may not just be reflective of absolute biomechanical stress magnitude, but also of variation in patterns of masticatory loading (Biewener et al., 1986; Hsieh et al., 2001; Kopher and Mao, 2003; Rubin and Lanyon, 1984).

In addition, the relative influence of genetics and population history on mandibular robusticity compared to masticatory loading is unknown (Antón et al., 2011; Fukase and Suwa, 2008; Kaifu, 1997). Fukase and Suwa (2008) found evidence that some population-level differences in mandibular robusticity were present in early ontogeny, thereby challenging the accepted relationship between masticatory force and mandibular morphology. However, Fukase and Suwa (2008) did not calculate cross-sectional geometry, and they only analysed symphyseal morphology. In contrast, Holmes and Ruff (2011) found that there was progressive development of greater rigidity and strength in the mandibles of populations with a harder diet, thus supporting the functional adaptation of the mandible to biomechanical loadings during development. It will be important for future bioarchaeological studies to include, when possible, juveniles in the analysis, to track mandibular shape changes over time within a population.

6.7 Conclusions

The effect of masticatory loading on jaw shape has often guided interpretations of morphological variation in recent humans. In particular, patterns of mandibular variation are thought to reflect differences in skeletal loading associated with shifts in food preparation and subsistence strategies. This study has identified diachronic variation in mandibular robusticity between hunter-gatherer, agro-pastoralists and agricultural samples in ancient Nubia. In particular, the development of intensive agriculture in ancient Nubia led to a decrease in overall mandibular rigidity, especially in symphyseal and molar I_x and I_{max} . The observed trend was stronger in males than females. While differential biomechanical loading induced by diet has been shown to influence mandibular robusticity, caution is needed when drawing conclusions

from this study due to the modest sample sizes available. Future research should focus on further clarifying of the relationship between mandibular robusticity, subsistence strategy and dietary composition in additional populations from ancient Nubia.

7 Oral Health

7.1 Introduction

Oral health is strongly influenced by dietary intake, food processing and patterns of subsistence strategy. As such, researchers study the frequency and severity of dental pathologies to contribute towards a better understanding of diet, food-preparation techniques and overall health in past human populations, particularly when considering the biological effect of the transition to agriculture (De Groote et al., 2018; Eshed et al., 2006; Hillson, 1996, 2001; Humphrey et al., 2014; Larsen, 2015; Larsen et al., 1991; Lukacs, 1989, 2008; Powell, 1985; Starling and Stock, 2007; Turner II, 1979; Walker et al., 1986). Around the world, the agricultural transition drastically changed the human diet to one largely based on carbohydrates (Larsen, 2015; Lukacs, 1989, 1992; Saunders et al., 1997; Turner II, 1989). Many studies have shown that agricultural populations had poorer oral health than their predecessors, as inferred by an increasing number of carious lesions, abscesses and ante-mortem tooth loss (AMTL) (Hillson, 2001; Lukacs, 1992; Powell, 1985; Turner II, 1979). However, other studies have not found an association between agriculture and poor oral health, indicating that this relationship is influenced by the types of cultivated crops and food processing practices present within a given population (e.g. Eshed et al., 2006; Tayles et al., 2000).

This section of the research investigated the relationship between oral health and changing diet and subsistence strategies in Upper Nubia from the Sudanese Neolithic through to the Meroitic period (c. 5000 cal BC–AD 350). The first objective was to explore patterns of dental wear and oral pathology (including caries, calculus, periodontal disease, AMTL and linear enamel hypoplasia [LEH]) with increasing reliance on agricultural food products. The second objective was to investigate differences in oral health between males and females both within and between samples over time. By focusing on several indicators of oral health throughout agricultural intensification in ancient Nubia, the study aimed to investigate how diachronic changes in oral health relate to diet and subsistence strategy. As the majority of dental pathologies are age-related, there will also be discussion of how the age distribution of the samples may have contributed to the observed variation in dental disease.

7.2 Studying oral health in archaeological populations

Teeth are abundant in the archaeological record and are frequently utilised by bioarchaeologists to answer research questions related to the diet and overall health of past individuals and populations. Studies in modern populations show that the frequency of dental pathologies are positively correlated with socioeconomic status and the overall health of an individual (Dye and Thornton-Evans, 2010; Gift and Atchison, 1995; Hujoel, 2009; Jamieson et al., 2011; Mashoto et al., 2010; Samuelson et al., 1971). However, there are inherent limitations and biases in any study of health based on skeletal material (Milner et al., 2008; Reitsema and McIlvaine, 2014; Temple and Goodman, 2014). Researchers often rely on the presence and frequency of diagnostic skeletal lesions in an individual to reflect health, but this methodology may not be consistent with how 'health' is assessed in living populations (Goodman and Martin, 2002; Temple and Goodman, 2014; Wilson, 2014; Yaussy and DeWitte, 2019). First defined by Wood and colleagues (1992), the 'osteological paradox' suggests that because many diseases take time to visually manifest in the skeleton, the presence or absence of lesions does not necessarily imply the good or bad health of an individual. For example, a higher frequency of skeletal lesions within an individual may, in fact, indicate better health as compared with an individual without any lesions who may have died before a pathological condition left any physical evidence on the skeleton (Siek, 2013; Wood et al., 1992). To limit the influence of the osteological paradox, this study used oral health as one indicator of dietary intake, rather than a reflection of the overall health of an individual. The following sections provide background information on the indicators of oral health that were analysed in this study: dental wear, caries, calculus, LEH, periodontal disease and AMTL.

7.3 Dental pathology background

7.3.1 Dental wear

Dental 'wear' is a generalised term that refers to the age-progressive loss of dental enamel. The pattern and severity of dental wear in a population can provide information about dietary toughness and abrasiveness, as well as levels of paramasticatory activities. Most of the dental wear observed in archaeological human populations is the result of attrition and/or abrasion (Powell, 1985; Burnett, 2016). 'Attritional' wear results from direct tooth-on-tooth contact during routine mastication or paramasticatory behaviour. Attrition primarily affects the

occlusal and interproximal surfaces of the teeth and can, over time, result in the overall reduction of tooth size. Severe attrition can also initiate other dental processes, such as continuous eruption, mesial drift and/or changes to the angle of the anterior dentition to maintain contact between highly worn teeth (D'Incau et al., 2012; Kaifu et al., 2003).

Dental 'abrasion' results from contact between teeth and foreign substances introduced into the oral cavity (Powell, 1985; Burnett, 2016). Abrasive materials may be introduced with food or during paramasticatory practices (Irish and Turner II, 1987, 1997; Milner and Larsen, 1991; Ortner, 2003; Pindborg, 1970; Powell, 1985; Turner II and Machado, 1983). For example, many plants contain materials such as siliceous phytoliths that can be abrasive when consumed (Baker et al., 1959; Lucas et al., 2013; Rabenold and Pearson, 2014; Sanson et al., 2007). Abrasive contaminants can also be introduced from the local environment (e.g. windblown sand) (Burnett, 2016) or food processing techniques (e.g. particles from grinding stones). Dental abrasion was common in past human populations but has gradually decreased over time as modern diets have become increasingly soft and free of exogenous abrasive particles (Burnett, 2016; Ganss et al., 2002; Hinton, 1982).

Dietary composition also affects the observed pattern of dental wear. Diets high in fibre, characteristic of hunter-gatherer populations, tend to cause flat wear across the occlusal surface; softer diets, such as those consumed by agriculturalists, often cause a concave wear pattern on the dental occlusal surface (Larsen, 1995; Smith, 1984). However, severe attrition resulting from specific, repetitive chewing and paramasticatory activities can result in wear patterns that significantly deviate from the above generalised patterns (Kieser et al. 2001; Kaifu et al. 2003).

The study of tooth wear in archaeological human populations can provide insight into a population's diet, subsistence practices and food preparation techniques (Deter, 2009; Eshed et al., 2006; Hillson, 1996, 2001; Hinton, 1981; Kaifu, 1999; Larsen, 2015; Lukacs, 2008; Molnar, 1971a; Powell, 1985; Smith, 1984). It is often difficult to differentially diagnose dental wear that is caused by attrition or abrasion without the analysis of microwear using advanced microscopy (Kaidonis, 2008). As such, bioarchaeologists often broadly classify dental wear as a mechanical process that results from dietary composition and other masticatory behaviours (Larsen, 1998). Dental wear has been used to study the subsistence patterns of archaeological populations from the Americas (Molnar, 1971; Watson, 2008; Deter, 2009), Australia and the Pacific (Brown and Molnar, 1990; Turner and Cacciatore, 1998; Kieser et al., 2001a,b), Asia (Turner II, 1979; Lukacs and Pastor, 1988; Tayles et al., 2000), the Near East (Dahlberg, 1960; Carbonell, 1966; Smith, 1972; Smith et al., 1984; Eshed et al., 2006; Caglar et al., 2007), Europe (Bonfiglioli et al., 2003; Esclassan et al., 2009; Lavelle, 1970; Lubell et al., 1994) and Africa (Greene et al., 1967; Armelagos and Rose, 1972; Jurmain, 1990; Forshaw, 2009; Gamza and Irish, 2010). The majority of this research has identified a decrease in dental wear severity over time attributed to improvements in food processing, the increased availability of softer agricultural foods and the reduced paramasticatory use of the dentition (Brace, 1962; Deter, 2009; Molleson et al., 1993; Molnar, 1971a; Pindborg, 1970; Powell, 1985; Smith, 1984).

However, there is substantial variation in the severity of dental wear observed both within and between populations from different regions (Clement and Hillson, 2012; Littleton et al., 2013). High rates of wear have been documented in agricultural populations living in areas where abrasive contaminants are easily introduced into the diet (e.g. deserts), or in populations heavily reliant on tools such as stone grinders for food preparation (Beckett and Lovell, 1994; Carbonell, 1966; Dahlberg, 1960; Greene et al., 1967; Larsen, 1995; Molnar, 1971a; Scott and Turner II, 1988; Smith, 1972; Wells, 1975). It is, therefore, important to consider dental wear patterns within the cultural and local environmental context of a given population.

7.3.2 Dental caries

The analysis of dental caries in archaeological human populations is frequently used by researchers to infer and compare the dietary behaviours of past human populations (e.g. De Groote et al., 2018; Humphrey et al., 2014; Larsen, 1995, 2006). Dental caries, also called tooth decay or cavities, result from the progressive demineralisation of enamel and dentin by acids produced during the fermentation of dietary carbohydrates (Hillson, 2008; Larsen, 2015; Powell, 1985). Caries are most likely to occur where dental plaque accumulates, primarily in the interproximal surfaces and occlusal fissures of tooth crowns (Mays, 1998). Carious lesions are often a precursor to other serious dental pathologies such as AMTL, periapical lesions and localised or systemic infections (Ortner, 2003).

The transition from a hunter-gatherer subsistence strategy to one based on agriculture was typically associated with a shift to the regular consumption of fermentable carbohydrates (particularly sucrose), which increased the level of cariogenic bacteria present in the dental plaque (Gibbons, 2012; Hillson, 2008; Larsen, 1995, 2006; Menaker, 1980; Ortner, 2003; Temple, 2016; White, 1975). Compared with sucrose, starch has lower overall cariogenicity

due to slow oral digestion (Frostell et al., 1967). However, the cariogenicity of sucrose increases when cooked at a high temperature. The introduction of pottery and its use in cooking starch-based foods may have been a significant trigger for the increase in caries frequency often observed before the widespread consumption of cultivated grains and carbohydrates (Wrangham, 2009). Although carbohydrate consumption is viewed as the primary cause of dental caries, the disease process is multifactorial and can be affected by age, sex, hormone levels, salivary flow rate and the composition of oral bacteria (Larsen et al., 1991; Lukacs, 2008; Lukacs and Largaespada, 2006; Maat and Van der Velde, 1987; Temple and Larsen, 2007).

The relationship between subsistence strategy and the prevalence of dental caries has been extensively documented throughout the world (e.g. Armelagos and Rose, 1972; Armelagos et al., 1984; Beckett and Lovell, 1994; De Groote et al., 2018; Douglas, 2006; Eshed et al., 2006; Humphrey et al., 2014; Lanfranco and Eggers, 2010; Larsen et al., 1991; Lukacs, 1992; Meiklejohn et al., 1984; Munoz, 2017; Nicklisch et al., 2016; Rose et al., 1993; Tayles et al., 2000; Temple and Larsen, 2007, 2013; Turner II, 1979; Willis and Oxenham, 2013). However, not all agricultural transitions were associated with an increase in the frequency and severity of dental caries, particularly in Asia where agricultural diets were more commonly rice-based (Douglas, 2006; Oxenham et al., 2006; Pietrusewsky and Douglas, 2002; Pietrusewsky and Tsang, 2003; Tayles et al., 2000, 2009; Willis and Oxenham, 2013). In addition, abrasive carbohydrate-based diets (e.g. those including grit from stone-ground flour or windblown sand) tend to be less cariogenic than diets with more refined foods because severe dental wear can reduce the size of occlusal fissures (Armelagos and Rose, 1972; Carbonell, 1966; Chazel et al., 2005; Dahlberg, 1960; Eshed et al., 2006; Greene, 1972; Jurmain, 1990; Walker et al., 1986). In addition, trace minerals present in the soil and groundwater, particularly cariostatic calcium phosphate and fluoride, can reduce the cariogenicity of the foods cultivated in that area (Hillson, 1979; Sutfin et al., 1970; Schamschula et al., 1978). Furthermore, the importance of carbohydrate-rich wild plant foods and the presence of pottery-faciliated food processing in some pre-agricultural populations may be underestimated, thereby affecting the trends and inferences based on observed dental caries prevalence in these populations (Humphrey et al., 2014; Turner II and Machado, 1983). It is clear that many factors, including diet, can influence caries prevalence in human populations.

7.3.3 Dental calculus

Dental calculus is the mineralised form of dental plaque, a natural biofilm found on the surface of teeth that consists of food remains and bacteria (Hillson, 1996; Lieverse, 1999). Dental plaque often forms around the gum-line in areas adjacent to the mineral-secreting salivary glands, such as the lingual surfaces of the anterior teeth or the buccal surfaces of the posterior teeth (Brothwell, 1981; Lukacs, 1989; Hillson, 1996; Waldron, 2009). Dental calculus is composed of minerals derived from saliva or gingival crevicular fluid, primarily calcium phosphates and organic/inorganic particles introduced by bacteria, saliva, or diet (Warinner et al., 2014; White, 1991). The rate and degree of calculus formation can be influenced by oral hygienic practices (Jepsen et al., 2011), salivary flow and alkalinity, hydration levels and diet (Hillson, 1996; Lieverse, 1999; Lieverse et al., 2007; Littleton and Frohlich, 1989; Lukacs, 1992). The severity of dental plaque has been correlated with other oral pathologies such as caries and periodontal disease (Peterson et al., 2013; Wang et al., 2013) and overall poor health (e.g. Adolph et al., 2017; DeStefano et al., 1993; Sumi et al., 2007).

Dental calculus has been common throughout human history and, due to its durability, preserves well in the archaeological record (Adler et al., 2013). The influence of dietary consumption and subsistence strategy on calculus presence and severity in human populations has been investigated in archaeological populations around the world (e.g. Bonfiglioli et al., 2003; Delgado-Darias et al., 2006; Eshed et al., 2006; Harris et al., 1998; Irei et al., 2008; Lillie and Richards, 2000; Listi, 2011; Littleton and Frohlich, 1989, 1993; Lukacs, 1989, 2017; Mickleburgh and Pagán-Jiménez, 2012; Okumura and Eggers, 2005; Pietrusewsky et al., 1997; Slaus et al., 2011; Valentin et al., 2006). Although high levels of calculus are generally linked with agricultural diets, research has shown that elevated levels can occur in populations with both high carbohydrate and high protein diets (Hillson 1979; Turner 1979; Lukacs 1989; Larsen 1995). It is also important to note that the severity of dental calculus in archaeological skeletal remains may not accurately reflect the true levels of dental calculus present in the individual. Calculus deposits can be easily removed from the dentition through taphonomic processes or during curation and the 'cleaning' of the skeletal remains. Therefore, the true levels of dental calculus in a population may be higher than those recorded through analyses of calculus in a skeletal sample.

7.3.4 Linear enamel hypoplasia (LEH)

LEH is caused by the disruption of normal enamel formation during development, and manifests on the surface of adult dentition as visible bands of reduced enamel thickness (Hillson, 1996; Larsen, 2015; Waldron, 2009). As a non-specific indicator of 'stress', LEH is often viewed as the result of metabolic or environmental stressors such as malnutrition, infection or parasites (Ortner, 2003). However, LEH bands can also result from a variety of rare genetic conditions or due to localised trauma; although it is important to note that the presence of LEH due to these causes tend to be easily differentiated from those caused by systemic stress (Suckling, 1989; Hillson and Bond, 1997; Hillson, 2005, 2014). The terms 'stress' and 'health' are often misrepresented in a bioarchaeological context and, due to the complexity of tooth formation processes, it can be difficult to correctly identify the cause of a visible hypoplasia in an adult (Hillson, 2014; Hillson and Rose, 2012; Temple and Goodman, 2014). Accordingly, the prevalence of LEH should only be used as a very general indicator of 'life-history' for a sample or individual, and must be cautiously interpreted (Hillson, 2014).

Researchers have incorporated analyses of LEH into studies of archaeological populations to gauge overall nutritional stress experienced due to changes in subsistence strategy and dietary composition (Cook and Buikstra, 1979; Goodman and Armelagos, 1985; Goodman and Rose, 1990; Hutchinson and Larsen, 1988; McHenry and Schulz, 1976; Munoz, 2017; Sciulli, 1977, 1978; Starling and Stock, 2007; Van Gerven et al., 1990). There has been specific interest in the frequency of LEH observed in Holocene populations following the transition to an agricultural-based subsistence strategy (Cohen and Armelagos, 1984; Goodman and Rose, 1990; Hershkovitz and Gopher, 2008; Klaus and Tam, 2010; Larsen, 1995; Starling and Stock, 2007; Wittwer-Backofen and Tomo, 2008). Many studies have found an increase in the prevalence of LEH after the shift to an agriculture-based subsistence, with the general consensus that an over-reliance on domesticated plants, coupled with challenges associated with a sedentary lifestyle (growing population density, poor sanitation and increased exposure to zoonotic diseases), may have led to a decline in nutrition quality, an increase in infection rates and a subsequent rise in physiological stress indicators. A study of Egyptian and Nubian populations during the agricultural intensification in the Nile Valley supports the claim that early agriculture was associated with high stress and poor health (as reflected by LEH frequency), but that the health of agriculturalists improved substantially in later populations alongside increasing dietary heterogeneity, urbanisation and trade (Starling and Stock, 2007).

7.3.5 Periodontal disease and ante-mortem tooth loss (AMTL)

Periodontal disease is caused by an immune response to the bacteria in the dental plaque on the surface of the dentition. The disease manifests as either an acute or chronic infection of the periodontium (the supporting structure for teeth within the jaws, composed of the bony alveolus, gingiva, cementum and periodontal ligament) (Hildebolt and Molnar, 1991; Holt and Ebersole, 2005; Nelson, 2016). Acute periodontal infections tend to heal without leaving permanent signs on the bony jaw. In chronic infections, the inflammation can lead to bone resorption if the periodontal ligament pulls away from the underlying alveolar structure (Hillson, 2001; Nelson, 2016). If left untreated, chronic periodontal disease will continue to weaken the periodontal ligament and expose the roots until the tooth is eventually lost (Cochran, 2008; Di Benedetto et al., 2013; Hildebolt and Molnar, 1991; Sima et al., 2014). Infection of the alveolar tissue near the tooth root can also result in the formation of an abscess (accumulation of pus). Osteoclastic activity will form a fistula (cavity) inside the bone that may open to the surface to release pressure through the oral cavity. When there is a clear opening to the fistula in the alveolar bone of the jaw, it is possible to identify this as a periapical abscess (Hillson, 2001; Nelson, 2016). In addition to acting as an indicator of overall oral health, severe periodontal disease has also been correlated with several serious diseases such as cardiovascular disease, diabetes and some cancers (DeWitte, 2012; Kuo et al., 2008).

AMTL can be caused by a variety of factors including severe dental caries, periodontal disease, periapical lesions (Larsen, 1995), inadequate oral hygiene, excessive mechanical stress on the teeth and jaws (Larsen, 2015) and/or trauma (Hillson, 2001). The prevalence of periodontal disease and AMTL in archaeological populations has been studied throughout the world (Beckett and Lovell, 1994; Bernal et al., 2007; Buzon and Bombak, 2010; De Groote et al., 2018; Domett and O'Reilly, 2009; Douglas, 2006; Eshed et al., 2006; Forshaw, 2009; Karsten et al., 2019; Keenleyside, 2008; Listi, 2011; Lukacs, 1989, 1992, 2007; Oxenham and Tayles, 2006; Pietrusewsky, 1989; Smith et al., 1984; Turner, 2015). In general, prehistoric agriculturalists exhibit higher rates of periodontal disease and AMTL than hunter-gatherer populations.

AMTL is predominantly observed in the molar row, as the molar dentition are more susceptible to periodontal disease, dental caries and wear. AMTL can also be caused by the continuous eruption of heavily worn teeth (Buzon and Bombak, 2010; Clarke and Hirsch, 1991; Hillson, 1996) or, in some cases, deliberate tooth extraction. Teeth may be extracted to reduce pain and discomfort from an infection but in some populations, teeth (most often the incisors) were deliberately removed for cultural reasons (referred to as evulsion or ablation) (De Groote et al., 2018). Many of the factors that can cause AMTL are age-progressive, with older individuals generally exhibiting a higher incidence of AMTL than younger individuals from the same population (Ogden, 2008). Once alveolar remodelling has progressed to the point where there is no longer evidence of the tooth socket, it can be difficult to determine the exact cause of tooth loss in an individual in an archaeological context.

7.4 Sex differences in oral health

Numerous researchers have observed that women's oral health was more negatively affected by the transition to agriculture than men's (particularly with regards to caries and AMTL prevalence) (Cohen and Crane-Kramer, 2007; Fields et al., 2009; Larsen et al., 1991; Lukacs, 1996, 2017; Lukacs and Largaespada, 2006; Masotti et al., 2013; Michael et al., 2017; Walter et al., 2016; Watson et al., 2010; Willis and Oxenham, 2013). Sex differences in oral health are often interpreted using two, not mutually exclusive, models: dietary-behavioural hypotheses and sex-based physiological hypotheses (Fields et al., 2009; Klaus and Tam, 2010; Larsen et al., 1991; Lukacs, 1996, 2008, 2017; Lukacs and Largaespada, 2006; Temple and Larsen, 2007; Watson et al., 2010). The dietary-behavioural models interpret differences in oral health between males and females as the result of differences in dietary consumption associated with social hierarchy and sexual division of labour (Lukacs and Largaespada, 2006). The higher proportion of cariogenic foods in the diets of agricultural women as compared with the higher protein diets of men (e.g. Kelley et al., 1991; Klaus and Tam, 2010; Larsen, 2015; Larsen et al., 1991; Lukacs, 1996; Lukacs and Pal, 1993; Novak, 2015; Tayles et al., 2000; Temple and Larsen, 2007; Walker and Hewlett, 1990) may be driving the observed sex differences in oral health (particularly with regards to caries prevalence).

The sex-based physiological hypotheses focus on the influence of biology and fertility on oral health. Some researchers have noted that females' permanent dentition erupts earlier than males', thereby increasing the likelihood of developing more severe carious lesions by exposing the dentition to a cariogenic environment for a longer period (Al Habashneh et al., 2005; Lukacs and Largaespada, 2006). However, the difference in dental eruption patterns between males and females is most likely not significant enough to cause the observable differences in oral health. It may be that the higher caries prevalence observed in females is related to hormonal differences related to fertility and salivary production (Lukacs, 1996, 2008, 2017; Lukacs and Largaespada, 2006; Watson et al., 2010). With the agricultural transition, researchers have found a relationship between an increasingly sedentary lifestyle, greater carbohydrate consumption and a rise in fertility rates (Armelagos et al., 1991; Eshed et al., 2004; Lukacs, 2008, 2011; Lukacs and Largaespada, 2006; Sellen and Mace, 1997). The increase in oestrogen experienced during pregnancy has been shown to alter oral flora and reduce salivary production, increasing the likelihood of caries development in pregnant women (Arantes et al., 2009; Burakoff, 2003; Fields et al., 2009; Kolenbrander and Palmer, 2004; Laine, 2002; Lukacs and Largaespada, 2006; Marsh, 2004; Silk et al., 2008; Steinberg, 2000). In addition, menopause has long been associated with bone loss, and research has identified that menopause can lead to a reduction in bone mineral density of the jaw, alveolar bone loss and AMTL (Hildebolt, 1997; Jeffcoat et al., 2000; Watson et al., 2010; Yang et al., 2003). However, if sex differences in oral health were simply related to biological factors the observed trends should be universal, and they are not (Douglas, 2006; Larsen, 1983; Šlaus et al., 2018; Temple and Larsen, 2007; Watson et al., 2010). Although it is important to understand and consider the influence of biological factors (such as hormones and reproductive history) on oral health, cultural factors (e.g. division of labour and dietary preferences) also have a considerable impact on overall oral health and disease susceptibility (Carvalho et al., 2019; Lukacs, 2011).

7.5 Materials and methods

7.5.1 Materials

For the R12, KAW, KER and KUS samples, all left-sided teeth that could be reliably attributed to a mandible were analysed. If the left-sided tooth was absent (and there were no signs of dental disease of the alveolar socket), then the right-side antimere was used. The JSA sample was not available for direct dental analysis and, therefore, the oral health of the JSA sample was not included in this portion of the study. Due to differences in methodological approach and potential for inter-observer error, oral health data for the JSA sample available from other published sources were not included in this analysis.

The sex and age of the individuals were determined based on standard osteological methods (Buikstra and Ubelaker, 1994; **Appendix A.1**). Due to the small sample size of older adults, age categories were consolidated into two groups representing younger (\leq 35 years old) and older (>35 years old) individuals. In total, the dental analyses were performed on 515 adult

mandibular teeth. The sample sizes of the mandibular dentition studied by sample, sex and age category are shown in **Table 7.1**. The KER sample (n=200) had the largest sample size of mandibular dentition, followed by R12 (n=156), KAW (n=99) and KUS (n=60).

		Рори	lation	
Mandibular Dentition	R12	KAW	KER	KUS
Individuals (n) ^a	25	17	49	10
Left side $(n)^{b}$				
I ₁	19	7	2	6
I_2	17	6	12	7
C_1	17	10	14	7
P ₃	19	13	24	7
\mathbf{P}_4	18	15	31	7
\mathbf{M}_1	22	17	39	8
M_2	22	17	38	10
M_3	22	14	40	8
Sex $(n)^{c}$				
Male	61	75	84	36
Female	95	24	95	24
Age $(n)^d$				
Younger Adult	34	69	106	41
Older Adult	122	30	68	19
Total (n) ^b	156	99	200	60

Table 7.1 Summary of the mandibular dental study sample by population

^aNumber of adult individuals examined; ^bMaximum number of left mandibular teeth examined, some parameters could not be recorded for all teeth; ^cMaximum number of teeth examined by sex, some individuals could not be sexed; ^dMaximum number of teeth examined by age, younger adults ≤35 years old, older adults >35 years old; some individuals could not be aged. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

The mandibular dentition were also analysed by tooth class: incisor, canine, premolar and molar (**Table 7.2**) (Gagnon and Wiesen, 2011). Analysis by tooth type facilitates the investigation of how dental pathologies vary by tooth morphology and location in the mouth (Hillson, 2001). In addition, analysis within tooth classes helps to minimise the effect of differential preservation bias on the overall dental analyses.

		Populat	ion	
Mandibular Dentition	R12	KAW	KER	KUS
Tooth class				
Incisor	36	13	14	13
Canine	17	10	14	7
Premolar	37	28	55	14
Molar	66	48	117	26
Total	156	99	200	60

Table 7.2 Tooth class sample sizes by population

Left mandibular dentition; Incisor: I₁ and I₂; Canine: C₁; Premolar: P₃ and P₄; Molar: M₁, M₂ and M₃. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

7.5.2 Methods

The mandibular dentition was assessed for the presence and/or severity of five dental traits: dental wear, caries, calculus, LEH and periodontal disease (**Table 7.3**). The methodology that was used to record the dentition was chosen to limit the biases that arise from analysing dental pathology in prehistoric populations (Hillson, 2001).

Dental Pathology	Scoring System	References
Wear	1-8	Smith (1984); Buikstra and Ubelaker (1994)
Carriag	+/-; 1–4	Metress and Conway (1975); Turner (1979); Powell
Carles		(1985); Buikstra and Ubelaker (1994)
Calculus	+/-; 1–3	Brothwell (1972, 1981); Dobney and Brothwell
Calculus		(1987); Buikstra and Ubelaker (1994)
LEH	+/-	Guatelli-Steinberg (2003); Starling and Stock (2007)
Periodontal disease	+/-	Clarke et al., (1986); Tal (1985)

Table 7.3 Standards for scoring dental pathology

References indicate the scoring methodology that was used for each dental pathology based on severity; +/-, present or absent. LEH: linear enamel hypoplasia.

The number of mandibular teeth present, absent ante-mortem (as evidenced by partial or complete socket resorption) and/or absent post-mortem (as evidenced by completely unresorbed sockets) was recorded per individual. Each tooth that was present was recorded as complete, partially broken, or 'root' if the crown was absent. When heavy wear or poor preservation limited the accurate analysis of a dental pathology, such as calculus, caries or LEH, the tooth was excluded from that analysis (and noted as 'not recordable condition'). The variation in sample size between the study samples, due in part to the poor preservation of the sample populations, limited certain statistical analyses. Many of the dental pathologies analysed here (particularly dental wear, caries and periodontal disease) are age-related conditions. Therefore, the observed prevalence and severity of these pathologies can be heavily influenced by the age distribution of the sample. Therefore, the distribution of the dental sample by population, tooth and age category is provided for each analysis. Statistical analyses were also conducted by age categories to determine if the trends observed from the combined age analysis mirrored those within each age group. In addition, patterns of oral health can be influenced by biological and/or behavioural differences between males and females (see **Section 7.4**). Therefore, for each dental pathology the distribution of the sample by population, tooth and sex is provided and separate statistical analyses by sex were conducted.

7.5.2.1 Dental wear

Various scoring systems have been proposed to record dental wear (e.g. Molnar, 1971; Scott, 1979; Molnar et al., 1983; Richards, 1984; Dreier, 1994), reduction of crown height (Tomenchuk and Mayhall, 1979) and the angle of wear (Molnar, 1971; Hall, 1976; Smith, 1984). Smith (1984) produced a simplified version of an earlier ordinal dental wear scale (Murphy, 1959), by collapsing the wear patterns into single sets by tooth type. Smith's (1984) 8-stage grading system, with '8' classified as the most severe wear, is widely accepted for use in archaeological populations and was used in this study to quantify dental wear (Buikstra and Ubelaker, 1994) (**Table 7.3**). The simplified nature of the scale reduces both inter- and intra-observer error. To account for the age-related influence on severity and patterns of dental wear, the dental wear score for each tooth was divided by the dental wear score of the first molar for that individual (Zakrzewski, 2012). These scores were then used to compare differences in the observed patterns of dental wear between samples.

7.5.2.2 Dental caries

For each tooth, all surfaces were observed macroscopically for the presence or absence of a carious lesion. A carious lesion was considered present if there was clear penetration and tissue breakdown of the enamel, as distinguished from tooth discolouration (Buikstra and Ubelaker, 1994; Cucina et al., 2011; Halcrow et al., 2013; Hillson, 2001; Lukacs, 1989). Caries frequency was reported as a proportion of the total observed teeth (number of teeth with at least one carious lesion/total number of teeth observed), as well as calculated separately by tooth type (due to differential susceptibility of various tooth forms) (Larsen et al., 1991; Moore and Corbett, 1975; Turner II, 1979). When a carious lesion was present, the severity of the lesion was scored from 1–4 (representing slight, slight-moderate, moderate or severe carious lesions) (**Table 7.3**) (Metress and Conway, 1975; Powell, 1985; Turner II, 1979). The scores are defined as: (1) pitting or slight fissure; (2) involvement of less than half of the tooth; (3) involvement of more than half of the tooth; or (4) complete destruction of enamel with socket exposed (Metress and Conway, 1975).

7.5.2.3 Dental calculus

Each tooth was evaluated for the presence or absence of dental calculus. If present, the dental calculus severity was scored on a scale of 1–3 (mild, moderate, or severe) (**Table 7.3**) (Brothwell, 1981; Dobney and Brothwell, 1987; Judd, 2012). The location of the calculus was also recorded as buccal or lingual.

7.5.2.4 Linear enamel hypoplasia (LEH)

Teeth were evaluated for the presence or absence of LEH by a visual examination of the buccal/labial surface of each crown (Goodman and Rose, 1990; Buikstra and Ubelaker, 1994). For this analysis, an enamel hypoplasia was defined as a horizontal band with reduced thickness of enamel (FDI, 1982; Goodman and Rose, 1990; Guatelli-Steinberg, 2003; Starling and Stock, 2007; Temple, 2007). It has been noted in several studies that the anterior teeth, particularly the canines, are more susceptible to LEH lesions compared with premolars and molars (Goodman and Armelagos, 1985; Goodman and Rose, 1990, 1991). Although this has led some researchers to only analyse certain tooth classes to limit potential sample bias (Keita and Boyce, 2001), in this study – primarily due to the fragmentary nature of the samples used – all teeth positively attributed to a mandible were scored for the presence or absence of LEH (Goodman and Armelagos, 1985; Guatelli-Steinberg, 2016). The frequency of LEH in each population was examined separately by tooth class to address the potential for sample bias in LEH susceptibility.

7.5.2.5 Periodontal disease

Reliable identification and scoring methods for periodontal disease in archaeological samples based on alveolar resorption is problematic because many factors, such as continuous eruption, can affect the distance between the cemento-enamel junction (CEJ) and the alveolar crest (AC) (Clarke and Hirsch, 1991; Haytac et al., 2013; Kaifu et al., 2003; Lavigne and Molto, 1995; Nelson, 2016; Newman, 1999; Tal, 1985; Varrela et al., 1995; Whittaker et al., 1985). Many bioarchaeological studies consider CEJ and AC measurements ≥ 2 mm on any surface of the tooth crown to be potentially pathological (Clarke et al., 1986; De Groote et al., 2018; DeWitte, 2012; Hillson, 1996; Wasterlain et al., 2011). However, some researchers insist that visual inspection of the alveolar surface morphology is the only reliable method of diagnosing periodontal disease in skeletal material (Kerr, 1988; Klaus and Tam, 2010; Vodanović et al., 2012; Wasterlain et al., 2011). Therefore, accurate documentation of periodontal disease in skeletal material (Kerr, 1988; Klaus and Tam, 2010; Vodanović et al., 2012; Wasterlain et al., 2011). Therefore, accurate documentation of periodontal disease in skeletal material (Kerr, 1988; Klaus and Visual inspection of the AC for porosity (Klaus and Tam, 2010; Vodanović et al., 2012; Vodanović et al., 2010; Vodanović et al., 2012).

In this study, periodontal disease was recorded as present or absent for each tooth using the methods of Tal (1985) and Clarke and colleagues (1986): if a ≥ 2 mm distance was observed between the CEJ and the AC with accompanying evidence of porosity and lipping, the tooth was marked 'present' for periodontal disease (**Table 7.3**) (Griffin, 2014). Limited sample sizes and poor levels of preservation prevented more detailed classification in this study (Strohm and Alt, 1998).

7.5.3 Statistical analysis

Summary statistics by sample for each dental pathology were generated in IBM SPSS Statistics for Mac, version 22 (IBM Corp., Armonk, N.Y., USA). For the dental pathologies that were scored on a scale (wear, caries and calculus), Kruskal-Wallis tests were used to identify significant differences between samples (significance level $p \le 0.05$). Following significant Kruskal-Wallis tests, Mann-Whitney tests were used to identify significant pairwise relationships between samples (significance level $p \le 0.008$ following a Bonferroni correction). Mann-Whitney tests were also used to identify significant differences in these dental pathologies (wear, caries and calculus) between sex and age categories in each sample (significance level $p \le 0.05$). For the dental pathologies that were scored based on the presence or absence of the pathology (caries, calculus, periodontal disease and LEH), Pearson Chi-Square tests were used to identify significant differences in prevalence between samples (significance level $p \le 0.05$). In addition, Pearson Chi-Square tests were used to identify significant differences between sex and age categories in each sample for the above dental pathologies (significance level $p \le 0.05$).

7.6 Results

7.6.1 Dental wear

The mean dental wear scores (each tooth score was divided by the score for M_1 of that individual) by sample and tooth are shown in **Figure 7.1** and **Table 7.4**. There were statistically significant differences in dental wear across time periods for P_4/M_1 (p<0.001), M_2/M_1 (p=0.03) and M_3/M_1 (p=0.002) (**Table 7.5**). For each of these tooth combinations, KER had the highest mean dental wear score and KUS had the lowest. With regards to significant pairwise comparisons, KER had significantly higher mean dental wear for P_4/M_1 compared with R12, KAW and KUS. For M_3/M_1 , KER had significantly higher dental wear than KAW (**Table 7.5**). A full breakdown of the dental wear sample sizes by tooth, sex and age can be found in **Appendix D.1**.

	Populat					lation						
		R12			KAW			KER			KUS	
Tooth	п	Mean	SD	п	Mean	SD	п	Mean	SD	п	Mean	SD
I_1/M_1	19	0.72	0.26	7	0.77	0.27	1	0.67	-	6	0.83	0.19
I_2/M_1	17	0.69	0.23	6	0.59	0.24	8	0.68	0.39	7	0.65	0.29
C_1/M_1	17	0.80	0.20	10	0.75	0.29	9	0.92	0.19	6	0.71	0.17
P_{3}/M_{1}	19	0.81	0.22	13	0.68	0.16	15	0.81	0.23	6	0.71	0.20
P_4/M_1	18	0.72	0.11	15	0.70	0.17	22	0.89	0.15	6	0.69	0.10
M_2/M_1	22	0.76	0.19	16	0.79	0.15	32	0.88	0.17	8	0.75	0.12
M_3/M_1	21	0.61	0.19	14	0.52	0.22	30	0.70	0.17	7	0.44	0.23

Table 7.4 Descriptive statistics for mandibular dental wear by tooth and population

Left mandibular dentition; dental wear severity was scored for each tooth on a 1–8 scale (Smith, 1984) and divided by the score of M_1 of that individual (Zakrzewski, 2012). **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; SD: standard deviation.



Figure 7.1 Mean mandibular dental wear scores by tooth and population

Left mandibular dentition; dental wear severity was scored for each tooth on a 1–8 scale (Smith, 1984) and divided by the score of M_1 of that individual (Zakrzewski, 2012). **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

 Table 7.5 Kruskal-Wallis and Mann-Whitney tests comparing dental wear by population

Tooth	n	Н	р	Mann-Whitney tests
I_1/M_1	33	1.59	0.66	N/A
I_2/M_1	38	0.95	0.81	N/A
C_1/M_1	42	4.54	0.21	N/A
P_{3}/M_{1}	53	2.90	0.46	N/A
P_4/M_1	61	20.73	<0.001	KER>R12, KAW, KUS
M_2/M_1	78	8.96	0.03	No significant results
M_{3}/M_{1}	72	14.88	0.002	KER>KAW

Kruskal-Wallis level of significance $p \le 0.05$; Mann-Whitney level of significance $p \le 0.008$, arrows indicate direction of significant relationship between populations. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *H*: Kruskal-Wallis test statistic; *n*: sample size.

When mean dental wear values were compared between males and females from the same sample, there were limited significant differences. The only significant differences were in KAW for P_3/M_1 and in KUS for I_1/M_1 , for which males had higher mean dental wear values

than females (see **Appendix D.1** for full Mann-Whitney results by sex). When dental wear severity was assessed between samples separately for males and females, the results mirrored that of the pooled-sex comparison (**Figure 7.2**). Males were significantly different for P_4/M_1 and M_3/M_1 , and females were significantly different for P_4/M_1 (**Table 7.6**). There were no significant pairwise comparisons for males for P_4/M_1 , but females from KER had significantly higher values than females from R12 and KAW. Males from KER had significantly higher mean dental wear than males from KAW M_3/M_1 .

Tuble 710 Hubiku	i wanis and ma	in winning tests to	i dentai weai bet	ween populations by sex
Male				
Tooth	n	H	р	Mann-Whitney tests
I_1/M_1	18	2.41	0.49	N/A
I_2/M_1	21	2.84	0.42	N/A
C_1/M_1	21	3.15	0.37	N/A
P_{3}/M_{1}	25	0.86	0.84	N/A
P_4/M_1	31	10.03	0.018	No significant results
M_2/M_1	43	6.08	0.11	N/A
M_{3}/M_{1}	40	9.13	0.028	KER>KAW
Female				
Tooth	n	H	р	Mann-Whitney tests
I_1/M_1	15	0.09	0.77	N/A
I_2/M_1	17	4.15	0.25	N/A
C_1/M_1	21	2.58	0.46	N/A
P_{3}/M_{1}	28	5.77	0.12	N/A
P_4/M_1	30	13.67	0.003	KER>R12, KAW
M_2/M_1	35	3.03	0.39	N/A
M_{2}/M_{1}	32	5 4 3	0.14	N/A

Table 7.6 Kruskal-Wallis and Mann-Whitney tests for dental wear between populations by sex

Kruskal-Wallis level of significance $p \le 0.05$; Mann-Whitney level of significance $p \le 0.008$, arrows indicate direction of significant relationship between populations. **R12**: NDRS R12, Neolithic (c. 5000– 4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *H*: Kruskal-Wallis test statistic; *n*: sample size.



Figure 7.2 Mean dental wear for a) males and b) females

Left mandibular dentition; dental wear severity was scored for each tooth on a 1–8 scale (Smith, 1984) and divided by the score of M₁ of that individual (Zakrzewski, 2012). **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

7.6.2 Dental caries

There was a low prevalence of carious lesions in R12 and KUS, and all caries observed were classified as slight or slight-moderate severity (0.6% and 3.8% respectively, tooth count) (**Table 7.7**). KER had the highest frequency of slight and slight-moderate carious lesions (7.4%) and was the only population with moderate and severe carious lesions (0.5%) (**Table 7.7**). No dental caries were recorded in the KAW population. The level of caries severity was significantly higher in the KER population than in R12 (p=0.001) and KAW (p=0.004) (**Appendix D.2**).

Population, n (%)							
Severity	R12	KAW	KER	KUS			
Absent	153 (99.4)	99 (100.0)	175 (92.1)	51 (96.2)			
1	1 (0.6)	-	8 (4.2)	-			
2	-	-	6 (3.2)	2 (3.8)			
3	-	-	1 (0.5)	-			
4	-	-	-	-			
Total present	1 (0.6)	0 (0.0)	15 (7.9)	2 (3.8)			

Table 7.7 Prevalence and severity of carious lesions by population (combined dentition)

Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985; % number of affected teeth/total *n* for each population x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size.

In addition to the severity of caries, the presence or absence of caries was recorded for each tooth and examined between populations (**Figure 7.3**; **Table 7.7**). There were significant differences between populations in the frequency of carious lesions, with KER having significantly more caries (7.9%) than all other populations (**Figure 7.3**; **Table 7.7**; **Appendix D.2**). The dental caries sample size by tooth type is shown in **Table 7.8**. Awareness of the distribution of the sample by tooth type is important because morphologically complex teeth, such as the premolars and the molars, are more susceptible to carious lesions. Although the sample sizes indicate that, proportionally, each sample was comprised of more posterior dentition compared with the other samples. Analysis by tooth type indicated that most of the caries observed in the samples were in the molar dentition (see **Appendix D.2**). The implications of tooth type distribution, especially considering the high caries prevalence observed in the KER sample, will be further explored in the Discussion.

	Population, n						
Tooth Type	R12	KAW	KER	KUS			
Incisor	55	18	16	17			
Canine	29	14	15	7			
Premolar	54	45	74	27			
Molar	104	82	216	41			

Table 7.8 Dental caries sample size by tooth type and population

Incisors: I₁ and I₂; Canine: C₁; Premolar: P₃ and P₄; Molar, M₁, M₂ and M₃. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size.

As the observed prevalence of dental caries may be influenced by the sex of an individual, it is important to understand the sex distribution of the sample populations. The sex distribution by tooth type of each sample can be found in Table 7.9. Although the ratio of male to females was relatively equal in the KER sample, the KAW and KUS samples had more males than females, and the R12 sample had more females than males. For the combined dentition, females in R12, KER and KUS had more severe caries and a higher prevalence of caries than their male counterparts, although these comparisons were only statistically significant in the KUS sample (p=0.038) (see full results in **Appendix D.2**).



Figure 7.3 Prevalence of carious lesions by population (combined dentition)

Combined left mandibular dentition; %: *n* of dentition with at least one carious lesion/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

	R1	2	KA	W	KE	R	KU	JS
Sex	Male	Female	Male	Female	Male	Female	Male	Female
I ₁	9	20	10	7	2	2	6	3
I_2	9	17	0	1	6	6	5	3
C ₁	10	19	9	5	8	7	4	3
P ₃	12	13	16	6	8	20	7	4
P ₄	10	19	18	5	17	29	10	4
M_1	13	22	21	6	38	32	9	4
M_2	11	23	23	7	38	34	10	5
M_3	14	21	19	6	37	37	9	4
Total	88	154	116	43	154	167	60	30
		-						
	R1	.2	KA	W	KE	R	KU	JS
Age	R1 Younger	2 Older	KA Younger	W Older	KE Younger	R Older	KU Younger	JS Older
Age I ₁	R1 <u>Younger</u> 8	2 Older 21	KA <u>Younger</u> 8	W Older 2	KE Younger 1	CR Older 3	KU <u>Younger</u> 8	J S Older 1
Age I ₁ I ₂	R1 Younger 8 5	2 Older 21 21	KA Younger 8 7	W Older 2 1	KE Younger 1 6	R Older 3 6	KU <u>Younger</u> 8 6	JS Older 1 2
Age I ₁ I ₂ C ₁	R1 Younger 8 5 6	2 Older 21 21 23	KA Younger 8 7 8	W Older 2 1 6	KE <u>Younger</u> 1 6 7	<u>Older</u> 3 6 8	KU Younger 8 6 4	Older 1 2 3
Age I ₁ I ₂ C ₁ P ₃	R1 Younger 8 5 6 4	2 Older 21 21 23 21	KA Younger 8 7 8 15	W Older 2 1 6 7	KE Younger 1 6 7 14	Older 3 6 8 13	KU Younger 8 6 4 7	Older 1 2 3 4
Age I ₁ I ₂ C ₁ P ₃ P ₄	R1 Younger 8 5 6 4 7	2 Older 21 23 21 22	KA Younger 8 7 8 15 15 17	W Older 2 1 6 7 6	KE Younger 1 6 7 14 26	Older 3 6 8 13 19	KU Younger 8 6 4 7 9	Older 1 2 3 4 5
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁	R1 Younger 8 5 6 4 7 8	2 Older 21 23 21 22 22 27	KA <u>Younger</u> 8 7 8 15 17 19	W Older 2 1 6 7 6 8	KE Younger 1 6 7 14 26 41	2 R <u>Older</u> 3 6 8 13 19 27	KU Younger 8 6 4 7 9 9 9	Older
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁ M ₂	R1 Younger 8 5 6 4 7 8 8 9	2 Older 21 21 23 21 22 27 25	KA Younger 8 7 8 15 17 19 21	W Older 2 1 6 7 6 8 9	KE Younger 1 6 7 14 26 41 46	Older 3 6 8 13 19 27 24	KU Younger 8 6 4 7 9 9 9 9 9	Older 1 2 3 4 5 4 6
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁ M ₂ M ₃	R1 Younger 8 5 6 4 7 8 9 8 9 8	2 Older 21 23 21 22 27 25 27 25 27	KA Younger 8 7 8 15 17 19 21 21 17	W Older 2 1 6 7 6 8 9 8	KE Younger 1 6 7 14 26 41 46 43	Older 3 6 8 13 19 27 24 29	KU Younger 8 6 4 7 9 9 9 9 9 8	JS Older 1 2 3 4 5 4 6 5 5

Table 7.9 Dental caries sample size by population, tooth, sex and age

Younger adults: ≤35 years old; older adults: >35 years old. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

As the frequency and severity of dental caries can be influenced by the age of an individual, it would be expected that older individuals would demonstrate more frequent and/or severe dental caries. Therefore, it is important to understand the age distribution of the sample populations to determine if the results are influenced by a disproportionate number of younger/older adults. The sample sizes for each sample by tooth and age category can be found in Table 7.9. For the KAW and KUS samples, there were almost twice as many teeth analysed for the younger age category than the older age category. In R12, it was the older age category that had the higher representation in the sample. Although the sample sizes were more balanced in the KER sample, dentition from younger individuals was more prevalent. Direct comparisons of dental caries severity between age groups within each sample showed that older adults had more severe carious lesions than younger adults in R12 and KUS, but not KER. However, these observed differences were not statistically significant (see **Appendix D.2**). The potential impact of the sex and age distribution of the pooled-sex dental caries analyses presented here will be further explored in the Discussion.

7.6.3 Dental calculus

The KAW sample had the highest percentage of teeth affected by calculus deposition (68.1%), followed by KER (53.3%), KUS (41.5%) and R12 (27.3%) (**Figure 7.4**; **Table 7.10**). Overall, KAW had significantly higher calculus severity than R12 (p<0.001), KER (p=0.002) and KUS (p<0.001) (**Table 7.10**). KER also had significantly higher median calculus severity than R12 (p<0.001; **Table 7.10**). R12 had the lowest levels of calculus compared with the other samples.





Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent, 1, mild, 2, moderate, 3, severe; %: number of affected teeth/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth.

The sex and age distributions of each sample population by tooth can be found in Table 7.11. Overall, there was a higher proportion of males represented in the KAW and KUS samples, and a higher proportion of females represented in the R12 sample. Males and females were relatively equally represented in the KER sample. Males had higher mean calculus severity compared with females within the R12, KER and KUS samples, but this difference was only significant in the KER sample (p=0.033) (**Figure 7.5**; see **Appendix D.3** for full results).

There was a higher proportion of younger individuals represented in the KAW, KER and KUS samples. Younger adults had more severe calculus than older adults within the R12,

KAW and KUS samples (Figure 7.6; see Appendix D.3 for full results), but the difference between younger and older individuals was only significant in the KAW sample (p=0.024).

			Tooth Cl	lass <i>n</i> (%)		_
	Calculus					Total n
Population	Severity	Incisor	Canine	Premolar	Molar	(%)
R12	Absent	26 (76.5)	12 (70.6)	26 (70.3)	48 (72.7)	112 (72.7)
	Mild	5 (14.7)	4 (23.5)	6 (16.2)	15 (22.7)	30 (19.5)
	Moderate	3 (8.8)	1 (5.9)	4 (10.8)	3 (4.5)	11 (7.1)
	Severe	-	-	1 (2.7)	-	1 (0.6)
	Total (n)	34	17	37	66	154
KAW	Absent	6 (46.2)	4 (40.0)	4 (14.8)	17 (36.2)	31 (32.0)
	Mild	4 (30.8)	3 (30.0)	18 (66.7)	22 (46.8)	47 (48.5)
	Moderate	3 (23.1)	2 (20.0)	3 (11.1)	6 (12.8)	14 (14.4)
	Severe	-	1 (10.0)	2 (7.4)	2 (4.3)	5 (5.2)
	Total (n)	13	10	27	47	97
KER	Absent	7 (50.0)	5 (41.7)	30 (55.6)	49 (42.6)	91 (46.7)
	Mild	5 (35.7)	4 (33.3)	20 (37.0)	60 (52.2)	89 (45.6)
	Moderate	2 (14.3)	2 (16.7)	4 (7.4)	6 (5.2)	14 (7.2)
	Severe	-	1 (8.3)	-	-	1 (0.5)
	Total (n)	14	12	54	115	195
KUS	Absent	4 (36.4)	2 (33.3)	8 (66.7)	17 (70.8)	31 (58.5)
	Mild	6 (54.5)	3 (50.0)	4 (33.3)	7 (29.2)	20 (37.7)
	Moderate	1 (9.1)	1 (16.7)	-	-	2 (3.8)
	Severe	-	-	-	-	-
	Total (n)	11	6	12	24	53
		Kru	skal-Wallis to	est		
n	H	df	р	Manr	n-Whitney <i>pos</i>	st-hoc
				KAV	V > R12, KER,	KUS
499	43 95	3	<0.001		KER > R12	

Table 7.10 Descriptive statistics and Kruskal-Wallis test for calculus severity by population and tooth class

Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent; 1, mild; 2, moderate; 3, severe; *n*, number of affected teeth; %, number of affected teeth/total *n* x 100; Kruskal-Wallis test based on combined dentition; Kruskal-Wallis test significance at $p \le 0.05$; Mann-Whitney test significance $p \le 0.008$; arrows indicate direction of significant relationship between populations. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; df: degrees of freedom; *H*: Kruskal-Wallis test statistic.

1	R1	2	KA	W	KE	R	KU	JS
Sex	Male	Female	Male	Female	Male	Female	Male	Female
I ₁	9	20	10	0	2	2	6	3
I_2	9	17	7	1	6	7	5	3
C ₁	10	19	9	5	10	8	4	3
P ₃	12	13	16	6	11	20	7	4
P ₄	10	19	17	5	18	29	10	4
M_1	13	22	20	6	36	32	9	4
M_2	11	23	23	7	38	32	10	5
M_3	14	21	19	6	37	37	9	4
Total	88	154	121	36	158	167	60	30
	D1	•	T7 A	**7	171	T	T/T	IC
	KI	2	KA	w	KE	<i>ι</i> K	NU	5
Age	KI Younger	Older	KA Younger	w Older	KE Younger	Older	KU Younger	Older
Age I ₁	KI Younger 8	2 Older 21	KA Younger 8	W Older 2	KE Younger 1	Older 3	KU Younger 8	Older 1
Age I ₁ I ₂	Younger 8 5	Older 21 21 21	KA Younger 8 7	V Older 2 1	KE Younger 1 6	Older 3 7	Younger 8 6	0lder 1 2
Age I ₁ I ₂ C ₁	Younger 8 5 6	2 Older 21 21 23	KA Younger 8 7 8	Older 2 1 6	KE Younger 1 6 8	Older 3 7 10	Younger 8 6 4	Older 1 2 3
Age I1 I2 C1 P3	Younger 8 5 6 4	2 Older 21 21 23 21	KA Younger 8 7 8 15	Older 2 1 6 7	Younger 1 6 8 17	Older 3 7 10 13	Younger 8 6 4 7	Older 1 2 3 4
Age I ₁ I ₂ C ₁ P ₃ P ₄	Younger 8 5 6 4 7	2 Older 21 23 21 22 22	KA Younger 8 7 8 15 16	Older 2 1 6 7 6	Younger 1 6 8 17 27	Older 3 7 10 13 19	Younger 8 6 4 7 9	Older 1 2 3 4 5
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁	Younger 8 5 6 4 7 8	2 Older 21 21 23 21 22 27	KA Younger 8 7 8 15 16 18	V Older 2 1 6 7 6 8	Younger 1 6 8 17 27 41	Older 3 7 10 13 19 25	Younger 8 6 4 7 9 9 9	Older 1 2 3 4 5 4
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁ M ₂	Younger 8 5 6 4 7 8 9	2 Older 21 23 21 22 27 25	KA <u>Younger</u> 8 7 8 15 16 18 21	V Older 2 1 6 7 6 8 9	Younger 1 6 8 17 27 41 46	Older 3 7 10 13 19 25 22	Younger 8 6 4 7 9 9 9 9 9 9 9 9	Older 1 2 3 4 5 4 6
Age I1 I2 C1 P3 P4 M1 M2 M3	Younger 8 5 6 4 7 8 9 8	2 Older 21 23 21 22 27 25 27	KA Younger 8 7 8 15 16 18 21 17	W Older 2 1 6 7 6 8 9 8 8	Younger 1 6 8 17 27 41 46 43	Older 3 7 10 13 19 25 22 29	Younger 8 6 4 7 9 9 9 8	Older 1 2 3 4 5 4 6 5

 Table 7.11 Calculus sample size by population, tooth, sex and age

Younger adults, ≤35 years old; older adults, >35 years old. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).





Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent, 1, mild, 2, moderate, 3, severe; %: number of affected teeth/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

192



Figure 7.6 Calculus severity by age (combined dentition) within (a) R12, (b) KAW, (c) KER and (d) KUS populations.

Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent, 1, mild, 2, moderate, 3, severe; %, number of affected teeth/total *n* x 100; younger adults, \leq 35 years old; older adults, >35 years old. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

7.6.4 LEH

The population from KAW had the highest percentage of teeth with at least one LEH band present (10.4%), followed by KER (7.4%), R12 (6.5%) and KUS (5.7%) (**Figure 7.7**; **Table 7.12**). The prevalence of LEH was found to be independent of population for both the combined dentition (χ^2 =1.66, *p*=0.45; **Appendix D.4**), and when each tooth class was analysed separately (**Appendix D.4**).



Figure 7.7 Prevalence of LEH by population for combined dentition (tooth count)
%: number of affected teeth/total *n* x 100; R12: NDRS R12, Neolithic (c. 5000–4000 cal BC);
KAW: NDRS P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350). LEH: linear enamel hypoplasia.

When the presence of LEH was compared between sexes within each sample, males had a higher prevalence than females in both the R12 and KAW samples (**Figure 7.8**; **Appendix D.4**). Conversely, for the KER and KUS samples, females had higher LEH prevalence than males (**Figure 7.8**; **Appendix D.4**). However, none of these relationships were statistically significant (**Appendix D.4**).

_	n (%)					
Population	Incisor	Canine	Premolar	Molar	Total	
R12	1 (2.9)	2 (11.8)	2 (5.4)	5 (7.6)	10 (6.5)	
KAW	2 (15.4)	2 (20.0)	2 (7.7)	4 (8.5)	10 (10.4)	
KER	-	3 (21.4)	6 (12.0)	5 (4.4)	14 (7.4)	
KUS	-	1 (16.7)	2 (16.7)	-	3 (5.7)	

Table 7.12 Prevalence of LEH within each population and tooth class (tooth count)

Left mandibular dentition. *n*: sample size; %: number of affected teeth/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). LEH: linear enamel hypoplasia.





Left mandibular dentition. %: number of affected teeth/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). LEH: linear enamel hypoplasia.

7.6.5 Periodontal disease

The KER population had the highest level of periodontal disease (72.1%) while the KUS population had the lowest (3.6%) (**Figure 7.9**). The prevalence of periodontal disease varied significantly between populations (χ^2 =80.22, *p*<0.001; **Appendix D.5**) and the KER sample had significantly higher disease frequency compared with the other samples.



Figure 7.9 Prevalence of periodontal disease by population for combined dentition (tooth count)

Left mandibular dentition; %: *n* affected dentition/total *n* x 100. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

The age and sex distribution within each sample and by tooth can be found in Table 7.13. The samples from the KAW and KUS populations had a higher proportion of males, and the sample from R12 had a higher proportion of females. The proportion of males and females within the KER periodontal disease sample was similar. Within the R12 and KAW populations, females had a higher incidence of periodontal disease than males. The opposite trend was found within the KER and KUS samples, where males had a higher prevalence of periodontal disease compared to their female counterparts (**Figure 7.10a**). The differences in periodontal disease prevalence between males and females were statistically significant within the R12 (χ^2 =6.37, p=0.012) and KER (χ^2 =17.27; p<0.001) samples (**Figure 7.10a**; **Appendix D.5**).

	R12		KAW		KER		KUS	
Sex	Male	Female	Male	Female	Male	Female	Male	Female
I ₁	4	7	4	0	2	2	3	0
I_2	6	7	2	1	7	7	2	0
C ₁	7	14	2	2	11	8	1	0
P ₃	5	9	6	3	12	20	4	0
P ₄	5	14	9	1	19	29	5	0
M_1	11	18	13	5	38	32	8	3
M_2	10	18	15	6	38	34	8	3
M_3	8	13	11	6	37	36	8	1
Total	56	100	62	24	164	168	39	7
	R12		KAW		KER		KUS	
Age	Younger	Older	Younger	Older	Younger	Older	Younger	Older
I ₁	2	9	3	1	1	3	3	2
I_2	2	11	2	1	6	8	1	3
C ₁	5	16	2	2	8	11	1	0
P ₃	3	11	5	4	16	15	3	1
P ₄	3	16	8	2	28	19	5	8
M_1	5	24	13	5	41	27	8	3
M_2	6	22	15	6	46	24	8	3
7.5								
\mathbf{M}_{3}	4	17	11	6	42	29	7	2

Table 7.13 Periodontal disease sample size by population, tooth, sex and age

Younger adults \leq 35 years old, older adults >35 years old. **R12**: NDRS R12, Neolithic (5000 – 4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (2500 – 2050 BC); **KER**: Kerma, Kerma Classique (1750 – 1500 BC); **KUS**: Kawa (R18), Meroitic (350 BC – AD 350).

There was a greater proportion of younger individuals within the KAW, KER and KUS samples (Table 7.13). Within each sample, there was a higher prevalence of periodontal disease among older adults compared to younger adults, but this was only significant in the KER sample (χ^2 =7.25, *p*=0.007) (**Figure 7.10**; **Appendix D.5**).



Combined left mandibular dentition; %: *n* affected dentition/total *n* x 100; younger adults, ≤35 years old; older adults, >35 years old. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

198
7.7 Discussion

Using the analysis of dental wear and pathologies from four ancient Nubia populations, the aim of this study was to explore the relationship between oral health and dietary composition over a period that included the intensification of agricultural practises in this region. Before the results from each analysis are discussed below, it is important to note that the frequency and severity of dental pathologies observed can be influenced by the sex and age distribution of the sample population. Therefore, understanding the age and sex composition of each sample is necessary to interpret the overall results. As the progression of many dental pathologies is age-related (particularly dental wear, dental caries and periodontal disease), it would be expected that a sample with a higher proportion of younger individuals would have an overall lower prevalence/severity of these dental pathologies compared with the true level in the population. In addition, previous archaeological studies have shown that females often have worse oral health compared with their male counterparts (particularly with regards to dental caries) (e.g. Cohen and Crane-Kramer, 2007; Larsen et al., 2001; Lukacs and Largaespada, 2006; Watson et al., 2010). Therefore, samples with a relatively higher proportion of females may have different levels of oral health compared with more equally distributed samples. The age and sex distribution of each sample, and the possible implications on the results, will be discussed alongside the archaeological evidence for diet in each of the following sections.

7.7.1 Dental wear

The relationship between dental wear and age has been researched extensively, and although some studies have found little correlation (e.g. Santini et al., 1990), many studies have found moderate to high correlation between age and severity of dental wear (Mays, 2002; Miles, 2001; Molnar et al., 1983; Tomenchuk and Mayhall, 1979). In fact, dental wear is often used to estimate age in archaeological material (Brothwell, 1963; Hillson, 1996; Kieser et al., 1983; Lovejoy, 1985; Miles, 1963, 2001; Nowell, 1978). Since dental wear is an age-progressive process, the current study adjusted the dental wear score for each tooth by the score for M_1 of the same individual to, in part, correct for the influence of age on dental wear severity.

The relationship between dental wear and dietary composition in past human populations has been explored by many researchers (Anderson, 1965; Eshed et al., 2006;

Forshaw, 2009, 2014; Greene et al., 1967; Hillson, 1979; Littleton and Frohlich, 1993; Molnar, 1971a; Powell, 1985; Scott and Turner II, 1988; Smith, 1984). In this study, the level of dental wear varied significantly between the ancient Nubian populations examined. In general, the KER sample (c. 1750–1500 BC) had the most severe dental wear of the populations. Although there were no significant differences between samples in the anterior dentition, for the posterior dentition (P₄, M₂ and M₃), the KER sample had the highest levels of tooth wear and the KUS sample (c. 350 BC–AD 350) had the least severe tooth wear. The trends observed when males and females were analysed separately mirrored the results for the pooled-sex analyses.

Previous studies have shown that, in general, agriculturalists had less severe dental wear compared with non-agricultural groups (Anderson, 1965; Armelagos and Rose, 1972; Cassidy, 1984; Eshed et al., 2006; Kennedy, 1984; Lubell et al., 1994; Pastor, 1992; Powell, 1985; Smith, 1984; Walker, 1978). Therefore, it is not surprising that KUS had the lowest dental wear for the posterior dentition. However, the KER sample represents a primarily agricultural population and these individuals exhibited the most severe dental wear. In fact, severe tooth wear has been observed before in agricultural populations based in the ancient Nile Valley (Beckett and Lovell, 1994; Smith and Wood-Jones, 1910; Vagn Nielsen, 1970; Wells, 1975). Throughout the Kerma period, there was significant interaction and trade between the Egyptians and Nubians, and this influenced the diet of the Kerma population (O'Connor, 1993). The severe dental wear observed in the KER sample may have been caused by excessive grit present in the diet due to a reliance on bread consumption, a food product introduced by the ancient Egyptians (Leek, 1966, 1972, 1973; Soames and Southam, 1998). There is evidence from other studies that a gritty substance was introduced into the diet during the Kerma Moyen period (Judd, 2001a; Smith, 1984). However, it is not clear whether the dietary grit was introduced during the harvesting or processing of grain (i.e. through the use of flint-tooth sickle tools and/or grinding stones) or was the result of contamination from desert sand (Forshaw, 2009; Jurmain, 1990; Leek, 1972; Littleton and Frohlich, 1993; Macchiarelli, 1989; Miller, 2008; Powell, 1985; Smith, 1984).

Although not significant, the Sudanese Neolithic R12 sample had dental wear severity for I₂, C₁ and P₃ comparable to the KER sample. Previous research has shown that dental wear severity varied between Sudanese Neolithic populations, with some demonstrating high levels of wear (Coppa and Macchiarelli, 1983; Crivellaro, 2001; Judd, 2008) and others with relatively low dental wear severity (e.g. Gebel Ramlah, Lower Nubia; Kobusiewicz et al., 2004). The presence of lingual surface attrition of the maxillary anterior teeth (LSAMAT) in several R12 individuals has led previous researchers to infer the presence of paramasticatory behaviours within this population (Crivellaro, 2001; Judd, 2012). It is possible that such paramasticatory behaviours may have contributed to the observation of severe dental wear in the anterior dentition in the R12 sample compared with the other samples in this study.

For the Nubian populations analysed, males had more severe dental wear than females within the R12, KER and KUS samples. This trend was statistically significant only in the KER sample. Studies investigating sex differences in dental wear have yet to find a conclusive trend (Davies and Pedersen, 1955; Goldstein, 1932; Kieser et al., 1985; Lovejoy, 1985; Lunt, 1978; Molnar, 1971a; Molnar et al., 1983; Tomenchuk and Mayhall, 1979; Turner II and Cadien, 1969). For the R12, KER and KUS samples in this study, there appears to be a divergence in dietary intake or paramasticatory behaviours between males and females that has resulted in differential patterns of dental wear.

7.7.2 Dental caries

Dental caries is one of the most commonly analysed dental pathologies used to infer diet and subsistence strategy in past human populations (Larsen, 1995, 2006). Many studies have shown that agricultural populations consuming a high proportion of dietary carbohydrates have increased frequency and severity of dental caries compared with non-agricultural populations (Cohen and Armelagos, 1984; Hillson, 1979; Larsen, 1981; Larsen et al., 1991; Meiklejohn et al., 1984; Milner, 1984; Newbrun, 1982; Turner II, 1979; Ubelaker, 1980). However, the relationship between caries frequency and subsistence strategy varies drastically by geographical region (Hershkovitz, 1998; Larsen, 2015; Meiklejohn et al., 1984; Turner II, 1979), and it can be difficult to differentiate the populations with mixed subsistence strategies from those with emergent agricultural practices (Hillson, 2001; Lukacs, 1992, 1996). Therefore, it is important to compare caries frequency between populations from similar regions.

This study found significant differences in caries prevalence and severity between the Nubian samples. The KER sample had a significantly higher prevalence and severity of caries compared with the earlier R12 and KAW samples. In addition, the Meroitic KUS sample had significantly higher caries severity than the Kerma Ancien KAW sample. In this study the caries frequency for each sample was calculated as 0.6% for R12, 0.0% for KAW, 7.9% for KER and 3.8% for KUS (tooth count: number of dentition with one carious lesion/number of

teeth observed). It is important to note here that the KER sample had a high proportion of posterior dentition compared with anterior dentition, and this is potentially problematic because dentition with complex morphology (e.g. the premolars and molars) are more susceptible to developing carious lesions than teeth with less complex morphology. As such, the percentage of carious lesions that was observed in KER may reflect the high number of posterior teeth within the sample. Therefore, potential limitations to the interpretation based on differences in tooth type composition should be considered. The frequency of dental caries observed in each sample are discussed below within the context of results from studies of similar populations and the archaeological information available for each population.

During the Sudanese Neolithic, there was a gradual shift for Nubian populations to replace some of their traditional subsistence strategies with aspects of animal domestication and cereal agriculture. Analysis of phytoliths from plant depositions within burials and the starch from dental calculus from R12 and an Early Neolithic cemetery from Ghaba in central Sudan has provided evidence that domesticated cereal was present in these populations c. 7000 BP (Out et al., 2016). The data suggests that, to some extent, cereal cultivation was practised by the R12 population. However, Nubians during this period still relied heavily on fishing and river resources, and their diet included a high proportion of wild C4 plants (sorghum in particular) and protein derived from bovine milk (Caneva, 1988; Caneva et al., 1993; Caneva and Gautier, 1994). The proteins and minerals absorbed orally from animal-based diets, such as calcium and phosphate, can limit the formation of dental plaque and lower overall cariogenic risk by modifying pH levels, increase salivary production and/or promote remineralisation (Duggal et al., 1991; Hillson, 1996; Lukacs and Largaespada, 2006; Pathak et al., 2016). In addition, the isotopic evidence indicates that the Neolithic Nubian diet included fewer carbohydrates than later agricultural groups in Nubia, a finding consistent with the low level of caries evident in the R12 sample in this study (Caneva, 1988; Caneva et al., 1993; Caneva and Gautier, 1994). Experimental evidence from rats has also shown that the C4 plant sorghum can be cariostatic (Schmid et al., 1988).

Isotopic evidence has demonstrated that overall, the diet during the Kerma Ancien period (KAW sample) was similar to the Neolithic period, with high levels of consumption of both cattle and wild cariostatic C4 plants (sorghum and millet) (Iacumin et al., 1998). This study found no evidence of dental caries within the KAW sample analysed here, a result that is consistent with a previous study finding low caries rates in the same Kerma Ancien population (Judd, 2001b). A study of another Kerma Ancien population from the Northern

Dongola Reach site of H29 also found low caries frequency (1-2%) (Whiting, 2018). Although wheat and barley phytoliths have been found in a burial context at the Kerma Ancien H29 site (Ryan, 2018), similar domesticated plant remains have not been found from habitation sites. The consistently low caries rates that have been found in Kerma Ancien populations throughout the Dongola Reach reflects the interpretation derived from archaeological and isotopic evidence that these populations primarily relied on livestock management and the consumption of animal protein for subsistence (Iacumin et al., 1998; Whiting, 2018).

Although some studies have found that agricultural populations demonstrate an inverse relationship between dental wear severity and caries prevalence (Buzon and Bombak, 2010; Eshed et al., 2006; Larsen, 1995; Leek, 1972; Littleton and Frohlich, 1993; Maat and Van der Velde, 1987; Powell, 1985), the KER sample in this study had both high levels of dental wear and dental caries. A similar study analysing dental pathology in ancient Egyptian populations also found that the severity of dental wear and the frequency of dental caries increased concurrently over time (Zakrzewski, 2012). The inverse relationship between dental wear and dental caries has been suggested to be a result of heavily worn tooth crowns preventing cariogenic food substances from adhering to the tooth surface, thus limiting the formation of carious lesions (Greene, 1972). However, high levels of dental wear may facilitate access of cariogenic substances to the exposed dental pulp (Armelagos, 1969; Hillson, 2001). There has also been a suggestion that dental wear and caries are independent of each other (Meiklejohn et al., 1988, 1992).

Isotopic and archaeobotanical evidence has shown that populations during the Kerma Classique period had similar diets to Middle Kingdom Egyptians, with a high proportion of the C3 winter crops emmer wheat and barley (Fuller, 2004b; Iacumin et al., 1998). In addition, there is archaeobotanical evidence that a diverse range of fruits may have supplemented the Kerma Classique diet (Fuller, 2004b). The current study found a dental caries prevalence of 7.9% (tooth count) in the KER sample, which was significantly higher than previous populations and may reflect a high proportion of cariogenic carbohydrates in the diet. Previous analyses on caries prevalence within the Kerma population used in this study have provided caries frequencies of around 2% (total sample size not provided; both mandibular/maxillary teeth included; Triambelas, 2014) and 5% (total sample size of 1891 teeth; both mandibular and maxillary; Buzon and Bombak, 2010). The differences in caries frequency observed between studies is most likely due to a combination of differences in sample size and differences in the dentition analysed (this study only considered mandibular dentition).

It is important to note that the KER sample represents a population from a highly hierarchical Nubian state that maintained extensive trade networks (Edwards, 2004; Gatto and Zerboni, 2015). Inequality within the Kerma population is evidenced by the disparity in burial practices and grave goods between royal and non-royal individuals (Buzon, 2011; Chaix and Grant 1993). The KER sample in this study includes both high and low status individuals, and it is possible that higher status individuals may have had a different diet due to their position, thus influencing the rates of dental caries observed in the KER sample. Additional analyses will be required to understand the differences in diet between different classes of individuals within the Kerma population and how any dietary differences may have influenced the prevalence and severity of dental caries observed between the two groups.

In this study, caries frequency was markedly reduced following the Kerma period (7.9% in KER compared with 3.8% in KUS). The Meroitic populations in ancient Nubia increased their agricultural output due, in part, to the introduction of sorghum and the adoption of the water wheel for irrigation (saqia) (Fuller, 2004a; Martin et al., 1984; Wetterstrom, 1993). With a shift to intensive agriculture and the concomitant change in dietary composition, it would be expected that Meroitic populations would have relatively higher rates of dental caries compared with previous populations. However, low caries frequency in Meroitic populations has been observed in other studies. One study reported a frequency of 1.3% for a Meroitic population near Gabati (Judd, 2012) and another reported 0.8% for a Meroitic population from the central Sudan at the site of Al Khiday (Jakob, 2010). As was mentioned in the context of Neolithic populations, sorghum has been shown to be cariostatic in mice experiments (Schmid et al., 1988). Therefore, the cultivation of, and subsequent reliance on, dietary sorghum by Meroitic populations may account for the low levels of caries in these populations compared with other agricultural populations. Furthermore, the decrease in caries frequency observed between the KER and KUS samples may be influenced by non-dietary factors, such as improving environmental conditions and/or hygienic practices, as has been suggested for the reduction in dental caries observed between Predynastic and Dynastic ancient Egyptians (Grilletto, 1973).

Previous studies of Egyptian and Nubian populations have found higher caries prevalence and severity in females compared with males (Beckett and Lovell, 1994; Buzon and Bombak, 2010; Hillson, 1979; Judd, 2001b; Whiting, 2018); this trend was also observed in this study (the only statistically significant difference between males and females was in the KUS sample). Egyptian cultural depictions of agriculture during the Kerma period support the presence of a sexual division of labour (Brier and Hobbs, 2008), and sexual division of labour

has been shown in other populations to be accompanied by dietary differences (Gamza and Irish, 2010; Hill and Hurtado, 1989; Larsen, 1983, 1984; Temple and Larsen, 2007; Walker and Hewlett, 1990). However, more research is needed to clarify if there was sexual division of labour in the Nubian populations in this study, and how/if this then translated into different diets for males and females within each population. Sex differences in oral health are not consistently observed in past human populations (Esclassan et al., 2009; Keenleyside, 2008; Powell, 1988; Trombley et al., 2019), and can be influenced by a complex set of behavioural and biological factors (Carvalho et al., 2019).

Age-progressive caries frequency has been reported in studies of archaeological populations (Corbett and Moore, 1976; Moore and Corbett, 1975; Whiting, 2018). Dental caries form through the progressive demineralization of dental enamel, which cannot be remodelled. Therefore, the prevalence and severity of dental caries is often correlated with the age of an individual (Hillson, 2008; Temple, 2011, 2016; Temple and Larsen, 2007, 2013; Trombley et al., 2019). In this study, older individuals had more severe dental caries than younger individuals in the R12 and KUS samples. However, there were no differences found in caries prevalence between age categories within each sample. It may be that the younger adults and older adults were consuming different foods that would alter the progression of carious lesions. Caries rates can also be affected by the presence of AMTL in older populations, as carious teeth may be lost or removed, resulting in an observed caries frequency that is lower than the true occurrence within the population (Hillson, 2001). Differences in age distribution between the samples in this study (KAW and KUS had a larger proportion of younger individuals than the other samples) may affect the overall pooled age and sex analyses, as samples with a higher proportion of younger individuals are likely to have a lower frequency of dental caries compared with the true frequency in the population. It is important that dietary inferences using dental caries are made cautiously and are considered alongside evidence from other dental pathologies.

7.7.3 Dental calculus

Research has shown that increased rates of dental calculus in archaeological populations have been associated with both high protein and high carbohydrate diets (Hillson, 1979; Larsen, 1995; Lieverse, 1999; Lukacs, 1989; Turner II, 1979). In addition, calculus deposits in skeletal remains can be damaged and/or removed accidentally during curation, resulting in underestimates of calculus severity in past human populations. Therefore, it can be

difficult to infer the dietary composition of an archaeological population based on levels of dental calculus (Roberts and Manchester, 2005). The current study found that the level of calculus deposits was significantly higher in the KAW sample compared with the other populations. The KER sample had the second highest level of calculus, followed by the KUS and R12 samples.

Isotopic ratios during the Kerma Ancien period have indicated that animal protein was consumed in higher quantities during this period than subsequent periods (Iacumin et al., 1998). High levels of calculus severity in the KAW sample may, therefore, reflect the dietary importance of animal meat and/or secondary by-products. A relatively higher reliance on animal protein in the KAW sample is also supported by the low caries rates observed within this sample. An inverse relationship between caries and calculus has been found in several previous studies (Bonsall, 2014; Douglas, 2006; Lukacs, 2017; Oxenham, 2006). Although the formation of dental caries and dental calculus favours opposing oral environments (acidic versus alkaline, respectively; Manji et al., 1989), there is some evidence that severe calculus and high frequency of dental caries within a population (as observed in the KER sample) are reflective of a carbohydrate-based diet (Keenleyside, 2008; Lieverse, 1999). However, factors other than dietary composition, such as poor dental hygiene, paramasticatory practices and trauma that adversely affects chewing, can all influence calculus formation in an individual (Lieverse, 1999; Roberts and Manchester, 2005).

Within the R12, KER and KUS samples, males had significantly higher calculus severity than females (this was only significant within the KER sample). Differences in calculus severity may be due to sex-based differences in access to, and consumption of, protein (Lillie and Richards, 2000) or due to differences in the mineral content and production of saliva (Lieverse, 1999). Previous studies have shown that males often have higher rates of calculus deposits compared with females in both modern (Beiswanger et al., 1989; Buckley, 1980) and archaeological populations (Lillie and Richards, 2000; Lukacs, 2017). However, some studies have found that females have higher calculus severity than males (Yaussy and DeWitte, 2019), or that there is low/no correlation between sex and calculus severity (Delgado-Darias et al., 2006; Keenleyside, 2008; Macpherson et al., 1995; Slaus et al., 2011).

The differential age and sex distributions of the samples analysed here may limit the interpretations of diet based on dental calculus severity for the pooled sex/age analysis. The KAW and KUS samples had a higher proportion of males, and the R12 sample had a higher proportion of females. In addition, the KAW, KER and KUS samples had a higher proportion

of younger adults. Within the R12, KAW and KUS samples, the younger adults had higher calculus severity than older adults (only significant within the KAW sample). Calculus formation is partly age-related, and it would be expected that younger populations would have lower levels of dental calculus than older individuals (Beiswanger et al., 1989; Hillson, 2008; Macpherson et al., 1995; Slaus et al., 2011). However, some studies of archaeological populations have found higher calculus severity in younger individuals (Delgado-Darias et al., 2006; Yaussy and DeWitte, 2019). It is possible that there were age-related differences in paramasticatory and/or hygienic behaviour, but the results observed here may also reflect inadvertent damage to, or removal of, the calculus deposits during excavation or curation.

The results from previous studies regarding the correlation between dental calculus severity and a high protein or carbohydrate diet are not conclusive (Lieverse, 1999; Roberts and Manchester, 2005), and it has been suggested that dental calculus was common in all past human populations, regardless of dietary composition (Hershkovitz et al., 1997; Pietrusewsky and Douglas, 2002; Roberts and Manchester, 2005). Therefore, it is important to be cautious when interpreting diet in past populations based on dental calculus severity. Instead of quantifying the amount of dental calculus within an individual, it may be more informative for future studies to extract biomolecules from dental calculus to identify past diets (Hardy et al., 2009).

7.7.4 Periodontal disease

The presence and severity of periodontal disease within an individual can be reflective of dietary composition, but it can also be indicative of overall systemic health/stress (Garcia et al., 2001; Hujoel, 2009). A recent study estimated that in the modern, global population, the prevalence of periodontal disease falls between 20–50% (tooth count) (Nazir, 2017). In past human populations, some researchers have found high rates of periodontal disease in agriculturalists with a predominately carbohydrate-based diet (Clarke et al., 1986; Fyfe et al., 1993; Larsen, 2015; Lavelle and Moore, 1969; Moore and Corbett, 1983; Rathbun, 1984), while others have found no relationship between levels of periodontal disease and dietary composition (Held, 1989; Kennedy, 1984; Kerr, 1991).

In this study, the KER sample had significantly higher rates of periodontal disease by tooth count (72.1%) than the KAW (44.4%), R12 (29.9%) or KUS (3.6%) samples. The high rates of periodontal disease within the KER sample fit within the general pattern of poor oral

health for this sample. However, there is a suggestion that periodontal disease is over diagnosed in skeletal material, as heavy tooth wear (as is present in the KER posterior dentition) can initiate continuous dental eruption, which can be difficult to differentiate from periodontal disease in skeletal remains (Clarke et al., 1986; Newman, 1999; Roberts and Manchester, 2005; Whittaker et al., 1985). In addition, continuous dental eruption due to severe dental wear is often more severe in the mandible (Glass, 1991). Although alveolar porosity is often used to identify periodontal disease (as it was in this study), it is not unique to periodontal disease and, thus, caution is needed for interpreting the results from this study.

There were significant differences in the prevalence of periodontal disease between males and females in the R12 and KER samples. Females had significantly higher rates of periodontal disease than males in the R12 sample, but males had higher rates than females in the KER sample. The rise in female fertility associated with the adoption of agriculture, and the resultant hormonal effects, have been linked to the increase in periodontal disease observed in females from agricultural populations (Watson et al., 2010). In addition, all the samples in this study had higher rates of periodontal disease in older individuals, as would be expected due to the age-related trajectory of periodontal disease (Costa, 1982; Goldberg et al., 1976; Kerr, 1991; Watson, 1986; Whiting, 2018).

One of the challenges with analysing levels of periodontal disease in past human populations is that there is a lack of standardisation between studies with regards to classifying and recording periodontal disease in skeletal remains (Brothwell, 1981; Karn et al., 1984; Levers and Darling, 1983; Lukacs, 1989). Post-mortem damage to the jaw (particularly the maxilla) can mimic bone loss around tooth roots and be mistaken for periodontal disease (Scott and Turner II, 1997). Changes to the alveolar bone can also reflect non-masticatory factors such as vitamin deficiencies (e.g. scurvy) and osteoporosis (Atkinson and Hallsworth, 1983; Atkinson and Woodhead, 1968; Brickley and Ives, 2006; Hildebolt, 1997). The methodology used in this study may overestimate the reported frequency of periodontal disease in these samples by inadvertently including incidences of gingivitis, the precursor to periodontal disease in an individual can be reflective of factors relating to genetics, the environment, diet, and/or hygienic practices; observed levels can also be influenced by the specific methodology used. It is, therefore, important to consider the inferences from periodontal disease together with other evidence of oral health within these samples.

7.7.5 LEH

This study found that there were no significant differences in LEH prevalence between samples, although the KAW sample had the highest prevalence of LEH (10.4%) and the KUS sample had the lowest (5.7%) (R12=6.5%, KER=7.4%; tooth count). In the R12 sample, males had higher incidence of LEH than females, whereas the opposite trend was found in the KER sample. The current sample fits the trend reported in previous studies (Cohen, 1989; Cohen and Armelagos, 1984; Larsen, 2006; Starling and Stock, 2007; Steckel and Rose, 2002) that early agriculturalists show signs of higher levels of physiological stress and poor health (by proxy of LEH frequency) relative to hunter-gatherers in similar environments. A related study of LEH in Nubian populations found the prevalence of LEH in the hunter-gatherer Jebel Sahaba population at 6.5% and the Kerma population at 6.1% (Starling and Stock, 2007). The health of agriculturalists improved substantially with increasing urbanisation and trade that accompanied the formation of the Nubian settled agricultural "proto-city-states" (Kemp, 1989). In addition, the KAW sample was not only an early agro-pastoral community, but is thought to represent a rural society of lower socioeconomic status than individuals from urban centres, as represented by the KER sample (Adams, 1977; Welsby, 1996b, 2018). It is, therefore, possible that the high frequency of LEH in the KAW sample compared with the other samples reflects their socioeconomic status and limited access to resources.

7.8 Conclusions

High dental wear present with low caries and calculus rates characterised the Sudanese Neolithic R12 population, suggesting an abrasive diet of semi-processed wild plants and meat, rather than a heavy reliance on domesticated cereals (Judd, 2008). Although recent archaeobotanical data has suggested that domesticated cereal production (e.g. wheat and barley) was present in some form in the R12 population (Out et al., 2016), a dietary change to an intensive carbohydrate-rich diet was not reflected in the rates of caries. This suggests that carbohydrates made up a relatively small proportion of the R12 diet. The Kerma Ancien KAW population was characterised by low dental wear and caries rate, but a high calculus rate. These elevated calculus rates, especially when compared to the R12 sample, may be attributable to the reliance on animal products during the period, particularly cattle, indicated by nitrogen isotopic levels (Iacumin et al., 1998). In addition, the KAW sample represents a pastoral rural

population that may have had even less reliance on domesticated and wild plants than the preceding R12 population.

The economy of the Kerma Classique (KER) population was based on intensive agriculture of emmer wheat and barley (Chaix and Grant, 1993; Iacumin et al., 1996, 1998) and domestication of cattle and caprines, with some hunting (Chaix, 1993). The conclusions from the archaeological and isotopic research were supported by the oral health observations in the KER sample, who had the highest rates of caries and periodontal disease of all the ancient Nubian populations in this study. The KER sample also had the highest dental wear severity, which may be due to the introduction of abrasive particles through increased bread consumption (Bonnet, 1997; Judd, 2001a). The carbon isotopic ratios and calculus levels from Kerma indicate that caprine consumption was an important component of the diet (Iacumin et al., 1998).

The Meroitic KUS sample in this study was characterised by moderate dental wear, caries severity and calculus. The dental pathology findings support the archaeological evidence that Meroitic populations had a diverse diet that was reliant on agricultural products (Fuller, 2004a; Martin et al., 1984; Rowley-Conwy, 1989; Wetterstrom, 1993). The overall improvement of dental disease as evidenced across various dental pathology parameters compared with the KER sample particularly indicates that the KUS sample may have had greater dietary diversity and possibly increased hygienic practices.

Age was a significant factor in dental pathology frequency and severity, as would be expected based on the age-progressive nature of many of the dental pathologies analysed. Sex-specific differences in oral health were not universal across populations or pathology, but females did tend to have more severe dental caries and LEH, particularly within the KER sample. There was also a trend for males to have more severe dental wear in the R12, KER and KUS populations. The differences between males and females were likely due to a combination of inherent biological causes as well as external cultural influences (Carvalho et al., 2019; Lukacs, 2011). Future research should conduct isotopic analyses separately for males and females to determine if there was sex-specific variation in dietary consumption.

The dental wear and dental pathologies analysed here allowed for patterns of oral health amongst ancient Nubian populations to be compared to shifts in subsistence patterns and dietary consumption. A combination of archaeological, isotopic and archaeobotanical evidence was used to reconstruct the ancient diet of these populations as accurately as possible. These analyses contribute to the understanding of the biological effect of agricultural intensification in the Northern Dongola Reach from the Sudanese Neolithic through to the Meroitic period (c. 5000 cal BC–AD 350).

8 Dental Metrics

8.1 Introduction

An early Holocene dental reduction trend in human populations has been observed around the world (Brace, 1966, 1976, 1979b, 1980; Brace and Hinton, 1981; Brace and Mahler, 1971; Brace et al., 1987; Brace and Ryan, 1980; Brose and Wolpoff, 1971; Calcagno, 1989; Calcagno and Gibson, 1988; Christensen, 1998; Frayer, 1977, 1978; Hill, 2004; Huang et al., 2012; Kieser, 1990; Lieberman, 2011; Meiklejohn and Schentag, 1988; Organ et al., 2011; Pinhasi, 1998; Pinhasi et al., 2008; Smith, 1977; Soltysiak, 2007; Y'Edynak, 1983, 1989). Most of these studies attribute diet-related mechanisms to the observed dental reduction. Some studies have concluded that morphological change is associated with dietary composition, whereas others argue that the change is due to advances in food preparation technology, such as the use of pottery. However, the causal relationship between dental reduction and subsistence strategy (most notably at the agricultural transition) is complex and varies by population. It is important to examine diachronic dental size change in the context of regionspecific changes in subsistence strategy, food preparation techniques and dietary consistency.

This study assessed temporal trends in mandibular dental crown size between Upper Nubian populations from c. 5000 cal BC–AD 350 to evaluate the relationship between tooth size variation and dietary changes over time. Diachronic variation in dental size was assessed by mesiodistal (length) and buccolingual (width) measurements. In addition, established mechanisms for dental reduction such as the Probable Mutation Effect (PME), the Increasing Population Density Effect (IPDE) and the Selective Compromise Effect (SCE) were assessed in the context of this study.

8.2 Dental reduction mechanisms

Compared with other primates, modern humans have relatively small teeth and postcanine tooth rows in relation to their overall body size (Brace, 1963; Brace et al., 1987; Dahlberg, 1963; Gómez-Robles et al., 2017; Lucas, 2004; Wolpoff, 1971). Dental crown dimensions are complex phenotypic traits that are controlled by a combination of genetic, developmental and environmental factors. Although some studies have shown that there is a high heritability of dental crown diameters (e.g. Alvesalo and Tigerstedt, 1974; Bader and Lehmann, 1965; Dempsey and Townsend, 2001; Dempsey et al., 1995; Goose, 1971; Goose

and Lee, 1971; Harzer, 1987; Horowitz et al., 1958; Hughes et al., 2000; Townsend, 1980), many researchers view environmental and/or cultural factors as significant triggers for the observed diachronic dental crown reduction in recent human populations (e.g. Brace, 1979a; Brace et al., 1987; Calcagno and Gibson, 1988; Harris and Johnson, 1991; Pinhasi et al., 2008; Pinhasi and Meiklejohn, 2011; Y'Edynak and Fleisch, 1983).

Inter-population variability in tooth size and dental reduction trends have been studied around the world (e.g. Brace, 1978, 1980; Brace and Vitzthum, 1984; Christensen, 1998; Dahlberg, 1960; Frayer, 1978, 1984; Hill, 2004; Hillson and Fitzgerald, 2003; Huang et al., 2012; Larsen, 1981; Lukacs, 1984; Mockers et al., 2004; Pajević and Glišić, 2017; Smith et al., 1984, 1986; Y'Edynak and Fleisch, 1983), including within ancient Nubian populations (Anderson, 1968; Calcagno and Gibson, 1988; Calcagno, 1986, 1989; Carlson and van Gerven, 1977; Greene, 1972; Greene and Armelagos, 1972; Greene et al., 1967; Strouhal, 1968). Although many of the above studies show dental crown size reduction, the magnitude of this trend varies by tooth type and measurement used (mesiodistal versus buccolingual). In addition, some studies have demonstrated that tooth size does not decrease, and can even increase over time (e.g. Fernandes et al., 2013; Garn et al., 1969; Harper, 1994; Harris et al., 2001; Jacobs, 1994; Lavelle, 1972; Lindsten et al., 2002; Mockers et al., 2004; Y'Edynak, 1989).

Researchers have proposed several mechanisms to explain the observed dental reduction in recent human populations, and these can be broadly separated into three categories: genetic-based, natural selection, and/or developmental plasticity in response to environmental factors. The Probable Mutation Effect (PME) model for dental reduction is an example of a genetic-based, 'non-selection' mechanism (Brace, 1963, 1964; Brace and Mahler, 1971). According to the PME model, as selection for large teeth weakened (due to changes in food processing and dietary composition), non-functional genetic mutations relating to the dentition began to accumulate. Since most genetic mutations tend to interfere with the phenotypic development of a structure, such mutations are likely to limit the optimal growth of the tooth, leading to a reduction in tooth size (Brace, 1963, 1964). Specifically, Brace (1964) proposed that technological advancements in early Holocene populations (first cooking and then the development of pottery) led to softer diets that required less masticatory effort, and ultimately relaxed selection pressure for large teeth (Brace and Mahler, 1971; Brace et al., 1987). Therefore, the 'probable effect' of the relaxation of selective forces on dentition was a reduction in overall tooth size (Brace and Nagai, 1982; Brace, 1977, 1980, 1988, Brace et al.,

1984b, 1987; Brace and Vitzthum, 1984; Dahlberg, 1963; McKee, 1984). Brace and colleagues (1987) used this model to explain why, according to their research, the rate of dental reduction doubled with the adoption of agriculture around 10,000 years ago in certain regions.

The PME model for dental reduction proposes that genetic mutation can be the predominant mechanism for morphological change, but this model is difficult to test in archaeological and modern human populations (Brace, 1963, 1964). In addition, the PME model for dental reduction does not explain the dental variation present within early hominin species, or in more recent human populations (Brace et al., 1987). The credibility of a mutation-based genetic mechanism for dental reduction has also been questioned; the accumulation of random mutations is a slow process and selection typically acts on already existing variation (Bailit and Friedlaender, 1966; Brues, 1966; Calcagno, 1989; Calcagno and Gibson, 1988; Frayer, 1978; Holloway, 1966; Prout, 1964).

The Somatic Budget Effect (SBE) model presents natural selection as the driving force behind dental reduction in an environment where food preparation methods and dietary composition limit the necessity of large dental crown surface areas (Jolly, 1970; Kieser, 1990). In nutrient-poor conditions, selection favours individuals who can conserve energy and resources by forming small and efficient teeth (Bailit and Friedlaender, 1966; Greene, 1970; Jolly, 1970; Kieser, 1990; Smith, 1982). However, critics of the SBE model question whether the small amount of energy gained by the reduction of dental size would be significant enough to confer a tangible competitive advantage for that individual and drive selection processes (Brace et al., 1991; Calcagno, 1989).

The Increasing Population Density Effect (IPDE) model uses environmental factors, rather than a genetic or natural selection driven process, to explain dental reduction (Macchiarelli and Bondioli, 1986). The transition to agriculture was often associated with a general decline in health due to poor nutrition and an increase in the prevalence of diseases associated with a sedentary lifestyle (Larsen, 2015). The IPDE model proposes that the reduction in dental crown size associated with the agricultural transition is an allometric effect of smaller body sizes in such high-stress environments (Larsen, 1981; Macchiarelli and Bondioli, 1986). Some studies have found a low but positive correlation between tooth dimensions and body size in modern human populations (Garn et al., 1966, 1968), supporting the idea that differences in tooth size between human populations can be attributed to changes in body size (Brace et al., 1991; Macchiarelli and Bondioli, 1986). However, studies testing the IPDE model using diachronic human populations with associated stature and nutritional

data have shown that variation in dental crown size cannot be entirely explained by body size differences (Armelagos et al., 1989; Calcagno, 1989). In addition, some researchers argue that the correlation between dental and body size is not strong enough to support such a co-dependent reduction model (Garn et al., 1968; Henderson and Corruccini, 1976; Perzigian, 1981). Instead, researchers assert that dental size is more strongly correlated with the size of tooth supporting structures, such as the maxilla or mandible, rather than overall body size (Harris, 1998).

The Selective Compromise Effect (SCE) model for dental reduction is based on a selective compromise in tooth size between small teeth that are resistant to caries and overcrowding, with large teeth that are more resistant to severe dental wear (Calcagno, 1986, 1989; Calcagno and Gibson, 1988; Lucas et al., 1986). In populations consuming a hard diet, it is important to have large occlusal surfaces to prevent excessive wear from exposing the underlying dental pulp that can potentially lead to a life-threatening infection (Calcagno and Gibson, 1988). Although resistant to occlusal wear, larger teeth are much more susceptible to dental caries than smaller teeth (Armelagos, 1969; Brothwell, 1981; Calcagno and Gibson, 1991; Greene, 1972; Turner II, 1976, 1979, 1986, 1989; Van Reenen, 1966). In general, agricultural populations subsisting on soft cariogenic diets experience low levels of dental wear, with dental cusps remaining unworn during much of an individual's life. Consequently in agricultural populations, there may be selection for smaller and simpler teeth that are caries resistant, as the soft diet precludes the need for large, dental wear resistant teeth (Armelagos et al., 1989).

The functional-demand portion of the SCE model is based on the premise that through subsistence strategy shifts, particularly from hunting and gathering to agriculture, human populations experienced a decrease in the biomechanical stress on the masticatory apparatus due to improvements in food preparation techniques and an increased reliance on softer foods (Armelagos et al., 1989; Calcagno, 1986, 1989; Pinhasi et al., 2008; Soltysiak, 2007). The reduction in biomechanical stress and associated decline in bone and muscle stimulation resulted in a smaller masticatory complex, possibly predisposing an individual to dental crowding, impaction and malocclusion (Armelagos et al., 1989; Lieberman et al., 2004a). The selective challenge in agricultural populations is to maintain dental efficiency while preventing overcrowding, dental disease and life-threatening secondary infections such as gangrene, septicaemia or osteomyelitis (Calcagno and Gibson, 1988). However, the SCE model has been criticised by some researchers who claim that the increase in frequency of dental caries and

tooth crowding at the end of the Pleistocene could not be a selective force because at that point, 90% of the dental reduction and crown simplification had already occurred (Brace et al., 1991). Overall, populations are subject to a unique set of environmental constraints that alter the relative importance of the above selective pressures (dental caries, dental wear and masticatory stress).

Despite an abundance of early research that proposed the above hypotheses to explain dental reduction in human populations (the PME, SBE, IPDE and SCE), recent contributions to the debate have been limited (but see, Bernal et al., 2010; Harris and Lease, 2005; Hill, 2004; Pajević and Glišić, 2017; Pinhasi et al., 2008; Pinhasi and Meiklejohn, 2011). There is still no clear understanding of the relative importance of these different factors (natural selection, environment, genetics) in dental reduction at different points in recent human history (Guatelli-Steinberg, 2018). In addition, trends in tooth size vary by region, and the mechanisms involved may be region-specific. However, diet is a factor common to all of these mechanisms. Considering changes in subsistence strategy, food preparation and dietary consistency alongside dental size may therefore help to clarify the specific nature of the forces influencing dental reduction in past human populations.

Typically, anthropologists study tooth size by measuring the maximum crown diameter along the mesiodistal (MD; crown length) and buccolingual (BL; crown breadth) planes (Mayhall, 2000). There is debate over the most accurate method to measure dental dimensions in human populations (Falk and Corruccini, 1982; Fitzgerald and Hillson, 2008; Frayer, 1978; Goose, 1963; Hillson, 2005; Hillson et al., 2005; Karaman, 2006; Kieser, 1990; Moorrees and Reed, 1964; Pilloud and Hillson, 2012; Tobias, 1967), especially as many past human populations exhibit severe dental wear which can limit the accuracy of dental crown measurements. Methodological differences are particularly prevalent for the mesiodistal tooth length in the posterior dentition, because measurements can be taken either along the interproximal contact points parallel to the occlusal surface, or at the maximum width of the tooth crown in the mesiodistal plane (Buikstra and Ubelaker, 1994) (Figure 8.1). There is a general agreement that any methodology utilised to measure dental crown dimensions has limitations. Based on the general consensus among researchers (Hemphill, 2016), and the practicalities of the present research, in this study tooth measurements were performed according to the guidelines set by Buikstra and Ubelaker (1994) which, in turn, are based on the standards set by Moorrees and Reed (1957; 1964) and Mayhall (1992).

8.3 Materials and methods

8.3.1 Materials

The dental samples used in this study represent ancient Nubian populations from the NDRS site R12 (**R12**, c. 5000–4000 cal BC), NDRS site P37 (**KAW**, c. 2500–2050 BC), Kerma (**KER**, c. 1750–1500 BC) and the R18 site at Kawa (**KUS**, c. 350 BC–AD 350) (see **Chapter 4** for detailed information about the populations). Unfortunately, the dental sample of the JSA population was not available, and therefore JSA was not included in this portion of the study. Published data on JSA dental metrics were not considered here to prevent the introduction of methodological and inter-observer error into the analyses. Individuals in each sample were aged and sexed based on the standards outlined in **Appendix A.1**, and only adults were included in the analysis. Dental metric analyses were conducted only on the mandibular teeth because of the overall research objectives relating to diachronic change in mandibular size and shape.

Any study of dental trends in archaeological populations must consider the influence of dental wear. Dental wear was recorded for each tooth following Smith's (1984) methodology outlined in Buikstra and Ubelaker (1994) (see **Chapter 7** for dental wear analysis). The MD and BL measurements of tooth with extensive dental wear (an incisor or canine wear score of ≥ 5 , or a premolar/molar wear score ≥ 6) were not included in the data analysis due to the potential for recording reduced crown dimensions (Hillson, 1996; Pilloud and Hefner, 2016).

All permanent teeth that could be assigned to a position in the left-side of the mandibular dental arcade were measured, except when missing, worn or poorly preserved. In such cases, the corresponding right-side tooth was substituted. This is common practice since tooth crown diameters are correlated with those of their antimere (Lunt, 1969). Loose dentition that could be reliably associated with an individual and assigned to the correct anatomical position were also measured.

8.3.2 Methods

The MD and BL dental crown diameters were measured on the mandibular dentition following the methodology of Buikstra and Ubelaker (1994). In accordance with this protocol, the MD length of the posterior teeth was measured at the maximum width of the tooth crown. This methodology limits the influence of interproximal wear, allows for the inclusion of loose dentition, and mitigates any complications due to malocclusion (Buikstra and Ubelaker, 1994) (**Figure 8.1**). The BL measurement was taken as the widest diameter of the tooth, measured perpendicular to the mesiodistal plane (Buikstra and Ubelaker, 1994). The MD and BL diameters of the mandibular dentition were measured using fine point digital calipers with an accuracy of 0.1 mm.



Figure 8.1 Mesiodistal and buccolingual posterior dental measurements (from Buikstra and Ubelaker 1994)

To determine the rate of intra-observer error, 10 individuals were selected randomly and re-measured. A percentage difference was calculated between the two measurements for each individual and then averaged to obtain the mean intra-observer error (Calcagno, 1989; Pinhasi et al., 2008). The total intra-observer error in this study was 1.4%, which is comparable to the level of error in Calcagno's (1986) study (1.3%).

The Coefficient of Variation (CV) was calculated for each MD and BL measurement to provide a standardised way to compare the magnitude of morphological variation in the dentition (1) between samples, (2) between anterior (I_1 , I_2 , C_1) and posterior (P_3 , P_4 , M_1 , M_2 , M_3) teeth and (3) within each sample (Pinhasi and Meiklejohn, 2011; Pinhasi et al., 2008):

$CV = (SD/mean) \times 100$

SD, standard deviation and arithmetic mean (Sokal and Braumann, 1980).

The percentage difference in tooth dimensions across samples was calculated to determine the magnitude of dental size change that may have occurred over time between the four samples (Calcagno, 1989; Christensen, 1998; Hill, 2004):

[(mean_{older} – mean_{recent})/mean_{older}] x 100

mean_{older}, mean tooth measurement for older sample and mean_{recent}, mean tooth measurement for more recent sample.

8.3.3 Statistical analysis

To maximise sample sizes and increase statistical power, the male and female measurements for each population were combined. The male and female descriptive statistics for the mesiodistal and buccolingual measurements, along with independent sample *t*-tests between males and females within each sample, can be found in **Appendix E.1**. Although the following analyses were conducted on the raw combined data, analyses were also conducted on data in which the male values were adjusted to the female mean (**Appendix E.2**). A comparison of the means from the raw and adjusted data for each dental measurement can be found in **Appendix E.2**. Due to the similarity of values, it was decided to use the raw combined data to prevent any biases introduced through the adjusted data.

Summary statistics of the dental metrics by sample along with dental shape indices were generated in IBM SPSS Statistics for Mac, version 22 (IBM Corp., Armonk, N.Y., USA). Data were tested for normality using the Shapiro-Wilk Test. To assess differences between Nubian populations for the mesiodistal and buccolingual dental measurements, standard ANOVAs were used (significance level $p \le 0.05$). The Hochberg's GT2 *post-hoc* test was used to identify significant pairwise relationships between populations (significance level $p \le 0.05$). Welch's ANOVA and the Games-Howell *post-hoc* tests were used for measurements with a significant Levene's test for normality.

For analysis of the crown shape indices and CVs, the non-parametric Kruskal-Wallis test was used to identify significant differences between populations (significance level $p \le 0.05$). Follow-up Mann-Whitney tests were used to identify significant pairwise relationships between populations (significance level $p \le 0.008$ following a Bonferroni correction for multiple comparisons). For comparisons of CV values within each population by measurement (buccolingual versus mesiodistal) and tooth position (anterior versus posterior) independent samples *t*-tests were used (significance level $p \le 0.05$).

8.4 Results

8.4.1 Mesiodistal and buccolingual metrics

Descriptive statistics for the mesiodistal crown measurements for each population can be found in **Table 8.1** and **Figure 8.2**. The descriptive statistics for the mandibular buccolingual measurements are presented in **Table 8.4** and **Figure 8.3**.

Tooth	Population	n <i>n</i> Mean (mm)		SD	CV
Iı	R12	16	5.09	0.30	5.89
	KAW	6	5.04	0.62	12.30
	KER	2	4.97	0.17	3.42
	KUS	5	4.91	0.52	10.59
	R12	13	5.55	0.73	13.15
T.	KAW	6	5.90	0.47	7.97
12	KER	7	5.60	0.23	4.11
	KUS	5	5.69	0.28	4.92
	R12	14	6.50	0.52	8.00
C	KAW	10	6.78	0.41	6.05
CI	KER	8	5.88	0.75	12.76
	KUS	4	6.46	0.37	5.73
	R12	17	6.51	0.33	5.07
P.	KAW	12	7.17	0.50	6.97
13	KER	16	6.74	0.70	10.39
	KUS	5	6.39	0.63	9.86
	R12	17	6.94	0.54	7.78
P,	KAW	14	7.11	0.38	5.34
14	KER	25	7.01	0.57	8.13
	KUS	6	7.15	0.58	8.11
	R12	19	10.83	0.59	5.45
M	KAW	14	10.87	0.33	3.04
1411	KER	34	10.43	0.89	8.53
	KUS	5	11.17	0.29	2.60
	R12	18	10.73	0.79	7.36
Ma	KAW	15	10.63	0.67	6.30
1412	KER	36	10.71	0.87	8.12
	KUS	6	10.33	0.63	6.10
\mathbf{M}_3	R12	21	10.52	0.93	8.84
	KAW	14	10.62	0.67	6.30
	KER	39	10.63	1.12	10.54
	KUS	6	10.64	0.68	6.39

Table 8.1 Descriptive statistics by sample for the mandibular mesiodistal crown dimensions

R12, Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**, Kerma Ancien (c. 2500–2050 BC); **KER**, Kerma Classique (c. 1750–1500 BC); **KUS**, Meroitic (c. 350 BC–AD 350). *n*, sample size; SD, standard deviation; CV, coefficient of variation





Figure 8.2 Mesiodistal crown measurement (mm) for R12, KAW, KER and KUS populations (a) I₁, (b) I₂, (c) C₁, (d) P₃, (e) P₄, (f) M₁, (g) M₂ and (h) M₃
R12: Sudanese Neolithic (c. 5000–4000 cal BC); KAW: Kerma Ancien (c. 2500–2050 BC); KER: Kerma Classique (c. 1750–1500 BC); KUS: Meroitic (c. 350 BC–AD 350). Error bars represent 95% confidence interval.

223

Tooth	Population	п	Mean (mm)	SD	CV
I ₁	R12	16	3.54	0.59	16.67
	KAW	6	3.36	0.66	19.64
	KER	2	4.93	0.35	7.10
	KUS	4	2.92	0.54	18.49
	R12	13	3.60	0.64	17.78
т	KAW	6	3.18	0.45	14.15
12	KER	6	5.30	0.95	17.92
	KUS	5	3.38	0.72	21.30
	R12	15	5.03	0.53	10.54
C	KAW	10	4.29	0.53	12.35
\mathbf{C}_1	KER	3	5.85	0.66	11.28
	KUS	4	4.39	0.42	9.57
	R12	18	7.59	0.50	6.59
Р.	KAW	12	7.72	0.67	8.68
13	KER	16	7.60	0.66	8.68
	KUS	5	7.27	0.74	10.18
	R12	17	8.22	0.47	5.72
D.	KAW	14	8.23	0.65	7.90
14	KER	25	8.14	0.80	9.83
	KUS	5	7.78	0.22	2.83
	R12	19	10.68	0.64	5.99
M	KAW	15	10.58	0.72	6.81
1411	KER	31	10.46	0.77	7.36
	KUS	6	10.53	0.32	3.04
\mathbf{M}_2	R12	18	10.35	0.62	5.99
	KAW	15	10.19	0.63	6.18
	KER	36	10.41	0.65	6.24
	KUS	6	10.03	0.50	4.99
\mathbf{M}_3	R12	21	9.99	0.84	8.41
	KAW	15	10.17	0.59	5.80
	KER	38	9.98	0.90	9.02
	KUS	6	9.65	0.16	1.66

Table 8.2 Descriptive statistics by sample for the mandibular buccolingual dental dimensions

R12: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). *n*: sample size; SD: standard deviation; CV: coefficient of variation





Figure 8.3 Mean buccolingual crown measurement (mm) for the R12, KAW, KER, and KUS populations (a) I_1 , (b) I_2 , (c) C_1 , (d) P_3 , (e) P_4 , (f) M_1 , (g) M_2 and (h) M_3

R12: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). Error bars represent 95% confidence interval.

Tooth	n	F	р	Hochberg's GT2
I ₁	28	0.23	0.87	-
I_2	30	0.69^{a}	0.58	-
C ₁	35	4.29	0.012	KAW>KER
P ₃	49	4.24	0.01	KAW>R12
P4	61	0.38	0.77	-
M_1	71	4.22^{a}	0.018	KUS>KER ^b
M_2	74	0.44	0.73	-
M_3	76	0.058	0.98	-

Table 8.3 ANOVAs and *post-hoc* tests for mesiodistal tooth measurements

^aWelch Statistic; ^bGames-Howell *post-hoc* test; **R12**: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). ANOVAs significant at $p \le 0.05$ in bold; Hochberg's GT2 *post-hoc* test significant at $p \le 0.05$ for the populations indicated: directional arrow indicates the significant size relationship between the populations. *n*: sample size; *F*: ANOVA test statistic.

There were significant differences between populations in the mesiodistal dimensions of C₁ (F(3,32)=4.29, p=0.012), P₃ (F(3,46)=4.24, p=0.01) and M₁ (F(3,68)=4.22, p=0.018) (**Table 8.3**). Following *post-hoc* analysis, the mesiodistal dimension of C₁ from the KAW sample was significantly larger than KER (p=0.008); KAW was also significantly larger in mesiodistal P₃ than R12 (p=0.013) (**Table 8.3**). For M₁, the KUS sample was significantly larger than the KER sample (p=0.009) (**Table 8.3**).

Tooth	п	F	р	Hochberg's GT2		
		-	-	KAW>KUS		
I_1	27	5.23	0.006	KER>R12, KAW, KUS		
\mathbf{I}_2	30	11.83	<0.001	KER>R12, KAW, KUS		
				KER>R12, KAW, KUS		
C ₁	31	8.89	<0.001	R12>KAW		
P ₃	50	.63	0.60	-		
P ₄	60	3.42 ^a	0.033	R12>KUS ^b		
\mathbf{M}_{1}	70	0.39	0.76	-		
M_2	74	0.90	0.45	-		
M ₃	78	4.17 ^a	0.013	KAW>KUS ^b		

Table 8.4 ANOVAs and post-hoc for buccolingual dental dimensions

^aWelch's ANOVA; ^bGames-Howell *post-hoc*; **R12**: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). ANOVAs significant at $p \le 0.05$ in bold; Hochberg's GT2 *post-hoc* test significant at $p \le 0.05$ for the populations indicated: directional arrow indicates the significant size relationship between the populations. *n*: sample size; *F*: ANOVA test statistic.

There were significant differences in buccolingual measurements between the Nubian samples for I₁ (*F*(3, 24)=5.23; *p*=0.006), I₂ (*F*(3, 27)=11.83; *p*<0.001), C₁ (*F*(3, 28)=8.89; *p*<0.001), P₄ (*F*(3, 57)=3.42, *p*=0.033) and M₃ (*F*(3, 75)=4.17, *p*=0.013) (**Table 8.4**). *Post-hoc*

analyses showed that for I_1 , I_2 and C_1 the KER sample had significantly larger buccolingual dimensions than the other samples (**Table 8.4**). For both I_1 and M_3 , the buccolingual dimension from KAW was significantly larger than KUS. In addition, the buccolingual dimension of R12 dentition was significantly larger than KAW for C_1 and KUS for P_4 (**Table 8.4**).

Mesiodistal			Buccolingual				
I ₁	R12	KAW	KER	I ₁	R12	KAW	KER
KAW	-0.98	-	-	KAW	5.08	-	-
KER	-2.36	-1.39	-	KER	39.27	46.73	-
KUS	-3.54	-2.58	-1.21	KUS	-17.51	-13.1	-40.77
I 2	R12	KAW	KER	I ₂	R12	KAW	KER
KAW	6.31	-	-	KAW	-11.67	-	-
KER	0.90	-5.08	-	KER	47.22	66.67	-
KUS	2.52	-3.56	1.61	KUS	6.11	6.29	-36.23
C ₁	R12	KAW	KER	C ₁	R12	KAW	KER
KAW	4.31	-	-	KAW	-14.72	-	-
KER	-9.54	-13.27	-	KER	16.3	36.36	-
KUS	-0.62	-4.72	9.86	KUS	-12.72	2.33	-24.96
P ₃	R12	KAW	KER	P ₃	R12	KAW	KER
KAW	10.14	-	-	KAW	1.71	-	-
KER	3.53	-6.00	-	KER	0.13	-1.55	-
KUS	-1.84	-10.88	-5.19	KUS	-4.22	-5.83	-4.34
P ₄	R12	KAW	KER	P ₄	R12	KAW	KER
KAW	2.45	-	-	KAW	0.12	-	-
KER	1.01	-1.41	-	KER	-0.97	-1.09	-
KUS	3.03	0.56	2.00	KUS	-5.35	-5.47	-4.42
M_1	R12	KAW	KER	M ₁	R12	KAW	KER
KAW	0.37	-	-	KAW	-0.93	-	-
KER	-3.69	-4.05	-	KER	-2.06	-1.13	-
KUS	3.14	2.76	7.09	KUS	-1.40	-0.47	0.67
M ₂	R12	KAW	KER	M ₂	R12	KAW	KER
KAW	-0.93	-	-	KAW	-1.55	-	-
KER	-0.19	0.75	-	KER	0.58	2.16	-
KUS	-3.73	-2.82	-3.55	KUS	-3.09	-1.57	-3.65
M ₃	R12	KAW	KER	M ₃	R12	KAW	KER
KAW	0.95	-	-	KAW	1.8	-	-
KER	1.05	0.094	-	KER	-0.10	-1.87	-
KUS	1.14	0.19	0.094	KUS	-3.40	-5.11	-3.31

Table 8.5 Percentage difference in mesiodistal and buccolingual mandibular dimensions between populations

R12: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). A reduction in tooth size is indicated by (-).

The percentage differences between samples for both the mesiodistal and buccolingual measurements are shown in **Table 8.5**. The magnitude of change in dental measurements between samples, expressed as percentage differences, have often been calculated in previous dental metric studies (Calcagno, 1989; Christensen, 1998; Hill, 2004). However, these values were not assessed using statistical methods and, therefore, although trends in the magnitude of change can be observed, but the statistical significance of such trends cannot be determined. A negative value indicates that the more recent sample had a smaller measurement in that dimension than the older sample. In addition, the larger the absolute value of the percentage difference, the greater the magnitude of change in the dental measurement between the two samples.

8.4.2 Coefficient of variation analyses

There were no significant differences between mesiodistal and buccolingual CVs for the combined dentition, or when the anterior and posterior dentition were analysed separately (**Figure 8.4**; **Appendix E.3**). However, when mesiodistal and buccolingual CVs were combined and analysed by dental position, within the R12 (t(5.46)=2.68, p=0.04) and KAW (t(5.61)=2.85, p=0.031) samples the anterior dentition had significantly higher CVs than the posterior dentition (**Appendix E.3**).

Overall, there was no significant difference between mesiodistal (H(3)=2.15, p=0.54) and buccolingual (H(3)=1.00, p=0.80) CVs between samples (**Figure 8.4**). There were also no significant differences between samples in buccolingual CVs when the anterior (H(3)=1.51, p=0.68) and posterior (H(3)=6.58, p=0.088) dentition were analysed separately. However, there were significant differences in mesiodistal CVs in the posterior dentition (H(3)=8.61, p=0.035), but no *post-hoc* pairwise comparisons were significant (**Figure 8.4**). In addition, although there were no significant differences between samples when the CVs of the anterior dentition were significantly different (H(3)=1.14, p=0.77), the CVs of the posterior dentition were significantly different (H(3)=11.16, p=0.011). *Post-hoc* analysis showed that the KER sample had higher CVs for their posterior dentition than the KAW population (U=11.5, p=0.004).



Figure 8.4 Population dental metric CV for mesiodistal and buccolingual measurements by (a) anterior dentition (I_1 , I_2 , C_1) and (b) posterior dentition (P_3 , P_4 , M_1 , M_2 , M_3)

R12: Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**: Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma Classique (c. 1750–1500 BC); **KUS**: Meroitic (c. 350 BC–AD 350). Calculated by BL/MD x 100 (BL: buccolingual width; MD: mesiodistal length); CV: coefficient of variation.

8.5 Discussion

This study found that the mesiodistal (MD) length of most of the mandibular dentition did not differ significantly between Upper Nubian samples spanning the period from the Sudanese Neolithic (c. 5000–4000 cal BC) through to the Meroitic (c. 350 BC–AD 350). Statistically significant differences between samples in MD measurements were limited to C₁ (KAW>KER), P₃ (KAW>R12) and M₁ (KUS>KER). Analysis of the percentage differences in MD between samples indicated that there was a slight reduction trend for I₁ and P₃ starting with the KAW sample. Previous studies have shown MD reductions over time in the mandibular canine (Pajević and Glišić, 2017) and third molar (Armelagos et al., 1989; Pajević and Glišić, 2017), but have failed to find significant changes in MD length in mandibular incisors and first/second molars (Huang et al., 2012; Pajević and Glišić, 2017; Pinhasi et al., 2008). It is clear that across populations, there is neither a clear reduction trend nor consensus over which teeth are most affected by changes in MD length.

For the buccolingual (BL) width of the mandibular anterior dentition (I_1, I_2, C_1) , the most striking result was that the agriculturalist KER sample had significantly larger BL width than the other samples. Although not statistically analysed, both males and females from the KER sample also had the highest BL width values for the anterior dentition (Appendix E.1). Minor increases in the anterior dental size have been observed previously (Pajević and Glišić, 2017), particularly between Lower Nubian agriculturalist populations and earlier groups (Calcagno, 1986). Increases in tooth size among more recent human populations have been attributed, by some, to genetic differences (Jacobs, 1994; Mockers et al., 2004), reduced interproximal wear (Calcagno, 1986; Harper, 1994) or the result of improved nutrition and health (Brook et al., 2009; Harris et al., 2001; Lindsten et al., 2002). However, there is no evidence for significant genetic discontinuity between the Nubian populations included in this study, nor is there evidence of significant differences in health based on comparisons of stature (see Appendix A.2). Dental wear analyses in Chapter 7 demonstrated that overall, the KER sample had the most severe dental wear compared with the other samples (particularly in the posterior dentition). Although individuals with severe dental wear were excluded from the dental metric analysis, and interproximal wear is more likely to affect the MD length rather than BL width, it may be that the consistent severity of dental wear observed in the KER sample influenced the BL measurements. In addition, previous research has questioned the overall reliability of anterior teeth BL diameter measurements (Pajević and Glišić, 2017). Within the anterior dentition, there were other statistically significant differences between samples in I_1 (KAW>KUS) and C_1 (R12>KAW).

In contrast to the anterior dentition, there were reduction trends in the BL measurements of the posterior dentition (particularly P₃, P₄ and M₃). Statistically significant differences were found for P₄ (R12>KUS) and M₃ (KAW>KUS). Previous studies have found a decrease in the BL width of posterior dentition over time (Brace et al., 1987; Christensen, 1998; Hill, 2004; Pajević and Glišić, 2017; Pinhasi et al., 2008; Soltysiak, 2007). Although some studies have found a decrease in the BL width for all dentition (Brace et al., 1987; Pinhasi et al., 2008), many have found that posterior dental reduction is more marked than that of the anterior teeth (Hill, 2004; Sofaer, 1973; Sofaer et al., 1971). The differences in dental size trends between the anterior and posterior dentition in the Kerma population have been observed previously, with studies finding that between agriculturalist and intensive agriculturalist populations, there was a levelling of anterior tooth size but a lower, continued rate of reduction for the posterior teeth (Calcagno, 1986, 1989).

There were no significant differences in CVs between MD and BL dimensions for the combined dentition within each sample, or when the anterior and posterior dentition were analysed separately (Pinhasi and Meiklejohn, 2011). However, the anterior dentition (I₁, I₂, C₁) had significantly higher CV values than the posterior dentition (P₃, P₄, M₁, M₂, M₃), which was particularly significant in the R12 and KAW samples. These results are similar to those of Pinhasi and Meiklejohn (2011), who found that European Late Mesolithic and Neolithic populations had significantly higher CVs in the anterior dentition compared with the posterior dentition, but this pattern was not found among later Holocene groups. Relatively lower CVs may indicate the presence of selective pressures acting on the posterior dentition and not the anterior dentition. However, in the scope of this study, it may be that the high CVs in the anterior dentition are reflective of measurement reliability in the anterior dentition and smaller sample sizes.

The results from the MD and BL dental measurements in this study show that there was no universal change in the overall size of the dentition, and most of the diachronic variation in size was observed in the BL dimension. With regards to the IPDE model of dental reduction, changes in dental size are an allometric effect of nutritional stress and body size change (Harris et al., 2001; Larsen, 1981; Macchiarelli and Bondioli, 1986). The IPDE mechanisms for dental reduction predict that over time, dental metric change should occur equally in all areas of the dentition across all periods, and this was not observed in this study. In addition, changes in body stature were not significant between the populations (**Appendix A.2**). With regards to the Probable Mutation Effect (PME) model for dental reduction, the random genetic drift associated with the mechanism may express itself in random degrees of dental reduction such as are observed in this study. However, the observation that the BL measurements and the posterior dentition were the most affected is likely too specific and function-related to be a result of the PME mechanism.

Some researchers have attributed the specific pattern of dental reduction observed over time to the functional-masticatory hypothesis, as part of the Selective Compromise Effect (SCE) model (Armelagos et al., 1989; Pinhasi et al., 2008; Soltysiak, 2007). This model suggests that in an environment of high cariogenic soft food consumption (such as following the agricultural transition), there is a selective tendency toward smaller teeth and jaws to avoid malocclusions and dental diseases that could be potentially life-threatening (Calcagno, 1989; Christensen, 1998; Larsen, 2015). The SCE model does not necessarily predict a universal reduction in dental size over time, but rather that selective pressures will differentially influence specific dimensions and teeth. In fact, the SCE predicts that the MD measurement (reflecting the length of the dentition and, therefore, influencing malocclusion) or the posterior dentition (most likely to be affected by dental caries) will be the measurements most affected by a selective force. Although studies of malocclusion have not been conducted for the Nubian samples in this study, there was no evidence of dental crowding or malocclusion in any of the populations. Therefore, it seems that malocclusion and dental crowding were unlikely to be strong selective forces in these samples from ancient Nubia.

The fact that the breadths of the dentition were decreasing rather than the mesiodistal dimensions (and particularly within the posterior dentition) supports the caries resistant part of the SCE model (Christensen, 1998; Greene, 1970). If malocclusion was the primary selective pressure, lengths of the teeth (MD) should be more affected than breadths (BL) (Calcagno and Gibson, 1991; Pinhasi et al., 2008; Sofaer, 1973). Therefore, for the Nubian samples in this study, the negative effects of caries and periodontal disease may have been a more significant selection pressure than malocclusions. The data presenting percentage differences in tooth dimensions over time shows that the largest reductions, particular in BL width, occurred between the KER and the KUS samples. An increasing reliance on agricultural products in the later populations (KER and KUS) may have influenced selection for smaller teeth in the KUS population, supporting the caries resistance hypothesis. However, the results of this study did

not show clear evidence of selection for smaller buccolingual dimensions (as evidenced by low CV values) nor was there a uniform reduction trend in this dimension.

Small sample sizes for the populations also prevented separate analysis of dental size variation for males and females (descriptive statistics and *t*-tests for male and female dental measurements can be found in **Appendix E.1**). For many of the dental measurements, there were no statistically significant differences between male and female dental measurements in each sample. The significant differences that were seen were primarily in the KAW sample, and in the mesiodistal M₂ and M₃ measurement (**Appendix E.1**). Previous studies have found that males, on average, have larger teeth (as quantified by maximum BL and MD crown or cervical lengths) than females, although the values do overlap (e.g. Alvesalo, 1971; Ateş et al., 2006; Cardoso, 2008; Garn et al., 1967; Kondo et al., 2005; Mitsea et al., 2014; Pajević and Glišić, 2017; Schwartz and Dean, 2005; Sorenti et al., 2019; Stroud et al., 2014; Townsend and Alvesalo, 1985a,b; Zakrzewski, 2012; Zorba et al., 2011). The canines are the most dimorphic teeth, and male canines can be between 5–10% larger than those of their female counterparts (Pajević and Glišić, 2017; Paramkusam et al., 2014; Singh et al., 2015; Viciano et al., 2015). The degree of sexual dimorphism is lowest within the anterior dentition (excluding the canine) (Hillson, 1996, 2005; Schmidt, 2016).

Previous studies have shown that males and females demonstrate different trends in dental size variation over time. The majority of the significant results and greater size reduction is often observed for females (Calcagno, 1989; Hill, 2004; Larsen, 1981) and this has been attributed to subsistence transitions more significantly affecting the diet of females compared with males (Larsen, 1981). Results from the oral health analyses in **Chapter 7** found that females from the R12, KER and KUS populations had a higher prevalence and severity of dental caries than their male counterparts (although this observation was statistically significant only in the KUS population). The observed dental metric difference between males and females may therefore be influenced by differences in dietary consumption (as inferred by patterns of oral health) (Hinton et al., 1980; Perzigian, 1976).

Analyses of dental metric change over time were conducted on both the raw combined measurements (presented in this chapter) and the combined measurements in which the male values were adjusted to the female mean (following the methodology described in Ackermann et al., 2006; **Appendix E.2**). The analysis of each set of data produced similar results, although there were more significant differences in the MD measurements for the raw combined data. As using adjusted data for analyses introduces an unknown level of error into interpretation, it
was decided to primarily focus on the results that used the raw combined data. A limitation of this approach is that the distribution of males and females for each dental measurement may have influenced the mean value. However, there were few significant differences between the male and female values for each of the dental measurements. In addition, due to the similarity of the results based on the raw or adjusted data, it is expected that any sex-related influence on the observed results was small and did not have a significant impact on the overall interpretation. Further research is required to analyse the potential differences in dental metric values and trends between males and females in the Nubian populations in this study.

In this study, only mandibular dentition was analysed to identify diachronic changes in dental metrics between the Upper Nubian samples. Previous studies have observed different patterns of dental metric change between the maxillary and mandibular dentition (Calcagno, 1986; Frayer, 1978; Pajević and Glišić, 2017), and specifically that dental reduction in the maxilla often exceeds that of the mandible (Brace et al., 1987; Hill, 2004; LeBlanc and Black, 1974; Lukacs, 1985; Sofaer, 1973; Sofaer et al., 1971; Wolpoff, 1971). Since the growth of the mandible is more plastic than the maxilla (Kieser, 1990), it may be able to adapt to accommodate larger teeth and prevent dental crowding. In contrast, malocclusion in the maxilla caused by disparate reduction trends in the dentition and bony structure (Kieser, 1990; Larsen, 2002) can cause serious dental infections, inducing a stronger selection pressure for smaller teeth in the maxilla. Analysing diachronic variation in the size of the maxilla and maxillary dentition was not possible in this study due to the poor preservation of the crania of these populations. However, based on the evidence from other studies, it is likely that there would be different dental metric trends observed in the mandibular and maxillary dentition of the Nubian populations in this study.

Many studies conclude that the majority of significant dental reduction in human populations occurred at the end of the Pleistocene (Brace et al., 1987; Calcagno, 1986, 1989; Calcagno and Gibson, 1988; Frayer, 1977; Hill, 2004; Sciulli and Mahaney, 1991). Brace and colleagues (1987, 1991) have argued that improvements in food preparation technology had a larger impact on tooth size reduction than changes in dietary composition. For example, studies using populations from Lower Nubia have demonstrated substantial dental reduction between Nubian Mesolithic populations and more recent groups (Brace and Mahler, 1971; Calcagno, 1986; Greene et al., 1967). However, a Late Palaeolithic/early Holocene population from Upper Nubia was not available for inclusion in this study. Therefore, the populations included

here may fail to capture early Holocene dental reduction in Upper Nubia caused by the production of pottery and increase in food processing (Sciulli and Mahaney, 1991).

In this study, the observed dental reduction over time was primarily observed in the posterior dentition and may be a result of selection against dental infection as hypothesised in the caries resistance portion of the SCE model (Armelagos et al., 1989; Calcagno, 1989; Pinhasi et al., 2008; Soltysiak, 2007). However, the high dental wear rates observed in the KER population indicate that the diet of Upper Nubian agricultural populations may have been more abrasive than other agricultural populations around the world (Judd, 2001a; Leek, 1966, 1972, 1973; Smith, 1984). Although research tends to focus on how differences in dietary hardness versus softness influences dental metrics (e.g. Corruccini, 1991; Larsen, 2015; Lieberman et al., 2004a), there are fewer studies that focus on the role of dietary abrasiveness on dental size. However, there is some evidence that a significant reduction in dietary abrasiveness, without a concomitant change in the hardness of food consumed, can initiate dental reduction (Hill, 2004). Therefore, it is possible that if the diet consumed by the Upper Nubian populations was abrasive, this may have counteracted some of the selection pressure to prevent dental caries, and may explain why the dental reduction trends measured in these samples are not as significant as reported elsewhere. More research is needed to understand the relationship between dietary abrasiveness, cariogenicity and dental size.

8.6 Conclusions

In this study, mesiodistal and buccolingual dental dimensions of the mandibular teeth were measured to study diachronic changes in dental crown size in relation to dietary shifts in Upper Nubia. The most pronounced trend was found in the BL diameter of the posterior dentition, with the Neolithic R12 sample demonstrating the largest BL widths for the mandibular posterior dentition. Notably, the agricultural sample from KER had the largest BL dimensions in the mandibular anterior dentition. A consistent temporal change in the MD diameter of the anterior and posterior mandibular dentition was not identified. It is possible that due to changes in food processing technology, the majority of the substantial dental reduction in the Upper Nubian populations occurred before the Sudanese Neolithic period and has not been captured by the populations included in this study. In addition, the abrasive diets of the agricultural populations in Upper Nubia may have limited selection pressures for smaller, caries-resistant dentition in place of larger teeth that could resist dental wear. Dental size

change can be difficult to explain without context from other analyses, due to the possible multifactorial effects on tooth size. It is important to analyse tooth size change within the context of mandibular size and oral health, which will be further explored in the Discussion in **Chapter 9**.

9 Discussion

9.1 Introduction

The present study assessed and quantified the differences in mandibular morphology and robusticity, oral health and dental metrics between populations from ancient Nubia. The populations studied represent cultural periods from the Late Palaeolithic through to the Meroitic, covering the transition from hunting and gathering, to early agro-pastoralism, and through agricultural intensification. The overarching goal of this study was to assess how patterns of mandibular morphology, dental size and oral health changed over time alongside shifting subsistence strategies. The first section of this chapter includes a brief summary of the main results, with reference to the research objectives outlined in **Chapter 4** for the mandibular linear measurements, mandibular cross-sectional geometry, oral health and dental metric analyses (**Chapters 5–8**). Secondly, the results from the above analyses are discussed collectively to form a detailed picture of the relationship between mandibular and dental morphological change and subsistence strategy in ancient Nubia. The chapter concludes with a discussion of the limitations of this dataset and presents potential avenues for future research.

9.2 Revisiting hypotheses and results

9.2.1 Mandibular osteometrics

Mandibular linear measurements were used to explore variation in mandibular size and shape associated with changes in dietary composition and subsistence strategy in ancient Nubia. Based on evidence from animal experiments, the clinical literature and previous archaeological research, it was predicted that within these Nubian populations, an increasing reliance on agricultural products would be associated with mandibular gracilisation due to an overall decrease in biomechanical stress. Due to the gradual adoption of agricultural practices in ancient Nubia, it was predicted that the most notable differences in mandibular size and shape would be observed in the comparison of the hunter-gatherer population (JSA) with the later Upper Nubian populations. This prediction was supported by the results of this study, which showed that the majority of the statistically significant differences between samples in mandibular linear measurements were between the JSA and the later samples from Upper Nubia. Overall, the mandibles from JSA were longer, wider and had a more upright and larger ramus (both in width and height) than the other samples. In addition, the mandibular body of the JSA sample was taller than the other populations at the symphysis, mental foramen and molar region.

It was also predicted that changes in mandibular shape would continue over time within the more recent Upper Nubian samples, particularly in areas of masticatory functional significance, such as the ramus and gonial region. Although this study found fewer significant differences between the Holocene samples, there were clear trends over time for a reduction in the overall length of the mandible, decreased mandibular body height in the molar region, decreased width of the ramus and a more obtuse gonial angle. These metric results were not just an allometric reflection of concurrent decreases in body size and stature, because body size and stature were not significantly different between populations (**Appendix A.2**). In fact, the pattern of morphological change observed in the mandible was concentrated in functionally important regions, indicating that the mandible adapted specifically, rather than systemically, to variation in masticatory function.

When males and females were analysed separately, it was expected that males would have higher mandibular metric values due to larger overall body size. This prediction was supported for the majority of the measurements used in this study (although the differences between males and females were not always statistically significant). The notable exception to this trend was observed for the degree of the gonial angle, in which females had consistently more obtuse gonial angles compared with their male counterparts. A second hypothesis was that males and females would each display unique morphological trends, due to variation in dietary intake and/or a result of differential osseous response to biomechanical stimulus. In fact, males and females displayed similar morphological reduction trends, although the differences between samples were often more pronounced between males. In particular, the difference between the JSA and the later samples was more pronounced in males than in females. It is important to note that the sample sizes used in the sex analyses were often small and unequal between males and females. Therefore, it was difficult to assess the statistical significance of many of the sex-specific trends.

The results of this study support the trends observed in previous research showing that craniofacial gracilisation was associated with the adoption of agriculture in Lower Nubia (Carlson and Van Gerven, 1977; Galland et al., 2016; Martin et al., 1984; Small, 1981), and around the world (e.g. Katz et al., 2017; May et al., 2018; von Cramon-Taubadel, 2011). Importantly, the mandibles from the Upper Nubian samples were not just size-reduced versions

of the JSA mandibles, but continued to demonstrate a complex process of morphological change with more subtle dietary shifts. The differences in mandibular morphology within these samples were specific to functional regions of the mandible, such as the mandibular body and the ramus, which supports the idea that variation in masticatory loading associated with subsistence strategy transitions results primarily in localised shape changes relating to the functional areas of the mandible (Paschetta et al., 2010).

9.2.2 Mandibular cross-sectional geometry (CSG)

The long-term effect of dietary transitions on mandibular strength and robusticity was assessed by calculating biomechanical properties from cross-sections at the symphysis and in the molar region. Due to the relationship that has been observed between dietary variation, biomechanical loading and measures of overall mandibular size and robusticity (Antón et al., 2011; Hinton and Carlson, 1979; Holmes and Ruff, 2011; Kaifu, 1997; von Cramon-Taubadel, 2011), it was predicted that changes in dietary composition spanning subsistence transitions in ancient Nubia would lead to an overall decline in CSG values, indicative of a reduction in mandibular strength and robusticity. Within the symphysis, the hunter-gatherer sample (JSA) had significantly higher I_x and I_{max} compared with the other populations (reflective of greater symphyseal rigidity to vertical bending in the coronal plane; Daegling, 1989). However, between the later Upper Nubian samples, the symphyseal CSG properties remained consistent over time. In contrast, within the molar region there was a decline in I_x and I_{max} across all the samples. Molar I_x and I_{max} values represent the ability to resist parasagittal bending strains. In addition, the molar I_{y}/I_{x} ratio approached the value of one over time (reflecting the increasing circularity of the cross-section), driven largely by a reduction in I_x values. These results reflect a decrease in sagittal bending rigidity relative to transverse bending rigidity over time (represented by I_{y}) (Daegling, 1989; Daegling and Grine, 1991; Hylander, 1988; van Eijden, 2000).

When males and females were analysed separately, the results largely mirrored those observed for the pooled-sex analysis. However, males tended to have a more pronounced biomechanical reduction in terms of absolute values, particularly regarding symphyseal strength. Within the symphysis in males, the largest decrease in biomechanical strength occurred between the JSA and R12 samples; although it is interesting to note that the I_x , I_{max} and *J* CSG properties subsequently increased in the later samples. In contrast, for females the smallest symphyseal CSG values were not in the R12 sample, but in the KAW and KUS

samples. For both males and females, there was a reduction in the sagittal bending strength of the molar region (I_x and I_{max}), starting with the R12 sample.

The results from this study support the hypothesis that changes in dietary composition significantly affected mandibular strength and robusticity in the ancient Nubian samples analysed in this study. Overall, levels of mandibular rigidity decreased over time, particularly with respect to parasagittal bending of the molar region of the mandible (I_x and I_{max}). However, not all biomechanical properties were significantly different between samples, suggesting that the human mandible adapts specifically, rather than systemically, to the biomechanical stress produced during mastication.

9.2.3 Oral health

This portion of the study analysed the frequency and severity of dental pathologies (including dental wear, caries, calculus, linear enamel hypoplasia (LEH) and periodontal disease in the Upper Nubian samples (R12, KAW, KER and KUS). Based on the observations from other studies of oral health around the world, it was expected that these Nubian samples would experience worsening oral health alongside intensifying agricultural practices. Overall, the results from this study supported this hypothesis, as the frequency and severity of many of the oral pathologies included in this analysis increased with agricultural intensification. In particular, the agricultural Kerma Classique (KER) sample had the highest rates of dental caries and periodontal disease. Although rates of dental pathology remained high in the Meroitic (KUS) sample, especially with regards to dental caries, there was a slight improvement in comparison with the preceding KER sample. Improved oral health in the KUS sample may be reflective of increased agricultural crop diversification in the population, which included the introduction of cariostatic domesticated sorghum (Fuller, 2004a; Rowley-Conwy, 1989; Wetterstrom, 1993). It is important to note that compared with the other population samples, the KER sample had the highest proportion of complex, posterior dentition. As these teeth are the most susceptible to dental caries formation, the high caries frequency observed in the KER sample may simply reflect the tooth composition of the sample. Therefore, inferences based on these results may be limited.

In many regions of the world, dental wear has been shown to decrease in agricultural populations due to the increased reliance on softer carbohydrates (Armelagos and Rose, 1972; Eshed et al., 2006; Lubell et al., 1994). Therefore, it was predicted that as Nubian populations

increased their consumption of domesticated cereal products, the overall severity of dental wear would decrease. However, the KER sample had the most severe dental wear of all the populations (particularly in the posterior dentition). Previous studies have also observed severe dental wear in agricultural Nile Valley populations (Beckett and Lovell, 1994; Vagn Nielsen, 1970; Wells, 1975), and this may be reflective of the introduction of abrasive particles through bread consumption; a food product introduced by the Egyptians during the Kerma Moyen period (Judd, 2001a; Leek, 1966, 1972, 1973; Smith, 1984; Soames and Southam, 1998). The Sudanese Neolithic (R12) sample had relatively high dental wear in the anterior dentition (particularly C₁ and P₃), comparable to the KER sample. Lingual surface attrition of the maxillary anterior teeth (LSAMAT) has been observed in individuals from the R12 population (Crivellaro 2001; Judd, 2012). The presence of LSAMAT may indicate that individuals from R12 engaged in paramasticatory behaviours that may have also caused severe wear in the anterior mandibular dentition observed in this R12 sample. The Kerma Ancien (KAW) and Meroitic (KUS) samples had the lowest levels of dental wear.

Previous studies have found that early agriculturalists often have higher levels of physiological stress and poor health (inferred by LEH frequency) compared with their non-agriculturalist predecessors (Cohen, 1989; Cohen and Armelagos, 1984; Larsen, 2006; Starling and Stock, 2007; Steckel and Rose, 2002). Based on this previous research, it was hypothesised that the incidence of LEH would be lowest in the Meroitic sample (KUS), due to improving health following urbanisation and dietary diversification. The results showed that the KAW sample had the highest frequency of LEH and the KUS sample had the lowest, but there were no statistically significant differences between populations. The high frequency of LEH in the KAW sample may be reflective of their low socioeconomic status, especially when compared with the individuals from the urban Kerma centre (KER) (Adams, 1977; Welsby, 1996b). However, the relationship between LEH and overall health is not fully understood (Cohen, 1977), and it was beyond the scope of this study to identify the driver behind the physiological stress that may have induced LEH development in these samples. In addition, dental calculus severity was highest within the KAW sample, which may reflect the prevalence of animal protein (meat and/or secondary products) in the diet of this rural, primarily herding population (Iacumin et al., 1998).

Differences in oral health between males and females was analysed because previous research has shown that women's oral health was more negatively affected by the onset of agriculture than males, particularly with regards to the frequency of dental caries (Beckett and

Lovell, 1994; Frayer, 1989; Hillson, 1979; Walker et al., 1986). Divergent oral health trends in males and females have been previously explained using both behavioural (division of labour and/or differential access to dietary resources) and/or biological factors (fertility, hormones and/or genetics) (Carvalho et al., 2019; Lukacs, 2011). This study found that in every population, females had higher dental caries severity than males (although this trend was only statistically significant in the KUS sample). In addition, females had higher rates of LEH in the agricultural KER sample than males. Dental wear severity was similar between males and females from the same population. It is likely that a complex set of genetic, reproductive and cultural factors all contributed to the observed differences in male and female oral health in this study. Future research should concentrate on sex-specific analysis of dental calculus and isotopic signatures to directly compare the diets of males and females.

It is important to note that dental wear and most of the dental pathologies analysed in this study are age-related processes, in which older individuals will have a more severe/higher frequency of these pathologies compared with younger individuals. Therefore, the age distribution of each sample, and how this distribution compares between samples, is important to interpreting the observed prevalence and severity of these pathologies. The KAW and KUS samples had a higher proportion of younger individuals for many of the analyses, and the R12 sample had a higher proportion of older individuals. The age distribution in the KER sample was relatively even. Differences in age distribution may impact the results from this oral health analyses, and therefore, caution is needed when interpreting the results.

9.2.4 Dental metrics

To evaluate the relationship between tooth size variation and changes in subsistence strategy, this study analysed the mesiodistal (MD) and buccolingual (BL) dimensions of the mandibular dentition from the Upper Nubian sample populations (R12, KAW, KER and KUS). Previous studies have observed dental size reduction associated with changes in food processing technology and dietary consumption (e.g. Calcagno, 1989; Hill, 2004; Pinhasi et al., 2008). Therefore, it was predicted that within this study, the size of the mandibular dentition would reduce over time with agricultural intensification, and the smallest dentition would be observed in the Meroitic (KUS) sample. If dental reduction occurred, this trend was expected to best fit within the Selective Compromise Effect (SCE) model, which suggests that in an environment of highly cariogenic and soft food consumption (such as following the agricultural transition), there would be a selective tendency towards smaller teeth and jaws to avoid the

potentially life-threatening complications caused by dental crowding, malocclusions and dental disease (Calcagno, 1989; Christensen, 1998; Larsen, 2015).

Surprisingly, for the anterior dentition $(I_1, I_2 \text{ and } C_1)$, the agriculturalist KER sample had significantly larger BL width than the other populations. Minor increases in the size of anterior dentition over time has been observed previously in Lower Nubia (Calcagno, 1986), as well as in other areas of the world. This increase has been attributed to possible genetic differences (Jacobs, 1994; Mockers et al., 2004), reduced interproximal wear (Calcagno, 1986; Harper, 1994) or the result of improved nutrition and health in later populations (Brook et al., 2009; Harris et al., 2001; Lindsten et al., 2002). However, caution is required when interpreting these results, as overall reliability problems of BL measurements of the anterior dentition (Pajević and Glišić, 2017) coupled with relatively high dental wear may have influenced the KER measurements. Non-significant reduction trends in BL width were present in the posterior dentition (particularly P₃, P₄ and M₃), similar to those observed in previous studies (Brace et al., 1987; Christensen, 1998; Hill, 2004; Pajević and Glišić, 2017; Pinhasi et al., 2008; Soltysiak, 2007). There was no overall trend in the MD length of the mandibular dentition, although there was a slight reduction observed for I_1 and P_3 . As such, the overall length of the dental arch (estimated through MD length measurements) did not change significantly over time. Unfortunately, small sample sizes prevented statistical analysis of dental size variation independently for males and females.

This study did not find a consistent dental reduction trend over time in the Nubian samples. It is possible that the majority of the significant dental reduction occurred before the Sudanese Neolithic, as a result of improvements in food processing technology, rather than due to the changes in dietary composition over the agricultural transition (Brace et al., 1987, 1991; Sciulli and Mahaney, 1991). In addition, other studies have found that maxillary dental reduction exceeds that of the mandibular dentition (Brace et al., 1987; Hill, 2004; LeBlanc and Black, 1974; Lukacs, 1985; Sofaer, 1973; Sofaer et al., 1971; Wolpoff, 1971), so future research should include analysis of maxillary dentition for the populations in this study.

The results from this study do not fit completely within any established dental reduction mechanism. However, the dental size trends that were observed within these samples do indicate that mandibular dental breadth was decreasing more than length. Therefore, it is unlikely that any problems caused by dental crowding and malocclusions were selective forces for dental size change. It may be that selection for smaller dental size to limit the incidence of dental caries may have been affected by the abrasive diets of the agricultural populations, in which large teeth were still needed to resist dental wear. It is important to note that these dental size trends may also simply be reflective of normal human dental variation, rather than the result of a specific adaptive force.

9.3 Mandibular morphological change in Upper Nubia

It was expected that the hunter-gatherer JSA sample would be clearly morphologically divergent from the Upper Nubia population samples in both mandibular size and robusticity. As predicted, this study showed that the JSA mandibles had the largest mean for both linear measurements and raw CSG compared with the Upper Nubian populations. However, the mandibles of the Dongola Reach samples were not just size-reduced versions of the earlier JSA mandibles, and the observed diachronic differences in morphology within these samples were associated with areas functionally relevant to mastication. This was particularly apparent in analysis of the size-standardised CSG. In contrast to the raw values, the size-standardised I_{y} and I_{min} values were not significantly different between the JSA and later samples within the symphysis or molar region. This result supports the findings from the mandibular metric data, in which there were no significant differences in symphyseal or molar body breadth between the JSA and later samples. In contrast, there were significant differences in the size-standardised I_x and I_{max} values at the symphysis between the JSA and later samples, as well as a temporal reduction trend in I_x and I_{max} values in the left molar region (particularly evident following the R12 sample). Again, these CSG data support the findings from the mandibular metric results, which showed a significant decrease in the height of the symphysis and mandibular body in the molar region over time.

The observation that size-standardised I_x and I_{max} values at the symphysis did not change between the Holocene populations may indicate that these measures were not only reflective of adaptation to mechanical loading, but tied more closely to overall variation in lower facial shape (i.e. brachyfacial or dolichofacial; Holton et al., 2014). Previous research has also shown that although symphyseal form may be influenced by biomechanical loading to a degree, morphological adaptation to masticatory loading in the symphysis is, in fact, limited (Carlson and Van Gerven, 1977; Fukase and Suwa, 2008; Kaifu, 1997; Martin and Danforth, 2009; Mays, 2015; Moore et al., 1968; Pinhasi et al., 2008; Rando et al., 2014; Smith et al., 1984). Therefore, CSG variation in the mandibular molar region may better reflect adaptation to masticatory loading. Notably, size-standardised TA (total area of the cross-section) was not significantly different between any of the samples. Therefore, although the shape of the mandibular body was changing significantly (particularly in I_x , I_{max} and height), there was no change in the overall size of the cross-section. Modification in cross-sectional shape was also demonstrated by the increase in the robusticity and shape indices within the molar region (I_y/I_x and breadth/height) over time. High values in these indices have been associated with a greater resistance to the strain caused by transverse bending and torsion (Daegling, 1989; Daegling and Grine, 1991; Hylander, 1988; van Eijden, 2000). However, in this case the increasing circularity of the molar region was driven by a decrease in sagittal bending rigidity (represented by I_x and I_{max}), and the values representative of transverse bending rigidity (I_y and I_{min}) do not change significantly over time.

The period from c. 5000 cal BC to AD 350 in Upper Nubia represented a period of increasing production of, and reliance on, cereal agriculture. This study examined mandibular and dental morphological variation in samples from four Dongola Reach populations (R12, KAW, KER and KUS). Within the Dongola Reach samples, there was a reduction of the overall length of the mandible (ML3 and LML), corpus height in the molar region (LH), and width of ramus (LRB), as well as an increase in the gonial angle (GA).⁸ Results from animal and clinical studies have shown that both bite force magnitude and masticatory muscle size are inversely correlated with the size of the gonial angle (Ingervall and Helkimo, 1978; Kasai et al., 1994, 1997; Kiliaridis et al., 1995; Ringqvist, 1973; Sondang et al., 2003; Throckmorton et al., 2000; Tuxen et al., 1999). Therefore, an increasingly obtuse GA over time is reflective of smaller masticatory muscles and a reduction in bite force. Concurrently, a decrease in the overall width of the ramus (LRB) was observed, and this indicates a smaller attachment area for the masseter and medial pterygoid and, indirectly, reflects smaller overall masticatory muscles.

This study showed that although there were reductions both in mandibular metric and size-standardised CSG over time, these reductions did not necessarily occur concurrently. Comparison of the mandibular metric and size-standardised CSG reduction trends indicate that the overall size of the mandible (mandibular metric values) reduced before strength relative to size (size-standardised CSG). Specifically, the overall length of the mandible, height of the

⁸ ML3: mandibular length measured from the infradentale to the midsagittal point of the goniongonion chord (BGoB); LML: lower mandibular length measured from the gnathion to the midsagittal point of the condyle-condyle chord (BCoB); LH: height of the left mandibular body measured between M₁ and M₂; LRB: least ramus breadth measured perpendicularly to the height of the ramus; GA: gonial angle formed by the inferior border of the corpus and the posterior border of the ramus.

mandibular corpus in the molar region and the width of the ramus decreased steadily from the JSA sample through the Upper Nubian samples. In contrast, the reduction in size-standardised CSG (particularly in the molar region) and the increase in the size of the gonial angle was most apparent when comparing the R12 sample with the later samples. The observation that cross-sectional strength relative to size and gonial angle measurements were similar between the JSA and R12 samples may reflect that despite evidence for the beginnings of cereal cultivation (Madella et al., 2014; Out et al., 2016), the R12 population still relied primarily on wild plant and animal consumption.

The ancient Nubians have long been associated with a 'porridge and pot' diet, which was in contrast with the 'bread and oven' diets characteristic of the ancient Egyptian and Near Eastern populations (Haaland, 2007). Sorghum porridge, and most likely beer, were common in the ancient Nubian diet from at least the Sudanese Neolithic through to the Meroitic period (Haaland, 2007). Over time, the increasing presence of ovens found in Nubian settlements, particularly during the Kerma period, indicates not only changing diet, but also the growing incorporation of Egyptian staple food products into the diet of the ancient Nubians (Fuller and Gonzalez Carretero, 2018). In particular, during the Kerma period, bread was baked primarily for elite consumption and for use during funerary rituals (Haaland, 2012). Therefore, higher status individuals may have had more access to Egyptian-style bread and beer (made from emmer wheat and barley), and lower socioeconomic individuals continued to rely on the traditional sorghum porridge and beer (Haaland, 2012). The differences observed in mandibular morphology and oral health in the later Nubian samples included in this study, particularly between the KAW, KER and KUS samples, may reflect differences in diet due to the socioeconomic composition of the individuals within each sample. Additional analyses of similar populations will be required to understand if the trends observed in this study are reflective of a broader picture of dietary and morphological change, or are reflective of the hierarchical composition of each population involved in this research.

Dietary toughness, as opposed to dietary abrasiveness, is also important to differentiate, as each has a unique effect on the overall biomechanical strain on the mandible (Van Ankum, 2018). In general, tough foods, such as meat and fibrous plants, require higher bite force and more chewing cycles than abrasive foods (Van Ankum, 2018). Bite force magnitude is proportional to masticatory muscle strain and the resulting magnitude of biomechanical stress on the mandible (Ingervall and Bitsanis, 1987; Ledogar et al., 2016). High levels of dental wear within a population do not necessarily indicate a mechanically tough diet and repetitive

masticatory loading, as abrasive diets can induce high levels of dental wear per chew cycle (Antón et al., 2011). Overall, the KER sample in this study had the most severe dental wear compared with the other Upper Nubian samples, but the results from the mandibular metric and CSG analyses showed that the KER sample fits within the general reduction of mandibular size and biomechanical robusticity over time. Different mechanical signals from cross-sectional data compared with dental wear patterns has been observed before (Organ et al., 2006). This highlights the importance of using a holistic approach to infer diet in past human populations; in this case, one that uses evidence from both dental wear patterns and bone morphology to distinguish between dietary toughness and abrasive, and overall levels of masticatory loading. Future research should include dental microwear analysis as this may be able to differentiate between wear due to mechanically tough diets and wear due to an abrasive diet.

To infer bite force based on mandibular morphology, the absolute size of the mandible may not be as important as the length to width ratio. Kieser and colleagues (1996; 1999) have shown that for a given jaw width, the longer the mandible the lower the bite force on the working-side. Between the Upper Nubian samples, the absolute widths of the mandible and dental arch remained relatively constant, while the overall length reduced over time. Although not always significant, for most of the length to width ratios (ML1, ML2 and ML3 to BCoB and BGoB; LML/BGoB), the highest ratio was found in the R12 sample, and declined within more recent agricultural samples to the JSA value or even lower. If one assumes that the long mandibles of the JSA reflect high bite force then, taken in isolation, the length/width ratios would appear to indicate that bite force efficiency increased over time in the Upper Nubian samples.

However, the relationship between external morphology and biomechanical output is not straight-forward. By using finite element analysis (FEA) molar biting simulations, Stansfield and colleagues (2018) found that although the shorter bodies of 'modern' mandibles were more efficient at bite force generation relative to a sample of Upper Palaeolithic mandibles, the modern mandibles were less able to resist the biomechanical strains produced during mastication. Specifically, the modern mandibles with more obtuse gonial angles experienced higher levels of wishboning strain throughout the mandibular corpus compared with the Upper Palaeolithic mandibles (Stansfield et al., 2018). This result demonstrates that during mastication, the mandible works as a functional unit, and it can be difficult to interpret the biomechanical impact of changing one mandibular parameter, such as a length or width measurement, in isolation. Therefore, data including measures of external morphology and internal strength and rigidity are needed to make a complete interpretation of mandibular biomechanics. In this study, although the decreasing length/width ratios of the Upper Nubian samples may create the optimal anatomy for greater biting efficiency in an FEA simulation, the concomitant reduction in size-standardised CSG properties and increase in gonial angle indicate that these mandibles were likely less able to resist bending stresses due to mastication. Modern mandibular morphology is likely to be reflective of overall patterns of facial reduction and retraction, rather than an adaptation to increase biting efficiency (Stansfield et al., 2018).

Dental crowding and malocclusion in agricultural and modern populations has been observed in previous studies (e.g. Corruccini and Beecher, 1982; von Cramon-Taubadel, 2011). This observation has often been attributed to the softer/more processed diets of agriculturalists leading to a decrease in mechanical loading that reduced the rate of growth and development of the bony jaw in comparison with the related dentition (Garn et al., 1968; Lieberman et al., 2004; Shea and Gomez, 1988; Vinyard et al., 2019; Wolpoff, 1985). As expected, this study showed that the bony structure of the mandible was more responsive to changes in mechanical loading than the mandibular dentition. However, for these samples, the gracilisation of the mandible without a concomitant reduction in dental size did not appear to lead to dental crowding or malocclusion. This may be because within the Upper Nubian samples, the overall length of the mandible was decreasing, but the dental arch length (DAL) did not decrease significantly.

Furthermore, despite some studies showing that the spatial requirements of the developing dentition can influence mandibular size and shape (in addition to biomechanical factors; Corruccini and Beecher, 1982; Smith, 1983; Wolpoff, 1975; Wood, 1978), this study did not find a clear relationship between posterior dentition width (BL) and mandibular corpus morphology. Despite slight BL width reduction trends for P₃, P₄ and M₃, indicators of corpus robusticity and size in the molar region (i.e. I_y/I_x) declined at a relatively faster rate than the BL width of the dentition. Other studies have also found little evidence for a direct relationship between molar width (BL) and distal mandibular corpus 'robusticity' (breadth/height of the corpus; Daegling and Grine, 1991; Plavcan and Daegling, 2006). More research is needed to understand the developmental integration of the jaw and dentition, and how biomechanical stress during development can influence the epigenetic mechanisms of growth in the masticatory complex (Boughner and Dean, 2004; Corruccini, 1984; Lieberman, 2011).

The results from this study support the conclusions of the masticatory-functional hypothesis (Carlson and Van Gerven, 1977), and identify the mechanism of phenotypic plasticity to explain the overall gracilisation of the mandible following the shift to agricultural practices in ancient Nubia. Although the populations in this study were selected to limit the influence of gene flow on the morphological results, it is beyond the scope of this study to determine if the morphological changes observed were completely the result of adaptation, or whether other differences between the populations might be influencing the morphology. Although there is much still to be discovered about the relationship between mandibular morphology and diet in humans, this study provides a better understanding of the role of subsistence change in driving patterns of mandibular morphological variation in human populations.

9.3.1 Sex-specific mandibular morphological trends

When it was possible in this study, males and females were analysed separately to identify sex-specific trends. The differences that were observed between males and females included both the magnitude and chronological timing of certain mandibular morphological trends. Regarding mandibular metrics, the major morphological distinction for males occurred between the hunter-gatherer (JSA) and the R12/KAW samples. For females, although JSA still had the highest mean for many of the linear measurements, the major decrease was observed in the later agricultural KER and KUS samples. In addition, although males and females displayed similar trends for the CSG properties, males had a larger overall reduction trend in absolute values, particularly in molar I_x and I_{max} . There are several processes that may be driving the observed differences between males and females, and these include both cultural (e.g. variation in paramasticatory behaviour and/or differences in food consumption) and biological (e.g. differential osseous response to mechanical loading due to hormones and/or genetics) factors.

For many populations, the adoption of agriculture was accompanied by cultural changes, such as division of labour and complex social hierarchies, that may have led to sex differences in dietary consumption. Previous studies of postcranial strength within the Nile Valley have shown evidence for changing activity levels for both males and females following the transition to agriculture (Stock et al., 2011). The evidence indicates that the initial adoption of agriculture led to a significant reduction in the mechanical loading of the skeleton for males, whereas a modest decrease in the mechanical loading of the skeleton for females occurred later

during the formation of the Egyptian state (Stock et al., 2011). Sexual division of labour is often be accompanied by significant differences in diet between males and females (Hill and Hurtado, 1989; Temple and Larsen, 2007; Walker and Hewlett, 1990). Sex differences in diet may manifest as men having greater access to protein sources, such as fish and meat, while females rely more heavily on plants and carbohydrates (Hayden, 1979; Larsen, 1983, 1984). In addition, studies that have analysed changing stature over time within the Nile Valley have found that a pronounced increase in stature was observed in males compared with females (Zakrzewski, 2003). Different trends regarding stature over time may reflect sex differences in diet and nutrition, possibly as a result of sexual division of labour or increasing social complexity, or may in fact be a result of different biological responses to improvements in diet between males and females (Zakrzewski, 2003).

Differences in mandibular morphology between males and females may also relate to biological differences in the osseous response to the same masticatory stress. For example, males typically exhibit stronger bite forces, especially during adolescence when the bone is most responsive to biomechanical stress (Hatch et al., 2000; Helkimo et al., 1977; Ingervall and Minder, 1997; Kovero et al., 2002; Mountain et al., 2011; Raadsheer et al., 1999; Rentes et al., 2002). Hormonal differences between males and females may also influence the pattern of observed morphological variation. Additional research is necessary to understand the relationship between sex, biomechanical loading and bone remodelling in the masticatory complex.

The oral health results from this study showed different patterns of dental pathology by sex within the samples. Females had higher caries prevalence compared with males within the R12, KER and KUS samples. However, these results were only statistically significantly within the KUS population (which may be related to limitations in sample size). The often observed decline in female oral health associated with agriculture is most likely not only due to dietary change, but is reflective of broader demographic changes that included an increase in fertility rates (Lukacs, 2008, 2011; Watson et al., 2010; Willis and Oxenham, 2013). Pregnancy is associated with a weakened immune system and, therefore, a higher fertility rate would place females at increased risk of poor oral health, regardless of changes in diet (Lukacs, 2008). However, more information is required concerning the division of labour and the distribution of food resources in the populations included in this study. Future research will need this cultural information, combined with more research on how sex influences bone remodelling in

males and females, in order to more accurately interpret the different patterns of male and female morphological trends observed here.

9.4 Limitations and future directions

9.4.1 Mandible and cranial integration

Although the mandible can adapt to variation in masticatory strain and evolve independently of the cranium (Galland et al., 2016; Preuschoft and Witzel, 2002; von Cramon-Taubadel, 2011), there are still strong patterns of morphological integration within the skull (Bastir et al., 2004; Bookstein et al., 2003; Lieberman, 2011; Polanski, 2011; Polanski and Franciscus, 2006; Rosas et al., 2008). The shape of the skull is highly constrained, and the majority of observed human cranial variation can be explained using population history models related to migration and gene flow, rather than phenotypic plasticity during the life of an individual (Harvati and Weaver, 2006; Relethford, 2004; Roseman, 2004; Smith, 2009; von Cramon-Taubadel, 2014, 2017). However, the "masticatory-functional hypothesis" was not formed based solely on changes in mandibular morphology, but also through the observation that agriculturalists had smaller, less prognathic faces and more globular brain cases (Carlson and Van Gerven, 1977).

Relatively few studies have investigated how the cranium and mandible adapt concurrently to variation in dietary consumption (but see Galland et al., 2016; Katz et al., 2017; von Cramon-Taubadel, 2011). However, the above studies have shown that changes in the cranium, particularly the facial region, are often observed alongside the more pronounced changes to the mandible. Although poor cranium preservation within the samples in this study prevented any analysis of the relationship between cranial and mandibular robusticity and shape changes over time, future research should investigate the functional integration and patterns of morphological change between the mandible and the cranium in ancient Nubian populations. The comparison of cranial and mandibular morphological changes may elucidate the chewing mechanisms and musculature that are most affected by changes in dietary consumption. In addition, the analysis of the cranium would provide information regarding the population history and genetic continuity of the populations, and allow researchers to better determine whether morphological changes were due to plastic adaptations to changes in dietary consistency or reflective of population history.

9.4.2 Internal mandibular morphology

In this study, solid-section models were used to quantify mandibular CSG because CT-scanning was not available. Therefore, analysis of the internal morphology of the mandible was not possible. Bone structure is dynamic, and cortical and trabecular bone can change in response to biomechanical load in a relatively short period of time throughout the life of an individual (Barak et al., 2011; Huang et al., 2013; Ruff et al., 2006). Although a solid-section cross-sectional model has been shown to provide an accurate estimation of biomechanical properties (Holton et al., 2015; Macintosh et al., 2013; Stock and Shaw, 2007), it is possible that there were differences in how the mandible internally adapted to masticatory stress at both the sample and individual level that could not be detected using the methods employed in this research. For example, Toro-Ibacache and colleagues (2019) found that mandibular cortical bone distribution was similar in low- and high-load groups, despite the external gracility of the low-load mandibles. Similarly, studies have found a relationship between dietary toughness and trabecular bone anisotropy in the mandibular condyle of mice (Balanta-Melo et al., 2018).

Future research should aim to use methodology that allows analysis of the internal morphology of the mandible to determine how the external/internal morphological structures change in relation to each other over time. Specifically, future work should focus on the relationship between masticatory biomechanical loading and trabecular bone structure (e.g. trabecular bone thickness, bone volume fraction and/or orientation; Coiner-Collier et al., 2018).

9.4.3 Nubian population sample

It is important to examine morphological changes associated with subsistence strategy transitions in populations for which there is good evidence of biological continuity, in order to identify variation due to phenotypic plasticity and adaptation. The Northern Dongola Reach samples used in this study (R12, KAW, KER and KUS) were selected because they presented an opportunity to investigate the effect of subsistence strategy transitions on mandibular morphology and oral health while, in part, controlling for genetic and geographic variation. Although there has not yet been any analysis on the biological relationship between all of the Northern Dongola Reach populations included in this study, there is no archaeological evidence of major migration or population replacement from the Sudanese Neolithic period in the Kerma region (Edwards, 2004). However, a certain level of admixture from outside populations can

be expected, especially in the later Kerma and Meroitic populations which were part of a large state with extensive trading routes (Phillipson, 2005; Wilkinson, 1999). Future studies should focus on the genetic relatedness of the populations in the Northern Dongola Reach to identify the relationships between these populations.

It was important to include a hunter-gatherer population in this study, but unfortunately there are a limited number of Epipalaeolithic archaeological sites in Upper Nubia, and most of these sites are not associated with any skeletal remains. Therefore, the Late Palaeolithic Jebel Sahaba (JSA) population from Lower Nubia was included in the study. There is some debate over the relationship between the JSA population and later Nubian populations (Franciscus, 1995; Greene, 1972; Groves and Thorne, 1999; Holliday, 2015). Dental (Irish 2000, 2005) and postcranial (Raxter, 2011) research has found morphological differences between the JSA and KER populations, suggesting genetic discontinuity. Based on evidence from cranial shape analysis, Galland and colleagues (2016) placed the time of genetic discontinuity in Lower Nubia between the Mesolithic (Epipalaeolithic) and Neolithic. Although within the context of this study it was not possible to determine whether observed differences between the JSA hunter-gatherers and later populations were due to genetic or adaptive mechanisms, it was important to use JSA as an outlier population to compare with the later populations. It is clear that due to the ambiguity in the genetic relatedness between the JSA and the Upper Nubian populations in this study, along with a relatively large temporal gap of over 4000 years between the JSA and R12 population, future analyses should, if possible, include an Upper Nubian Epipalaeolithic population in the analysis.

In general, due to the preservation levels of the samples used in this study, the sample sizes for analyses were relatively small, especially when males and females were analysed separately. This means that some of the observations of morphological change in the mandible were trends, rather than reflective of statistical significance. However, non-statistically significant trends are still useful, particularly as guidance for future research. Although currently it would not be possible to increase the sample sizes for the populations used in this study (due to absolute numbers of individuals and preservation levels), future analyses of mandibular and dental change should aim to include more populations within the region to increase the sample size of each chronological period.

9.5 Concluding remarks

Dietary transitions have been important drivers of health and morphological change in past human populations. The adoption of food production in ancient Nubia occurred gradually, with hunter-fisher-gatherers first adopting animal husbandry alongside their foraging and pottery production. These populations then systematically increased their reliance on cereal agriculture based on the local environmental conditions (Linseele, 2013). The continuity of the Upper Nubian populations in this study presented an opportunity to create a detailed picture of the biological and cultural context for subsistence strategy transitions in the ancient Nile Valley. By integrating the results from oral health, mandibular and dental metrics, as well as mandibular cross-sectional geometry, this study used a holistic approach towards understanding the biological effect of dietary transitions on the mandible and related dentition. The results presented here corroborate the findings from previous studies that have shown a substantial morphological change in the mandible during the transition from hunting and gathering to agriculture, thus supporting the underlying principles of the "masticatoryfunctional hypothesis" (Carlson and Van Gerven, 1977). This study expands our knowledge of the complex relationship between human biological variation and subsistence strategy transitions and provides the foundation for future work investigating how dietary factors influence the shape of the human skull.

10 References

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APPENDIX A GENERAL METHODOLOGY

A.1 Sex and age determination

Individuals were preferentially selected for inclusion in the study if they had associated postcranial material to allow for more accurate age and sex determination. When possible, the biological sex of each individual was determined using the pelvis. The pelvic traits that were assessed included the ventral arc, subpubic concavity, greater sciatic notch and ischiopubic ramus ridge (Buikstra and Ubelaker, 1994; Phenice, 1969; White and Folkens, 2005). In the absence of pelvic material, the sexually dimorphic features of the skull were used: nuchal crest; prominence and breadth of the mastoid process; prominence of the glabella; width of the supraorbital margin; and the mental eminence (Buikstra and Ubelaker, 1994; Mays, 1998; White and Folkens, 2005). However, it is important to note that previous studies have found that gracile skulls are characteristic of males from Northeast Africa, as compared with European males on whom the sexing standards are based (Lahr, 1996). Therefore, sex determination from the pelvis was preferred for the individuals in this study. Individuals for which sex could not be determined were marked as 'indeterminate' and only included in the pooled sex analyses.

Only adult individuals were included in this study, and adulthood was determined by eruption of M3 and the fusion of the clavicle (when present) (Buikstra and Ubelaker, 1994; Ubelaker, 1989). When possible, each individual was assigned to an age class in order to explore age as a factor when interpreting the results. Age was preferentially estimated based on the age-related change and degeneration of the pelvic pubic symphyseal joint (Brooks and Suchey, 1990) and auricular surface morphology (Lovejoy et al., 1985; Meindl and Lovejoy, 1989). For individuals without an associated pelvis, other criteria such as cranial suture closure and sternal rib end morphology were utilised, if available (Bass, 1995; Brooks and Suchey, 1990; Schwartz, 1995; Walker et al., 1991; White and Folkens, 2000). Individuals were grouped into three age categories: 20-35 years ('young adult'), 36-50 years ('middle adult') and 50+ years ('older adult'). For the samples included in this study, few individuals were classified as 'older adults'. Therefore, for the age-related analyses conducted in this study, the middle and older adult categories were combined to optimise sample size of this older age category. As with biological sex, individuals that could not be confidently assigned an age category were recorded as 'adult' and were only included in analyses with pooled age categories.

Each individual in this study was assigned sex and age by the current researcher (MB). Previous researchers have also estimated the age and sex of many of the individuals used in this study (see Judd, 2000, 2008), and this information was used to assess inter-observer error. There were only a few cases in which the age and sex assessment were not aligned, and in those cases the individual was included in the 'indeterminate' sex or 'adult' age category. Access to the primary Jebel Sahaba material was not available for the purposes of this study. Therefore, the sex assessments from a previous researcher (T. Davies – pers. comm.) were used in the current study. Unfortunately, age estimation of the individuals from Jebel Sahaba was not available. Therefore, the sample from Jebel Sahaba was not included in any age-specific analyses (although age-related analyses was primarily used to assess oral health in Chapter 7, for which the JSA sample was not available for analysis).

A.2 Stature and body mass

The dietary and social impacts of changes in subsistence strategy can dramatically influence the biology and health of human populations. Postcranial measurements can be used to estimate body mass and stature in past human populations and analyse how these measures changed over time in relation to subsistence strategy transitions (Angel, 1972; Bogin, 1999; Eveleth and Tanner, 1990; Larsen, 1984; Schweich and Knüsel, 2003; Steckel, 1995, 2009; Zakrzewski, 2003). In this study, the stature of individuals was estimated using long bone lengths, as there is a predictable relationship between long bone length and standing height (Auebach and Ruff, 2004; Buikstra and Ubelaker, 1994; Martin and Saller, 1957; Nikita et al., 2011; Raxter et al., 2006; Ubelaker, 1978). In recent years, region-specific equations to estimate stature and body mass have been developed. The closest region-specific equations for the ancient Nubian populations in this study were developed using Egyptian populations by Raxter and colleagues (2006, 2008, 2011) (**Table A.1**). Equations used to estimate stature preferentially use maximum femur length followed by bicondylar femur length; however, other long bone lengths can also be used (Raxter et al., 2008; Trotter and Gleser, 1951). In this study, the long bones were measured by hand with an osteometric board.

Measurement/Index	Formulae	References
Stature (STAT)	Males: 2.257(XFL) + 63.93 ± 3.218 2.253(BFL) + 64.76 ± 3.226 Females: 2.340(XFL) + 56.99 ± 2.517 2.341(BFL) + 57.63 ± 2.511	Raxter et al., 2006, 2008
Body Mass (BM)	2.268 x FHD – 36.5	Grine et al., 1995
	(2.741 x FHD – 54.9) * 0.90 (males) (2.426 x FHD – 35.1) *0.90 (females)	Ruff et al., 1991; Auerbach and Ruff, 2004
SD _S and SD _{BM}	[(male value – female value)/((male value + female value)/2)] *100	Borgognini Tarli and Repetto, 1986; Wells, 2012

Stature: XFL (femoral maximum length), BFL (femoral bicondylar length) and STAT (stature) are reported in centimetres. **Body Mass**: Calculated from the average of the two equations (Raxter, 2011). FHD, femoral head diameter anterior-posterior breadth, reported in millimetres, body mass reported in kilograms. SD_S, % sexual dimorphism in stature; SD_{BM}, % sexual dimorphism in body mass.

Estimating the body mass of past human populations is an important way to infer the overall health of a population and can be used to understand the impact of dietary shifts. The two primary methods to estimate body mass in past human populations are based on regression equations: the "morphometric" method uses bi-iliac breadth and stature measurements (Ruff, 2000; Ruff et al., 1997); and the "mechanical" method uses the femoral head diameter (FHD) (Auerbach and Ruff, 2004). Due to the poor level of preservation of the samples in the current study, these individuals were not expected to have associated and/or intact pelvises suitable to measure bi-iliac breadth. Therefore, the mechanical method to estimate body mass was used. Raxter (2011) compared body mass estimation methodologies and found that for Nubian males, the average of estimates made using Ruff and colleagues' (1991) sex-specific general equation and Grine and colleagues' (1995) formula proved the most accurate. Therefore, in this study body mass was calculated with the FHD and presented as the average of the two above equations (Auerbach and Ruff, 2004; Grine et al., 1995; Raxter, 2011; Ruff et al., 1991) (**Table A.1**). The FHD was measured using Mitutoyo digital calipers.

Sexual dimorphism (SD) is the difference in size between males and females in a population. As estimations of body mass and stature are an important way to assess overall health, it is important to understand if trends are similar for males and females within the same

population. Sexual dimorphism (as a percentage) was calculated for both stature and body mass within each population (Borgognini Tarli and Repetto, 1986; Wells, 2012). Descriptive statistics for estimated stature and body mass for each Nubian population are presented in **Table A.2** and **Table A.3**.

			Stature (cm	<u>1)</u>		Indepen	dent sam	ples <i>t</i> -test
Population	Sex	п	Mean	SD	% SD _S	t	df	р
JSA	Male	6	168.39	4.87	-			•
	Female	3	160.03	5.74				
					5.93	2.30	7	0.055
R12	Male	5	169.63	1.27				
	Female	12	156.95	7.83				
					7.77	3.54	15	0.003
KAW	Male	11	170.00	6.90				
	Female	4	160.35	4.20				
					5.84	2.59	13	0.022
KER	Male	13	169.15	5.99				
	Female	18	156.67	5.17				
					7.66	5.05	18	<0.001
KUS	Male	3	167.38	4.80				
	Female	5	155.03	5.55				
					7.66	3.18	6	0.019

Table A.2 Descriptive statistics for estimated stature and *t*-tests between males and females within each population

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000 – 9000 BC); **R12**: NDRS R12, Neolithic (c. 5000 – 4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500 – 2050 BC); **KER**: Kerma, Kerma Classique (c. 1750 – 1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC – AD 350). Stature calculated from formulae adapted by Raxter and colleagues (2006, 2008). *n*: sample size; SD: standard deviation; %SD_S: % sexual dimorphism stature (based on Borgognini Tarli and Repetto, 1986 and Wells, 2012); df: degrees of freedom. Independent samples *t*-test significant at $p \le 0.05$.

Independent samples *t*-tests were used to assess differences in stature and body mass between males and females within each sample. Males had significantly larger estimated stature compared with their female counterparts in the R12, KAW, KER and KUS samples (**Table A.2**; **Figure A.1a**). Females also had lower estimated body mass than males within each population, and this was significantly different in the R12, KAW and KER populations (**Table A.3**; **Figure A.1b**).

			Body mass	<u>(kg)</u>		<u>Indepen</u>	dent samp	oles <i>t</i> -test
Population	Sex	п	Mean	SD	% SD _{BM}	t	df	р
JSA	Male	5	67.98	7.32			-	
	Female	1	59.43	N/A				
					14.56			N/A
R12	Male	8	64.56	4.78				
	Female	9	58.39	3.88				
					10.04	2.93	14	0.01
KAW	Male	11	59.05	6.16				
	Female	4	51.56	4.71				
					13.54	2.19	13	0.047
KER	Male	12	63.02	7.40				
	Female	18	57.04	6.56				
					12.65	3.40	27	0.002
KUS	Male	3	62.62	11.94				
	Female	6	55.32	5.04				
					12.40	1.35	7	0.22

Table A.3 Descriptive statistics for estimated body mass and *t*-tests between males and females within each population

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000 – 9000 BC); **R12**: NDRS R12, Neolithic (c. 5000 – 4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500 – 2050 BC); **KER**: Kerma, Kerma Classique (c. 1750 – 1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC – AD 350). Body mass calculated from two sets of formulae (Grine et al., 1995; Raxter, 2011; Ruff et al., 1991); *n*: sample size; SD: standard deviation; %SD_{BM}: % sexual dimorphism body mass (based on Borgognini Tarli and Repetto, 1986 and Wells, 2012); df: degrees of freedom. Independent samples *t*-test significant at *p*≤0.05.



Figure A.1 Estimated (a) stature and (b) body mass for males and females within each Nubian population

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

When ANOVAs were used to identify significant differences in stature and body mass between Nubian populations over time, there were no significant differences found between any of the populations (**Table A.4** and **Table A.5**).

Sex	Population	п	Mean (cm)	SD	F (df1, df2)	р
Male						
	JSA	7	168.11	4.51		
	R12	5	169.63	1.27		
	KAW	11	170.00	6.90		
	KER	13	169.15	5.99		
	KUS	3	167.38	4.80		
					0.17 (4, 33)	0.95
Female						
	JSA	2	158.43	7.11		
	R12	12	156.95	7.83		
	KAW	4	160.35	4.20		
	KER	18	156.67	5.17		
	KUS	5	155.03	5.55		
					0.63 (4, 37)	0.65

Table A.4 ANOVAs for estimated stature differences between Nubian populations

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). cm: centimetres; df: degrees of freedom; *n*: sample size; SD: standard deviation; *F*: ANOVA test statistic; ANOVA significant at $p \le 0.05$.

Sex	Population	п	Mean (kg)	SD	F (df1, df2)	р
Male						
	JSA	5	67.98	7.32		
	R12	8	64.56	4.78		
	KAW	11	59.05	6.16		
	KER	12	63.02	7.40		
	KUS	3	62.62	11.94		
					1.63 (4, 34)	0.19
Female						
	JSA	1	59.43	N/A		
	R12	9	58.39	3.88		
	KAW	4	51.56	4.71		
	KER	18	57.04	6.56		
	KUS	6	55.32	5.04		
					1.20 (4,33)	0.33

Table A.5 ANOVAs for estimated body mass differences between Nubian populations

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). df: degrees of freedom; kg: kilograms; *n*: sample size; SD: standard deviation; *F*: ANOVA test statistic; ANOVA significant at $p \le 0.05$.

A.3 3D laser scanning

This section describes the methodology used to 3D laser scan the mandibles in this study and addresses why this method was chosen to answer the research questions in this study. More detailed methodology relating to how the 3D scans were subsequently used for specific analyses is included in the relevant results chapters (**Chapters 5 and 6**). All mandibles in this study were scanned by the author (MB), apart from the JSA population which was scanned by T. Davies.

The main aim of this study was to analyse mandibular size and shape over time, and this required that the appropriate methodology was selected. In this study, cross-sectional biomechanical principles were essential to analysing mandibular shape and robusticity over time. Cross-sectional geometric (CSG) properties use the distribution of cortical bone in a cross-section to infer the strength of bone in response to strain caused by torsion and bending (Davies et al., 2012; Lieberman et al., 2004b; Macintosh et al., 2014). As the calculation of CSG properties is based on the shape of a cross-section, it is important to use an accurate image of the bone in cross-section. Methods that can be used to capture the external, and in some cases internal, bone shape include x-rays, computed tomography (CT) scanning, 3D digitizers and periosteal moulding (e.g. Runestad et al., 1993; Stock, 2002; Stock and Shaw, 2007; Sumner et al., 1985; Trinkaus and Ruff, 1989). CT scanning is often preferred over other methods because it produces an image of both the external (periosteal) and internal (endosteal) bone contour (O'Neill and Ruff, 2004; Sumner et al., 1985). However, CT scanning facilities were not available for this study. In cases where CT scanning is not available, desktop 3D laser scanners have become widespread within biomechanics research (Davies et al., 2012; Kuzminsky and Gardiner, 2012; Macintosh et al., 2014). As a non-destructive and relatively quick process, 3D laser scanning is a valuable way to produce a high-definition 3D model of the bone that can then be studied using various software and techniques (Friess, 2012; Slice and Algee-Hewitt, 2015; Stoyanova et al., 2015; Weber, 2015).

This study used a NextEngineTM 3D laser scanner (www.nextengine.com) to 3D laser scan the mandibles, employing a technique adapted from the methodology of Davies and colleagues (2012). The scanner is made up of two parts: the scanning device, which uses structured light scanning, and a rotating AutoDriveTM rubber platform/turntable with an extendable rubber PartGripperTM arm to hold the mandible without causing any damage. In this study, the mandible was oriented so that the posterior ramus rested on the turntable, with the rubber gripper on the mental protuberance holding the mandible upright. Foam pads were

placed under the mandibular ramus to safely secure the mandible during the scanning process. The platform turntable was placed 17 inches away from the scanner (the length of the cable connecting the two devices and, therefore, the maximum distance). The scanner connects to a laptop running the ScanStudio HD Pro software.

Once the mandible was in place, a digital camera integrated within the NextEngine device captured high-resolution images from multiple views to register the colour and texture of the mandibular surface. Using triangulation between laser projections, the 3D scanner calculates the distance between points on the object to create an accurate, 3D model of the bone (White, 2015). Once a single scan is complete the turntable rotates and another scan is taken; this process is repeated until the desired number of scans are obtained (Weber and Bookstein, 2011). Each mandible was scanned with 12 rotations (i.e. each scan was taken at a 30° rotation from the previous one), to form a 360° mesh of coordinates. However, due to the orientation of the mandible on the turntable, some parts of the posterior surface of the symphysis and the medial aspects of the ramus were obscured. Therefore, additional scans were used to supplement those areas of the mandible. All the scans for each mandible were aligned into a single 3D model using the ScanStudio software. Appropriate conservation-approved adhesive labels were used on the mandible to help ensure accuracy during the alignment process in ScanStudio. For an intact mandible, the entire scanning process took approximately 45 minutes. However, when the mandible was fragmented, the process took significantly longer, as each individual fragment had to be scanned independently.

After the scanning process was complete, the scans were initially processed in ScanStudio, which included removing the unwanted images (such as parts of the turntable and foam pads) and digitally fusing the scans. This process resulted in a complete 3D model that showed the periosteal contour of the mandible (Algee-Hewitt and Wheat, 2016). The final mandibular model can be viewed in several ways: with a 'photo' surface to demonstrate texture; with a solid surface; with a mesh surface; or as a point cloud (Kuzminsky and Gardiner, 2012). The completed 3D digital models are created in both .scn and .xyz file formats, and many different analyses can be conducted on these models; the analyses relevant to this study will be discussed further in **Chapters 5 and 6**.

For bioarchaeological research, desktop 3D laser scanners and software programs can be used to reconstruct fragmentary skeletal elements. Although the mandible is a robust bone and, as such, is one of the most frequently found skeletal elements in an archaeological context, many of the mandibles associated with the populations in this study were in poor condition and broken into several pieces (**Figure A.2**). Traditional analytical methods, such as using digital calipers to measure linear distances and/or CT scanning to conduct cross-sectional analysis, would have been difficult or impossible based on the preservation state of the mandibles. However, by using 3D laser scanning, each fragment of the mandible could be scanned individually and then digitally fused to create a complete 3D representation of the original mandible (**Figure A.2**). In addition, software programmes such as Rapidform also have the option of digitally repairing 3D scans by "filling holes" or mirroring missing sides of an object (Kuzminsky and Gardiner, 2012). From the creation of a complete digital mandible, precise measurements were taken that would not have been possible on the actual mandibular specimen. In the context of this research, future researchers will now have access to the scanned mandibles without potential further damage to physical skeletal remains (Kuzminsky and Gardiner, 2012).





Figure A.2 Fragmented mandible and the reconstructed 3D model – R12 94 $\,$

APPENDIX B MANDIBULAR METRIC DATA

		ML	1/BGoB			ML	.2/BGoB			ML	.3/BGoB			ML	1/BCoB	
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	10	1.08	0.073	6.76	10	1.23	0.066	5.37	10	0.78	0.065	8.33	10	0.94	0.09	9.57
R12	7	1.17	0.088	7.52	7	1.35	0.078	5.78	7	0.83	0.097	11.69	7	0.97	0.099	10.21
KAW	14	1.13	0.087	7.70	14	1.31	0.11	8.40	15	0.8	0.094	11.75	11	0.96	0.044	4.58
KER	37	1.13	0.073	6.46	37	1.31	0.07	5.34	37	0.76	0.079	10.39	39	0.94	0.062	6.60
KUS	8	1.08	0.054	5.00	8	1.27	0.067	5.28	8	0.75	0.062	8.27	6	0.91	0.038	4.18
		ML	2/BCoB			ML	.3/BCoB			UM	L/BCoB			LM	L/BGoB	
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	10	1.07	0.088	8.22	10	0.68	0.076	11.18	10	0.93	0.093	10.00	10	0.86	0.071	8.26
R12	7	1.12	0.094	8.39	7	0.69	0.058	8.41	7	0.92	0.11	11.96	7	0.94	0.056	5.96
KAW	11	1.12	0.042	3.75	11	0.69	0.065	9.42	11	0.93	0.049	5.27	15	0.9	0.1	11.11
KER	39	1.09	0.057	5.23	39	0.63	0.06	9.52	38	0.9	0.057	6.33	37	0.86	0.07	8.14
KUS	6	1.07	0.032	2.99	6	0.66	0.04	6.06	6	0.9	0.052	5.78	8	0.82	0.057	6.95
		UM	L/LML			BM2	2B/BM1B			<u>BM2</u>	B/BCP3B			BM2	2B/BGoB	
Population	п	<u>UM</u> Mean	I <u>L/LML</u> SD	CV	п	<u>BM2</u> Mean	2 <u>B/BM1B</u> SD	CV	п	<u>BM2</u> Mean	<u>B/BCP3B</u> SD	CV	n	<u>BM2</u> Mean	2 <u>B/BGoB</u> SD	CV
Population JSA	<i>n</i> 10	<u>UM</u> Mean 1.24	L/LML SD 0.047	CV 3.79	<i>n</i> 10	<u>BM2</u> Mean 1.09	2 <u>B/BM1B</u> SD 0.024	CV 2.20	n 10	<u>BM2</u> Mean 1.79	<u>B/BCP3B</u> SD 0.079	CV 4.41	n 10	<u>BM2</u> Mean 0.6	2B/BGoB SD 0.033	CV 5.50
Population JSA R12	n 10 7	<u>UM</u> Mean 1.24 1.17	L/LML SD 0.047 0.043	CV 3.79 3.68	n 10 8	<u>BM2</u> Mean 1.09 1.1	2B/BM1B SD 0.024 0.033	CV 2.20 3.00	n 10 8	<u>BM2</u> Mean 1.79 1.84	B/BCP3B SD 0.079 0.2	CV 4.41 10.87	<i>n</i> 10 7	<u>BM2</u> Mean 0.6 0.64	2 <u>B/BGoB</u> SD 0.033 0.037	CV 5.50 5.78
Population JSA R12 KAW	n 10 7 11	<u>UM</u> Mean 1.24 1.17 1.21	L/LML SD 0.047 0.043 0.052	CV 3.79 3.68 4.30	n 10 8 15	<u>BM2</u> Mean 1.09 1.1 1.12	2B/BM1B SD 0.024 0.033 0.022	CV 2.20 3.00 1.96	n 10 8 15	<u>BM2</u> Mean 1.79 1.84 1.82	B/BCP3B SD 0.079 0.2 0.14	CV 4.41 10.87 7.69	n 10 7 15	BM2 Mean 0.6 0.64 0.65	2B/BGoB SD 0.033 0.037 0.05	CV 5.50 5.78 7.69
Population JSA R12 KAW KER	n 10 7 11 35	<u>UM</u> Mean 1.24 1.17 1.21 1.26	L/LML SD 0.047 0.043 0.052 0.06	CV 3.79 3.68 4.30 4.76	n 10 8 15 35	BM2 Mean 1.09 1.1 1.12 1.11	2B/BM1B SD 0.024 0.033 0.022 0.045	CV 2.20 3.00 1.96 4.05	n 10 8 15 36	BM2 Mean 1.79 1.84 1.82 1.86	B/BCP3B SD 0.079 0.2 0.14 0.12	CV 4.41 10.87 7.69 6.45	n 10 7 15 35	BM2 Mean 0.6 0.64 0.65 0.65	2B/BGoB SD 0.033 0.037 0.05 0.038	CV 5.50 5.78 7.69 5.85
Population JSA R12 KAW KER KUS	n 10 7 11 35 6	<u>UM</u> Mean 1.24 1.17 1.21 1.26 1.27	L/LML SD 0.047 0.043 0.052 0.06 0.061	CV 3.79 3.68 4.30 4.76 4.80	n 10 8 15 35 8	BM2 Mean 1.09 1.1 1.12 1.11 1.12	BM1B SD 0.024 0.033 0.022 0.045 0.049	CV 2.20 3.00 1.96 4.05 4.38	n 10 8 15 36 8	<u>BM2</u> Mean 1.79 1.84 1.82 1.86 1.84	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14	CV 4.41 10.87 7.69 6.45 7.61	n 10 7 15 35 8	BM2 Mean 0.6 0.64 0.65 0.65 0.64	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034	CV 5.50 5.78 7.69 5.85 5.31
Population JSA R12 KAW KER KUS	<i>n</i> 10 7 11 35 6	UM Mean 1.24 1.17 1.21 1.26 1.27 BM2	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB	CV 3.79 3.68 4.30 4.76 4.80	n 10 8 15 35 8	BM2 Mean 1.09 1.1 1.12 1.11 1.12 BM1	2B/BM1B SD 0.024 0.033 0.022 0.045 0.049 B/BCP3B	CV 2.20 3.00 1.96 4.05 4.38	n 10 8 15 36 8	BM2 Mean 1.79 1.84 1.82 1.86 1.84 BM1	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 12 0.14	CV 4.41 10.87 7.69 6.45 7.61	n 10 7 15 35 8	BM2 Mean 0.6 0.64 0.65 0.65 0.65 0.64 BM2	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB	CV 5.50 5.78 7.69 5.85 5.31
Population JSA R12 KAW KER KUS Population	n 10 7 11 35 6 n	<u>UM</u> Mean 1.24 1.17 1.21 1.26 1.27 <u>BM2</u> Mean	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB SD	CV 3.79 3.68 4.30 4.76 4.80 CV	n 10 8 15 35 8 <i>n</i>	<u>BM2</u> Mean 1.09 1.1 1.12 1.11 1.12 <u>BM1</u> Mean	2B/BM1B SD 0.024 0.033 0.022 0.045 0.045 0.049 B/BCP3B SD	CV 2.20 3.00 1.96 4.05 4.38 CV	n 10 8 15 36 8 <i>n</i>	<u>BM2</u> Mean 1.79 1.84 1.82 1.86 1.84 <u>BM1</u> Mean	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 0.12 SD	CV 4.41 10.87 7.69 6.45 7.61 CV	n 10 7 15 35 8 <i>n</i>	BM2 Mean 0.6 0.64 0.65 0.65 0.64 Mean	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB SD	CV 5.50 5.78 7.69 5.85 5.31 CV
Population JSA R12 KAW KER KUS Population JSA	<i>n</i> 10 7 11 35 6 <i>n</i> 10	UM Mean 1.24 1.17 1.21 1.26 1.27 BM2 Mean 0.52	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB SD 0.044	CV 3.79 3.68 4.30 4.76 4.80 CV 8.46	<i>n</i> 10 8 15 35 8 <i>n</i> 10	BM2 Mean 1.09 1.1 1.12 1.11 1.12 BM1 Mean 1.64	2B/BM1B SD 0.024 0.033 0.022 0.045 0.049 B/BCP3B SD 0.058	CV 2.20 3.00 1.96 4.05 4.38 CV 3.54	n 10 8 15 36 8 n 10	BM2 Mean 1.79 1.84 1.82 1.86 1.84 Mean 0.55	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 0.12 0.14 0.12 0.13	CV 4.41 10.87 7.69 6.45 7.61 CV 6.00	<i>n</i> 10 7 15 35 8 <i>n</i> 10	BM2 Mean 0.6 0.64 0.65 0.64 Mean Mean 0.48	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB SD 0.042	CV 5.50 5.78 7.69 5.85 5.31 CV 8.75
Population JSA R12 KAW KER KUS Population JSA R12	n 10 7 11 35 6 n 10 7	UM Mean 1.24 1.17 1.21 1.26 1.27 BM2 Mean 0.52 0.53	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB SD 0.044 0.044	CV 3.79 3.68 4.30 4.76 4.80 CV 8.46 8.30	n 10 8 15 35 8 <i>n</i> 10 7	BM2 Mean 1.09 1.1 1.12 1.11 1.12 BM1 Mean 1.64 1.65	2B/BM1B SD 0.024 0.033 0.022 0.045 0.045 0.049 B/BCP3B SD 0.058 0.15	CV 2.20 3.00 1.96 4.05 4.38 CV 3.54 9.09	n 10 8 15 36 8 15 10 7	BM2 Mean 1.79 1.84 1.82 1.86 1.84 Mean 0.55 0.58	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 0.12 0.14 0.033 0.037	CV 4.41 10.87 7.69 6.45 7.61 CV 6.00 6.38	n 10 7 15 35 8 <i>n</i> 10 7	BM2 Mean 0.6 0.64 0.65 0.64 Mean Mean 0.48 0.49	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB SD 0.042 0.048	CV 5.50 5.78 7.69 5.85 5.31 CV 8.75 9.80
Population JSA R12 KAW KER KUS Population JSA R12 KAW	<i>n</i> 10 7 11 35 6 <i>n</i> 10 7 11	UM Mean 1.24 1.17 1.21 1.26 1.27 BM2 Mean 0.52 0.53 0.56	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB SD 0.044 0.044 0.026	CV 3.79 3.68 4.30 4.76 4.80 CV 8.46 8.30 4.64	n 10 8 15 35 8 <i>n</i> 10 7 11	BM2 Mean 1.09 1.1 1.12 1.11 1.12 BM1 Mean 1.64 1.65 1.62	2B/BM1B SD 0.024 0.033 0.022 0.045 0.049 B/BCP3B SD 0.058 0.15 0.097	CV 2.20 3.00 1.96 4.05 4.38 CV 3.54 9.09 5.99	n 10 8 15 36 8 n 10 7 11	BM2 Mean 1.79 1.84 1.82 1.86 1.84 BM1 Mean 0.55 0.58 0.58	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 0.12 0.14 0.12 0.14 0.12 0.14 0.12 0.14 0.12 0.14 0.12 0.14	CV 4.41 10.87 7.69 6.45 7.61 CV 6.00 6.38 7.24	<i>n</i> 10 7 15 35 8 <i>n</i> 10 7 11	BM2 Mean 0.6 0.64 0.65 0.64 0.65 0.64 BM2 Mean 0.48 0.49 0.5	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB SD 0.042 0.048 0.021	CV 5.50 5.78 7.69 5.85 5.31 CV 8.75 9.80 4.20
Population JSA R12 KAW KER KUS Population JSA R12 KAW KER	n 10 7 11 35 6 n 10 7 11 36	UM Mean 1.24 1.17 1.21 1.26 1.27 BM2 Mean 0.52 0.53 0.56 0.54	L/LML SD 0.047 0.043 0.052 0.06 0.061 2B/BCoB SD 0.044 0.026 0.029	CV 3.79 3.68 4.30 4.76 4.80 CV 8.46 8.30 4.64 5.37	n 10 8 15 35 8 n 10 7 11 35	BM2 Mean 1.09 1.1 1.12 1.11 1.12 BM1 Mean 1.64 1.65 1.62 1.66	2B/BM1B SD 0.024 0.033 0.022 0.045 0.049 B/BCP3B SD 0.058 0.15 0.097 0.095	CV 2.20 3.00 1.96 4.05 4.38 CV 3.54 9.09 5.99 5.72	n 10 8 15 36 8 n 10 7 11 35	BM2 Mean 1.79 1.84 1.82 1.86 1.84 Mean 0.55 0.58 0.59	B/BCP3B SD 0.079 0.2 0.14 0.12 0.14 0.12 0.14 0.033 0.037 0.042 0.035	CV 4.41 10.87 7.69 6.45 7.61 CV 6.00 6.38 7.24 5.93	n 10 7 15 35 8 <i>n</i> 10 7 11 35	BM2 Mean 0.6 0.64 0.65 0.64 0.65 0.64 0.65 0.64 0.65 0.64 0.65 0.64 0.65 0.64 0.64 0.64 0.64 0.64 0.64 0.64 0.64 0.48 0.49 0.5 0.49	2B/BGoB SD 0.033 0.037 0.05 0.038 0.034 1B/BCoB SD 0.042 0.042 0.048 0.021 0.023	CV 5.50 5.78 7.69 5.85 5.31 CV 8.75 9.80 4.20 4.69

 Table B.1 Descriptive statistics for the mandibular metric ratios

		BC3I	PB/BGoB			BCP	3B/BCoB			DA	L/BM2B			DA	L/ML1	
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV
JSA	10	0.33	0.031	9.39	10	0.29	0.034	11.72	10	0.62	0.039	6.29	10	0.34	0.03	8.82
R12	7	0.36	0.039	10.83	7	0.3	0.049	16.33	8	0.59	0.053	8.98	7	0.32	0.032	10.00
KAW	11	0.36	0.023	6.39	11	0.31	0.013	4.19	15	0.57	0.09	15.79	11	0.34	0.051	15.00
KER	35	0.35	0.028	8.00	35	0.3	0.020	6.67	36	0.59	0.073	12.37	35	0.34	0.046	13.53
KUS	6	0.36	0.019	5.28	6	0.3	0.026	8.67	8	0.55	0.038	6.91	6	0.33	0.023	6.97
		DA	L/ML3		_	MR	RB/LRB		_	LI	RB/RH		_	\mathbf{M}	RB/RH	
Population	п	Mean	SD	CV	п	Mean	SD	CV	п	Mean	SD	CV	n	Mean	SD	CV
JSA	10	0.48	0.027	5.63	13	1.3	0.057	4.38	9	0.65	0.06	9.23	9	0.84	0.071	8.45
R12	7	0.45	0.049	10.89	17	1.29	0.073	5.66	18	0.56	0.052	9.29	17	0.72	0.072	10.00
KAW	11	0.48	0.058	12.08	15	1.24	0.073	5.89	15	0.62	0.061	9.84	14	0.77	0.097	12.60
KER	35	0.5	0.061	12.20	39	1.37	0.067	4.89	39	0.55	0.072	13.09	39	0.74	0.082	11.08
KUS	6	0.46	0.023	5.00	9	1.35	0.068	5.04	9	0.56	0.061	10.89	9	0.76	0.067	8.82
		<u>BGo</u>	B/BCoB			MI	.1/ML2									
Population	п	Mean	SD	CV	п	Mean	SD	CV								
JSA	7	0.87	0.046	5.29	11	0.87	0.034	3.91								
R12	7	0.83	0.084	10.12	13	0.87	0.025	2.87								
KAW	11	0.87	0.053	6.09	14	0.86	0.025	2.91								
KER	37	0.83	0.043	5.18	39	0.86	0.032	3.72								
KUS	6	0.85	0.049	5.76	9	0.85	0.02	2.35								
JSA: Jebel Sal	naba, I	Late Palaeo	lithic (c. 13	000–9000	BC); R	12: NDRS	R12, Neol	ithic (c. 500	00-400	00 cal BC);	KAW: ND	DRS P37, K	lerma A	Ancien (c. 2	2500-2050	BC);

KER: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **ML1**: mandibular length gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length gnathion to condyle; **ML3**: mandibular length infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length gnathion to gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch length from infradentale to midsagittal BM2B; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *n*: sample size; SD: standard deviation, CV: coefficient of variation.

Indices	n	Н	df	р
ML1/ML2	86	2.86	4	0.58
ML1/BGoB	76	7.94	4	0.094
ML2/BGoB	76	11.93	4	0.018
ML3/BGoB	77	4.76	4	0.31
ML1/BCoB	73	4.55	4	0.34
ML2/BCoB	73	6.76	4	0.15
ML3/BCoB	73	9.99	4	0.041
UML/BCoB	72	3.30	4	0.51
LML/BGoB	77	9.98	4	0.041
UML/LML	85	20.88	4	<0.001
BM2B/BM1B	76	6.05	4	0.20
BM2B/BCP3B	77	5.35	4	0.25
BM2B/BGoB	75	12.32	4	0.015
BM2B/BCoB	70	12.13	4	0.016
BM1B/BCP3B	78	2.98	4	0.56
BM1B/BGoB	75	9.59	4	0.048
BM1B/BCoB	71	6.74	4	0.15
BCP3B/BGoB	76	5.22	4	0.27
BCP3B/BCoB	72	7.73	4	0.10
DAL/BM2B	77	9.14	4	0.058
DAL/ML1	84	4.98	4	0.29
DAL/ML3	86	12.07	4	0.017
MRB/LRB	93	32.71	4	<0.001
LRB/RH	94	24.88	4	<0.001
MRB/RH	92	15.48	4	0.004
BGoB/BCoB	71	7.60	4	0.11

Table B.2 Kruskal-Wallis tests for mandibular metric indices

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **ML1**: mandibular length gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length gnathion to condyle; **ML3**: mandibular length infradentale to midsagittal gonion-gonion chord; **BG0B**: bigonial breadth; **BC0B**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length from infradentale to midsagittal arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *n*: sample size; *H*: Kruskal-Wallis test statistic; degrees of freedom=4; Kruskal-Wallis level of significance *p* ≤ 0.05 .

					Mann-V	Whitney U	-tests p (r)	
Calculated ratio	Population	n	MR	JSA	R12	KAW	KER	KUS
ML2/BGoB	JSA	10	18.80	-	0.011	0.053	0.002	0.11
	R12	7	51.14	-0.62	-	0.41	0.24	0.083
	KAW	14	39.93	-0.39	-0.18	-	0.82	0.54
	KER	37	42.19	-0.45	-0.18	-0.03	-	0.21
	KUS	8	32.50	-0.38	-0.45	-0.13	-0.28	-
ML3/BCoB	JSA	10	44.30	-	0.63	0.78	0.059	0.52
	R12	7	48.57	-0.12	-	0.89	0.042	0.25
	KAW	11	46.91	-0.06	-0.03	-	0.025	0.27
	KER	39	29.97	-0.27	-0.30	-0.32	-	0.23
	KUS	6	38.83	-0.16	-0.32	-0.27	-0.18	-
LML/BGoB	JSA	10	37.10	-	0.025	0.44	0.90	0.25
	R12	7	58.86	-0.54	-	0.38	0.009	0.011
	KAW	15	44.60	-0.16	-0.19	-	0.28	0.061
	KER	37	36.43	-0.02	-0.39	-0.15	-	0.18
	KUS	8	25.38	-0.27	-0.66	-0.39	-0.2	-
UML/LML	JSA	11	44.82	-	0.001	0.21	0.29	0.24
	R12	13	19.46	-0.67	-	0.081	<0.001	0.001
	KAW	14	33.36	-0.25	-0.34	-	0.018	0.038
	KER	38	50.53	-0.15	-0.50	-0.33	-	0.30
	KUS	9	58.00	-0.26	-0.69	-0.43	-0.15	-
BM2B/BGoB	JSA	10	16.20	-	0.019	0.015	0.001	0.033
	R12	7	37.86	-0.57	-	0.86	0.47	0.91
	KAW	15	40.13	-0.49	-0.04	-	0.71	0.85
	KER	35	43.43	-0.51	-0.11	-0.05	-	0.47
	KUS	8	37.63	-0.50	-0.03	-0.04	-0.11	-
BM2B/BCoB	JSA	10	19.70	-	0.63	0.005	0.011	0.051
	R12	7	29.86	-0.12	-	0.11	0.47	0.48
	KAW	11	49.73	-0.61	-0.37	-	0.042	0.07
	KER	36	36.86	-0.37	-0.11	-0.30	-	0.64
	KUS	6	34.17	-0.49	-0.20	-0.44	-0.07	-
BM1B/BGoB	JSA	10	19.10	-	0.079	0.035	0.002	0.062
	R12	7	39.43	-0.43	-	0.81	0.83	0.82
	KAW	15	40.20	-0.42	-0.05	-	0.70	0.52
	KER	35	42.86	-0.46	-0.03	-0.06	-	0.30
	KUS	8	35.00	-0.44	-0.06	-0.13	-0.16	-

 Table B.3 Mann-Whitney tests for mandibular metric ratios

					Mann-V	Whitney <i>U</i> -	tests p (r)	
Calculated ratio	Populatio n	п	MR	JSA	R12	KAW	KER	KUS
DAL/ML3	JSA	11	42.82	-	0.14	0.73	0.166	0.21
	R12	13	29.15	-0.30	-	0.57	0.003	0.30
	KAW	16	37.38	-0.07	-0.11	-	0.038	0.87
	KER	37	53.41	-0.20	-0.41	-0.28	-	0.051
	KUS	9	35.22	-0.28	-0.22	-0.03	-0.29	-
MRB/LRB	JSA	13	38.08	-	0.52	0.02	0.001	0.057
	R12	17	34.53	-0.12	-	0.086	<0.001	0.043
	KAW	15	21.73	-0.44	-0.3	-	<0.001	0.004
	KER	39	62.62	-0.45	-0.49	-0.62	-	0.663
	KUS	9	57.89	-0.41	-0.40	-0.59	-0.06	-
LRB/RH	JSA	13	65.77	-	0.006	0.66	0.008	0.030
	R12	18	38.17	-0.50	-	0.013	0.64	0.88
	KAW	15	61.73	-0.08	-0.43	-	0.019	0.053
	KER	39	41.79	-0.37	-0.06	-0.32	-	0.97
	KUS	9	40.78	-0.46	-0.03	-0.40	-0.01	-

Table B.3 continued

Above the diagonal are *p*-values and below the diagonal are the corresponding *r* values. Mann-Whitney tests level of significance $p \le 0.005$. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **ML1**: mandibular length gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length gnathion to condyle; **ML3**: mandibular length infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length gnathion to gonion-gonion chord; **GML**: length from gnathion to M₃; **DAL**: dental arch length from infradentale to midsagittal BM2B; **BCP3B**: dental arch breadth at C/P₃; **BM1B**: dental arch breadth at M₁; **BM2B**: dental arch breadth at M₂; *n*: sample size; MR: mean rank; *r*: effect size.

Measurement	Population	t	df	р	Measurement	Population	t	df	р
ML1	JSA	2.11	9	0.065	CrH	JSA	3.12	10	0.011
	R12	0.56	11	0.59		R12	0.83	16	0.42
	KAW	2.16	13	0.05		KAW	1.47	14	0.16
	KER	4.33	37	<0.001		KER	4.90	36	<0.001
	KUS	1.64	7	0.14		KUS	1.65	7	0.14
ML2	JSA	3.10	9	0.013	GA	JSA	-3.53	10	0.005
	R12	0.31	11	0.77		R12	-2.20	19	0.041
	KAW	1.78	12	0.10		KAW	-1.63	14	0.13
	KER	5.61	37	<0.001		KER	-2.10	36	0.043
	KUS	1.80	7	0.11		KUS	-0.21	7	0.84
ML3	JSA	4.23	9	0.002	UML	JSA	2.32	4.28	0.077
	R12	1.04	11	0.32		R12	-0.083	11	0.94
	KAW	0.56	13.535	0.59		KAW	3.70	12.91	0.003
	KER	3.19	37	0.003		KER	3.95	36	<0.001
	KUS	0.66	7	0.53		KUS	0.85	7	0.42
BGoB	JSA	1.93	8	0.089	LML	JSA	4.08	9	0.003
	R12	-0.29	5	0.78		R12	2.70	12	0.019
	KAW	2.41	13	0.032		KAW	0.95	14	0.36
	KER	5.08	35	<0.001		KER	4.39	37	<0.001
	KUS	-0.009	6	0.99		KUS	0.57	7	0.59
BCoB	JSA	1.12	8	0.30	DAL	JSA	1.90	9	0.089
	R12	-1.58	5	0.18		R12	1.73	11	0.11
	KAW	1.14	9	0.28		KAW	-0.28	15	0.78
	KER	5.20	37	<0.001		KER	-0.65	35	0.52
	KUS	0.20	4	0.85		KUS	0.60	7	0.57

Table B.4 Independent *t*-tests between males and females for mandibular linear measurements

Measurement	Population	t	df	р	Measurement	Population	t	df	р
LRB	JSA	2.34	10	0.041	BCP3B	JSA	-0.62	8	0.55
	R12	-0.24	17	0.82		R12	1.03	8	0.33
	KAW	1.41	14.37	0.18		KAW	-0.039	15	0.97
	KER	1.93	37	0.062		KER	3.17	36	0.003
	KUS	1.95	7	0.093		KUS	-0.87	6	0.42
MRB	JSA	2.20	10	0.052	BM1B	JSA	0.63	8	0.55
	R12	-1.00	15	0.33		R12	2.06	6	0.085
	KAW	1.15	13	0.27		KAW	1.27	13	0.23
	KER	3.07	35.59	0.004		KER	4.66	35	<0.001
	KUS	1.43	7	0.20		KUS	0.009	6	0.99
RH	JSA	2.33	10	0.042	BM2B	JSA	0.99	8	0.35
	R12	3.23	16	0.005		R12	0.19	6	0.85
	KAW	1.15	13	0.27		KAW	2.21	13	0.046
	KER	3.81	37	0.001		KER	4.60	34	<0.001
	KUS	1.47	7	0.19		KUS	0.88	6	.41
GML	JSA	2.76	9	0.022					
	R12	1.73	11	0.11					
	KAW	-0.20	15	0.85					
	KER	1.65	35	0.11					
	KUS	0.72	7	0.49					

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **ML1**: mandibular length gnathion to midsagittal condyle-condyle chord; **ML2**: mandibular length gnathion to condyle; **ML3**: mandibular length infradentale to midsagittal gonion-gonion chord; **BGoB**: bigonial breadth; **BCoB**: bicondylar breadth; **LRB**: least ramus breadth; **MRB**: maximum ramus breadth; **RH**: ramus height; **CrH**: coronoid height; **GA**: gonial angle; **UML**: upper mandibular length from infradentale to midsagittal condyle-condyle chord; **LML**: lower mandibular length gnathion to gonion-gonion chord; **GML**: length from gnathion to M3; **DAL**: dental arch length from infradentale to midsagittal BM2B; **BCP3B**: dental arch breadth at C/P3; **BM1B**: dental arch breadth at M1; **BM2B**: dental arch breadth at M2; *t*: t-test statistic; df: degrees of freedom; level of significance at $p \le 0.05$.

Measurement	Population	t	df	р	Measurement	Population	t	df	р
SH	JSA	3.09	9	0.013	SB	JSA	1.58	9	0.15
	R12	-0.23	11	0.82		R12	-0.20	12	0.85
	KAW	3.26	13	0.006		KAW	1.09	14	0.29
	KER	2.22	33	0.033		KER	0.84	36	0.41
	KUS	4.44	6	0.004		KUS	0.68	6	0.53
SR	JSA	-0.18	9	0.86	SS	JSA	3.00	9	0.015
	R12	-0.001	11	0.99		R12	-0.22	11	0.83
	KAW	-1.45	13	0.17		KAW	2.68	13	0.019
	KER	-0.41	33	0.69		KER	1.96	33	0.059
	KUS	-1.27	6	0.25		KUS	1.77	6	0.13
MH	JSA	2.68	10	0.023	MB	JSA	0.26	9	0.80
	R12	1.28	19	0.22		R12	-1.06	19	0.31
	KAW	0.38	15	0.71		KAW	0.94	15	0.36
	KER	4.45	37	<0.001		KER	1.46	37	0.15
	KUS	0.87	6.525	0.42		KUS	-0.29	7	0.78
MR	JSA	-1.46	9	0.054	MS	JSA	1.43	9	0.19
	R12	-1.76	19	0.095		R12	-0.19	19	0.85
	KAW	0.57	15	0.58		KAW	0.96	15	0.35
	KER	-0.92	37	0.37		KER	3.40	37	0.002
	KUS	-0.69	7	0.51		KUS	-0.06	7	0.95
LH	JSA	1.50	7	0.18	LB	JSA	1.30	5.05	0.25
	R12	0.31	17	0.76		R12	-0.28	17	0.78
	KAW	0.62	14	0.55		KAW	-0.27	14	0.79
	KER	4.34	33	<0.001		KER	-0.23	34	0.82
	KUS	-0.18	6	0.86		KUS	0.77	6	0.47

 Table B.5 Independent *t*-tests between males and females for cross-sectional linear measurements

Measurement	Population	t	df	р	Measurement	Population	t	df	р
LR	JSA	0.19	7	0.91	LS	JSA	1.43	7	0.20
	R12	-0.076	6.89	0.94		R12	-0.26	17	0.80
	KAW	-0.73	14	0.48		KAW	0.20	12.61	0.84
	KER	-2.78	33	0.009		KER	1.75	33	0.09
	KUS	0.77	6	0.47		KUS	0.53	6	0.62
RH	JSA	3.10	8	0.015	RB	JSA	0.94	8	0.37
	R12	1.16	14	0.27		R12	-0.75	15	0.47
	KAW	0.68	13	0.51		KAW	-1.26	13	0.23
	KER	4.04	31	<0.001		KER	-0.94	34	0.35
	KUS	0.56	6	0.60		KUS	1.58	6	0.17
RR	JSA	-0.94	7.26	0.38	RS	JSA	1.91	8	0.09
	R12	-0.87	6.66	0.42		R12	-0.081	14	0.94
	KAW	-1.38	3.13	0.26		KAW	-0.38	13	0.71
	KER	-2.75	31	0.01		KER	0.54	31	0.59
	KUS	0.88	6	0.41		KUS	1.57	6	0.17

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **SH**: symphyseal height; **SB**: symphyseal breadth; **SR**: symphyseal breadth; **SR**: symphyseal breadth; **SR**: symphyseal breadth; **SR**: mental foramen neight; **MB**: mental foramen breadth; **MR**: mental foramen robusticity index; **MS**: mental foramen size; **LH**: left M_1/M_2 breadth; **LR**: left M_1/M_2 robusticity index; **LS**: left M_1/M_2 size; **RH**: right M_1/M_2 breadth; **RR**: right M_1/M_2 breadth; **RR**: right M_1/M_2 breadth; **RR**: right M_1/M_2 breadth; level of significance at $p \le 0.05$.

Measurement	Population	t	df	р	r
Height	JSA	-7.06	7	<0.001	.94
	R12	1.17	12	0.26	.32
	KAW	0.54	13	0.60	.15
	KER	-2.25	30	0.032	.38
	KUS	2.35	6	0.057	.69
Breadth	JSA	1.87	7	0.10	.58
	R12	0.091	12	0.93	.03
	KAW	-2.31	13	0.038	.54
	KER	-2.21	33	0.034	.36
	KUS	-0.12	6	0.91	.05
Robusticity Index	JSA	4.26	7	0.004	.85
	R12	-0.57	12	0.58	.16
	KAW	-2.70	13	0.018	.60
	KER	0.16	30	0.88	.03
	KUS	-0.72	6	0.50	.28
Size	JSA	-1.93	7	0.095	.59
	R12	0.76	12	0.46	.21
	KAW	-2.35	13	0.036	.55
	KER	-2.84	30	0.008	.46
	KUS	0.65	6	0.54	.26

Table B.6 Dependent *t*-tests comparing cross-sectional measurements from the left and right mandibular corpus at M_1/M_2

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Robusticity index: breadth/height; size: height x breadth x $\pi/4$; *t*: test statistic; df: degrees of freedom; test significant at $p \le 0.05$; *r*: effect size.

Measurement	F (df1, df2)	р	Hochberg	s's GT2 post-hoc tests
SB	0.036 (4, 82)	0.99		-
MB	0.79 (4, 29.74)	0.54		-
LH	12.77 (4, 83)	<0.001		JSA>all
LB	1.27 (4, 83)	0.28		-
RB	0.43 (4, 81)	0.79		-
Kruskal-Wallis	n	Н	р	Mann-Whitney tests
SH	82	31.08	<0.001	JSA>all
SR	82	23.48	<0.001	JSA>all
SS	82	19.73	0.001	JSA>all
MH	99	22.46	<0.001	JSA>all
MR	98	19.84	0.001	JSA>R12, KAW, KER
MS	98	9.23	0.056	-
LR	88	6.89	0.14	-
LS	88	16.85	0.002	JSA>KER, KUS
RH	82	27.44	<0.001	JSA>all
RR	82	13.65	0.008	JSA>KAW, KUS
RS	82	16.31	0.003	JSA>KER, KUS

Table B.7. ANOVAs and *post-hoc* tests for cross-sectional linear measurements (pooled sex)

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **SH**: symphyseal height; **SB**: symphyseal breadth; **SR**: symphyseal robusticity index; **SS**: symphyseal size; **MH**: mental foramen height; **MB**: mental foramen breadth; **MR**: mental foramen robusticity index; **MS**: mental foramen size; **LH**: left M₁/M₂ height; **LB**: left M₁/M₂ breadth; **LR**: left M₁/M₂ robusticity index; **LS**: left M₁/M₂ size; **RH**: right M₁/M₂ height; **RB**: right M₁/M₂ breadth; **RR**: right M₁/M₂ robusticity index; **RS**: right M₁/M₂ size; robusticity index: breadth/height; size: height x breadth x $\pi/4$; *F*: ANOVA test statistic; df1/df2: degrees of freedom 1/2; ANOVA level of significance $p \le 0.05$; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; *n*: sample size; *H*: Kruskal-Wallis test statistic; Kruskal-Wallis level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.005$.

Measurement	F (df1, df2)	р	ω	Hochberg's GT2 post-hoc tests
ML1	6.77 (4, 41)	<0.001	.33	JSA>R12, KAW, KER, KUS
ML2	10.15 (4, 40)	<0.001	.45	JSA>R12, KAW, KER, KUS
BGoB*	9.97 (3, 37)	0.001	.40	JSA>KAW, KER, KUS
BCoB*	11.66 (3, 34)	<0.001	.46	JSA>KAW, KER, KUS; KAW <ker< th=""></ker<>
LRB	18.20 (4, 47)	<0.001	.57	JSA>R12, KAW, KER, KUS
MRB	17.68 (4, 44)	<0.001	.58	JSA > R12, KAW, KER, KUS; R12 <ker< th=""></ker<>
RH	2.60(4, 44)	0.049	.12	No sig. results
CrH	3.13 (4, 43)	0.024	.15	No sig. results
GA	2.17 (4, 46)	0.088	N/A	N/A
UML	17.40 (4, 40)	<0.001	.59	JSA>R12, KAW, KER, KUS
GML	0.58 (4, 42)	0.68	N/A	N/A
BCP3B*	1.77 (3, 37)	0.053	N/A	N/A
BM1B*	4.56 (3, 36)	0.008	.21	JSA>KAW, KUS
BM2B*	1.17 (3, 36)	.34	N/A	N/A
	Kruskal-	Wallis and N	Iann-Whitne	y tests
Measurement	n	$H\left(\mathrm{df} ight)$	р	Mann-Whitney tests
ML3	46	18.37 (4)	0.001	JSA>KAW, KER
LML	47	22.24 (4)	<0.001	JSA>KAW, KER
DAL	46	14.65 (4)	0.005	JSA>KAW, KER

Table B.8. Male ANOVAs and *post-hoc* tests for mandibular measurements

*ANOVAs run without R12 population; ^aWelch's ANOVA. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *F*: ANOVA test statistic; df1/df2: degrees of freedom 1/2; ANOVA level of significance $p \le 0.05$; ω : effect size; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; *n*: sample size; *H*: Kruskal-Wallis test statistic; K-W level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.055$.

Measurement	F (df1, df2)	р	ω	Hochberg's GT2 post-hoc tests			
SH	23.72 (4, 38)	<0.001	.68	JSA>R12, KAW, KER, KUS			
MH	15.30 (4, 47)	<0.001	.52	JSA>R12, KAW, KER, KUS			
MB	1.00 (4, 46)	0.42	N/A	N/A			
LH	8.96 (4, 41)	<0.001	.67	JSA>R12, KAW, KER, KUS			
LB	0.67 (4, 41)	0.62	N/A	N/A			
RH	19.42 (4, 38)	<0.001	.63	JSA>R12, KAW, KER, KUS			
RB	0.92 (4, 40)	0.46	N/A	N/A			
Kruskal-Wallis and Mann-Whitney tests							
Measurement	n	$H(\mathrm{df})$	р	Mann-Whitney tests			
SB	45	0.44 (4)	0.98	N/A			
SS	43	17.19 (4)	0.002	JSA>KAW, KER			
SR	43	12.49 (4)	0.014	JSA <kaw< th=""></kaw<>			
MS	51	6.98 (4)	0.14	N/A			
MR	51	15.92 (4)	0.003	JSA <kaw, ker<="" th=""></kaw,>			
LR	46	4.11 (4)	0.39	N/A			
LS	46	8.20 (4)	0.08	N/A			
RR	43	11.59 (4)	0.021	JSA <kaw< th=""></kaw<>			
RS	43	14.564 (4)	0.006	JSA>KAW, KER			

 Table B.9. Male ANOVAs and *post-hoc* tests for cross-sectional linear measurements and calculated values

^aWelch's ANOVA. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *F*: ANOVA test statistic; df1/df2: degrees of freedom 1/2; ANOVA level of significance $p \le 0.05$; ω : effect size; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; *m*: manple size; *H*: Kruskal-Wallis test statistic; K-W level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.05$.

Measurement	F (df1, df2)	р	Ø	Hochberg's GT2 post-hoc tests
ML2	5.13 (4, 36)	0.002	.29	JSA>KER, KUS
ML3	5.78 (4, 37)	0.001	.31	JSA>KER
BGoB	5.60 (4, 30)	0.002	.35	JSA>KAW, KER
BCoB	2.21 (4, 29)	0.092	N/A	N/A
LRB	12.80 (4, 39)	<0.001	.52	JSA>R12, KAW, KER, KUS
MRB	12.48 (4, 38)	<0.001	.52	JSA>R12, KAW, KER, KUS
RH	1.35 (4, 39)	0.27	N/A	N/A
CrH	1.17 (4, 40)	0.34	N/A	N/A
GA	1.01 (4, 40)	0.42	N/A	N/A
LML	9.26 (4, 37)	<0.001	.44	JSA>KER, KUS; R12>KER, KUS
UML	7.17 (4, 36)	<0.001	.38	JSA>R12, KAW, KER, KUS
GML	0.72 (4, 35)	0.58	N/A	N/A
BM1B	4.54 (4, 32)	0.005	0.28	JSA>R12, KER
	Kruskal-W	Vallis and Ma	ann-Whitne	y tests
Measurement	n	$H\left(\mathrm{df} ight)$	р	Mann-Whitney tests
ML1	41	12.96 (4)	0.011	No significant results
DAL	41	12.21 (4)	0.016	No significant results
BCP3B	40	9.09 (4)	0.06	N/A
BM2B	36	9.96 (4)	0.041	No significant results

Table B.10 Female ANOVAs and post-hoc tests for mandibular measurements

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *F*: ANOVA test statistic; df1/df2: degrees of freedom 1/2; ANOVA level of significance $p \le 0.05$; ω : effect size; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; *n*: sample size; *H*: Kruskal-Wallis test statistic; K-W level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.005$.

Measurement	F (df1, df2)	р	ω	Hochberg's GT2 post-hoc tests
SH	9.04 (4, 34)	<0.001	.45	JSA>R12, KAW, KER, KUS
SB	0.31 (4, 37)	0.87	N/A	N/A
MB	1.00 (4, 41)	0.42	N/A	N/A
LH	3.97(4, 36)	0.009	.23	JSA>KER
RB	0.87 (4, 36)	0.49	N/A	N/A
	Krus	kal-Wallis and	Mann-Whitne	ey tests
Measurement	n	<i>H</i> (df)	р	Mann-Whitney tests
SS	39	6.60 (4)	0.16	N/A
SR	39	10.24 (4)	0.037	No sig. results
MH	46	7.39 (4)	0.12	N/A
MS	46	6.51 (4)	0.16	N/A
MR	46	4.84 (4)	0.30	N/A
LB	42	6.74 (4)	0.15	N/A
LR	41	5.57 (4)	0.23	N/A
LS	41	8.54 (4)	0.074	N/A
RH	39	9.83 (4)	0.043	No sig. results
RR	39	4.35 (4)	0.36	N/A

 Table B.11 Female ANOVAs and *post-hoc* tests for cross-sectional linear measurements and calculated values

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *F*: ANOVA test statistic; df1/df2: degrees of freedom 1/2; ANOVA level of significance $p \le 0.05$; ω : effect size; Hochberg's GT2 *post-hoc* test level of significance $p \le 0.05$; *n*: sample size; *H*: Kruskal-Wallis test statistic; K-W level of significance $p \le 0.05$; Mann-Whitney tests level of significance $p \le 0.005$.
APPENDIX C MANDIBULAR CROSS-SECTIONAL GEOMETRY DATA

Measurement	Population	t	df	р
ТА	JSA	2.80	7	0.026
	R12	1.55	12	0.15
	KAW	0.49	13	0.63
	KER	0.68	32	0.51
	KUS	-0.097	6	0.93
I_x	JSA	4.33	7	0.003
	R12	1.56	12	0.14
	KAW	1.15	14	0.27
	KER	-0.39	32	0.70
	KUS	0.34	6	0.75
I_y	JSA	0.52	7	0.62
	R12	1.37	12	0.20
	KAW	0.60	14	0.56
	KER	0.51	32	0.61
	KUS	-0.56	6	0.60
I _{max}	JSA	4.52	7	0.003
	R12	1.74	12	0.11
	KAW	1.11	14	0.29
	KER	-0.72	32	0.48
	KUS	0.098	6	0.93
I _{min}	JSA	1.57	7	0.16
	R12	1.14	12	0.28
	KAW	0.56	14	0.59
	KER	2.08	32	0.046
	KUS	-0.216	6	0.84
J	JSA	4.30	7	0.004
	R12	1.77	12	0.46
	KAW	1.06	14	0.31
	KER	-0.225	32	0.82
	KUS	0.03	6	0.98

Table C.1 Dependent t-tests between left and right molar regions for CSG properties

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). CSG: cross-sectional geometry; *t*: dependent *t*-test statistic; df: degrees of freedom; level of significance $p \le 0.05$.

<u>Cross-section</u>											
	Symp	hysis			Left	Molar			Right N	Molar	
JSA	t	df	р	JSA	t	df	р	JSA	t	df	р
ТА	2.18	9	0.057	TA	1.87	7	0.10	ТА	2.09	8	0.07
I_x	3.54	9	0.006	I_x	1.95	7	0.093	I_x	2.35	8	0.047
I_y	2.42	6.58*	0.048	I_y	1.23	7	0.26	I_y	1.47	8	0.18
I _{max}	3.64	9	0.005	Imax	1.97	7	0.09	Imax	2.33	8	0.048
Imin	1.25	9	0.24	Imin	1.40	7	0.20	I_{min}	1.40	8	0.20
J	3.27	9	0.01	J	1.99	7	0.087	J	2.24	8	0.055
R12	t	df	р	R12	t	df	р	R12	t	df	p
TA	-1.16	12	0.27	TA	0.32	11	0.76	TA	0.03	13	0.98
I_x	-1.25	12	0.24	I_x	1.03	12	0.32	I_x	1.76	13	0.10
I_y	-0.95	12	0.36	I_y	-0.53	12	0.61	I_y	-0.66	13	0.52
Imax	-1.26	12	0.23	Imax	1.04	12	0.32	Imax	1.77	13	0.10
Imin	-0.93	12	0.37	I _{min}	-1.16	12	0.27	I_{min}	-0.96	13	0.36
J	-1.23	12	0.24	J	0.68	12	0.51	J	1.19	13	0.25
KAW	t	df	р	KAW	t	df	р	KAW	t	df	р
ТА	4.21	13	0.001	TA	0.49	12	0.63	TA	-0.74	13	0.47
I_x	2.89	13	0.013	I_x	1.03	13	0.32	I_x	-0.32	13	0.75
I_y	2.72	13	0.017	I_y	0.33	13	0.74	I_y	-1.17	13	0.27
I _{max}	2.87	13	0.013	Imax	1.00	13	0.34	I _{max}	-0.41	13	0.69
I _{min}	2.92	13	0.012	Imin	0.67	10.32*	0.52	I_{min}	-1.06	13	0.31
J	3.1	13	0.008	J	0.91	13	0.38	J	-0.58	13	0.57
KER	t	df	р	KER	t	df	р	KER	t	df	р
TA	2.40	31	0.022	TA	2.33	34	0.026	TA	1.45	33	0.16
I_x	1.94	31	0.061	I_x	3.98	34	<0.001	I_x	3.61	33	0.001
I_y	2.20	31	0.035	I_y	0.77	34	0.45	I_y	0.022	33	0.98
I_{max}	2.02	31	0.052	Imax	3.61	34	0.001	I _{max}	3.29	33	0.002
I_{min}	1.99	31	0.055	Imin	1.05	34	0.30	I_{min}	0.18	33	0.86
J	2.17	31	0.038	J	3.26	34	0.003	J	2.69	33	0.011
KUS	t	df	р	KUS	t	df	р	KUS	t	df	р
TA	1.09	6	0.32	TA	-0.18	6	0.86	TA	1.27	6	0.25
I_x	1.88	6	0.11	I_x	-0.34	6	0.75	I_x	0.54	6	0.61
I_y	0.78	6	0.46	I_y	-0.63	6	0.55	I_y	0.69	6	0.52
I _{max}	1.85	6	0.11	I _{max}	-0.67	6	0.53	I _{max}	0.23	6	0.83
I_{min}	0.87	6	0.42	I _{min}	0.072	6	0.95	I_{min}	1.86	6	0.11
J	1.68	6	0.14	J	-0.47	6	0.66	J	0.71	6	0.50

Table C.2 Independent t-tests for sex differences in CSG properties

*Equal variances not assumed. **JSA**: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *t*: dependent *t*-test statistic; df: degrees of freedom; level of significance $p \le 0.05$.

Measurement	п	Н	df	р	Mann-Whitney tests
Symphysis				-	
I _x /BM2B	70	9.41	4	0.052	-
I _x /BGoB	69	3.19	4	0.53	-
I _y /ML3	78	17.05	4	0.002	KER>R12
I _{max} /BGoB	69	3.61	4	0.46	-
Imax/BM2B	70	10.46	4	0.033	JSA>KAW, KUS
$I_{min}/ML3$	78	18.09	4	0.001	KER>JSA, R12
I_y/I_x	81	4.138	4	0.39	-
I_{min}/I_{max}	81	18.83	4	0.001	JSA <r12, kaw,="" ker,<="" td=""></r12,>
					KUS
Left M1/M2					
I _x /ML2	76	14.68	4	0.005	JSA>KER
I _x /ML3	78	1.79	4	0.77	-
I _x /LML	78	2.95	4	0.57	-
I _y /BGoB	71	9.96	4	0.041	No sig. results
I _y /BM2B	73	3.88	4	0.42	-
$I_{max}/ML2$	77	12.11	4	0.017	JSA>KER
I _{max} /ML3	78	1.99	4	0.74	-
I _{max} /LML	78	3.74	4	0.44	-
Imin/BGoB	71	8.12	4	0.087	-
$I_{min}/BM2B$	73	3.4	4	0.49	-
I_{min}/I_{max}	83	13.21	4	0.010	JSA <kaw, kus<="" td=""></kaw,>
I_y/I_x	83	10.78	4	0.029	No sig. results
Right M1/M2					
I _x /ML2	74	3.01	4	0.56	-
I _x /ML3	76	5.67	4	0.23	-
I _x /LML	76	2.73	4	0.61	-
I _y /BGoB	69	12.30	4	0.015	JSA <r12< td=""></r12<>
I _y /BM2B	70	4.60	4	0.33	-
I _{max} /ML2	74	2.36	4	0.67	-
$I_{max}/ML3$	76	6.89	4	0.14	-
I _{max} /LML	76	4.87	4	0.30	-
Imin/BGoB	69	9.54	4	0.049	No sig. results
$I_{min}/BM2B$	70	2.29	4	0.68	-
I _{min} /I _{max}	83	17.89	4	0.001	KAW>JSA, KER
I_v/I_x	83	11.41	4	0.022	No sig. results

Table C.3 Kruskal-Wallis and Mann-Whitney tests for CSG measurement indices

JSA: Jebel Sahaba, Late Palaeolithic (c. 13000–9000 BC); **R12:** NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). **ML2**, mandibular length gnathion to condyle; **ML3**, mandibular length infradentale to midsagittal gonion-gonion chord; **BGoB**, bigonial breadth; **BCoB**, bicondylar breadth; **LML**, lower mandibular length gnathion to gonion-gonion chord; **BM2B**, dental arch breadth at M₂. CSG: cross-sectional geometry; df: degrees of freedom; *n*: sample size; *H*: Kruskal-Wallis test statistic; Kruskal-Wallis level of significance $p \le 0.05$; Mann-Whitney test level of significance $p \le 0.005$.

APPENDIX D ORAL HEALTH DATA

D.1 Dental Wear

Table D.1.1 Dental wear sample size by population for tooth, sex and age								
	R 1	2	KA	W	KE	R	KU	JS
Sex	Male	Female	Male	Female	Male	Female	Male	Female
\mathbf{I}_1	7	12	7	0	1	0	3	3
I_2	7	10	5	1	5	3	4	3
C ₁	6	11	7	3	5	4	3	3
P ₃	8	11	9	4	5	10	3	3
P ₄	7	11	11	4	10	12	3	3
M_1	9	13	13	4	19	18	5	3
M_2	9	13	12	4	17	15	5	3
M_3	8	13	10	4	17	13	5	2
Total	61	94	74	24	79	75	31	23
1 otui	01	74	/ 4	24	1)	15	51	23
1000	R1	1 <u>2</u>	KA	W	KE	\mathbf{R}	KU	 J S
Age	R1 Younger	2 Older	KA Younger	W Older	KE Younger	CR Older	KU Younger	JS Older
Age I ₁	R1 Younger 4	Older 15	KA Younger 5	W Older 2	KE Younger 0	CR Older 1	SI KU Younger 5	JS Older 1
Age I ₁ I ₂	R1 Younger 4 3	Older 15 14	KA Younger 5 5	24 W Older 2 1	KE Younger 0 4	CR 0lder 1 4	51 KU Younger 5 5	23 JS Older 1 2
Age I ₁ I ₂ C ₁	R1 Younger 4 3 4	J4 Older 15 14 13	KA <u>Younger</u> 5 5 6	24 W Older 2 1 4	KE Younger 0 4 4 4	73 CR Older 1 4 5	51 KU Younger 5 5 4	23 JS Older 1 2 2
Age I ₁ I ₂ C ₁ P ₃	R1 Younger 4 3 4 4 4	12 0lder 15 14 13 15	KA Younger 5 5 6 9	24 W Older 2 1 4 4	KE Younger 0 4 4 8	Older 1 4 5 6	5 5 5 4 5	23 JS Older 1 2 2 1
Age I ₁ I ₂ C ₁ P ₃ P ₄	R1 Younger 4 3 4 4 4 4 4	J4 Older 15 14 13 15 14	KA Younger 5 5 6 9 11	V Older 2 1 4 4 4 4	KE Younger 0 4 4 8 13	73 CR Older 1 4 5 6 8	51 KU Younger 5 5 4 5 5 5 5	23 JS Older 1 2 2 1 1 1
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁	R1 Younger 4 3 4 4 4 5	J4 Older 15 14 13 15 14 17	KA Younger 5 5 6 9 11 12	W 0lder 2 1 4 4 5	KE Younger 0 4 4 8 13 22	1 4 5 6 8 14	KU Younger 5 5 4 5 5 5 1	23 JS Older 1 2 2 1 1 1 6
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁ M ₂	R1 Younger 4 3 4 4 4 4 5 5 5	J4 12 Older 15 14 13 15 14 17 17	KA Younger 5 6 9 11 12 11	24 W Older 2 1 4 4 4 5 5 5	KE Younger 0 4 4 8 13 22 22 22	1 4 5 6 8 14 9	KU Younger 5 5 4 5 5 5 1 6	23 JS 0lder 1 2 2 1 1 6 2
Age I ₁ I ₂ C ₁ P ₃ P ₄ M ₁ M ₂ M ₃	R1 Younger 4 3 4 4 4 5 5 5 5	J4 12 Older 15 14 13 15 14 17 16	KA Younger 5 5 6 9 11 12 11 9	V 0lder 2 1 4 4 5 5 5	KE Younger 0 4 4 8 13 22 22 19	1 4 5 6 8 14 9 10	KU Younger 5 5 4 5 5 1 6 5 5	23 JS Older 1 2 2 1 1 6 2 2 2

Table D.1.1 Dental wear sample size by population for tooth, sex and age

R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Younger adults \leq 35 years old, older adults >35 years old.

Population	Tooth	n	U	р
	I_1/M_1	19	39.0	0.80
	I_2/M_1	17	31.0	0.69
	C_1/M_1	17	30.5	0.80
R12	P_3/M_1	19	29.0	0.21
	P_4/M_1	18	26.0	0.25
	M_2/M_1	22	51.0	0.61
	M_3/M_1	22	51.5	0.97
	I_1/M_1	N/A	N/A	N/A
	I_2/M_1	6	1.0	0.37
KAW	C_1/M_1	10	5.5	0.24
	P_3/M_1	13	6.0	0.035
	P_4/M_1	15	10.0	0.076
	M_2/M_1	16	21.0	0.70
	M_3/M_1	14	19.0	0.88
	I_1/M_1	N/A	N/A	N/A
	I_2/M_1	8	5.5	0.55
	C_1/M_1	9	5.5	0.27
KFR	P_3/M_1	15	24.0	0.90
MLA	P_4/M_1	22	37.0	0.11
	M_2/M_1	32	81.5	0.076
	M_3/M_1	30	80.0	0.20
	I_{l}/M_{1}	6	0.0	0.037
	I_2/M_1	7	1.0	0.077
	C_1/M_1	6	3.0	0.50
KUS	P_3/M_1	6	3.5	0.66
	P_4/M_1	6	4.0	0.822
	M_2/M_1	8	7.5	1.00
	M ₃ /M ₁	7	4.5	0.84

Table D.1.2 Mann-Whitney tests comparing dental wear by sex within each Nubian population

R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; *U*: Mann-Whitney test statistic; N/A: not applicable due to sample size; *p*: significance at $p \le 0.05$.

D.2 Dental caries

Table D.2.1 Kruskal-Wallis and Mann-Whitney tests comparing carious lesion severity be	etween
populations (combined dentition)	

n	Н	р	Mann-Whitney post-hoc
496	17.48	0.001	KER > R12, KAW
Combined left mandibular	dentition; dental caries score	red 1-4 according to Turn	er 1979 and Powell 1985. R12 :
NDRS R12. Neolithic (c.	5000-4000 cal BC): KAW	: NDRS P37, Kerma And	cien (c. 2500–2050 BC): KER:

Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; df: degrees of freedom; *p*: two-tailed significance set at $p \le 0.05$; Mann-Whitney test level of significance $p \le 0.008$; arrows indicate direction of significant relationship between populations.

Table D.2.2 Prevalence of carious lesions by population and chi-square analysis (combined dentition)

Population	n (total n)	% with caries	χ^2 (df)	p ^a
R12	1 (154)	0.6		
KAW	0 (99)	0.0		
KER	15 (190)	7.9		
KUS	2 (53)	3.8		
Total	396		20.67 (3)	<0.001

^aLikelihood ratio. Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500– 2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; %: number of affected teeth/total *n* for each population x 100; $p \le 0.05$ significant; Cramer's V=.188.

(combined dentition)				
Population	Sex	п	MR	р
	Male	59	77.00	
R12	Female	95	77.81	
	Total	154		0.43
	Male	75	50.00	
KAW	Female	24	50.00	
	Total	99		1.00

92

98

190

36

17

53

92.05

98.73

26.00

29.12

0.073

0.038

Male

Female

Total

Male

Female

Total

KER

KUS

Table D.2.3 Mann-Whitney tests comparing carious lesion severity by sex within each population (combined dentition)

Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*, sample size; MR, mean rank; *p*, two-tailed significance set at $p \le 0.05$.

Population	Age	п	MR	р
	Younger Adult	34	77.00	
R12	Older Adult	120	77.64	
	Total	154		.60
	Younger Adult	69	50.00	
KAW	Older Adult	30	50.00	
	Total	99		1.00
	Younger Adult	105	95.26	
KER	Older Adult	80	90.04	
	Total	185		.17
	Younger Adult	34	26.78	
KUS	Older Adult	19	27.39	
	Total	53		.67

Table D.2.4 Mann-Whitney tests comparing caries severity by age category within each population (combined dentition)

Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; MR: mean rank; df: degrees of freedom; *p*: two-tailed significance set at $p \le 0.05$; younger adults ≤ 35 years old, older adults ≥ 35 years old.

Donulation	Sov	Sov <u><i>n</i>(%)</u>		Totol	-
Population	Sex	Absent	Present	Total n	p
	Male	59 (100.0)	-	59	
R12	Female	94 (98.1)	1 (1.1)	95	
	Total			154	1.00^{b}
	Male	75 (100.0)	-	75	
KAW	Female	24 (100.0)	-	24	
	Total			99	_c
	Male	88 (95.7)	4 (4.3)	92	
KER	Female	87 (88.2)	11 (11.2)	98	
	Total			190	0.079ª
	Male	36 (100)	-	36	
KUS	Female	15 (88.2)	2 (11.8)	17	
	Total			53	0.099 ^b

Table D.2.5 Chi-square tests of caries prevalence by sex and population (combined dentition)

^aSignificance based on Pearson chi-square ($p \le 0.05$); ^bSignificance based on Fisher's exact test ($p \le 0.05$); ^cNo statistics are computed because caries is a constant. Combined left mandibular dentition. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; %: *n* of affected teeth/total *n* x 100.

Demails 4 ² and	Age	n ((%)		-
	Category	Absent	Present	n	p
	Younger adult	34 (100.0)	-	34	
R12	Older adult	118 (99.2)	1 (0.8)	119	
	Total	152	1	153	1.00 ^b
	Younger adult	69 (100.0)	-	69	
KAW	Older adult	47 (100.0)	-	47	
	Total	116	-	116	_c
	Younger adult	94 (89.5)	11 (10.5)	105	
KER	Older adult	76 (95.0)	4 (5.0)	80	
	Total	170	15	185	0.18 ^a
	Younger adult	33 (77.1)	1 (2.9)	34	
KUS	Older adult	18 (94.7)	1 (5.3)	19	
	Total	51	2	53	1.00 ^b

Table D.2.6 Chi-square tests for dental caries prevalence between age categories (combined dentition)

^aSignificance based on Pearson Chi-square ($p \le 0.05$); ^bSignificance based on Fisher's Exact Test ($p \le 0.05$); ^cNo statistics were computed because caries is a constant. Combined left mandibular dentition. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; %: *n* of affected teeth/total *n* x 100; younger adults \le 35 years old, older adults >35 years old.

		Tooth Class n (%)				
Population	Caries Severity	Incisor	Canine	Premolar	Molar	
	Absent	34 (100.0)	17 (100.0)	37 (100.0)	66 (98.5)	
R12	Stages 1 and 2	-	-	-	1 (1.5)	
	Stages 3 and 4	-	-	-	-	
	Absent	13 (100.0)	10 (100.0)	28 (100.0)	48 (100.0)	
KAW	Stages 1 and 2	-	-	-	-	
	Stages 3 and 4	-	-	-	-	
	Absent	13 (100.0)	11 (100.0)	50 (100.0)	101 (87.1)	
KER	Stages 1 and 2	-	-	-	14 (12.1)	
	Stages 3 and 4	-	-	-	1 (0.9)	
	Absent	11 (100.0)	5 (83.3)	12 (100.0)	24 (95.8)	
KUS	Stages 1 and 2	-	1 (16.7)	-	1 (4.2)	
	Stages 3 and 4	-	-	-	-	

Table D.2.7 Carious lesion severity by tooth class

Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

Tooth Class	n	Н	df	р	M-W
Incisor	71	0.0	3	1.00	N/A
Canine	44	6.33	3	0.096	N/A
Premolar	127	0.0	3	1.00	N/A
Molar	254	13.71	3	0.003	No Sig.

 Table D.2.8 Kruskal-Wallis and Mann-Whitney tests comparing dental caries severity by tooth class

Combined left mandibular dentition; dental caries scored 1–4 according to Turner 1979 and Powell 1985. *n*: sample size; df: degrees of freedom; Kruskal-Wallis level of significance, $p \le 0.05$; Mann-Whitney level of significance, $p \le 0.008$; arrows indicate direction of significant relationship between populations.

D.3 Dental calculus



Figure D.3.1 Calculus severity by population (combined dentition) for (a) males and (b) females
Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent;
1, mild; 2, moderate; 3, severe. R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); KAW: NDRS
P37, Kerma Ancien (c. 2500–2050 BC); KER: Kerma, Kerma Classique (c. 1750–1500 BC); KUS: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth; %: number of affected teeth/total *n* x 100.





Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent; 1, mild; 2, moderate; 3, severe. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth; %: number of affected teeth/total *n* x 100; younger adults, \leq 35 years old; older adults >35 years old.

Kruskal-Wallis Test	Category	n	Н	р	Mann-Whitney post-hoc
	Male	263	17.69	<0.001	KAW, KER>R12
Sex					KAW>R12, KER,
	Female	236	29.12	< 0.001	KUS
					KAW>R12, KER,
Age	Younger Adult	243	21.56	<0.001	KUS
_	Older Adult	251	26.18	<0.001	KAW, KER>R12

Table D.3.1 Kruskal-Wallis and Mann-Whitney tests for calculus severity between sex and age of different populations (combined dentition)

Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent; 1, mild; 2, moderate; 3, severe. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth; %: number of affected teeth/total *n* x 100; *H*: Kruskal-Wallis test statistic; df: degrees of freedom, 3; Kruskal-Wallis test significance at $p \le 0.005$; Mann-Whitney test significance at $p \le 0.008$; younger adults ≤ 35 years old, older adults >35 years old; arrows indicate direction of significant relationship between populations.

Table D.3.2 Descriptive statistics and Mann-Whitney tests for calculus severity by sex within each population (combined dentition)

		n (
Population	Calculus severity	Male	Female	р
	Absent	42 (71.2)	70 (73.7)	
	Mild	12 (20.3)	18 (18.9)	
R12	Moderate	4 (6.8)	7 (7.4)	
	Severe	1 (1.7)	-	
	MR	78.80	76.69	0.72
	Absent	27 (37.0)	4 (16.7)	
	Mild	33 (45.2)	14 (58.3)	
KAW	Moderate	9 (12.3)	5 (20.8)	
	Severe	4 (5.5)	1 (4.2)	
	MR	46.53	56.52	0.10
	Absent	37 (38.9)	54 (54)	
	Mild	49 (51.9)	40 (40)	
KER	Moderate	8 (8.4)	6 (6)	
	Severe	1 (1.1)	-	
	MR	105.91	90.49	0.033
	Absent	19 (52.8)	12 (70.6)	
	Mild	15 (41.7)	5 (29.4)	
KUS	Moderate	2 (5.6)	-	
	Severe	-	-	
	MR	28.65	23.50	0.19

Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent; 1, mild; 2, moderate; 3, severe. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth; %: number of affected teeth/total *n* x 100; MR: mean rank; Mann-Whitney test significance at $p \le 0.05$.

	<u> </u>				
Population	Calculus Severity	Younger Adult	Older Adult	р	
	Absent	23 (67.6)	89 (74.2)		
	Mild	5 (14.7)	25 (20.8)		
R12	Moderate	6 (17.6)	5 (4.2)		
	Severe	-	1 (0.8)		
	MR	83.09	75.92	0.29	
	Absent	18 (26.9)	13 (43.3)		
	Mild	32 (47.8)	15 (50)		
KAW	Moderate	12 (17.9)	2 (6.7)		
	Severe	5 (7.5)	-		
	MR	52.97	40.13	0.024	
	Absent	54 (50.0)	32 (39.0)		
	Mild	48 (44.4)	41 (50.0)		
KER	Moderate	6 (5.6)	8 (9.8)		
	Severe	-	1 (1.2)		
	MR	90.11	102.60	0.084	
	Absent	18 (52.9)	13 (68.4)		
	Mild	16 (47.1)	4 (21.1)		
KUS	Moderate	-	2 (10.5)		
	Severe	-	-		
	MR	28.00	25.21	0.47	

Table D.3.3 Descriptive statistics and Mann-Whitney tests for calculus severity by age within each population (combined dentition)

Left mandibular dentition; calculus severity scored 0–3 following Brothwell (1972, 1981): 0, absent; 1, mild; 2, moderate; 3, severe. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: number of affected teeth; %: number of affected teeth/total *n* x 100; MR: mean rank; younger adults \leq 35 years old, older adults >35 years old; Mann-Whitney test significance at *p* \leq 0.05.

D.4 Linear enamel hypoplasia (LEH)

	1 0		
п	χ^2	df	р
493	1.66	3	0.45
I oft mandibular dont	ition: n: sampla siza: x^2 : Poarson chi	, squara tast statistic: df	dagraas of freedom: n two

Table D.4.1 Chi-square test comparing rates of LEH by population (combined dentition)

Left mandibular dentition; *n*: sample size; χ^2 : Pearson chi-square test statistic; df: degrees of freedom; *p*, two-tailed significance set at *p*≤0.05; LEH: linear enamel hypoplasia.

Table D.4.2 Chi-square tests comparing rates of LEH by tooth class

Tooth Class	п	χ²	р
Incisor	70	4.58	0.21
Canine	47	0.61	0.90
Premolar	125	1.88	0.60
Molar	251	4.20	0.24

Left mandibular dentition; *n*: sample size; χ^2 : Pearson chi-square test statistic; df: degrees of freedom; *p*: two-tailed significance set at *p*≤0.05.

Donulation	Sow	<i>n</i> (%)		Totol a	-
ropulation	Sex	Absent	Present	Total n	p
	Male	54 (91.5)	5 (8.5)	59	
R12	Female	90 (94.7)	5 (5.3)	95	
	Total			154	0.51 ^a
	Male	64 (88.9)	8 (11.1)	32	
KAW	Female	22 (91.7)	2 (8.3)	24	
	Total			96	1.00^{a}
	Male	88 (94.6)	5 (5.4)	93	
KER	Female	88 (90.7)	9 (9.3)	97	
	Total			190	0.30 ^b
VIIC	Male	34 (94.4)	2 (5.6)	36	
KUS	Female	16 (94.1)	1 (5.9)	17	
	Total			53	1.00 ^a

Table D.4.3 Chi-square tests for LEH prevalence between sexes by population (tooth count)

^aFisher's Exact Test; ^bPearson Chi-Square. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Left mandibular dentition; LEH: linear enamel hypoplasia; *n*: sample size; %, *n* affected dentition/total *n* x 100; *p*: two-tailed significance set at $p \le 0.05$.

D.5 Periodontal Disease

Table D.5.1 Chi-square test comparing periodontal disease between populations for combined dentition

п	χ^2	df	р
398	80.22	3	<0.001

Left mandibular dentition; *n*: sample size; χ^2 : Pearson chi-square test statistic; df: degrees of freedom; *p*: two-tailed significance set at *p*≤0.05.

Table D.5.2 Prevalence of periodontal disease within each population and tooth class (tooth class)
--

	<u> </u>				
Population	Incisor	Canine	Premolar	Molar	Total
R12	0	0	5 (20)	27 (49.1)	32 (29.9)
KAW	2 (33.3)	1 (33.3)	2 (18.2)	19 (55.9)	24 (44.4)
KER	7 (50.0)	8 (57.1)	40 (74.1)	87 (75.7)	142 (72.1)
KUS	0	0	0	1 (5.0)	1 (3.6)

R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). Left mandibular dentition; *n*: sample size; χ^2 : Pearson chi-square test statistic; df: degrees of freedom; *p*: two-tailed significance set at *p*≤0.05

		5	2 I	
Tooth class	χ^2	df	р	Cramer's V
Incisor	15.09	3	0.002 ^a	0.549
Canine	12.98	3	0.005 ^a	0.583
Premolar	33.05	3	<0.001 ^b	0.565
Molar	39.85	3	<0.001 ^a	0.422

Table D.5.3 Chi-square tests of periodontal disease by tooth type

Left mandibular dentition; *n*: sample size; χ^2 : Pearson chi-square test statistic; df: degrees of freedom; *p*: two-tailed significance set at *p*≤0.05.

Donulation	Corr	<i>n</i> (%)	Tatal	7	
Population	Sex	Absent	Present	Total n	p	
	Male	36 (83.7)	7 (16.3)	43		
R12	Female	39 (60.9)	25 (39.1)	64		
	Total				0.012 ^a	
KAW	Male	23 (62.2)	14 (37.8)	37		
	Female	7 (41.2)	10 (58.8)	17		
	Total				0.15 ^a	
	Male	14 (14.4)	83 (85.6)	97		
KER	Female	41 (41.0)	59 (59)	100		
	Total				<0.001 ^a	
	Male	23 (95.8)	1 (4.2)	24		
KUS	Female	4 (100.0)	0	4		
	Total				1.00 ^b	

Table D.5.4 Chi-square tests for prevalence of periodontal disease by sex (tooth count)

^aSignificance based on Pearson's Chi-square; ^bSignificance based on Fisher's Exact Test. Combined left mandibular dentition. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; %: percentage of dentition affected by periodontal disease; *p*: two-tailed significance set at $p \le 0.05$.

		<i>n</i> (%)	T ()	
Population	Age	Absent	Present	lotal	р
	Younger Adult	19 (86.4)	3 (13.6)	22	-
R12	Older Adult	56 (65.9)	29 (34.1)	85	
	Total			107	0.061 ^a
KAW	Younger Adult	22 (61.1)	14 (38.9)	36	
	Older Adult	8 (44.4)	10 (55.6)	18	
	Total			54	0.25 ^a
	Younger Adult	36 (33.6)	71 (66.4)	107	
KER	Older Adult	14 (16.5)	71 (83.5)	85	
	Total			192	$\mathbf{0.007^{a}}$
	Younger Adult	23 (100.0)	-	23	
KUS	Older Adult	4 (80.0)	1 (20.0)	5	
	Total			28	0.18^{b}

Table D.5.5 Chi-square tests for prevalence of periodontal disease by age (tooth count)

^aSignificance based on Pearson's Chi-square; ^bSignificance based on Fisher's Exact Test. Combined left mandibular dentition. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; %: percentage of dentition affected by periodontal disease; *p*: two-tailed significance set at $p \le 0.05$; younger adults ≤ 35 years old, older adults >35 years old.

APPENDIX E DENTAL METRIC DATA

E.1 Dental Metric Sex Descriptive Statistics

I_1			I				
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	6	10	5.19	0.32	5.03	0.29	
KAW	6	0	5.04	0.62	-	-	
KER	1	1	4.85	N/A	5.09	N/A	
KUS	2	3	4.66	0.77	5.09	0.35	
I_2							
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	5	8	5.89	0.55	5.35	0.78	
KAW	5	1	5.87	0.52	6.03	N/A	
KER	5	3	5.24	0.78	5.63	0.33	
KUS	2	3	5.7	0.078	5.69	0.39	
C ₁							
	Sample size (n)		Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	7	8	6.99	1.24	6.44	0.39	
KAW	7	3	6.97	0.32	6.34	0.16	
KER	5	3	6.04	0.82	5.61	0.67	
KUS	1	3	6.05	N/A	6.59	0.31	
P ₃							
	Sample	size (n)	Male		Female		
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	7	10	6.65	0.42	6.41	0.23	
KAW	7	5	7.40	0.50	6.84	0.26	
KER	6	10	6.87	0.59	6.66	0.78	
KUS	1	4	5.65	N/A	6.57	0.54	
\mathbf{P}_4							
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	8	9	7.09	0.46	6.81	0.60	
KAW	9	5	7.23	0.36	6.91	0.35	
KER	12	14	7.01	0.64	6.86	0.77	
KUS	2	4	7.17	0.83	7.14	0.57	

Table E.1.1 Descriptive statistics for mesiodistal dental measurements by population and sex

\mathbf{M}_{1}	i					
	Sample	size (n)	Male		Femal	le
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD
R12	8	11	11.07	0.57	10.66	0.57
KAW	10	5	10.94	0.34	10.34	0.84
KER	18	16	10.47	1.02	10.39	0.74
KUS	2	4	11.38	0.42	10.76	0.55
\mathbf{M}_2	i					
	Sample	size (n)	Male		Femal	le
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD
R12	8	10	11.16	0.63	10.39	0.75
KAW	10	5	10.88	0.61	10.12	0.49
KER	20	16	11.02	0.86	10.31	0.72
KUS	2	4	10.66	0.77	10.17	0.59
M_3						
	Sample	size (n)	Male		Femal	le
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD
R12	8	13	10.53	1.03	10.52	0.91
KAW	10	5	11.31	1.49	10.17	0.46
KER	21	18	10.86	1.33	10.35	0.76
KUS	2	4	11.27	0.13	10.33	0.61

Table E.1.1 continued

R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). *n*: sample size; N/A: not applicable; SD: standard deviation.

Tooth	Population	df	t	р
	R12	14	1.02	0.32
Ŧ	KAW	N/A		
11	KER	N/A		
	KUS	3	-0.89	0.44
	R12	11	1.36	0.20
т	KAW	4	-0.28	0.79
12	KER	5	-0.24	0.82
	KUS	3	0.006	0.99
	R12	12	0.52	0.61
C	KAW	8	3.17	0.013
C_1	KER	6	0.76	0.48
	KUS	2	-1.53	0.27
	R12	15	1.53	0.15
р	KAW	10	2.26	0.047
F 3	KER	14	0.57	0.58
	KUS	3	-1.51	0.23
	R12	15	1.08	0.30
р	KAW	12	1.62	0.13
F4	KER	23	-0.043	0.97
	KUS	4	0.063	0.95
	R12	17	1.58	0.13
M.	KAW	12	1.22	0.25
1411	KER	32	0.26	0.80
	KUS ^a	1.10	1.14	0.44
	R12	16	2.31	0.034
М.	KAW	13	2.44	0.030
1412	KER	34	2.65	0.012
	KUS	4	0.88	0.43
	R12	19	0.026	0.98
М.	KAW	12	2.34	0.037
1113	KER ^a	32.56	1.49	0.15
	KUS ^a	3.47	2.97	0.049

Table E.1.2 Independent samples *t*-tests comparing male and female mesiodistal measurements in each population

^aEqual variances not assumed. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). df: degrees of freedom; *t*: test statistics; *t*-test significant $p \le 0.05$.

I ₁			1				
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	6	10	3.46	0.59	3.59	0.62	
KAW	6	0	3.36	0.66	-	-	
KER	1	1	5.17	N/A	4.68	N/A	
KUS	2	3	3.87	1.72	3.02	0.62	
I_2			1				
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	5	9	3.56	0.77	3.62	0.61	
KAW	5	1	3.25	0.46	2.82	N/A	
KER	5	3	6.35	0.38	4.46	0.41	
KUS	2	3	3.69	1.15	3.17	0.48	
C ₁							
	Sample size (n)		Male		Femal	'e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	7	8	5.11	0.54	4.95	0.54	
KAW	7	3	4.34	0.60	4.16	0.37	
KER	4	3	7.29	0.70	5.82	0.63	
KUS	1	3	4.15	N/A	4.46	0.48	
P ₃					-		
	Sample	size (n)	Male		Female		
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	8	10	7.57	0.64	7.60	0.39	
KAW	7	5	8.07	0.67	7.24	0.28	
KER	6	10	7.77	0.74	7.49	0.62	
KUS	1	4	7.59	N/A	7.19	0.83	
P4							
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	8	9	8.25	0.39	8.19	0.55	
KAW	9	5	8.58	0.48	7.60	0.39	
KER	12	13	8.39	0.82	7.90	0.73	
KUS	2	4	8.71	0.83	7.70	0.13	

Table E.1.3 Descriptive statistics for buccolingual dental measurements by population and sex

M_1							
	Sample size (n)		Male		Female		
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	8	11	10.73	0.58	10.64	0.72	
KAW	10	5	10.63	0.88	10.48	0.30	
KER	16	15	10.6	0.77	10.31	0.76	
KUS	2	4	10.64	0.23	10.47	0.38	
M_2							
	Sample	size (n)	Male		Female		
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	
R12	8	10	10.58	0.65	10.17	0.55	
KAW	10	5	10.33	0.62	9.92	0.63	
KER	20	16	10.72	0.56	10.02	0.56	
KUS	2	4	10.36	0.05	9.86	0.56	
M ₃							
	Sample	size (n)	Male		Femal	e	
Population	Male	Female	Mean (mm)	SD	Mean (mm)	SD	

 Table E.1.3 continued

R12 8 13 9.93 0.88 10.03 0.84 KAW 5 9.74 10 10.39 0.55 0.4 KER 20 18 10.19 1.03 9.74 0.7 9.93 KUS 2 4 0.74 9.71 0.092 R12: NDRS R12, Neolithic (c. 5000–4000 cal BC); KAW: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350).

n: sample size; N/A: not applicable; SD: standard deviation.

Tooth	n Population	df	t	р
I ₁	R12	14	-0.43	.68
	KAW	N/A		
	KER	N/A		
	KUS ^a	2	-0.51	.66
I_2	R12	12	-0.15	.88
	KAW	4	0.86	.44
	KER	4	6.00	.004
	KUS ^a	1.239	0.61	.63
C ₁	R12	13	0.57	.58
	KAW	8	0.48	.65
	KER	1	1.29	.42
	KUS	2	-0.57	.63
P ₃	R12	16	-0.11	.91
	KAW	10	2.57	.028
	KER	14	0.82	.43
	KUS	3	0.43	.69
P ₄	R12	15	0.27	.79
	KAW	12	3.89	.002
	KER	23	1.56	.13
	KUS	3	2.89	.063
M_1	R12	17	0.27	.79
	KAW	13	0.35	.73
	KER	29	1.07	.29
	KUS	4	0.56	.61
M_2	R12	16	1.44	.17
	KAW	13	1.21	.25
	KER	34	3.75	.001
	KUS	4	1.18	.30
M_3	R12	19	-0.27	.79
	KAW	13	2.35	.035
	KER	36	1.54	.13
	KUS	3	-3.05	.056

Table E.1.4 Independent samples *t*-tests comparing male and female buccolingual measurements in each population

^aEqual variances not assumed. **R12**: NDRS R12, Neolithic (c. 5000–4000 cal BC); **KAW**: NDRS P37, Kerma Ancien (c. 2500–2050 BC); **KER**: Kerma, Kerma Classique (c. 1750–1500 BC); **KUS**: Kawa (R18), Meroitic (c. 350 BC–AD 350). df: degrees of freedom; N/A: not applicable; *t*: test statistics; *t*-test significant $p \le 0.05$.

E.2 Dental metrics sex-adjusted data

For the dental metric sex-adjusted data, the male values were corrected to the female mean prior to analysis. This correction was completed to reduce the potentially confounding effect of sexual dimorphism whilst maintaining adequate sample sizes for analysis (Ackermann et al. 2006): adjusted male value = original male value + (mean females – mean males).

Tooth	n	F	р	Hochberg's GT2
I ₁	28	0.046	0.99	N/A
I_2	31	1.37	0.27	N/A
C ₁	36	3.27	0.033	R12>KER
P ₃	50	2.42	0.078	N/A
P ₄	62	0.50	0.69	N/A
\mathbf{M}_{1}	73	1.05	0.38	N/A
M_2	75	0.47	0.70	N/A
M_3	81	0.34	0.80	N/A

Table E.2.1 ANOVAs and Hochberg's GT2 *post hoc* comparing sex-adjusted mesiodistal dental measurements between populations

n: sample size; F: ANOVA test statistic; N/A: not applicable; ANOVA significance at $p \le 0.05$; Hochberg's GT2 *post-hoc* test significant at $p \le 0.05$; arrows indicate direction of significance.

 Table E.2.2 ANOVAs and Hochberg's GT2 post hoc comparing sex-adjusted buccolingual dental measurements between populations

Tooth	п	F	р	Hochberg's GT2
I ₁	28	4.04	0.018	KER>KAW, KUS
I_2	32	8.34	<0.001	KER>R12, KAW, KUS
				KER>R12, KAW, KUS
C ₁	35	14.53	<0.001	R12>KAW
P ₃	50	1.34	0.27	N/A
P ₄	62	4.55	0.013 ^a	R12>KAW
M_1	70	0.91	0.44	N/A
M_2	74	0.77	0.52	N/A
M_3	80	0.74	0.54 ^a	N/A

^aWelch statistic. *n*: sample size; F: ANOVA test statistic; N/A: not applicable; ANOVA significance at $p \le 0.05$; Hochberg's GT2 *post-hoc* test significant at $p \le 0.05$; arrows indicate direction of significance.





Figure E.2.1 Mean values for mesiodistal dental measurements for the raw and sex-adjusted combined data (a) I₁, (b) I₂, (c) C₁, (d) P₃, (e) P₄, (f) M₁, (g) M₂ and (h) M₃

R12, Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**, Kerma Ancien (c. 2500–2050 BC); **KER**, Kerma Classique (c. 1750–1500 BC); **KUS**, Meroitic (c. 350 BC–AD 350). Error bars represent 95% confidence intervals.







R12, Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**, Kerma Ancien (c. 2500–2050 BC); **KER**, Kerma Classique (c. 1750–1500 BC); **KUS**, Meroitic (c. 350 BC–AD 350). Error bars represent 95% confidence intervals.

E.3 Dental metric CV data

	Mesiodistal				Buccolingual			<u>t-test</u>		
Population	n	Mean (mm)	SD	n	Mean (mm)	SD	df	t	p	
R12	8	7.69	2.58	8	9.71	4.92	14	-1.029	0.32	
KAW	8	6.78	2.64	8	10.19	4.84	14	-1.746	0.10	
KER	8	8.25	3.18	8	9.68	3.70	14	-0.829	0.42	
KUS	8	6.79	2.63	8	9.01	7.43	8.726	-0.797	0.45 ^a	

Table E.3.1 Independent samples *t*-tests comparing CVs for the mesiodistal and buccolingual measurements within each population

^aEqual variances not assumed. **R12**, Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**, Kerma Ancien (c. 2500–2050 BC); **KER**, Kerma Classique (c. 1750–1500 BC); **KUS**, Meroitic (c. 350 BC–AD 350). CV: coefficient of variation; df: degrees of freedom; *n*: sample size; SD: standard deviation; *t*-test significant $p \le 0.05$.

Table E.3.2 Independent samples *t*-tests comparing CVs for the anterior and posterior measurements

 within each population

	Anterior Posterior				<u>t-test</u>				
Population	n	Mean (mm)	SD	n	Mean (mm)	SD	df	t	р
R12	6	12.01	4.73	10	6.72	1.30	5.46	2.68	0.04 ^a
KAW	6	12.08	4.79	10	6.33	1.52	5.61	2.85	0.031 ^a
KER	6	9.43	5.59	10	8.68	1.34	5.35	0.32	0.76 ^a
KUS	6	11.77	6.72	10	5.58	3.08	6.29	2.13	0.075 ^a

^aEqual variances not assumed. **R12**, Sudanese Neolithic (c. 5000–4000 cal BC); **KAW**, Kerma Ancien (c. 2500–2050 BC); **KER**, Kerma Classique (c. 1750–1500 BC); **KUS**, Meroitic (c. 350 BC–AD 350). CV: coefficient of variation; df: degrees of freedom; *n*: sample size; SD: standard deviation; *t*-test significant $p \le 0.05$.