1   A new zooarchaeological application for geometric

2   morphometric methods: Distinguishing *Ovis aries*

3   morphotypes to address connectivity and mobility of

4   prehistoric Central Asian pastoralists

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Abstract

Geometric morphometric methods (GMM), which were developed to characterize the shape and size of biological organisms, have been applied within zooarchaeology over the past decade to address animal domestication processes and to refine morphological criteria to differentiate between taxa. However, there has been limited utilization of these methods to discriminate between populations of the same taxa to challenge and refine other key archaeological issues, such as migration and connectivity in prehistory. Presented here is a novel application of a three-dimensional landmark based geometric morphometric approach to address the nature of long distance trade and connectivity on the prehistoric Silk Road. The similarity of Bronze and Iron Age archaeological cultures along this steppe route has encouraged characterisations of these people as nomads, with highly mobile, integrated, and connected human and animal populations. However, the interconnectedness of domestic animal populations, in particular sheep (*Ovis aries),* the foundation of this prehistoric pastoral economy, has never been examined. This study utilized geometric morphometric methods to quantify geometric morphometric variance of *O. aries* astragali between three geographically disparate settlement sites within a single Final Bronze age cultural and chronological context. Significant differences between morphotypes revealed that protracted mobility patterns were unlikely and that while animal exchange may have occurred, it was not pervasive enough to produce a uniform sheep morphotype across central and southeastern Kazakhstan. The result of this new application of geometric morphometric methods challenges models of uniform and undifferentiated long distance mobility and economic connectivity between the peoples of the Silk Road.

KEYWORDS: GEOMETRIC MORPHOMETRICS; ZOOARCHAEOLOGY; PASTORALISM; OVIS ARIES; BRONZE AGE; CENTRAL ASIA; THREE-DIMENSIONAL DIGITISATION

Introduction

Trade, connectivity, and mobility are key components in the study of early globalisation processes. The Central Asian steppe was a key region for the transfer of agricultural goods between Asia and Europe, and is well known as the Silk Road in the historical period, which was underpinned by trade, widescale mobility and migration (Jones et al., 2011; Miller et al., 2016; Spengler et al., 2016). Yet the degree and role of mobility in the formation of social networks and cultural change is still poorly described. Demic models of cultural change have recently found new support with the

50 publication of human genetic data indicating mass migrations both from and within the Central

51 Asian steppe in the Early Bronze Age (Allentoft et al., 2015; Chernykh et al., 2008; Damgaard et al.,

52 2018b, 2018a; Frachetti, 2011; Haak et al., 2015; Kuzmina, 2008; Narasimhan et al., 2018). However,

53 cultural diffusion models are still preferred to describe the gradual cultural changes of the Late and

54 Final Bronze Age in Central Asia prior to the increasing social inequality and technological advances

55 associated with the Early Iron Age. These pastoral economies, with little evidence of agricultural

56 production, are based upon animals, and as these animals are mobile assets, it has long been

57 assumed that mobility was a key feature of both human and animal populations. The scale of

58 interaction between human settlements through this period is disputed, with models of long

59 distance mobility over thousands of kilometres influenced by ethnographic examples and

60 widespread material cultures (Kuzmina, 2007). These compete with localised network models that

61 emphasize limited pastoral circuits, such as vertical transhumance and tethered mobility, that link

62 together to form broad networks of material culture exchange (Bendrey et al., 2010; Frachetti, 2009;

63 Rouse and Cerasetti, 2018). Recent archaeological research has supported the latter, with increasing

64 evidence for localised lifeways and economies that share an overarching material culture (Haruda,

65 2018; Motuzaite Matuzeviciute et al., 2015; Spengler et al., 2013; Ventresca Miller et al., 2017).

66 While traditional zooarchaeological analysis has contributed to this debate, morphological variability

67 of animal bones has not yet been explored. Osteological remains contain ecomorphological variation

68 that vary by population, and especially for postcranial elements can signal local ecological

69 adaptation. Geometric morphometrics capture and measure this variation, which makes this

70 method ideal for directly addressing archaeological questions of connectivity and exchange.

71   As a small, mobile herd animal, sheep are ubiquitous across prehistoric steppe archaeological

72 contexts dating from the Early Bronze Age as part of a pastoral package of horse, cattle, and goats,

73 (Bendrey, 2011; Haruda, 2018; Outram et al., 2012). Zooarchaeological assemblages are analysed as

74 palimpsests, with animal remains from the same chronological context within a site analysed as one

75 unit to assess economic patterns at a particular settlement for that period (Reitz and Wing, 1999). It

76 is unclear if Central Asian sheep flocks were part of a single highly intermixed flock, in the same

77 manner as predominant material culture groups. Ethnographically in the nineteenth and twentieth

78 centuries, livestock were exchanged between pastoral families and to secure social contracts

79 (Abramzon, 1971; Gardner and Shayakhmetov, 2006; Hudson, 1938; Krader, 1955; Olcott, 1987).

80 These types of exchanges led to the development of a Central Asian fat-tailed sheep landrace that

81 was found throughout the region during this historical period, but has since been lost due to

82 admixture with European breeds in the past century. (Mason and Porter, 2002; Olcott, 1987;

83 Robinson and Milner-Gulland, 2003; Youatt, 1837). Animal exchange in prehistory would have also

84   resulted in regionally similar flocks that were not isolated and continually subject to admixture.

85   Uniform long-distance mobility patterns practised by pastoralists across the region would have

86   encouraged similar osteological morphotypes adapted for extensive seasonal migrations that

87   overrode the influence of local ecology (Kuzmina, 2007). Both social contracts secured by animal

88   exchange and long distance mobility would lead to a homogeneous sheep flock across the Central

89   Asian steppe, which can be tested via geometric morphometric methods.

90   The power of geometric morphometric methods lies in the ability to detect small but significant

91   changes in shape between groups of specimens whilst retaining the element of shape information

92   related to size. These significant differences are often lost in traditional quantitative and qualitative

93   measurement methods (Zelditch et al., 2012). Zooarchaeologists have used size differences to

94   examine the effects of domestication and cultural change, but have only been able to roughly

95   describe shape quantitatively using ratios of linear measurements or logarithm methods (Albarella,

96   2002, 1997a; Sykes et al., 2013; Thomas, 2005; Zeder et al., 2006). While linear measurements of

97   appendicular skeletal elements are useful in zooarchaeology for species delineation and in certain

98   archaeological contexts, such as the size change of a species through time (Albarella, 1997b; Davis,

99   2000; Rowley-Conwy, 1998; Sykes et al., 2013), the confounding factor of size upon these elements

100   can cloud attempts to distinguish between populations and early emerging landraces. Guidelines

101   developed in the middle of the last century for identifying sheep breed types, such as the 'fat-tailed'

102   sheep typical of the steppe, utilize withers heights which are calculated using greatest lengths of

103   appendicular limb bones (Tsalkin, 1961). These measurements are affected by ontogenetic variables,

104   which are biological variables that impact bone morphology such as sex and nutritional level, and

105   have since been found to be unreliable for discriminating between breeds of sheep (Popkin et al.,

106   2012).

107   Geometric morphometrics have been used to explore domestication and population variation,

108   with specific focus upon the morphology of skulls and teeth (Bopp-Ito et al., 2018; Drake et al., 2015;

109   Duval et al., 2018; Owen et al., 2014). Other skeletal elements which are more resistant to density-

110   mediated attrition, such as calcanei, have been used successfully in ecomophological and

111   archaeological investigations of variability between populations (Barr, 2014; Bignon et al., 2005;

112   Curran, 2012; Plummer et al., 2015, 2008; Pöllath et al., 2019). Measurement of morphological

113   variation of zooarchaeological remains requires careful selection of a skeletal element that is both

114   taphonomically robust as well as appropriate for measuring inherited traits that address the

115   archaeological research question.

116   The astragalus has the least amount of growth out of all appendicular elements in the *O. aries*

117   skeleton and only occurs via appositional growth across the medio-lateral axis (Popkin et al., 2012).

118   Nutritional level, sexual dimorphism, and remodelling affect the astragalus the least out of all post-

119   cranial elements as it is completely enclosed within the joint and does not have a secondary

120   ossification centre (Pöllath et al., 2019). This element is a key bone in the ankle joint of the animal,

121   and works as a pivot point to convert motion both distally and dorsally. Working in concert with the

122   calcaneus, the astragalus controls for the degree of flexibility and stability in this joint. The

123   morphology of the distal articulation and the shape of the plantar articular surface together form a

124   disc cam, improving efficiency of stride for cursors (Barr, 2014). The astragalus has been noted as

125   effective as an ecomorphological indicator in studies of bovid post-cranial elements to reveal the

126   ecological and topographical environment of ancient animals (Curran, 2015; DeGusta and Vrba,

127   2005; Plummer et al., 2008; Pöllath et al., 2019). The environment of a ruminant flock, even within

128   the same species, drives selection towards a more efficient ankle joint for movement through the

129   closed or open environments, with populations living in closed environments with extensive

130   vegetative cover or mountainous gradients possessing ankle joints which are optimized for mobility

131   and powerful movement. Populations in open environments, such as the steppe or savanna, have

132   ankle joints optimized for speed and stability (Curran, 2012; Plummer et al., 2008). The astragalus is

133   a robust element that survives well taphonomically and is resistant to density-mediated attrition and

134   as this element the least affected by ontogenetic variables, the astragalus is an excellent specimen

135   for measuring inherited osteological morphology that reflects site palaeoecology (Lyman, 1994).

136   Shape variation between individuals is to be expected, however overall morphology of the

137   astragalus across a population of *O. aries* represents an ecomorphotype for that particular

138   population.

139   As osteological remains contain ecomorphological variation that is influenced by human-

140   mediated mobility patterns and dispersals across the ancient landscape, morphotypes particular to a

141   locality would indicate that inherited morphotypes are specific for that palaeoecology, while a

142   general morphotype that is uniform across sites and regions would indicate interbreeding between

143   regional flocks or a high degree of long-distance mobility to negate the effect of a specific

144   environmental influence around site environs. As zooarchaeological collections are palimpsests that

145   represent the animals which were deposited during the period of occupation of the site, these

146   remains represent a sample of animals during the occupation periods. Here, specimens from each

147   site are referred to as a population, which refers to a geographically distinguished group of animals

148   that occurred as a zooarchaeological palimpsest during a period of interest (Pöllath et al., 2019).

149   Thus, this novel study evaluates osteological morphology between Final Bronze Age *Ovis aries*

150 populations to test whether flock homogeneity aligns with material cultural homogeneity as a proxy

151 for describing the degree of connection between human settlements.

Materials and Methods

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153 *Ovis aries* astragali were selected from zooarchaeological assemblages from three Final Bronze Age

154 settlement sites in central and southeastern Kazakhstan, a region encompassing roughly 450,000

155 km^2. These specimens are from the publicly held archaeological collections of E.A. Bukhetov

156 Karaganda State University, Karaganda and the Margulan Institute for Archaeology, Almaty. No

157 permits were required for the described study. Neonatal specimens and those with surface damage

158 that would affect landmark placement were excluded from the study. Both left and right specimens

159 were selected except in cases in which entire articulated skeletons were excavated within a single

160 context, in which case the left astragalus was selected. Astragali were identified to species

161 according to qualitative characteristics (Boessneck, 1969; Fernandez, 2001; Prummel and Frisch,

162 1986; Zeder and Lapham, 2010) and this was tested using geometric morphometric methods

163 (Haruda, 2017).

164 The Final Bronze Age sites of Kent, Serektas, and Turgen, are located in different agro-climatic

165 zones with varying degrees of topographic variation (Haruda, 2018) (Fig 1). Kent is a large

166 archaeological settlement with one hundred and thirty pit houses and located at 925 m a.s.l. in the

167 central Kazakh highlands within Karkaralinsk National Park. This area is characterized by granitic

168 outcrops which rise to 1350 m a.s.l. within the park boundary and have a higher biodiversity than

169 the surrounding steppe. It is forested with pine and birch while the surrounding semi-arid steppe is

170 largely comprised of dry fescue type grasses and *Artemisia* spp. Kent is dated by ceramic typology to

171 the Final Bronze Age (1300-900 BCE) and belongs to the Begazy-Dandybaevsky material culture

172 group (Epimakov et al., 2005; Evdokimov and Varfolomeev, 2002). Previous zooarchaeological

173 analysis has shown that this settlement was heavily reliant upon sheep and goat which formed 63%

174 of recovered identifiable remains (NISP) and were likely raised for meat with a majority of the

175 population slaughtered before reaching four years of age (Haruda, 2018; Outram et al., 2012). Eight

176 astragali from *Ovis aries* originate from this site and are housed at the Bukhetov Karaganda State

177 University in Karaganda, Kazakhstan (SI Table 1).

Fig 1. Location of archaeological sites

180   Serektas is located at 776 m a.s.l. in the semi-arid steppe located midway between the Tien Shan

181   mountains 100 km to the south and the shores of Lake Balkhash 150 km to the north. The site is a

182   small settlement comprised of a pit house with multiple phases of renovation and occupation.

183   Serektas is also dated to the Late and Final Bronze Age by the presence of Begazy-Dandybaevsky

184   ceramics (Yermolaeva, 2001, 2000). The zooarchaeological profile of this site is similar to Kent, with

185   ovicaprids comprising 48% of NISP, although over half of the population survived past four years of

186   age (Haruda, 2018). Ten *Ovis aries* astragali originate from this site and are housed at the Margulan

187   Institute of Archaeology in Almaty, Kazakhstan.

188   Turgen is located at 1900 m a.s.l in a lightly wooded conifer valley within the foothills of the Tien

189   Shan mountain range. The Turgen valley originates at the foot of a glacier at approximately 3500 m

190   a.s.l and emerges onto the Semirech'ye alluvial plain near the modern city of Talgar at 1000 m a.s.l.

191   The site, located midway up the ravine, is comprised of two pit houses and two nearby cemeteries.

192   and also is dated by the presence of Begazy-Dandybaevsky ceramics from Late and Final Bronze Age

193   (Goriachev, 2011a, 2011b; Roberts et al., 2019). Despite the difference in microclimate and rainfall,

194   the zooarchaeological signature at Turgen is very similar to the other two site, as 53% of NISP are

195   ovicaprid, with a strong indication for meat consumption, with less than 10% of the population

196   surviving past four years (Haruda, 2018). Twenty-one *Ovis aries* astragali from this site contributed

197   to this study and are also housed at the Margulan Institute of Archaeology in Almaty, Kazakhstan.

Digitising and Landmarking

199   A suite of fifteen landmarks selected for this analysis follow a previously published set of

200   landmarks (Haruda, 2017) and describe the shape of the *O. aries* astragalus following quantitative

201   and qualitative zooarchaeological literature (Boessneck, 1969; Fernandez, 2001; Prummel and

202   Frisch, 1986; von den Driesch, 1976; Zeder and Lapham, 2010) as well as literature which describes

203   landmark methods for the appendicular morphology of *Cervidae* (Curran, 2015, 2012; Sykes et al.,

204   2013) (Fig 2). Specimens were scanned using a Next Engine 3D Laser Scanner with a dimensional

205   accuracy of ± .381 mm at a resolution of 2500dpi with Scan Studio HD software. These scans were

206   aligned to at least an accuracy of ±0.02mm and fused together into a single three-dimensional mesh.

207   Once scans were trimmed, aligned and fused, they were imported as cloud data (.ply) into Landmark

208   Editor (Wiley et al., n.d.). Landmarks were located on each specimen visually and with the assistance

209   of plantar-dorsal and proximal-distal axes according to landmark criteria and these files are

210   deposited in an open-access data repository (Haruda, 2017)(10.5281/zenodo.1188830).

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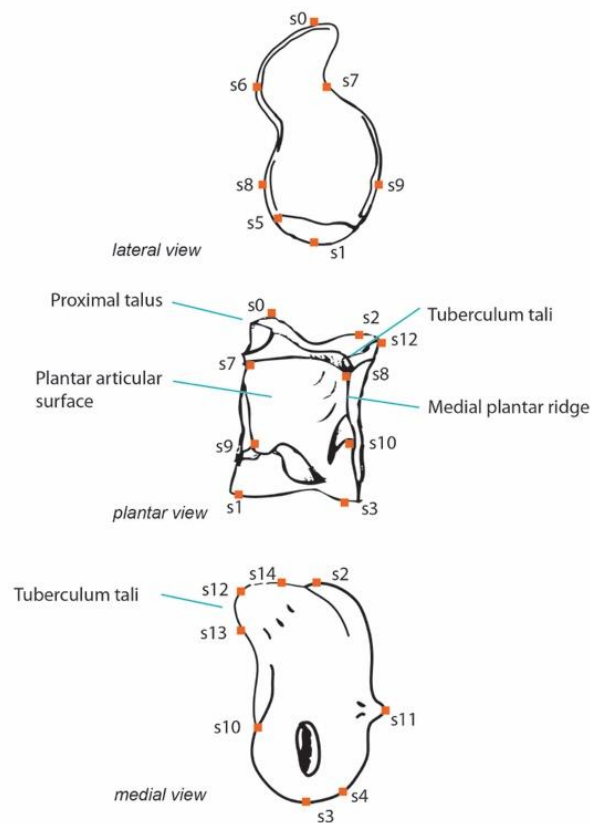
212

213   **Fig 2: Landmark locations**

Statistical Testing

215   The data were superimposed using a Generalized Procrustes Analysis (GPA) in MorphoJ to scale

216   all configurations to centroid size, translate them to the same location, and rotate them to the same

217   orientation and reflect them so both left and right specimens were comparable (Dryden and Marida,

218   1998; Klingenberg, 2011; Rohlf and Slice, 1990).

219   Measurement and replication error was quantified with a Procrustes ANOVA in MorphoJ on a

220   larger set of data from Serektas that incorporated two additional *Capra hircus* models which was

221   previously published (n = 12) (Haruda, 2017; Klingenberg, 2011; Klingenberg and McIntyre, 1998).

222   Specimens were scanned twice to create three-dimensional models, and each model was

223   landmarked twice, resulting in four sets of landmarks for each specimen. It was found that variation

224   between specimens was greater than between replicates, indicating that measurement error was

225   negligible (SI Table 2).

226   Statistical testing to investigate the influence of size and allometry as well as to explore variation

227   within the data was conducted using the packages Morpho and Geomorph in R (Adams et al., 2017;

228   Adams and Otárola-Castillo, 2013; R Core Team, 2017; Schlager, 2017). Significance of size variation

229   was tested with a Kruskal-Wallis test using log centroid size by site, and found a p value of 0.11

230   which was not significant for variation between sites. The presence of allometry was tested using a

231   multivariate regression of shape (Procrustes coordinates) upon size (log centroid size) with 1000

232   permutations and a randomised residual permutation procedure (RRPP) and allometry was not

233   found to be significant and size did not affect shape. To test for the effect of allometry across sites, a

234   single factor MANCOVA, with Procrustes coordinates as dependent, log centroid size as

235   independent, and sites as a factor with 1000 permutations and a RRPP also found that allometry was

236   not significant. Furthermore, a homogeneity of slopes test found that slopes of sites were parallel

237   and that allometry was not a significant effect between sites.

238   Due to the small sample size, large number of variables in comparison to specimens, and the

239   known problems with over fitting of classification rates with this type of data, the dimensionality of

240   the data was reduced using a Principal Components Analysis (PCA) in which components that

241   accounted for over 95% of variation were subsampled for a canonical variate analysis (CVA). The

242   CVA, paired with a leave-one-out cross validation, was used to test for differences in shape between

243   groups (Klingenberg and Montero, 2005; Viscosi and Cardini, 2011; Zelditch et al., 2012). To visualize

244   the variations between groups, a between-group PCA was utilized as this method does not

245   overestimate the extent of separation between groups. The mean shapes of groups and

246   visualizations of morphological variation were conducted by morphing the variation associated with

247   each principal component at a magnification of three standard deviations onto a three dimensional

248   model of the grand mean shape of all the specimens using the morphing functions of Geomorph

249   (Adams et al., 2017; Adams and Otárola-Castillo, 2013) (Fig 3). This method was also used to test

250   group membership using a permutation test of difference of average shape for pairwise

251   comparisons (Table 2).

Results and Discussion

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253   Permutation tests of the difference of average shape were significant (Table 1) across all

254   pairwise comparisons. The smallest Procrustes distance between groups was between Serektas and

255   Turgen. This is reflected in the cross-validated classification rates for the between-group PCA in

256   which Serektas and Turgen have a lower correct classification rate than Kent (Table 2). Cross-

257   validated classification rates for a canonical variate analysis with a reduced dimensionality return a

258   100% correct classification rate, indicating that there is slight overfitting using this type of analysis,

259   even with a reduction in dimensionality.

260   **Table 1. Pairwise Procrustes distances among site (above the diagonal) and p-values for the null hypothesis of equal**

261   **means (below the diagonal).**

	Kent	Serektas	Turgen
Kent	-	0.08800339	0.06858336
Serektas	0.0001	-	0.05934617
Turgen	0.0001	0.0001	-

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263   The first between-group principal component accounted for more than half of the shape

264   variation in the dataset [62.6%] while the second principal component accounted for a third of the

265   shape variation [37.3%]. Specimens from each of the three sites clearly clustered apart along both

266   the first and second principal components (Fig 3). Predicted shape variation along the first principal

267   component revealed variation in the orientation of the tuberculum tali, which lies medially to the

268   plantar articular surface that meets the calcaneus (Fig 2). The tuberculum tali was oriented laterally

269   towards the plantar articular surface for specimens with a positive value on the first principal

270   component, while it was oriented medially for those with negative values. Additionally, astragali

271   with positive values of the first principal component were elongated. Morphological variation along

272   the second principal component revealed a greater difference between the maxima of the proximal

273   and distal trochlea.

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277 **Table 2. Cross-validated classification results in percentages, with sample size in brackets**

|	bgPCA			CVA			
	Kent	Serektas	Turgen	Kent	Serektas	Turgen	None
Kent	100% (8)	0 %(0)	0% (0)	100% (8)	0% (0)	0% (0)	0% (0)
Serektas	0% (0)	90% (9)	10% (1)	0% (0)	80% (8)	0% (0)	20% (2)
Turgen	0% (0)	14.28% (3)	85.71% (18)	0% (0)	0% (0)	100% (21)	0% (0)
Overall classification accuracy: 89.7%				Overall classification accuracy: 94.9%			

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279   This landmark-based geometric morphometric method was able to reveal statistically significant

280 differences in morphology between astragali from three different archaeological sites. The

281 visualisation of shape variation along the first and second between groups principal components

282 indicated differences in the functionality of the ankle joint. The tuberculum tali, located on the

283 proximal medial corner of the plantar articular surface marks the full extent and angle of articulation

284 with the distal tibia. As the sustentaculum tali of the calcaneus slides along the plantar surface of the

285 astragalus, it follows the prominence of the plantar ridge. Any reduction in the prominence of

286 features such as this plantar ridge would result in a less stable and more mobile joint (Barr, 2014;

287 Plummer et al., 2015, 2008). The degree of mobility is marked by the relative size of the trochlea,

288 while stride length is marked by the location of a divot on the distal half of the plantar surface. The

289 relative increase in articular surface area on the plantar aspect increased stride length and efficiency

290 of movement but decreased power for intense bursts of motion. Conversely, squatter astragali with

291 robust trochlea with shorter plantar articular surfaces increased stride power and mobility with

292 fewer prominent features were characteristic of closed environments.

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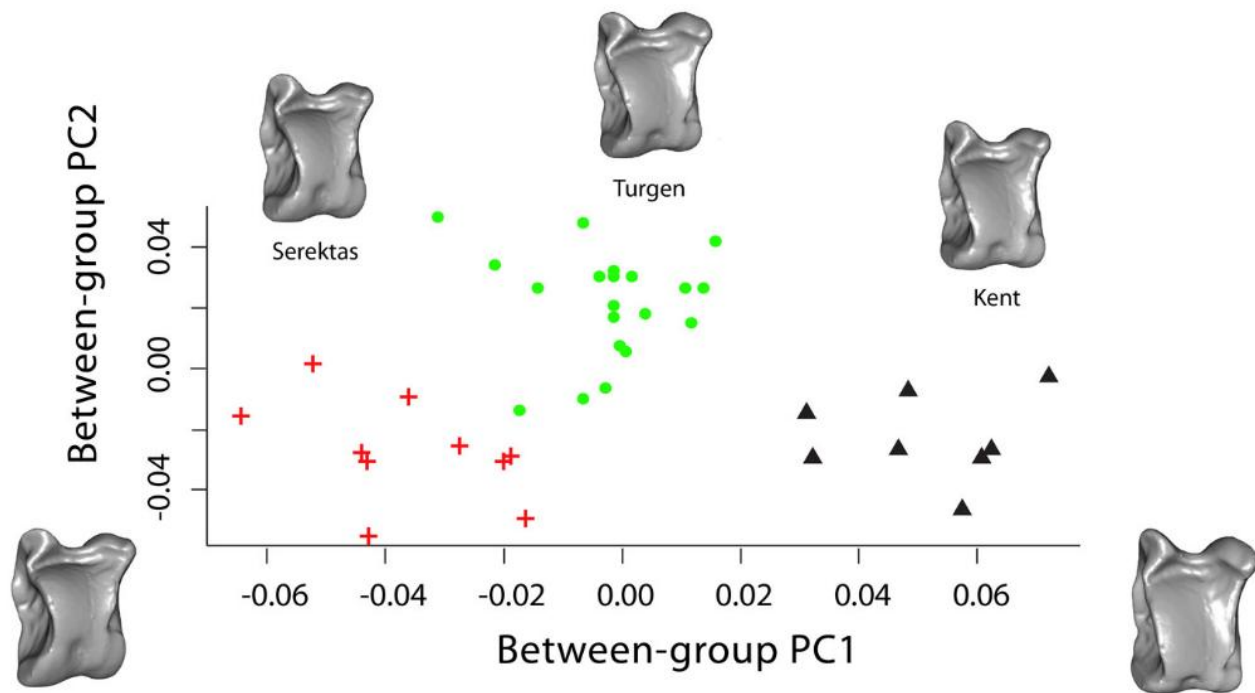
Fig 3. Between-group principal component analysis and average site shapes. Scatterplot of the scores along the first two between-group principal components. Overlaid are predicted shape changes along the first between-group principal component with a magnification factor of three and the average shape of astragali from each site.

Astragali from Serektas are relatively gracile and have morphological features including a less prominent tuberculum tali and proximal tali with a shallow groove. These astragali also have a shorter plantar articular surface and a prominent divot on the distal end of this surface, indicating a wider range of flexion on the distal end of the joint. The specimens from Turgen have a similar morphology to those from Serektas, with a less prominent tuberculum tali and a shorter plantar articular surface, however with even less prominent trochlea which would encourage even more joint mobility. In contrast, specimens from Kent are squat and robust and have a longer plantar articular surface, a more prominent tuberculum tali and plantar articular ridge as well as a more compact distal end, better for more efficient movement through open environments.

Specimens from Kent clearly possess morphological traits associated with open environments. In contrast, specimens from Turgen and Serektas have a more closed morphology, although these are not consistent for these two sites. The forested and vertiginous environment of Turgen is very different from the flatter topography surrounding Kent and Serektas. It is likely that specimens at Serektas had access to the foothills of the Tien Shan, as this site located only eighty kilometres from these mountains and thus individuals may have been grazed in both open and closed environments. Furthermore, the cross-validated classification results also indicate that there may have been some

314   connection between populations or exploitation of similar types of topography for some individuals

315   at Serektas and Turgen.

316   As established above, astragalus morphology is not affected by ontogenetic variables and is the

317   closest to a phenotypic expression of inherited traits, rather than reflecting plasticity driven by

318   variation in pasturage, proportions of sex hormones, or changes to morphology due to remodelling.

319   Recent GMM research on astragalar morphology has shown that variation in the width of the distal

320   end (the Bd measure in traditional von den Driesch 1976 linear measures) does vary by age, but not

321   by sex or environment (Pöllath et al., 2019). The morphotypes here show a range of variation across

322   the entire specimen, but variation at the distal end is not the most prominent area of variation.

323   Furthermore, previous herd profiles of sheep at these three sites show similar slaughter patterns,

324   with few animals surviving past three years of age. As astragali were selected once fully ossified,

325   which occurs at eighteen months of age, we can assume that this age range for this sample is

326   relatively narrow and that the variation between site morphotypes is not due to age related

327   slaughtering patterns.

328   The ankle joint is key to movement efficiency and thus survival. Animals which were unable to

329   efficiently move long distances to access distant pastures or move through closed environments and

330   evade predators were more likely not to pass on their genes to the next generation. Therefore, the

331   morphological signature of the astragalus is associated with the amount of cover and topography of

332   each site, which confirms the specificity of each population to a respective microenvironment and

333   can be called an ecomorphotype. This ecomorphological specificity indicates that mobility of these

334   sheep populations was limited to the local environment of the human settlement, and for example,

335   sheep at Turgen were not participating in long distance migrations across the relatively flat steppe,

336   nor were sheep at Kent utilizing vertiginous areas for pasture.

337   The clear separation of ecomorphotypes of sheep astragali in the Final Bronze Age can be the

338   result of two possibilities- the development of rapid ecomorphological adaptation or genetically

339   distinct sheep populations. These interpretations are not necessarily mutually exclusive. The genetic

340   structure of this ancient sheep population is not yet clear and it still remains to be seen whether

341   ancient sheep were introduced from the same founder population, or were the result of separate

342   introductions in the Early Bronze Age (Anthony, 2007). While the phenotypic link between some

343   elements in some species has been tested, such as for pigs, for this element in sheep, the direct

344   correlation between genetic variation and morphotype is not yet established. Furthermore, the

345   speed at which this ecomorphological adaptation occurred within populations is still not yet well

346   understood and necessitates future research.

347   Additionally, the quantification of the morphological variation between modern sheep breeds

348   and these ecomorphotypes would further serve to illustrate the relationship between ancient and

349   modern animal populations, particularly to explore whether these prehistoric sheep had similar

350   morphologies to modern sheep breeds, such as the historic fat-tailed Central Asian breed. However,

351   this is secondary to exploring the nature of the sheep flock homogeneity in the Final Bronze Age and

352   would not address questions of connectivity and exchange. Despite the origin of this particular

353   morphological plasticity, the geometric morphometric results point to isolated populations with little

354   animal exchange and separate, local pastoral mobility patterns in the Final Bronze Age within a

355   single shared cultural community that refutes hypotheses of a uniform and interconnected steppe-

356   wide sheep flock as well as long-distance mobility patterns.

357   These non-homogenous *O. aries* morphotypes support recent models of multi-scalar pastoral

358   exchange and interaction. First proposed as non-uniform interactions across the steppe (Frachetti

359   2009), the multi-scalar model was developed to describe the nature of sedentary/mobile interaction

360   (Rouse and Cerasetti, 2018) and applies well in this context to describe the nature of intra-cultural

361   exchange and connectivity between the central steppe and the southeastern region of Kazakhstan.

362   While material culture, burial customs, and architectural forms across this large region of central and

363   southeastern Kazakhstan were similar in the Final Bronze Age, variation between sheep

364   morphotypes indicates that local economies and scales of mobility were circumscribed in

365   comparison to the sphere of exchange of ideas, material culture, and modes of life.

366   Zooarchaeological analysis of herd structures of cattle, horses, and ovicaprids from these settlement

367   sites support this, as proportions of cattle in the Semirech'ye during the Late and Final Bronze Ages

368   are more similar to settlements of the same material culture located in more arid regions of the

369   central steppe (Haruda 2018). This is in contrast to broader patterns of domestic animal exploitation

370   across Eurasia during the Bronze Age, in which the proportions of cattle present at settlement sites

371   correlates strongly with annual precipitation and ecoregion (Bendrey, 2011; Outram et al., 2012).

372   Thus pastoralism as an economic mode is shared across this region, while the local practice, at least

373   for the management of sheep flocks, is locally circumscribed with little connectivity and exchange of

374   animals. However, mobility of other domesticated species, particularly those which would facilitate

375   human connectivity, such as horses and camels, is not yet know, and if studied, would further clarify

376   the degree of human interconnectivity during this period. It is clear that there is good evidence for

377   long distance exchange at this period and in the following Iron Age as millet and other crops moved

378   along the prehistoric Silk Road, yet the nature of this dispersal, whether diffusing slowly through

379   neighbouring communities, or via individuals moving long distances on horses is still unclear.

380   However, during this particular chronological context, long distance mobility and connectivity of

381   entire communities and their flocks of sheep can be excluded as a model for trade and connection

382   along the Silk Road.

383   Conclusion

384   Landmark based three-dimensional geometric morphometric methods using a post-cranial

385   element, the astragalus, on zooarchaeological remains successfully revealed significant

386   morphological variation between Final Bronze Age sheep located at different settlement sites. The

387   presence of these three distinct morphotypes challenges assumptions of *Ovis aries* flock

388   homogeneity and archaeological models which emphasize long distance mobility as an essential

389   component of pastoralism. This is some of the earliest direct evidence which indicates that

390   connectivity and exchange between settlements within a cultural community was complex and

391   multi-scalar. Comprehensive movements of people with their flocks across immense distances on

392   annual migrations no longer appears to be a likely model for prehistoric pastoral patterns and

393   human networks. Instead, communication and exchange of material culture and ideas occurred at

394   diffuse and varying scales which linked together human settlements across the prehistoric Silk Road.

395   Acknowledgments

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