

The people of Avaris: Intra-regional biodistance analysis using dental non-metric traits

Nina Maaranen^{*1}, Sonia Zakrzewski², Arwa Kharobi¹, Chris Stantis^{1,3},
Silvia Prell⁴, Manfred Bietak⁴, Holger Schutkowski¹

¹ Department of Archaeology and Anthropology, Bournemouth University,
Fern Barrow, Wallisdown, Poole BH12 5BB, UK
email: nina.maaranen@gmail.com (corresponding author)

² Department of Archaeology, University of Southampton,
Avenue Campus, Southampton, SO17 1BF, UK

³ Department of Anthropology, National Museum of Natural History,
Washington, District of Columbia, USA

⁴ Austrian Academy of Sciences,
Hollandstraße 11+13, 1020 Vienna, Austria

Abstract: *Dental non-metric traits have become widely used to estimate biological affinities, particularly by utilizing the Arizona State University Dental Anthropology System (ASUDAS). Here, we offer information from the Middle Bronze Age site of Avaris, located near modern Tell el-Dab'a in the Egyptian Nile Delta, that was ruled by the Hyksos kings during the Second Intermediate Period (circa 1640–1530 BCE).*

Dental non-metric traits were recorded from a sample of individuals (n=90) and analyzed using mean measure of divergence (MMD). Both intra- and inter-site analyses were conducted. The former compared the ancestry between locals and non-locals, defined isotopically by a recent study. The latter compared Avaris to other Egyptian sites to gauge its population distinctiveness.

Results indicated that individuals defined as locals and non-locals were not ancestrally different from one another. There was, however, a significant difference ($p < 0.01$) between the pooled locals and non-locals of Avaris and other Egyptian sites, regardless of spatial and/or temporal proximity. The results are in line with the archaeological evidence, suggesting Avaris was an important hub in the Middle Bronze Age eastern Mediterranean trade network, welcoming people from beyond its borders.

Key words: osteology; ASUDAS; dental anthropology; migration; Egypt

Introduction

Biological distance, or biodistance, is a sub-field of bioarchaeology that focuses on estimating the (dis)similarity of individuals and groups to reconstruct patterns such as kinship, social organization and population movement (Stojanowski & Schillaci

2006). The following is a study on people buried at Avaris, a Middle Kingdom (circa 2000–1640) and Second Intermediate Period (circa 1640–1530 BCE) trade hub located in the eastern Nile Delta. This study focuses on comparing Avaris to other Egyptian sites, using dental morphology.

There are numerous investigations using both genetic and phenetic data from ancient Egyptian samples (Berry & Berry 1967; Hawass et al. 2010; Hawass et al. 2012; Irish 2006; Keita & Godde 2019; Zakrzewski 2007) as well as Nubian samples (e.g., Godde 2009, 2013, 2018; Godde & Jantz 2017; Keita 2005). Where genetic studies are still limited and have focused more on the differences between past and present populations (Schuenemann et al. 2017), investigations relying on particular physical similarity have explored patterns among the ancient populations. Biodistance analyses using skeletal or dental shape assume that morphological similarity reflects underlying genetic closeness as phenotypic expressions become more prevalent among closely related individuals (Delgado et al. 2019; Hefner et al. 2016:3; Hubbard et al. 2015; Relethford 2004; Stojanowski & Schillaci 2006). Cranial and dental studies have suggested similar patterns of overall continuity and an “indigenous state formation process” (Zakrzewski 2007:501) while still experiencing small bursts of migration (Irish 2006; Keita 1992; Keita & Godde 2016; Prowse & Lovell 1996; Schillaci et al. 2009). Many of these studies have raised the need for more research and samples (Irish 2006; Zakrzewski 2007).

The ancient town of Avaris in the eastern Nile Delta is unique in Egyptian history, forming a mixture of Egyptian and non-Egyptian traditions. In its earliest occupation period during the Middle Kingdom 12th Dynasty (circa 2000–1800 BCE), material culture and settlement structures were consistent with Egyptian tradition, with few Aegean and Levantine imports (Bietak 2010:150). By the end of the 12th Dynasty, the archaeological record exhibits a combination of Egyptian and Near Eastern Middle Bronze Age (MBA) elements (Bader 2012; Bietak 2010:139; Bietak 1991a, 1991b; Forstner-Müller 2008; Schiestl 2009). These include Near Eastern temple types and artefacts, as well as burial and religious customs (Bietak 1996:36-41; Bietak 1981, 2007:428, 2009, 2019; Forstner-Müller 2008; Kopetzky 2010; Mourad 2015; Prell 2019a, 2019b, 2019c, 2020, 2021; Schiestl 2009). During the Second Intermediate Period, rulers of Avaris were passed down in historical sources as not of Egyptian origin (Gardiner 1916; Habachi 1972; Waddell 1940). This is implied even by the title, the Greek term Hyksos deriving from the ancient Egyptian *HKA.w-xAs.wt* meaning “rulers of foreign lands”. The Hyksos, a name that has sometimes lent itself for the entire time period and material culture in general (e.g., Schaeffer 1949), had a lasting influence on ancient Egyptian culture, from politics to religion (Bietak 2007:432; Mourad 2015, 2021).

The archaeological evidence from Avaris has provided a general idea of population provenance. Van Seters (1966:1-4) connected the Hyksos with the ethnic identifier *aAmw*, Asiatic, which had been used by Egyptians for Western Asiatics since the Old Kingdom (Strudwick 2005:335). The term is ambiguous in that it does not point to a clearly demarcated region in the eastern Mediterranean, consisting of at least the Levant (Altenmüller 2015; Marcus 2007; Mourad 2015:100-101,197,281).

Craniometric data has previously been used to compare Avaris with sites from Egypt, Nubia and the Near East, spanning from 2000 BCE to 100 CE (Winkler & Wilfing 1991:91-96). The metric data was analyzed with a hierarchical dendrogram which clusters the samples into a tree-like diagram, and placed Avaris far away from Saqqara, Abydos and several Theban samples. The closest samples, on the other hand, were from 5th century BCE Kamid el-Loz (Kunter & Poppa 1977) and 900–200 BCE Algeria (Chamla 1967). Because of poor preservation, sample sizes for each individual measurement were low for both males (sample number between one and six) and females (between one and fifteen). Another study by Randl-Gadora and Großschmidt (2002) compared 37 subadults from Avaris to larger regional samples (North Africa, Sub-Saharan Africa, West Africa and Western Europe) using dental nonmetric traits and least agreement of frequencies. In this study, the individuals grouped best with North Africa and Western Europe. Since these preliminary studies, advances have been made in recording standards and statistics and, as mentioned previously, more region-specific comparative material has also become available.

The research project “The Enigma of the Hyksos” made it possible to reassess a sample of human remains from Avaris using a host of different techniques. A recently published study utilized strontium ($^{87}\text{Sr}/^{86}\text{Sr}$) analysis to understand movement and migration within the people’s lifetimes (Stantis et al. 2020). In the cohort of 75 individuals, Stantis et al. (2020) found that 53% (40/75) of sampled individuals from Avaris had likely spent their childhood outside the Nile delta. The range of values was wide, suggesting potentially multiple origins for the migrants.

In addition to the isotope study, a sample of the available human remains from Avaris was recorded to investigate biodistance within the site and between other ancient Egyptian samples. Due to the poor preservation and incompleteness of the available skeletal material, dental non-metric traits provided the best approach to investigate biodistance between the people of the town and other ancient Egyptian sites (Figure 1). Dental nonmetric traits, also known as discrete, discontinuous or epigenetic traits, are accessory ridges, tubercles, styles and accessory cusps in crowns and deviations in root numbers (Scott & Turner 1988). These features are governed by circa 300 genes in interaction with epigenetic and environmental factors (Ramirez Rozzi 2016; Thesleff 2006; Townsend et al. 2009, 2012) which are considered stable enough for teeth to be ideal structures for biodistance analyses.

Two research questions premised on using dental nonmetric traits were posed for the Avaris material:

1. Are there significant differences in ancestry between the locals and non-locals of Avaris as determined by Stantis et al. (2020)? Since people arrived at the site during both the pre-Hyksos and Hyksos period (though in larger numbers during the pre-Hyksos period), we assume there are no significant differences between locals and non-locals.
2. How does Avaris cluster in relation to other Egyptian sites? Given previous studies of the site (Bader 2012:223, 2013; Raml-Gadora & Großschmidt 2002; Stantis et al. 2020; Winkler & Wilfing 1991), we hypothesize that, as a group,

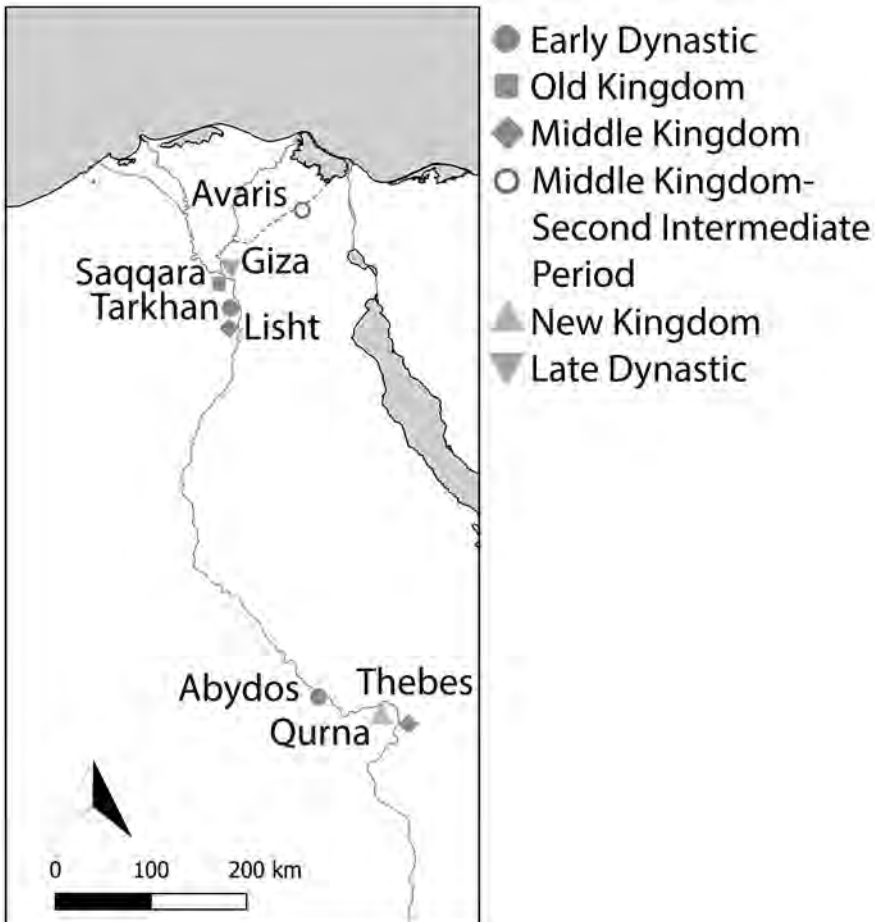


Figure 1. Map of sites mentioned. Giza also marks the location of modern Cairo. Map created by Nina Maaranen.

the Avaris assemblage will appear morphologically distant from ancient Egyptians.

Material

After decades of suspicion (Gardiner 1916:100-101; Habachi 1954), the archaeological site near modern Tell el-Dab'a, circa 105km north-east from Cairo, was confirmed as the ancient Hyksos capital of Avaris (AVA) by excavations led by the Austrian Archaeological Institute in Cairo and the Institute of Egyptology at the University of Vienna (Bietak 1975, 1981, 1996). Estimated at 250ha at its largest (Bietak 1991a:29), the site has several excavation areas (**Figure 2**). The study sample presented herein (n=90) derives from Area A/I (n=1), A/II (n=76) and F/I (n=13), spanning from the end of the 13th Dynasty (stratum G) to the 15th Dynasty (stratum D/2). Access to the material was permitted through the Anthropological Department of the Natural History Museum of Vienna, the Anthropological Department of the University of Vienna and the Medical University of Vienna (**Supplementary Table 1**, raw data available from author by request). All dental non-metric data from Avaris was recorded by Maaranen, and the remains were treated according to ethical guidelines (Brickley & McKinley 2001).

Temporal similarity is ideal when comparing regional differences (Stojanowski & Schillaci 2006) but there are few available collections from the Middle Kingdom and Second Intermediate Period for such comparative studies. We adopted an approach that has been used in previous investigations, expanding our analysis to a wider temporal window of Egyptian dynastic history, spanning from Early to Late Dynasties as described in **Table 1**. Details of the comparative material from Abydos (ABY), Giza (GIZ), el-Lisht (LIS), Qurna (QUR), Saqqara (SAQ), Tarkhan (TAR) and Thebes (THE) have also been compiled in **Table 1**. The data from these sites was collected by Irish (2006).

Methods

There are several methods for recording dental variation (Alt 1991; Alt et al. 1998; Zubov 1977), but the Arizona State University Dental Anthropology System (ASUDAS) has become the most widely used (Hanihara 2008; Irish 2005, 2015; Scott & Turner 1997). ASUDAS traits (**Table 2**) have been selected because of their durability, easy identification, good repeatability, heritability and lack of sexual dimorphism (Hanihara 1992; Hubbard et al. 2015; Scott 1973; Scott & Turner 1997; Turner et al. 1991). The traits deemed most useful were first compiled by Turner et al. (1991), including casts for further recording assistance. Further resources, such as more detailed descriptions and photographic atlases (Irish 2015; Scott & Irish 2013, 2017;

Scott & Turner 1997), have been produced since then to increase inter-observer reliability.

Data collection

Following recording guidelines (Scott & Irish 2017), dental nonmetric traits from the Avaris collection were recorded as present/absent or as a grade from absent to full expression (see Table 2, Figure 3). Though some traits can be recorded from several teeth, only one tooth per person was selected to express each trait to avoid duplication and bias. Additionally, the trait must always be considered from the same tooth in comparative studies. As an example, though shoveling (Figure 3a) can be recorded from all anterior teeth (e.g., upper and lower incisors and canines), only one upper central incisor was used in the analysis. For this study, the tooth was chosen to match the previous study (Irish 2006), a practice that is recommended in the recording standards as well (Scott & Irish 2017). The trait was recorded from the side with the stronger expression, assumed to best express the underlying genotype (Turner & Scott 1977).

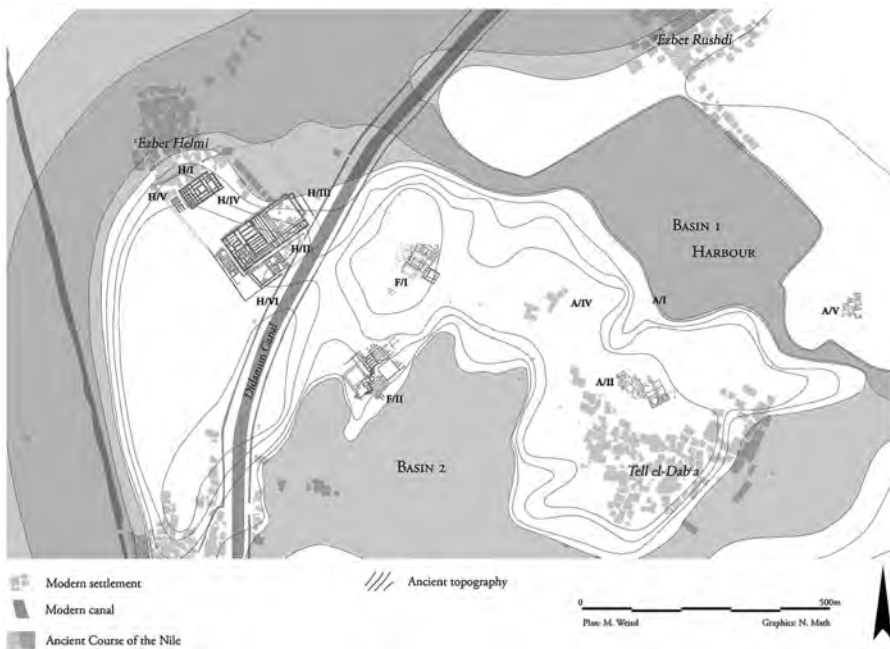


Figure 2. Map of Avaris/Tell el-Dab'a and its excavation areas. The study material was excavated from areas A/I, A/II and F/I. Map created by M. Weissl; graphics by N. Math. Image courtesy by the Hyksos Enigma project.

Table 1. Sample information from Avaris and comparative sites (from Irish 2006).

Site	Abbr.	n	Period	Description	Reference
Abydos	ABY	54	ED ¹ (dyn. 1–2)	Burials of officials and palace staff from a heavily disturbed cemetery near the king during 1–2 dyn.	Petrie 1902:1
Avaris	AVA	90	MK-SIP ² (dyn. 13–15)	Burials from Area A/I, A/II and F/I, consisting of jar, pit and chamber graves. Archaeological samples excavated in the late 1960s and early 1970s were exported to Vienna, Austria, after a find partition in The Museum of Egyptian Antiquities (Cairo, Egypt).	(see this study)
Giza	GIZ	62	LD ³ (dyn. 26–30)	Burials were discovered south of the Great Pyramid, circa 1–2km away. Little commentary on the burials exists apart from their dating (600–300 BCE).	Petrie 1907:29
el-Lisht	LIS	61	MK ⁴ (dyn. 12)	Necropolis for the Middle Kingdom capital Itjtawy, consisting of royal, noble and ordinary graves. The burials were excavated by the Metropolitan Museum of Art (1906–1934) in New York and the skeletal material is curated by the Smithsonian Institution, Washington, D.C., USA.	Baines & Malek 1982:133; Lythgoe 1909; Mace 1921
Qurna	QUR	67	NK ⁵ (dyn. 19–22)	Cemetery near Qurna mortuary temple. Field notes indicate finds were distributed between several institutions in Europe and North America.	Petrie 1909 after Irish 2006; Griffith Institute 2015
Saqqara	SAQ	41	OK ⁶ (dyn. 4)	Burials likely from the elite or royal cemetery in North Saqqara, curated by Musée de l’Homme, Paris, France.	Irish 2006
Tarqhan	TAR	51	ED ¹	Over 2000 burials were excavated, including both pit burials and mastabas. Notable finds include seal impressions of King Narmer.	Petrie et al. 1913; Griffith institute 2015
Thebes	THE	54	MK ⁴	The skulls were part of a larger collection acquired by the Austrian anthropologist Felix von Luschan. The collection was later sold to the American Museum of Natural History in New York, USA.	Irish 2006; Szemethy 2015:122

¹ Early Dynastic² Middle Kingdom – Second Intermediate Period³ Late Dynastic⁴ Middle Kingdom⁵ New Kingdom⁶ Old Kingdom

Statistical analysis – mean measure of divergence

Both intra- and inter-observer error tests were conducted to ensure agreement between data sets. Intra-observer error test was assessed on a sub-sample of individuals from Avaris, housed at the University of Vienna, while the inter-observer error test was conducted on a sample of individuals stored at Liverpool John Moores University. The intra-observer error was assessed using Spearman’s rank correlation coefficient. Inter-observer error test was conducted using Cohen’s kappa coefficient which measures the reliability between raters using nonparametric data. Biodistance was analyzed using modified mean measure of divergence, referred to as MMD henceforth (Harris & Sjøvold 2004; Sjøvold 1977, 1984; Smith 1972). It uses summary data to compare trait frequencies across groups, allowing it to cope with missing data, which has made

Table 2. List of ASUDAS dental traits (and abbreviations) recorded from the material.

Trait	Recorded	Abbreviation
Winging	Score	W
Labial curvature	Score	LC
Palatine torus	Score	PT
Shoveling	Score	S
Double-shoveling	Score	DS
Interruption groove	Present/Absent	IG
Tuberculum dentale	Score	TD
Pegged of reduced incisor	Score	UI2V
Mesial accessory ridge	Score	MAR
Distal accessory ridge	Score	DAR
Premolar accessory ridges	Score	PAR
Accessory cusps	Present/Absent	AC
Metacone size	Score	M
Hypocone size	Score	H
Bifurcated hypocone	Present/Absent	BH
Cusp 5	Score	C5_UM
Marginal ridge tubercles	Present/Absent	MRT
Carabelli cusp	Score	CC
Parastyle	Score	PA
Enamel extensions	Score	EE
Upper premolar root number	Count	RN_UP
Upper molar root number	Count	RN_UM
Congenital absence	Present/Absent	M3V
Odotome	Present/Absent	O
Tome's root	Score	TR
Lower premolar lingual cusp number	Count	CN
Anterior fovea	Score	AF
Mandibular torus	Score	MT
Groove pattern	x/y/+	GP
Rocker jaw	Score	RJ
Cusp number	Score	C5_LM
Cusp number	Score	C6
Cusp 7 size	Score	C7
Deflecting wrinkle	Score	DW
C1–C2 crest	Score	MDTC
Protostylid	Score	PR
Lower canine root number	Count	RN_LC
Lower molar root number	Count	RN_LM1 or LM2
Torsomolar angle	Present/Absent	TA_LM3
Mandibular molar pit tubercle	Score	MPT

the method extremely useful for material from archaeological contexts. If there is no difference between samples, MMD will resemble a normal distribution with a mean of 0 (Harris & Sjøvold 2004).

To create the frequency table, values must first be dichotomised into present (1) and absent (0). Though some traits have already been recorded as present and absent, the ones recorded by score/grade must be transformed according to trait thresholds or breakpoints, set by the investigator. With graded traits, the breakpoint often begins from a higher score, e.g. the breakpoint of shoveling is often 2, which excludes weak expressions to differentiate between individuals exhibiting strong trait expressions. The use of breakpoints has the benefit of decreasing inter- and intra-observer error by omitting weaker and sometimes difficult to see expressions, but it does come with the drawback of limiting inter-study comparisons if investigators have chosen different breakpoints. Since traits with different breakpoints are not comparable, several researchers have opted for using recommended standard breakpoints. The breakpoints

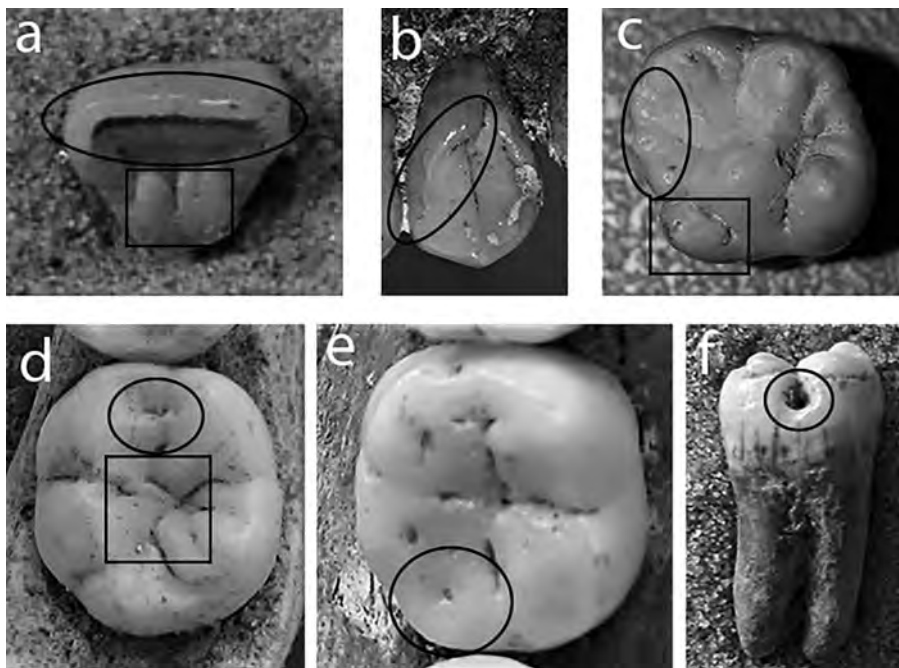


Figure 3. Examples of dental traits observed from the samples: a) shoveling (circle) and tuberculum dentale (square) on upper first incisor, b) mesial accessory ridge (circle) and slight distal accessory ridge on the opposite margin of upper canine, c) marginal ridge tubercles (circle) and Carabelli's cusp (square) on upper first molar, d) anterior fovea (circle) and Y-groove pattern (square) on lower first molar, e) worn but still visible cusp 5 (circle) on lower second molar, f) protostylid (circle) on lower second molar (with possible carious lesion in the pit). Image created by Nina Maaranen.

used in this study follow the morphological thresholds that have been assessed and recommended by prior research (Haeussler et al. 1988; Nichol 1990; Turner 1987).

MMD can be biased by too small a sample ($n < 10$), strongly correlated traits and traits that show no variation between samples. To ameliorate these issues, traits with less than 10 overall observations were excluded, so were traits exhibiting strong correlation based on Kendall's tau-b rank correlation coefficients ($\tau\text{-}b \geq 0.5$). The analysis was conducted in the R package *AnthropMMD* (Santos 2018) using the Anscombe angular transformation. The program was used to drop traits that did not contribute to variation (overall mean divergence or $MD \leq 0$). The resulting distance value increases with dissimilarity. Distances are considered statistically significant ($p = 0.05$) two standard deviations (2SD) apart.

Patterns can be visualized with multidimensional scaling (MDS) which creates a spatial representation of 1-to- n dimensions. It is a nonlinear dimension reduction technique that attempts to maintain the best dissimilarity between points in 2 or 3-dimensional space by assigning different points for several iterations until the best solution is found. There are two general methods for MDS, the metric/classical MDS and the nonmetric MDS (NMDS) that are used for continuous and rank data, respectively. As the MMD distance matrix derived from non-linear data, NMDS was used to visualize the distances.

Results

Intra-observer (Maaranen) and inter-observer (Maaranen and Irish) error tests indicated good agreement between recording events (Spearman's $\rho = 0.98$, $p < 0.00$, $n = 216$ observations) and between observers (Cohen's $\kappa = 0.8$, $p < 0.00$, $n = 281$ dichotomised observations), respectively. No trait within the Avaris dataset indicated strong inter-trait correlation.

The first MMD analysis was conducted using only Avaris, dividing the data set into locals and non-locals (S1-2) according to values published by Stantis et al. (2020). 63 of the 75 individuals (30 locals, 33 non-locals) used in the isotope study had teeth in good enough macroscopic condition for dental recording. Eight dental traits had enough observed cases (≥ 10) between groups; UM3 metacone size, UM2 hypocone size, UM2 bifurcated hypocone, UM1 Carabelli cusp, UM3 congenital absence, premolar odontomes, LP2 lingual cusp number and UM2 y-groove pattern. None of the traits showed positive variation (mean divergence or $MD > 0$), indicating there is no difference between the two groups. We accepted the null hypothesis, indicating no difference between groups.

Next, Avaris was compared to other Egyptian sites, including individuals not used in the isotope study. UI1 winging, palatine torus, LP1 Tome's root and LC root number had less than 10 observations. Some inter-trait correlations have been reported

Table 3. Traits, breakpoints and sample numbers after accounting for low sample numbers, inter-trait correlation and traits lacking overall variation. Avaris data from NM, comparative data from Irish (2006). Abydos (ABY), Thebes (THE) and Qurna (QUR) are Upper Egyptian sites. Tarqhan (TAR), Saqqara (SAQ), el-Lisht (LIS), Giza (GIZ) and Avaris (AVA) are Lower Egyptian.

Trait	Present	ABY	THE	QUR	TAR	SAQ	LIS	GIZ	AVA
Mesial accessory ridge UC	(1–3)	17	33	31	37	10	27	32	21
Carabelli's trait UM1	(2–7)	32	31	34	28	16	23	33	37
Enamel extension UM1	(1–3)	43	42	51	45	18	47	47	24
Root number UP1	(2+)	31	34	34	32	29	42	32	12
Congenital absence UM3	(-)	54	51	59	49	35	55	52	43
Lingual cusp LP2	(2–9)	25	37	35	18	12	12	21	23
Rocker jaw	(1–2)	36	53	52	43	37	37	51	19
Protostylid LM1	(1–6)	21	41	32	20	14	15	35	25
Torsomolar Angle LM3	(+)	32	40	37	36	23	26	35	18

Table 4. Traits, breakpoints and relative frequencies (%) after accounting for low sample numbers, inter-trait correlation and traits lacking overall variation. Avaris data from NM, comparative data from Irish (2006). Abydos (ABY), Thebes (THE) and Qurna (QUR) are Upper Egyptian sites. Tarqhan (TAR), Saqqara (SAQ), el-Lisht (LIS), Giza (GIZ) and Avaris (AVA) are Lower Egyptian.

Trait	Present	ABY	THE	QUR	TAR	SAQ	LIS	GIZ	AVA
Mesial accessory ridge UC	(1–3)	17.7	3.1	0.0	5.4	0.0	0.0	6.3	19.0
Carabelli's trait UM1	(2–7)	84.4	90.3	70.6	67.9	100.0	60.9	72.7	89.1
Enamel extension UM1	(1–3)	9.3	4.8	9.8	0.0	0.0	14.9	6.4	29.1
Root number UP1	(2+)	71.0	85.3	70.6	75.0	89.7	61.9	62.5	66.7
Congenital absence UM3	(-)	7.4	19.6	18.6	4.1	20.0	3.6	15.4	4.6
Lingual cusp LP2	(2–9)	76.0	70.3	54.3	77.8	66.7	66.7	61.9	93.0
Rocker jaw	(1–2)	30.6	22.6	9.6	16.3	24.3	32.4	13.7	5.2
Protostylid LM1	(1–6)	19.1	12.2	6.3	10.0	7.1	53.3	11.4	64.0
Torsomolar Angle LM3	(+)	9.4	22.5	2.7	5.6	0.0	30.8	2.9	27.8

in the Egyptian data by Irish (2006) between UI1 labial curvature and shoveling, UI1 shoveling and double-shoveling, LM1 C1–C2 crest and anterior fovea and LM1 cusp number and deflecting wrinkle (Irish 2006). These were omitted from further analysis. From the remaining traits, 12 did not contribute to the variation ($MD < 0$): peg-shaped UI2, UM2 hypocone size, UM2 root number, UM3 parastyle, P1–P2 odontome, LM1 cusp 6, LM1 root number, LM1 cusp 7, LM2 groove pattern, LM2 root number, LM2 cusp number and mandibular torus.

From the remaining nine traits, LM1 protostylid ($MD=11.2$), LM3 torsomolar angle ($MD=5.6$), UM1 Carabelli cusp ($MD=5.0$) and UM1 enamel extension

(MD=3.6) contributed most of the variation in the analysis. Protostylid, contributing most of the variation, is most frequent in the Avaris (64.0%) and el-Lisht (53.3%) samples and most infrequent in the Qurna (6.3%) sample. LM3 torsomolar angle was most frequent in el-Lisht (30.8%) and Avaris (27.8%) and infrequent in Saqqara (0%). Carabelli cusp was frequent in all site samples, from 60.9% to 100%, including Avaris (89.1%). The highest frequencies of enamel extension were noted in the Avaris (29.1%) and el-Lisht (14.9%) samples. More details are available in **Tables 3** and **4**, and further information on dental non-metric trait frequencies (including the traits not used in the MMD analysis) can be requested from the corresponding author.

According to the MMD analysis, Avaris was significantly different ($p < 0.01$) from every other group, whether Upper (Abydos, Qurna, Thebes) or Lower Egyptian (Giza, el-Lisht, Saqqara, Tarkhan) (**Supplementary Information Table 3**). There were significant differences between certain Egyptian samples as well, but overall, they clustered together (**Figure 4**). Egyptian sites were less than 3SD apart on average, regardless of their geographic location or date (ranging from Early to Late dynastic, specified in **Table 1**). On average, Avaris was 7SD apart from the other Egyptian sites, ranging between 3.2 and 11SD, well beyond the 0.05 significance level. Morphologically,

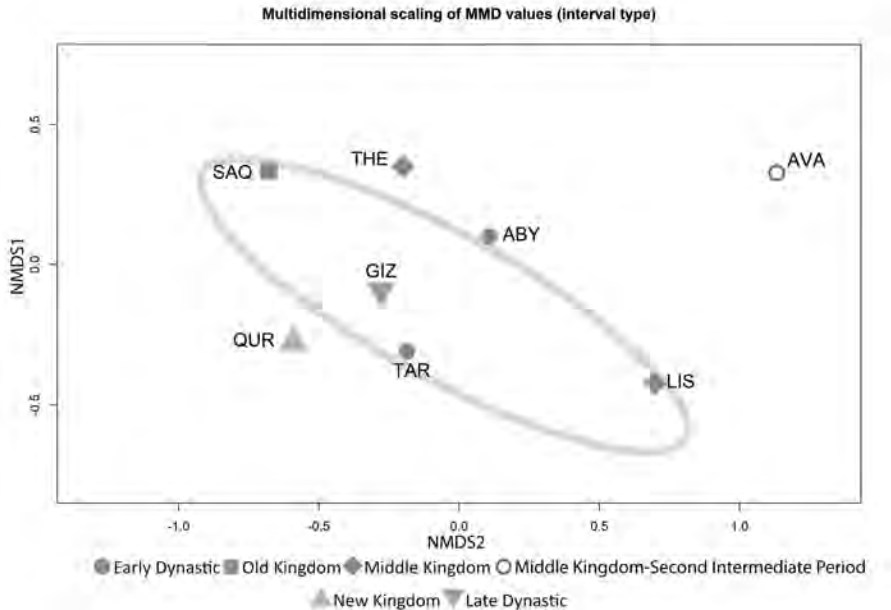


Figure 4. NMDS plot of the MMD distances. The ellipse marks the Lower Egyptian sites (excluding Avaris). ABY=Abydos, AVA=Avaris, GIZ=Giza, LIS=Lisht, QUR=Qurna, SAQ=Saqqara, TAR=Tarkhan, THE=Thebes. Graph by Nina Maaranen.

Avaris was closest to el-Lisht at 3.2SD away, a site that is similar both spatially and temporally.

Discussion

Two research questions were posed of the material. First, the biodistance between locals and non-locals was examined. According to the stable isotope study, migration to Avaris began in the pre-Hyksos era (Stantis et al. 2020). The oldest samples in the study dated to stratum G, the Middle Kingdom 13th dynasty. Small numbers of Syro-Palestinian cooking pots, used in local food production (Aston & Bietak 2004:156; Bader 2012, 2021:56), have been found from 12th Dynasty layers in Area F/I. Cooking ware has been regarded as the “internal domain” of a family or household and culturally more conservative, making it a potential indicator of cultural backgrounds (Burmeister 2000:540-542). Considering the results presented here and by Stantis et al. (2020), it is possible the pottery finds of the 12th Dynasty represent the onset of migration to Avaris. According to the MMD analysis, there was no difference between locals and non-locals; the people who had spent their childhood outside Egypt were closely related to the individuals with local values. Limitations in sample numbers meant MMD analysis of locals and non-locals could not be used in conjunction with sex or time periods. These differences within the Avaris sample will be explored further in the future when focussing solely on intra-site analysis (namely, Area A/II), utilizing a host of additional statistical techniques and further contextual information.

Recent study included $\delta^{18}\text{O}$ values as well to investigate mobility in Avaris (Stantis et al. 2021). The results of this study were generally similar to the previous investigation (Stantis et al. 2020), though five individuals with “local” $^{87}\text{Sr}/^{86}\text{Sr}$ biospheric values fell outside the group median in $\delta^{18}\text{O}$ values. Because there are multiple possible explanations for the difference, ranging from distinct diets to an origin somewhere else along the Nile Valley, the best way to incorporate the $\delta^{18}\text{O}$ data into further studies will be considered further in the intra-site analysis to come.

Second, Avaris was regarded in relation to other ancient Egyptian sites. Irish (2006) reported an overall dental homogeneity among dental samples from Abydos, Thebes, Qurneh, Tarkhan and Giza with el-Lisht and Saqqara as possible outliers. The Avaris sample was significantly different from other Egyptian sites ($p < 0.01$), making even the “Egyptian outliers” (Saqqara and el-Lisht) appear clustered with the other Egyptian sites (Figure 4). Together with the isotope results, this gives strong indication that the people settling in Avaris were not ancestrally close to Egyptian populations. El-Lisht was the morphologically closest site to Avaris, though still significantly different ($p = 0.005$). The relative closeness could be due to both spatial and temporal compatibility between the sites. The necropolis of el-Lisht consists of graves of royals, nobles and ordinary people (Mace 1921:10). A brief comment was noted from an el-

Lisht excavation report by Lythgoe (1909:122), from the bioanthropologist Hrdlička: “Only four foreign, broad skulls were found among over two hundred Egyptian, [...]. The broad crania are in all probability Asiatic, from north of the Semitic region.” The Illahun papyri also mention Asiatic settlements, the so-called *wnw.wt*, which supposedly existed in the vicinity of el-Lisht (Bietak 2022; Luft 1993). Though there is no record of how cranial shapes were assessed, it suggests the excavated individuals comprising this collection may have been morphologically (and ancestrally) diverse and perhaps marginally non-Egyptian.

When considering all the information together—the 12th Dynasty onset of the non-Egyptian archaeological evidence, the high percentage of first-generation movers of the pre-Hyksos era, and the biological closeness of the locals and non-locals but distinct difference to other Egyptian sites—it appears that migration to Avaris began early in its formation. There is ample of evidence for the presence of Near Eastern people in Egypt from the 12th Dynasty onwards (Luft 1993; Schneider 2003), assimilating to varying degrees into the Egyptian culture. Interestingly, movement appears to have slowed down during the Hyksos period, supported by the lower frequency of non-locals (Stantis et al. 2020) and a decrease in imported Levantine pottery (Vilain 2019:400, 2021) during the Hyksos period.

Though it is likely that the population of Avaris consisted of people of both Egyptian and non-Egyptian origin based on both textual and material evidence (Bietak 2016), the statistical analysis of the group places emphasis on the latter. The archaeological evidence of Avaris appears as a combination of both Egyptian and Near Eastern traditions (Bader 2012; Bietak 2010:139; Bietak 1991a, 1991b; Forstner-Müller 2008; Schiestl 2009), suggesting the presence of Egyptians and/or Egyptianized Asiatics. It could be that native Egyptians continued to bury their dead outside rather than within the city, making them absent from the data set, but this cannot be ascertained without further excavations.

If people of Egyptian ancestry did indeed live in the city as well, the distinctiveness of the Avaris sample when compared to the other Egyptian sites could be the result of some degree of population segmentation at the site. Migrants’ desire to perpetuate old collectives in new environments has been recorded in both archaeological and historical settlements (Smith 2010: 150), such as Kanesh (Larsen 2015), Kish (Charpin 1992) and Sippar (Harris 1975). Size and unity of the migrant population can also affect the formation of a group that is self-contained and promotes group member identity, particularly if the group is historically or ethnically distinct from the target population (Massey 1999; Tsuda & Baker 2015:310).

There is also the possibility that Avaris could reflect an unusually high degree of genetic drift, though this would be more difficult to interpret together with the isotope evidence. Contemporary samples from Egypt are scarce, but further work

will hopefully ameliorate this issue. Furthermore, different cemeteries in Avaris may represent different ethnic enclaves with potentially different migration backgrounds (Priglinger 2019). The majority of samples from Avaris in this study derived from Area A/II with too few individuals from the other cemeteries for a more extensive intra-site analysis. It is also possible that the Hyksos rulers, not present in this sample, did not share the same biological affinity as the “general population” of the city, creating yet another potential line of questioning for future research. The sample used in this study comprised individuals from all burial types (jar, pit and chamber burials), age groups and sexes from multiple time periods (from G to D/2, the end of the Middle Kingdom to the end of the Hyksos Period), making it at least generally representative of the site.

In addition to the practical issues, the methodological limitations may also have implications to the interpretations. Missing data, caused by poor preservation, was prominent in this study. The selection of MMD as the main statistical tool was able to combat the issue by employing frequency tables, but even this method has some caveats (discussed in Methods), which can limit the available variables and lead to loss of observable variation. Not using the full ASUDAS chart for analysis is not necessarily a detriment, however, as some traits have more utility than others (Rathmann & Reyes-Centeno 2020). Population affinity can be equally reliable when reconstructed with a smaller set of diagnostic traits.

Another issue concerns the use of dichotomised data. The phenetic appearance of dental traits can be either dichotomous or quasi-continuous (Scott & Turner 1988: 100) but MMD can only treat dichotomous data. By transforming the data into completely dichotomous sets, variation is lost. Furthermore, the results of the MMD analysis, like all other biodistance methods, are dependent on the samples used in the study. Though the relationships between sites generally remain similar, omitting or adding a group in the analysis changes the values and can cause alterations in interpretations, particularly with groups on the fringe of “significance” (close to the set p -value). Therefore, the results here reflect biodistances as represented by the samples and the available, dichotomised variables.

Keeping the limitations in mind, Avaris can be included in the larger discussion of Egyptian population history. Previous studies have found some variation between sites which has been interpreted as an indicator of immigration and gene flow during Egyptian history (Irish 2006; Keita 1992; Keita & Godde 2016; Prowse & Lovell 1996; Schillaci et al. 2009). Avaris forms a unique data point in the population history of ancient Egypt. Egypt’s interests in the eastern Mediterranean trade network throughout the pharaonic period are well known (Bietak 2007), demonstrated by the mere existence of Avaris, located in an access point to both road- and maritime networks (Bietak 1996:3). This work will hopefully act as a stepping-stone for more

synchronous analyses in the future as further data from the late Middle Kingdom and Second Intermediate Period become available. Especially other eastern Nile Delta sites, such as Tell el-Retaba and Tell el-Maskhuta, could open further insights into the eastern Nile Delta population structure.

Conclusions

Biodistance analyses on ancient Egyptian material are continuously increasing in number, improving our understanding of past population history. The analysis provided here builds on the work of Stantis et al. (2020) while also providing fresh insights from a different perspective in terms of movement and migration in Egypt, at the Middle Kingdom and Second Intermediate Period site of Avaris. The results of the biodistance study, using dental non-metric traits, support the archaeological evidence of a town with a substantial migrant element, likely born from Egypt's trade interests with the wider eastern Mediterranean region.

An entirely synchronic assessment of intra-regional differences was not possible here; to limit temporal effects, comparative sites were selected from the dynastic periods which overall have been noted to have less fluctuation (Irish 2006; Zakrzewski 2007). This study focussed on how Avaris related to other Egyptian sites, attempting to use as robust a data set as possible (i.e., pooling the data). For more nuanced work, further research on Avaris will include an intra-site analysis, employing further statistical tools and more contextual data, as well as an inter-regional analysis to compare Avaris to contemporary Near Eastern sites.

Acknowledgements

This project has received funding from the European Research Council under the European Union's Horizon 2020 research and innovation program (grant agreement No 668640). Special thanks are extended to Prof. Joel Irish for conducting an inter-observer error test with Maaranen to ensure agreement of data observations. Thanks are also due to collaborating institutions and persons: the Anthropology Institute of the University of Vienna, the Medical University of Vienna, Prof Großschmidt and the Natural History Museum of Vienna. Gratitude is also owed to the two reviewers, Prof. Michelle Buzon and Dr Kanya Godde, whose insightful comments helped improve the manuscript.

References

- Alt K. (1991), *Verwandtschaftsanalyse an Skelettmaterial. Methodenentwicklung auf der Basis odontologischer Merkmale*, Freiburg: Habil Schrift.

- Alt K.W., Rösing F.W., Teschler-Nicola M. (1998), *Dental anthropology: Fundamentals, limits and prospects*, New York: Springer.
- Altenmüller H. (2015), *Zwei Annalenfragmente aus dem frühen Mittleren Reich*, Hamburg: Buske Verlag.
- Aston D., Bietak M. (2004), *Tell El-Dab'a VIII: The classification and chronology of Tell El-Yahudiya ware*, Vienna: Austrian Academy of Sciences.
- Bader B. (2012), *Migration in archaeology: An overview with a focus on ancient Egypt* [in:] "Migrations: interdisciplinary perspectives", M. Messer, S.R. Wodak (eds.), Vienna: Springer, pp. 213-226.
- Bader B. (2021), *Material culture and identities in Egyptology. Towards a better understanding of cultural encounters and their influence on material culture*, Archaeology of Egypt, Sudan and the Levant 3, Vienna: Austrian Academy of Sciences.
- Bader B. (2013), *Cultural mixing in Egyptian archaeology: The 'Hyksos' as a case study*, Archaeological Review from Cambridge 28:257-286.
- Baines J., Malek J. (1982), *Atlas of ancient Egypt*, New York: Facts on File Publications.
- Berry A., Berry R. (1967), *Epigenetic variation in the human cranium*, Journal of Anatomy 101:361-379.
- Bietak M. (1975), *Tell el-Dab'a II. Der Fundort im Rahmen einer archäologisch-geographischen Untersuchung über das ägyptische Ostdelta*, Vienna: Austrian Academy of Sciences.
- Bietak M. (1981), *Avaris an Piramesse: Archaeological exploration in the Eastern Nile Delta*, Proceedings of the Egyptian Academy 65:225-289.
- Bietak M. (1991a), *Egypt and Canaan during the Middle Bronze Age*, Bulletin of the American Schools of Oriental Research 282:27-72.
- Bietak M. (1991b), *Tell el-Dab'a V*, Vienna: Austrian Academy of Sciences.
- Bietak M. (1996), *Avaris: The capital of the Hyksos*, London: British Museum Press.
- Bietak M. (2007), *Egypt and the Levant* [in:] "The Egyptian world", T. Wilkinson (ed.), New York: Routledge, pp. 417-448.
- Bietak M. (2009), *Near Eastern sanctuaries in the Eastern Nile Delta*, Bulletin d'Archéologie et d'Architecture Libanaises 6:209-228.
- Bietak M. (2010), *From where the Hyksos and where did they go?* [in:] "The Second Intermediate Period (Thirteenth-Seventeenth dynasties): Current research, future prospects", M. Marée (ed.), Leuven: Peeters, pp. 140-190.
- Bietak M. (2016), *The Egyptian community in Avaris during the Hyksos period*, Egypt and the Levant 26:263-274.
- Bietak M. (2019), *The spiritual roots of the Hyksos elite: An analysis of their sacred architecture part I* [in:] "The Enigma of the Hyksos", M. Bietak, S. Prell (ed.), Wiesbaden: Harrassowitz, pp. 45-64.
- Bietak M. (2022), *The 14th Dynasty in Tell el-Dab'a and a traumatic transition to the*

- Hyksos period* [in:] “Tell el-Dab’a XXVI: 50 Years of excavation and research in Tell el-Dab’a ancient Avaris (1966-2016)”, M. Bietak, E. Czerny, K. Kopetzky (eds.), Vienna: Austrian Academy of Sciences.
- Burmeister S. (2000), *Archaeology and migration: Approaches to an archaeological proof of migration*, *Current Anthropology* 41:539-567.
- Chamla M.-C. (1967), *La population du cimetiere méroïtique. Etude anthropologique*, Paris: Firmin Didot.
- Charpin D. (1992), *Immigrés, réfugiés et déportés en Babylonie sous Hammurabi et ses successeurs* [in:] “La circulation des biens, des personnes et des idées dans le Proche-Orient ancien. Actes de la XXXVIII^e Rencontre Assyriologique Internationale (Paris, 8–10 juillet 1991)”, D. Charpin, F. Joannès (eds.), Paris: Editions Recherche sur les civilisations, pp. 207-218.
- Delgado M., Ramirez L.M., Adhikari K., Fuentes-Guajardo M., Zanolli C., Gonzalez-Jose R., Canizales S., Bortolini M.C., Poletti G., Gallo C., Rothhammer F., Bedoya G., Ruiz-Linares A. (2019), *Variation in dental morphology and inference of continental ancestry in admixed Latin Americans*, *American Journal of Physical Anthropology* 168(3):438-447.
- Godde K. (2009), *An examination of Nubian and Egyptian biological distances: Support for biological diffusion or in situ development?*, *HOMO – Journal of Comparative Human Biology* 60(5):389-404.
- Godde K. (2013), *An examination of the spatial-temporal isolation model in Nubians*, *International Journal of Osteoarchaeology* 23(3):324-333.
- Godde K. (2018), *A new analysis interpreting Nilotic relationships and peopling of the Nile Valley*, *HOMO – Journal of Comparative Human Biology* 69(4):147-157.
- Godde K., Jantz R.J. (2017), *Evaluating Nubian population structure from cranial non-metric traits: Gene flow, genetic drift, and population history of the Nubian Nile Valley*, *Human Biology* 89(4):255-279.
- Forstner-Müller I. (2008), *Tell el-Dab’a XVI: Die Gräber des Areals A/III von Tell el-Dab’a*, Vienna: Austrian Academy of Sciences.
- Gardiner A.H. (1916), *The defeat of the Hyksos by Kamose: The Carnarvon tablet no. I*, *The Journal of Egyptian Archaeology* 3(1):95-110.
- Habachi L. (1954), *Khatâna-Qantîr: Importance*, *Annales du Service des Antiquités de l’Égypte* 52:443-559.
- Habachi L. (1972), *The second stela of Kamose and his struggle against the Hyksos ruler and his capital*, Glückstadt: J.J. Augustin.
- Haeussler A.M., Turner C.G., Irish J.D. (1988), *Concordance of American and Soviet methods in dental anthropology*, *American Journal of Physical Anthropology* 75:218.
- Hanihara T. (1992), *Dental and cranial affinities among populations of East Asia and*

- the Pacific: The basic populations in East Asia IV*, American Journal of Physical Anthropology 88:163-182.
- Hanihara T. (2008), *Morphological variation of major human populations based on nonmetric dental traits*, American Journal of Physical Anthropology 136:169-182.
- Harris R. (1975), *Ancient Sippar. A demographic study of an Old-Babylonian city (1894-1595 B.C.)*, Istanbul: Nederlands Historisch-Archaeologisch Instituut te Istanbul.
- Harris E.F., Sjøvold T. (2004), *Calculation of Smith's mean measure of divergence for intergroup comparisons using nonmetric data*, Dental Anthropology 17(3):83-93.
- Hawass Z., Gad Y.Z., Ismail S., Khairat R., Fathalla D., Hasan N., Ahmed A., Elleithy H., Ball M., Gaballah F., Wasef S., Fateen M., Amer H., Gostner P., Selim A., Zink A., Pusch C.M. (2010), *Ancestry and pathology in King Tutankhamun's family*, The Journal of the American Medical Association 303(7):638-647.
- Hawass Z., Ismail S., Selim A., Saleem S.N., Fathalla D., Wasef S., Gad A.Z., Saad R., Fares S., Amer H., Gostner P., Gad Y.Z., Pusch C.M., Zink A.R. (2012), *Revisiting the harem conspiracy and death of Ramesses III: Anthropological, forensic, radiological, and genetic study*, British Medical Journal 345:e8268.
- Hefner J.T., Pilloud M.A., Buikstra J.E., Vogelsberg C.C.M. (2016), *A brief history of biological distance analysis* [in:] "Biological distance analysis: Forensic and bioarchaeological perspectives", M.A. Pilloud, T. Hefner (eds.), London: Academic Press, pp. 3-22.
- Hubbard A.R., Guatelli-Steinberg D., Irish J.D. (2015), *Do nuclear DNA and dental nonmetric data produce similar reconstructions of regional population history? An example from modern coastal Kenya*, American Journal of Physical Anthropology 157:295-304.
- Irish J.D. (2005), *Population continuity vs. discontinuity revisited: Dental affinities among Late Paleolithic through Christian-era Nubians*, American Journal of Physical Anthropology 128:520-535.
- Irish J.D. (2006), *Who were the ancient Egyptians? Dental affinities among Neolithic through postdynastic peoples*, American Journal of Physical Anthropology 129:529-543.
- Irish J.D. (2015), *Assessing dental nonmetric variation among populations* [in:] "A companion to dental anthropology", J.D. Irish, G.R. Scott (eds.), Hoboken: John Wiley Sons Inc, pp. 265-286.
- Keita S.O. (1992), *Further studies of crania from ancient northern Africa: An analysis of crania from first dynasty Egyptian tombs using multiple discriminant functions*, American Journal of Physical Anthropology 87(3):245-254.
- Keita S.O. (2005), *History in the interpretation of the pattern of p49a, f Taql RFLP Y-chromosome variation in Egypt. A consideration of multiple lines of evidence*, Ameri-

- can Journal of Human Biology 17:559-567.
- Keita S. Godde K. (2016), *A preliminary analysis of diachronic craniometric geographical variation during the Predynastic – Early Dynastic period: Possible population implications for the theories of the merger of upper and lower Egypt*, Göttinger Miszellen 249:95-108.
- Kopetzky K. (2010), *Tell el-Dab'a XX: Die Chronologie der Siedlungskeramik der Zweiten Zwischenzeit aus Tell el-Dab'a*, Vienna: Austrian Academy of Sciences.
- Kunter M., Poppa R. (1977), *Kamid el-Loz. 4. Anthropologische Untersuchung der menschlichen Skelettreste aus dem eisenzeitlichen Friedhof*, Bonn: Habelt.
- Larsen M.T. (2015), *Ancient Kanesh: A merchant colony in Bronze Age Anatolia*, New York: Cambridge University Press.
- Luft U. (1993), *Asiatics in Illahun: A preliminary report* [in:] “Sesto Congresso Internazionale di Egittologia Atti Turin”, G.M. Zaccane, T.R. di Netro (eds.), Turin, pp. 291-297.
- Lythgoe A.M. (1909), *The Egyptian expedition*, The Metropolitan Museum of Art Bulletin 4:119-123.
- Mace A.C. (1921), *Excavations at Lisht*, The Metropolitan Museum of Art Bulletin 16:5-19.
- Marcus E.S. (2007), *Amenemhet II and the sea: Maritime aspects of the Mit Rahina (Memphis) Inscription*, Egypt and the Levant 17:137-190.
- Massey D.S. (1999), *Why does immigration occur? A theoretical synthesis* [in:] “The handbook of international migration: The American experience”, C. Hirschman, P. Kasinitz, J. DeWind (eds.), New York: Russel Sage Foundation.
- Mourad A.-L. (2015), *Rise of the Hyksos. Egypt and the Levant from the Middle Kingdom to the Early Second Intermediate Period*, Oxford: Archaeopress.
- Mourad A.-L. (2018), *Exploring change from the Twelfth to the Fifteenth Dynasty at Tell el-Dab'a*, Paper presented at American School of Oriental Research, Denver.
- Mourad A.-L. (2021), *The enigma of the Hyksos volume II. Transforming Egypt into the New Kingdom. The Impact of the Hyksos and Egyptian-Near Eastern relations, contributions to the archaeology of Egypt*, Nubia and the Levant 10, Wiesbaden: Harrassowitz.
- Nichol C.R. (1990), *Dental genetics and biological relationships of the Pima Indians of Arizona*, unpublished Ph.D. dissertation, Arizona State University.
- Petrie W.M.F. (1902), *Abydos*, London: Egypt Exploration Fund.
- Petrie W.M.F. (1907), *Gizeh and Rifeh*, London: Bernard Quaritch.
- Petrie W.M.F. (1909), *Qurneh*, London: Bernard Quaritch.
- Petrie W.M.F., Wainwright G.A., Gardiner A.H. (1913), *Tarkhan I and Memphis V*, London: Hazell Watson and Viney Ltd.
- Prell S. (2019a), *A ride to the netherworld: Bronze Age equid burials in the Fertile Cres-*

- cent [in:] “The enigma of the Hyksos”, M. Bietak, S. Prell (eds.), Wiesbaden: Harrassowitz, pp. 107-124.
- Prell S. (2019b), *Burial customs as cultural marker: A ‘global’ approach* [in:] “The enigma of the Hyksos”, M. Bietak, S. Prell (eds.), Wiesbaden: Harrassowitz, pp. 125-147.
- Prell S. (2019c), ‘Buckle up and fasten that belt!’ *Metal belts in the Early and Middle Bronze Age*, *Egypt and the Levant* 29:303-329.
- Prell S. (2020), *Hard to pin down – clothing pins in the eastern delta of Egypt and their diffusion in the Middle Bronze Age*, *Egypt and the Levant* 30:495-533.
- Prell S. (2021), *The Hyksos enigma, Volume III. Ausländische Bestattungssitten im Ost-delta Ägyptens – eine Spurensuche*, *Contributions to the Archaeology of Egypt, Nubia and the Levant* 11, Wiesbaden: Harrassowitz.
- Priglinger E. (2019), *Different aspects of mobility and migration during the Middle Kingdom*, *Egypt and the Levant* 29:331-353.
- Prowse T.L., Lovell N.C. (1996), *Concordance of cranial and dental morphological traits and evidence for endogamy in ancient Egypt*, *American Journal of Physical Anthropology* 101(2):237-246.
- Ramirez Rozzi F. (2016), *Diversity in tooth eruption and life history in humans: Illustration from a Pygmy population*, *Scientific Reports* 6:27405.
- Randl-Gadora U., Großschmidt K. (2002), *Nicht-metrische Zahnmerkmale bei hyksoszeitlichen (1640-1530 v. Chr.), Kinderskeletten aus Tell el Daba: Erste Ergebnisse*, *Egypt and the Levant* 11:289-299.
- Rathmann H., Reyes-Centeno H. (2020), *Testing the utility of dental morphological trait combinations for inferring human neutral genetic variation*, *Proceedings of the National Academy of Sciences of the United States of America* 117:10769-10777.
- Relethford J.H. (2004), *Boas and beyond: Migration and craniometric variation*, *American Journal of Human Biology* 16:379-386.
- Santos F. (2018), *AnthropMMD: An R package with a graphical user interface for the mean measure of divergence*, *American Journal of Physical Anthropology* 165:200-205.
- Schaeffer C.F.A. (1949), *Ugaritica II: Nouvelles études relatives aux découvertes de Ras Shamra*, Paris: P. Geuthner.
- Schiestl R. (2009), *Tell el-Dab’a XVIII. Die Palastnekropole von Tell el-Dab’a. Die Gräber des Areals F/II der Straten d/2 und d/1*, Vienna: Austrian Academy of Sciences.
- Schillaci M.A., Irish J.D., Wood C.C. (2009), *Further analysis of the population history of ancient Egyptians*, *American Journal of Physical Anthropology* 139:235-243.
- Schneider T. (2003), *Ausländer in Ägypten während des Mittleren Reiches und der Hyksoszeit Teil 2: Die ausländische Bevölkerung*, Wiesbaden: Harrassowitz.

- Schuenemann V.J., Peltzer A., Welte B., van Pelt W.P., Molak M., Wang C.C., Furtwängler A., Urban C., Reiter E., Nieselt K., Teßmann B., Francken, M., Harvati K., Haak W., Schiffels, S., Krause J. (2017), *Ancient Egyptian mummy genomes suggest an increase of Sub-Saharan African ancestry in post-Roman periods*, Nature Communications 8:15694.
- Scott G.R., Irish J.D. (2017), *Human tooth crown and root morphology: The Arizona State University Dental Anthropology System*, Cambridge: Cambridge University Press.
- Scott G.R. (1973), *Dental morphology: A genetic study of American white families and variation in living Southwest Indians*, unpublished Ph.D. dissertation, Arizona State University.
- Scott G.R., Irish J.D. (2013), *Anthropological perspectives on tooth morphology: Genetics evolution variation*, Cambridge: Cambridge University Press.
- Scott G.R., Irish J.D. (2017), *Human tooth crown and root morphology: The Arizona State University Dental Anthropology System*, Cambridge: Cambridge University Press.
- Scott G.R., Turner C.G. (1988), *Dental anthropology*, Annual Review of Anthropology 17:99-126.
- Scott G.R., Turner C.G. (1997), *The anthropology of modern human teeth: Dental morphology and its variation in recent human populations*, Cambridge: Cambridge University Press.
- Sjovold T. (1977), *Non-metrical divergence between skeletal populations*, Ossa 4:351-352.
- Sjovold T. (1984), *A report on the heritability of some cranial measurements and non-metric traits* [in:] "Multivariate statistical methods in physical anthropology", G.N. Van Vark, W.W. Howells (eds.), Dordrecht: Springer, pp. 223-246.
- Smith C.A.B. (1972), *Coefficients of biological distance*, Annals of Human Genetics 36:241-245.
- Smith M.E. (2010), *The archaeological study of neighborhoods and districts in ancient cities*, Journal of Anthropological Archaeology 29:137-154.
- Stantis C., Kharobi A., Maaranen N., Nowell G.M., Bietak M., Prell S., Schutkowski H. (2020), *Who were the Hyksos? Challenging traditional narratives using strontium isotope ($^{87}\text{Sr}/^{86}\text{Sr}$) analysis of human remains from ancient Egypt*, PLOS One 15(7):e0235414.
- Stantis C., Kharobi A., Maaranen N., Macpherson C., Bietak M., Prell S., Schutkowski H. (2021), *Multi-isotopic study of diet and mobility in the northeastern Nile Delta*, Archaeological and Anthropological Sciences 13:e105.
- Stojanowski C.M., Schillaci M.A. (2006), *Phenotypic approaches for understanding patterns of intracemetery biological variation*, American Journal of Physical Anthropology

- ogy 131:49-88.
- Strudwick N.C. (2005), *Texts from the Pyramid Age*, Atlanta: Society of Biblical Literature.
- Szemethy H. (2015), *The journey of Felix von Luschan to Egypt in 1889* [in:] “Egypt and Austria VIII”, I. Lazar (ed.), Koper: Univerza na Primorskem, pp. 101-127.
- The Griffith Institute, University of Oxford (2015), W.M. Flinders Petrie, available online.
- Thesleff I. (2006), *The genetic basis of tooth development and dental defects*, American Journal of Medical Genetics Part A 140:2530-2535.
- Townsend G., Bockmann M., Hughes T., Brook A. (2012), *Genetic environmental and epigenetic influences on variation in human tooth number size and shape*, Odontology 100:1-9.
- Townsend G., Harris E.F., Lesot H., Clauss F., Brook A. (2009), *Morphogenetic fields within the human dentition: A new clinically relevant synthesis of an old concept*, Archives of Oral Biology 54:S34-44.
- Tsuda T., Baker B. (2015), *Conclusion: migration and disruptions from prehistory to the present* [in:] “Migration and disruptions: Towards a unifying theory of ancient and contemporary migrations”, B. Baker, T. Tsuda (eds.), Gainesviell: University of Florida Press, pp. 296-331.
- Turner C.G., Scott G.R. (1977), *Dentition of Easter Islanders* [in:] “Orofacial growth and development”, A.A. Dahlberg, T.M. Graber (eds.), The Hague: Mouton, pp. 229-249.
- Turner II C.G. (1987), *Late Pleistocene and Holocene population history of East Asia based on dental variation*, American Journal of Physical Anthropology 73:305-321.
- Turner C.G., Nichol C.R., Scott G.R. (1991), *Scoring procedures for key morphological traits of the permanent dentition: The Arizona State University dental anthropology system* [in:] “Advances in dental anthropology”, M.A. Kelley, C.S. Larsen (eds.), New York: Wiley-Liss, pp. 13-32.
- Van Seters J. (1966), *The Hyksos: A new investigation*, New Haven: Yale University Press.
- Vilain S. (2019), *The foreign trade of Tell el-Dab'a during the Second Intermediate Period: Another glance at imported ceramics under Hyksos rule* [in:] “The crossroads III – A stranger in the house: Foreigners in ancient Egyptian and Near Eastern societies of the Bronze Age. Proceedings of an international conference held in Prague September 10-13 2018”, J. Mynářová, M. Kilani, S. Alivernini (eds.), Prague: Charles University Faculty of Arts, pp. 387-404.
- Vilain S. (2021), *A crisis? What crisis? Challenging times at Tell el-Dab'a during the Second Intermediate Period* [in:] “The enigma of the Hyksos, Volume IV. Changing clusters and migration in the Near Eastern Bronze Age. Collected papers of a

workshop held in Vienna, 4th–6th of December 2019”, M. Bietak, S. Prell (eds.), Contributions to the Archaeology of Egypt, Nubia and the Levant 12, Wiesbaden: Harrassowitz, pp. 315-332.

Waddell W.G. (1940), *Manetho*, London: Harvard University Press.

Winkler E., Wilfing H. (1991), *Tell el-Dab'a VI: Anthropologische Untersuchungen an den Skelettresten der Kampagnen*, Vienna: Austrian Academy of Sciences.

Zakrzewski S.R. (2007), *Population continuity or population change: Formation of the ancient Egyptian state*, American Journal of Physical Anthropology 132:501-509.

Zubov A.A. (1977), *Odontoglyphics: The laws of variation of the human molar crown microrelief* [in:] “Papers presented at a symposium held August 30 and 31 at the University of Chicago and submitted to the IXth International Congress of Anthropological and Ethnological Sciences, Chicago 1973”, A.A. Dahlberg, T.M. Graber (ed.), The Hague: Mouton, pp. 269-282.