1 **Reconstructing the diet of Kůlna 1 from the Moravian karst (Czech Republic)**

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24

Abstract

25

26   The dietary proclivities of an early adolescent Neandertal, Kůlna 1, are reconstructed using dental

27 microwear texture analysis. Examining the diet of Kůlna 1 provides new information about the lifeways and

28 paleoecological conditions faced by Neandertals living in the Moravian karst, an area of extensive anthropogenic

29 activity during Marine Isotope Stage (MIS) 3. Comparative samples include Hortus cave (n = 6), La Quina 5,

30 Malarnaud, Spy I, Krapina (n = 19), Vindija (n = 4) as well as human foragers, farmers and pastoralists (n = 181).

31 Kůlna 1 yields a relatively low value for anisotropy (*epLsar*) compared to most of the Neandertals investigated,

32 suggesting heterogeneous jaw movements typical of Holocene foragers. In contrast, Kůlna 1 exhibits one of the

33 highest Middle Paleolithic complexity (*Asfc*) values. Since elevated complexity is associated with Holocene humans

34 who consumed poorly processed, abrasive and mechanically hard resources, the diet of Kůlna 1 is reconstructed as

35 based largely on hard and brittle plant foods, perhaps available from an interval of higher temperatures during an

36 interstadial period of MIS 3 or possibly from other factors, including individual variation in diet preferences, food

37 availability, grit load, seasonality and group cultural traditions.

38 **Key words**: Hortus; La Quina 5; Malarnaud; Spy I; Dental Microwear Texture Analysis

42

1. Introduction

Evidence of Neandertal occupation has been recovered in the Moravian karst of the Czech Republic from Marine Isotope Stage (MIS) 6 to MIS 3. Among the most complete of the human remains is Kůlna 1, an early adolescent represented by a maxilla and associated with the Micoquian tool tradition of MIS 3 (Rink et al. 1996; Svoboda 2005; Neruda and Nerudová 2014). Kůlna cave is situated on the northern edge of the Moravian karstic formation near the village of Sloup, 30-35 km north of Brno, and is close to a number of Paleolithic sites in the central part of the Czech Republic, southern Poland and southern Germany (Fig. 1) (Rink et al. 1996; Svodoba 2005; Neruda and Nerudová 2014). The stratigraphy of Kůlna cave has been studied in detail via archaeological investigation between 1961-1976 and 1993-1996 under the direction of K. Valoch (Valoch 1988; Valoch et al. 2012), and recently under the direction of P. Neruda (Lisá et al. 2013; Neruda and Nerudová 2014).

Kůlna cave may have been occupied repeatedly by the same social group as a camp from autumn to spring and multiple activity areas within the cavern have been identified (Nerudová et al. 2014; Neruda 2017). Kůlna 1 was recovered from sector E of layer 7a, an area rich in lithic tools as well as Late Pleistocene animal bones, such as *Mammuthus primigenius*, *Rangifer tarandus*, *Equus* sp., *Ursus spelaeus* and *Bos primigenius*, dispersed around a small hearth. Electron spin resonance (ESR) estimates derived from equid, rhinoceros and cervid tooth enamel have been used to date layer 7a of Kůlna cave. They provide an average estimate of 46 ± 6 ka and a linear uptake (LU) date of 50 ± 5 ka (Rink et al. 1996). Radiocarbon dating of culturally modified bones from layer 7a range from 45.8 ± 2.4 ka calibrated before present (calBP) to 46.6 ± 2.6 ka calBP and corroborate the two ESR dates (Neruda and Nerudová 2014). Kůlna cave layer 7a is characterized as a period of oscillations of climatic extremes and is bracketed before and after by stadials. Layer 7a may have experienced a temperate climate with cold-adapted and interstadial fauna (Valoch 2002).

Kůlna cave layer 7a represents the final appearance of the Micoquian technology, characterized by the presence of bifacial backed knives and other bifacial tools, in addition to a large number of scrapers including "groszaki" and Quina types (Valoch 1988, 1995). The presence of side scrapers, retouchers from hard animal tissues, bones with cut-marks from processing and traces of anthropogenic fracturing and scraping indicate a wide range of human activities in the central living site (Neruda & Nerudová 2014; Neruda 2017). The wealth of modified bones suggests an intensive use of animal carcasses brought by the Neandertals to Kůlna cave. Many bone fragments from middle, large and very large animals were use as retouchers for lithic tools production. (Auguste

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71 2002; Neruda et al. 2011). There are other bone pieces such as mammoth ribs abraded on both ends that indicate a

72 number of activities (Valoch 1988). The majority of the bones are broken into small pieces. Cut-marks, surface

73 scraping and green fractures made when the bone was fresh are evident as well as the removal of cancellous bone

74 (Rink et al. 1996; Neruda et al. 2011). All of these features can be related to the consumption of marrow, trabecular

75 bone and fat (Sorensen & Leonard 2001; Snodgrass & Leonard 2009).

76   [Fig. 1]

77   Kůlna cave is close to several major Middle Paleolithic sites of eastern Central Europe (Fig. 1). These

78 include Šipka and Švédův stůl caves in the Czech Republic, Stajnia and Ciemna caves in southern Poland, Krapina

79 and Vindija caves in Croatia, Subalyuk cave in Hungary, and others (Ahern et al. 2013; Smith et al. 2015; Willman

80 et al. 2019; Fig. 1). Since only a cast of the Šipka lower jaw exists, the original having been destroyed in a fire at the

81 end of WWII, Kůlna 1 preserves the only well-dated permanent first maxillary molar known from the Czech

82 Republic prior to the end of MIS 3. Here we use dental microwear texture analysis (DMTA) to reconstruct the

83 dietary signal of Kůlna 1. Information about diet from the maxillary molar surface of Kůlna 1 can be compared to

84 paleoecological reconstructions (Svoboda 2005; Nerudová et al. 2014) and will add to the understanding of the

85 lifeways of the last Neandertals of Moravia by documenting the mechanical properties of the foods consumed.

86 *1.1. Dental microwear texture analysis*

87   Mastication of foods with hard parts or adherents deform tooth enamel, and this deformation is reflected in

88 the occlusal surface texture which dental microwear texture analysis was developed to describe (Scott et al. 2006,

89 2012; El Zaatari et al. 2011; Ungar et al. 2012; Arman et al. 2016; Schmidt et al. 2016, 2019, 2020). Surface texture

90 variables, such as complexity (*Asfc*) and anisotropy (*epLsar*), have been previously utilized to characterize the diets

91 of Plio-Pleistocene hominins (Scott et al. 2005, Ungar et al. 2012), Neandertals (El Zaatari et al. 2011, 2016;

92 Karrigar et al. 2016; Estalrrich et al. 2017; Krueger et al. 2017, 2019; Williams et al. 2018, 2019) and *Homo sapiens*,

93 both recent and prehistoric (El Zaatari 2010; Krueger 2015; Schmidt et al. 2016, 2019, 2020; Da-Gloria & Schmidt

94 2020). Area-scale fractal complexity (*Asfc*)—a calculation of enamel surface coarseness at different scales—is often

95 used as an indicator of hard food consumption (Scott et al. 2005, 2006, 2012; Calandra et al. 2012; DeSantis et al.

96 2013; Schmidt et al. 2019). Low complexity (*Asfc*) can be interpreted as evidence of a soft diet, i.e., one with

97 comparatively few hard foods capable of generating uneven dental micro-surfaces (Fig. 2). High values indicate a

98 very complex enamel surface, suggesting the individual consumed dietary items with physical and mechanical

99   properties capable of pitting the enamel (Scott et al. 2012, Hua et al. 2015). Another texture characteristic utilized is

100   the exact proportion length-scale anisotropy of relief (*epLsar*), or anisotropy. Anisotropy calculates the extent to

101   which surface striations share a common direction. Low values indicate striations in many directions and high values

102   indicate striations in a similar direction. In modern humans, low anisotropy is thought to relate to heterogeneity of

103   jaw movements while a high anisotropy signals more homogeneous movements (Fig. 2). A surface dominated by

104   parallel (i.e., high anisotropy) scratches has been interpreted to indicate a uniform masticatory action of the jaws

105   employed when tough, fibrous foods, or highly processed foods are consumed (Scott et al. 2006; Schmidt et al.

106   2019). Complexity (*Asfc*) and anisotropy (*epLsar*) are utilized in this study to infer the diet of Kůlna 1.

107   [Fig. 2]

108   *1.2. Previous dietary reconstructions of Neandertals*

109   The numerous cervid, bovid, mammoth, rhinoceros and equid bones along with the tools used to process

110   them at Neandertal sites signal a preference for mid- to large- or very large-bodied herbivores (Auguste 2002; Patou-

111   Mathis et al. 2005; Neruda & Lázn;čková-Galetová 2018). Stable isotopes also indicate Neandertals occupied the

112   trophic position of a top-level carnivore (Richards et al. 2000; Bocherens et al. 2001; Fiorenza et al. 2015; Wißing et

113   al. 2016). However, more recent studies of microwear and dental calculus suggest that Neandertal diets were more

114   variable than previously thought and that, like recent human foragers, Neandertals ate what was available to them.

115   (Hardy 2010; El Zaatari et al. 2011, 2016; Fiorenza et al. 2011; Henry et al. 2011, 2014; Hardy et al. 2012; Sistiaga

116   et al. 2014; Estalrrich et al. 2017; Power et al. 2018). The dietary proclivities of Neandertals have been found to

117   correlate with paleoecology such that colder open-steppe habitats are associated with meat-rich diets, and regions

118   with greater vegetation coverage are correlated with greater access to plant foods (El Zaatari et al. 2011, 2016;

119   Fiorenza et al. 2011). Conditions in the Moravian karst of Central Europe during MIS 3 may have been more similar

120   to open-steppe habitats than those with extensive tree resources, although the different levels of Kůlna cave may

121   have varied in habitat (Jelínek 1980, 1988; Svoboda 2005; Krueger et al. 2017, 2019).

122   *1.3. Plant foods*

123   Plant foods often include inadvertent grit and other hard particles such as phytoliths, seeds, pits and shells,

124   which tend to abrade and pit the enamel surface, leading to higher complexity values (Scott et al. 2006, 2012).

125   Dental microwear texture analysis shows some Neandertals during the late glacial period had relatively hard diets

126   from consuming unprocessed plant foods (El Zaatari et al. 2016; Estalrrich et al. 2017). Hard food mastication also

127 characterizes protohistoric and recent forager diets (El Zaatari et al. 2011, 2016; El Zaatari & Hublin 2014; Schmidt

128 et al. 2016, 2019). Hard food mastication is additionally evidenced in Late Pleistocene and Holocene forager diets

129 (El Zaatari et al. 2011, 2016; El Zaatari & Hublin 2014; Schmidt et al. 2016, 2019). In late Holocene foragers, it is

130 possible that meat consumption derives from a lack of available plant foods (El Zaatari 2010). When plant foods are

131 less common in a diet, complexity values tend to decrease. For example, Iron Age herders of the Mongolian steppe

132 consumed large amounts of meat and dairy products and had significantly lower values for molar microwear texture

133 complexity (*Asfc*) than agricultural contemporaries (Schmidt et al. 2016).

134 Paleolithic plant food consumption is also evidenced by fecal markers (Sistiaga et al. 2014), dental calculus

135 and stone tool residues (Hardy 2010; Hardy et al. 2012; Henry et al. 2011, 2014; Power et al. 2018; Power &

136 Williams 2018) as well as nitrogen isotopes (Naito et al. 2016). Dental calculus attests the use of starchy grasses,

137 roots and grass seeds at Neandertal sites in Europe and elsewhere (Henry et al. 2014; Power et al. 2018). The

138 consumption of plant foods is demonstrated by 19 microremains found in the dental calculus of Kůlna 1, which

139 document the use of Triticeae grass seeds and other locally available starch grains (Henry et al. 2014).

140 Neandertal diets often show a relationship between local habitat and plant resource availability, such as the

141 exploitation of date palms and other tree fruits at Shanidar (Henry et al. 2011). Vindija from a relatively temperate

142 period of MIS 3 exhibits lower complexity (*Asfc*), perhaps from a lack of hard plant foods, compared to Krapina

143 from a warmer interglacial of MIS 5 and a higher complexity value (Karriger et al. 2016). Krapina Neandertals also

144 exhibit elevated anisotropy (*epLsar*) compared to those at Vindija and most Holocene humans. Exactly what kinds

145 of food resources led to relatively high anisotropy (*epLsar*) at Krapina is unknown, but likely included tough fibrous

146 plant tissues (Karriger et al. 2016).

147 *1.4. Analytical considerations*

148 Complexity (*Asfc*) will reflect the extent to which the diet of Kůlna 1 contained foods that generate

149 complex surfaces (i.e., hard foods). Evidence of plant phytoliths in the dental calculus of Kůlna 1 indicate that hard

150 and/or unprocessed grass seeds comprised at least a portion of the diet (Henry et al. 2014). If complexity (*Asfc*) is

151 elevated in Kůlna 1, the individual probably consumed grass seeds and/or other hard foods within a few weeks of its

152 death. Given that there is no evidence of food processing tools at Kůlna, low complexity will be interpreted as

153 indicating a diet with fewer plant foods and likely more meat.

154   Neandertals, like Holocene foragers, tend to have jaw movements that lead to low anisotropy (*epLsar*),

155   which varies with available food and habitat. Therefore, we predict that the dental microwear texture of Kůlna 1 will

156   resemble those individuals from similar-aged sites and similar paleoecological conditions. For instance, Kůlna 1

157   should resemble La Quina 5 more than either Spy I from the terminus of MIS 3 or Malarnaud from interglacial MIS

158   5 (Table 1). Considering solely the central European sites, we expect Kůlna 1 to be more similar in anisotropy to

159   Neandertals at Vindija from a temperate interval of MIS 3 than those at Krapina from a relatively warm period of

160   MIS 5.

161   **2. Materials and Methods**

162   *2.1. Materials*

163   *2.1.1. Kůlna 1*

164   Kůlna 1 is a right maxillary fragment with M^1, permanent premolars and canine, and with crypts present for

165   I^1 and I^2. The individual has been aged to be 14-15 years old (Jelinek, 1967, Jelinek 1980, Rinke et al 1996),

166   although an investigation of calcification scores and attrition suggests Kůlna 1 is younger (11-12 years; Minugh-

167   Purvis 1988). Kůlna 1 is characterized as an early adolescent based on the observation that P^4 is unworn and

168   probably not quite fully erupted (Minugh-Purvis 1988). Additional support for the younger age estimate includes the

169   very minor attrition on P^3 and C^1 (Minugh-Purvis 1988) and only slight wear on M^1 (Stage 3, Smith 1984).

170   *2.1.2. Comparative fossil material*

171   The available comparative microwear texture sample covers an extensive range of the temporal and

172   ecogeographic variation known to characterize the European Neandertals. The comparative fossil sample can be

173   divided into two ecozones corresponding to the Mediterranean (Hortus) and continental (remaining Neandertals)

174   (Table 1). The continental ecozone included coniferous forests, patchy woodlands as well as open tundra (Fiorenza

175   et al. 2015). The Mediterranean ecozone was probably slightly warmer and drier than continental habitats but it may

176   have been subjected to more variation in extremes of cold and aridity (H. Lumley 1972; Lumley & Licht 1972;

177   Pillard 1972; M.-A. Lumley 1973).

178   The comparative fossil sample included six Neandertals from Hortus cave, which is located about 30 km

179   from Montpellier, France. The site has yielded a relatively large number of individuals dating to MIS 3 including

180   young adults Hortus IV, Hortus V, Hortus VI, Hortus VIII, older adult Hortus XI and the Hortus III child (de

181   Lumley, 1972; de Lumley & Licht, 1972; de Lumley, 1973; Lebègue et al., 2010; Pillard, 1972). The Hortus

182 Neandertals are from different phases (Table 1). These include the severe cold-dry of the chronologically later Phase

183 Vb; the slightly warmer and wetter habitat of Phase Va which is earlier than Phase Vb; and Phase IVb which is the

184 earliest of the phases and is characterized as warmer and wetter than Phase Va and Vb (Table 1).

185   In addition to the Hortus assemblage, La Quina 5, Malarnaud and Spy 1 are included. La Quina cave in

186 southwest France has been reconstructed as a cold and open habitat and is dated to 47-43 ka BP (Petite-Marie et al.

187 1971; Debénath & Jelinek 1998; Discamps & Royer 2017). Malarnaud is from the French Pyrenees and is dated to

188 the warmer last interglacial of MIS 5 (Petite-Marie et al. 1971). Spy I from northern Europe (Belgium) is dated to

189 late MIS 3 circa 36 ka BP, and derives from a cold-wet paleohabitat (Semal et al. 2009, 2011, 2013; Toussaint et al.

190 2011).

191   Additionally, we included the means and standard deviations from isolated molars of Vindija (n = 4) and

192 Krapina (n = 19) from Karriger et al. (2016). The Level G3 Vindija sample is from MIS 3 and dates to >42 ka BP

193 (Wild et al. 2001; Karriger et al. 2016), whereas Krapina derives from MIS 5e and is dated to 130 ka ± 10 ka BP

194 (Rink et al. 1995). Vindija can be described as temperate with some open grasslands (Miracle et al. 2010). Krapina

195 is likely from a warmer interglacial period (Table 1).

196   [Table 1]

197 *2.1.3. Human comparative sample*

198   The comparative sample includes the means and standard deviations from data on nine groups of foragers,

199 farmers and pastoralists (n = 181) collected at the University of Indianapolis (Table 2). We include farmers and

200 pastoralists for comparison because farmers tend to have higher anisotropy (*epLsar*) and pastoralists tend to have

201 lower complexity (*Asfc*) than foragers. These bioarchaeologically-derived groups are used to contextualize the

202 results because they include a range of foragers as well as farming and pastoral groups to provide a broad

203 comparative sample. Furthermore, the grass seed remnants and starch grains preserved in the dental calculus of

204 Kůlna 1 and other Neandertals may generate texture values that are atypical when compared to Holocene foragers

205 but still within the texture spectrum of non-foraging Holocene peoples (e.g., Schmidt et al. 2019). The nine human

206 groups span four continents and derive from Epipaleolithic, Neolithic and Early Bronze Age contexts. Since

207 different masticatory behaviors may result in similar microwear textures, we consider the physical and mechanical

208 characteristics of the foods consumed rather than any specific dietary resource utilized by this diverse comparative

209 sample.

210 *2.1.3.1. Sedentary foragers, hunter-gatherers and foragers with a few domesticates*

211   Six of the nine groups represent foragers including Epipaleolithic Natufians from Israel (n = 15) dated to 14

212 ka BP to 10 ka BP (Table 2). These sedentary hunter-gatherers had an abrasive diet of poorly processed, fibrous and

213 tough foods (Bar-Yosef 1998; Frazer 2011; Chiu et al. 2012). Natufians are known to have consumed acorns,

214 pistachios, almonds, wild emmer and other edible cereals, seeds and gazelle (Fagen 1995; Bar-Yosef 1998; Karriger

215 et al. 2016; Schmidt et al. 2019).

216   Early Holocene foragers from Lagoa Santa, Brazil (n = 23) were also included. This total comprises 14

217 subadults who were also analyzed separately since Kůlna 1 is an early adolescent. We included a subadult sample of

218 permanent molars because older children may exhibit microwear that can be attributed to having smaller ranges of

219 mandibular motion, and perhaps less muscle mass (Mahoney et al. 2016; Kelly et al. 2020). Although the difference

220 between permanent molar microwear texture of children older than 6 years and adults is minor, we cannot exclude it

221 from potentially impacting the results from Kůlna 1. The separate subadult sample from Lagoa Santa provides a

222 context to interpret any subtle differences between Kůlna 1 and the Neandertal adults examined. The subadult

223 sample from Lagoa Santa ranged from 7-19 years and comprised only permanent first molars. Lagoa Santa is a

224 collection of sites in Minas Gerais spanning 11 ka BP to 7 ka BP (Da-Gloria & Schmidt 2020). These paleoforagers

225 subsisted on small to medium-sized animals, fruits, nuts, grass seeds and tubers (Da-Gloria & Schmidt 2020).

226   From North America, we included Indiana Middle to Late Woodland hunter/gatherers who cultivated some

227 plants (n = 30) dated to 2 ka BP (Chui et al. 2012). These peoples collected hard nuts and seeds, fished, harvested

228 oil-rich *Chenopodium* seeds, as well as knotweed and sumpweed, and hunted for deer, rabbits and other small

229 animals (Yarnell 1993; Frazer 2010). We also included the somewhat earlier Indiana Archaic (Middle/Late) foragers

230 (n = 34) dated to 2.5 ka BP (Frazer 2010; Da-Gloria & Schmidt 2020), as well as Kentucky Archaic period foragers

231 (n = 13) dated to 3 ka BP (Karriger et al. 2016) (Table 2). These hunter-gatherers are characterized as abrasive food

232 consumers with a reliance on poorly processed, fibrous and tough foods, hard foods such as hickory nuts, as well as

233 deer, rabbit, fish, mussels, terrestrial plant resources and fewer domesticates than the Middle/Late Indiana Woodland

234 (Jefferies 2009; Schmidt et al. 2019, 2020).

235 *2.1.3.2. Farmers*

236   The comparative sample included farmers from the early Holocene, including Neolithic farmers of Israel (n

237 = 16) dated to 8 ka BP who had a diet comprising wheat, barely, sheep and goats with the addition of some wild

9

238 foods, such as cereal grains, small edible seeds, rye and fruit with pits (Fagen 1995; Dickinson 2006; Frazer 2010;

239 Chiu et al. 2012; de Gregory 2012). Early Bronze Age England (n = 21) from the Beaker tradition, dated to 4.5 ka

240 BP to 3.5 ka BP, was also included. These farmers consumed wheat, barley, rye and domestic animals with scarce

241 evidence of wild foods contributing to the diet (Harding 2000; Fitzpatrick 2011; Karriger et al. 2016; Schmidt et al.

242 2016). The diet was relatively hard, perhaps from grit introduced using rudimentary food processing technology,

243 perhaps limited to pulverization using grindstones and cooking (Table 2).

244 *2.1.3.3 Pastoralists*

245   Herders of the Asian steppe provide a contextual boundary by exemplifying a diet dominated by meat and

246 low in hard foods (Table 2). We included Neolithic Mongol Xiongnu herders of west, north and central Mongolia (n

247 = 29) dated to 3.2 ka–2.3 ka BP (Schmidt et al. 2016). The diet of these pastoralists was focused on meat as well as

248 milk and yoghurt from a variety of animal domesticates, including sheep, goats, cattle, camels, yaks and horses. The

249 main plant contribution to the diet was millet, which was traded for animal products (Knörzer 2000; Barfield 2001;

250 Di Cosmo 2002; Alt et al. 2003; Hanks 2010; Eng & Aldenderfer 2011: Makarewicz 2011; Machicek & Zubova

251 2012; Aldenderfer 2013; Murphy et al. 2013; Honeychurch 2014).

252   [Table 2]

253 *2.2. Methods*

254 *2.2.1. Molding*

255   The right M^1 of Kůlna 1 was molded at the Moravské zemské muzeum with President Plus Jet light body

256 polyvinylsiloxane (Coltène Whaledent) by Erik Trinkaus, and a positive cast was made with Epo-tek 301 epoxy by

257 JCW. Dental molds were created by FLW for eight Neandertals at Musée de l'Homme and the Centre Européen de

258 Recherches Préhistoire de Tautavel using polyvinylsiloxane (Coltène Whaledent). Additionally, a dental mold of the

259 right M^1 of Spy I on loan from the Royal Belgian Institute of Natural Sciences (Brussels) was provided by Patrick

260 Semal. High fidelity epoxy-resin dental casts of Hortus III, Hortus IV, Hortus V, Hortus VI, Hortus VIII, Hortus XI,

261 La Quina 5, Malaraud and Spy I were created at the Bioarchaeology Lab at Georgia State University.

262 *2.2.2. Scanning*

263   All of the dental casts were analyzed at the University of Indianapolis using a white-light confocal profiler

264 (Sensofar Plµ) at 100x magnification on facet 9, a Phase II facet experimentally known to experience crushing and

265 grinding of food particles during the power stroke when full occlusion of the maxillary and mandibular molars

266   occurs (Kay & Hiiemae 1974; Kay 1981; Krueger et al. 2008). For each specimen, four scans were automatically

267   stitched together to create a total study area of 242 x 182 μm. Surface data were imported into SolarMap 5.1.1 for

268   leveling and for removing extraneous debris on the surface. Both 2D and 3D representations were carefully

269   inspected to ascertain that the area was free of postmortem artefacts, films or casting defects (Fig. 3). The 3D

270   surface reconstructions were also examined to evaluate whether surface microwear was lacking taphonomic damage.

271   The surfaces were dominated by scratch and pit features consistent with those generated during mastication (Fig. 3).

272   The data clouds were subsequently analyzed using scale-sensitive fractal analysis within Sfrax® and Toothfrax®

273   software (Scott et al. 2006, 2012; Ungar et al. 2012; Schmidt et al. 2016, 2019) yielding complexity (*Asfc*) and

274   anisotropy (*epLsar*) that describe the micro-topography of the enamel surface. Whereas complexity (*Asfc*) records

275   the extent of hard object contact with the enamel surface during mastication typical of plant-based diets, anisotropy

276   (*epLsar*) describes the degree of microstriation patterning that occurs when tough foods or processed foods are

277   habitually consumed (Fig. 2).

278   [Fig. 3]

279   *2.2.3. Comparison of textural data*

280   Complexity (*Asfc*) and anisotropy (*epLsar*) values for Kůlna 1 are compared in a bivariate framework to

281   those of Hortus cave, with a 100% convex hull surrounding the sample, as well as three isolated Neandertal sites. In

282   addition, values for Kůlna 1 are compared to the means and standard deviations for complexity (*Asfc*) and

283   anisotropy (*epLsar*) in nine human groups, Hortus, Krapina and Vindija assemblages, as well as three isolated

284   Neandertals, the objective being to characterize the Kůlna 1 microwear texture in the context of Neandertal and

285   recent bioarchaeological populations in order to discern its dietary signature. A high complexity (*Asfc*) indicates an

286   uneven surface, which is found in humans consuming hard foods, like seeds and nuts. Anisotropy (*epLsar*) tends to

287   be low for foragers, when compared to farmers, indicating they have jaw movements in many directions, perhaps

288   because of their diverse diets requiring multiple chewing motions. Foraging groups with high anisotropy values

289   likely consumed unprocessed or poorly processed tough or fibrous foods (El Zaatari 2010; Schmidt et al. 2019).

290   **3. Results**

291   *3.1. Kůlna 1 compared to individual Neandertals*

292   The complexity (*Asfc*) of Kůlna 1 is relatively high and most closely resembles the value of Spy I

293   (Williams et al. 2019). Of the Hortus sample, the complexity value for Kůlna 1 is the most similar to that of Hortus

294   XI from Sub-Phase Va, who experienced a paleoecology characterized by moderate cold and some aridity (Fig. 4;

295   Tables 1 and 3). In contrast to Kůlna 1 and Hortus XI, La Quina 5 exhibits comparatively low complexity (*Asfc*)

296   (Fig. 4).

297   With respect to anisotropy (*epLsar*), Kůlna 1 is similar to older adult Hortus XI and La Quina 5 (Fig. 4).

298   Kůlna 1 also resembles subadult Malarnaud and the Hortus III child, albeit to a lesser extent. However, Kůlna 1

299   differs from Spy I and young adults from Hortus cave, including Hortus IV, Hortus V, Hortus VI and Hortus VIII,

300   all of whom present elevated values regardless of distinctions in chronology and paleoecology (Table 3). Like the

301   young and old Neandertals examined in this study, Kůlna 1 exhibits lower anisotropy (*epLsar*) than adults in their

302   prime.

303   [Fig. 4; Table 3]

304   *3.2. Kůlna 1 compared to Neandertal assemblages*

305   For complexity (*Asfc*), Kůlna 1 exceeds the range of variation observed at Hortus, Krapina and Vindija

306   (Fig. 5). With respect to anisotropy (*epLsar*), Kůlna 1 is similar to the mean for Vindija. However, Kůlna 1 with

307   relatively low anisotropy (*epLsar*) falls completely outside of the range of variation observed for the Krapina and

308   Hortus assemblages (Table 3; Fig. 6).

309   *3.3. Kůlna 1 in comparison to Epipaleolithic and Holocene human assemblages*

310   The only human group to exceed Kůlna 1 in complexity is early Holocene Lagoa Santa paleoforagers (Fig.

311   5). The complexity (*Asfc*) of Kůlna 1 is most similar to the mean of Middle/Late Indiana Woodland foragers, and

312   secondarily to Natufians and early Neolithic farmers from Israel. Kůlna 1 is the most distinct from Neolithic

313   Xiongnu herders from Mongolia (Fig. 5).

314   As might be expected, Kůlna is most similar to other foragers and least similar to food producers. For

315   anisotropy (*epLsar*), Kůlna 1 resembles foragers from the Americas. This is particularly true of Middle/Late Indiana

316   Woodland (Fig. 6). The anisotropy (*epLsar*) for Kůlna 1 is decidedly unlike that of the farmers and pastoralists as

317   well as Epipaleolithic Natufian foragers, all of whom have higher anisotropies compared to this early adolescent

318   from the Middle Paleolithic of Moravia (Fig. 6).

319   [Fig. 5 and Fig. 6]

320   **4. Discussion**

321 The dental microwear textures for Kůlna 1 can be compared to paleoecological reconstructions of Kůlna

322 cave. There are multiple Middle Paleolithic strata in Kůlna cave that record the end of the penultimate glacial MIS 6,

323 an interglacial period and an early Weichselian Glacial (Valoch 1988, 2002). Kůlna 1 is from layer 7a, which has

324 been correlated using loess samples to a cold climate. Fauna and vegetation from layer 7a indicate an interstadial but

325 still cold habitat characterized the period (Valoch 1989, 2002; Rink et al. 1996). Valoch (1989, 2002) characterizes

326 layer 7a using tree remains preserved as charcoal (Opravil 1988) and other analyses as resembling the conditions of

327 southern Scandinavia where moderate cold and wet habitats prevail. Evidence of mammoth and reindeer in layer 7a

328 alongside temperate tree species indicate a relatively recent shift from a colder habitat since the presence of large

329 fauna does not reflect short-term climatic events. The vegetal matter derived from charcoal remains includes

330 *Picea/Larix*, *Pinus* (the seeds of which can be eaten), *Acer*, *Corylus cf. avellana* and *Fraxinus*, suggesting the

331 variegated ecology surrounding Kůlna cave probably yielded a great quantity and diversity of plants. The plant

332 resources available to Kůlna 1, including grass seeds, underground storage organs and other plant foods (Hardy

333 2010; Henry et al. 2014), were certainly greater than those present in the earlier layers such as layer 6a. The cave is

334 situated on the border of the Moravian karst and open areas, and during layer 7a, stands of woodland were

335 interspersed with steppe landscape and open tundra. The climate was colder and drier than the present, and most of

336 the animals hunted were local to the Moravian karst (Nerudová et al. 2014).

337 Similar environments, including tundra interspersed with forests and woodlands, characterized the

338 paleoecology of Spy I (Semal et al. 2011, 2013). Although Spy cave of the Belgian Meuse river basin is over 1,000

339 km to the west of Kůlna cave, there is only a difference of about 200 km between Spy to the north and Kůlna to the

340 south. In addition, northwest Europe from where Spy cave is situated is protected from climatic extremes by warm

341 air circulating via the Gulf Stream and continental regions were probably, at times, comparatively colder. The fact

342 that Spy I resembles Kůlna 1 in complexity (*Asfc*) may reflect the use of plant foods with similar mechanical

343 properties, including seeds, but it could also reflect terrestrial grit adhering to underground storage organs, both of

344 which were Neandertal staples, even in relatively cold habitats (Hardy 2010; Henry et al. 2014; Power et al. 2018).

345 The elevated complexity (*Asfc*) of Kůlna 1 compared to most of the other Neandertals examined indicates

346 the consumption of hard particles such as nuts, seeds and seed casings as might be found in such plant foods as

347 *Pinus* seeds and nuts of *Corylus* that were noted in layer 7a (Valoch 1989). Mechanically resistant particles in

348 Middle Paleolithic diets could derive from the consumption of the hard parts of seasonally available plants, such as

349 grass seeds (Henry et al. 2011), or possibly from underground storage organs (Hardy 2010), terrestrial medicinal

350 herbs (Hardy et al. 2012) and/or starches (Hardy and Moncel 2011), all of which may have contributed inadvertent

351 grit during mastication. A combination of foods including hard and brittle items, and other resources that the

352 individual could acquire likely led to the relatively high degree of complexity (*Asfc*) characterizing Kůlna 1.

353   With respect to anisotropy (*epLsar*), Kůlna 1 falls close to Hortus XI, La Quina 5 and the mean value for

354 Vindija; these are all distinct from young adults of Hortus (Horus IV, Hortus V, Hortus VI and Hortus VIII), Spy I

355 and the mean for Krapina. The foragers of the Americas exhibit by far the most heterogeneous jaw movements,

356 represented by a distinct lack of patterning of striations compared to food producers and sedentary foragers. The fact

357 that Kůlna 1 most closely resembles these Paleoamerican foragers suggests a varied diet where complex movements

358 of the jaws were needed to process food resources.

359   The Kůlna 1 early adolescent is old enough to have assumed an adult-like jaw movement (Kelly et al.

360 2020). However, Kůlna 1 exhibits lower anisotropy (*epLsar*) compared to the Neandertal adults in this study,

361 including Spy I and Hortus young adults, all of whom exhibit much higher anisotropy values, suggesting the

362 individual likely ate more foods that required diverse jaw movements. Lower anisotropy (*epLsar*) in maturing

363 individuals compared to their adult counterparts is something that is seen among the Lagoa Santa human subadults

364 (Table 2; Fig. 6) and the El Sidròn Juvenile 1 Neandertal from MIS 3 of northern Spain (Estalrrich et al. 2017).

365 *4.2. Conclusions*

366   Observations of the enamel surface texture of Kůlna 1 offer evidence of hard plant food consumption in the

367 diets of the Moravian Neandertals of Central Europe. Several reasons may account for this high complexity (*Asfc*)—

368 higher than all other Neandertals examined except Spy I—such as greater mastication/consumption of plant foods,

369 or a lack of animal foods. Perhaps the consumption of plant foods relates to the part of the year when animals were

370 depleted. In such a scenario, plant food served as an additional source of energy, as it did at Kebara cave of Israel

371 from MIS 4 (Lev et al. 2005). It is also possible that the other Neandertals in our sample lived at a time when animal

372 resources were plentiful, whereas Kůlna 1 may have experienced a depleted supply of fauna resulting in a greater

373 reliance on plant foods. Although it is impossible to evaluate the validity of these competing interpretations, it

374 deserves to be mentioned that a greater reliance on plant foods may not be a preference among foragers (Hill and

375 Hurtado 1996; Kaplan et al. 2000). The possibility exists that the hard plant parts consumed by Kůlna 1 may have

376 been fallback foods when preferred items were scarce.

377   The dental calculus indicates mechanically challenging plant foods such as grass seed were consumed, and

378   the molar microwear texture of this individual is consistent with those results (Henry et al. 2014). Compared to layer

379   6a, layer 7a where Kůlna 1 was discovered, was a warmer interval. The less extreme coldness of layer 7a and the

380   proximity of Kůlna cave to different microhabitats (Valoch 1989, 2002), suggest that plants may have contributed

381   significantly to the diet.

382   Kůlna 1 exhibits high complexity (*Asfc*) and low anisotropy (*epLsar*), both of which occur in foragers of

383   the Americas. Most Holocene foragers have relatively low anisotropy compared to farmers and pastoralists. The

384   relatively low degree of anisotropy (*epLsar*) in many of these forager individuals, and perhaps Kůlna 1, resulted

385   from highly heterogeneous jaw movements required to masticate coarse, poorly processed foods.

398

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Figure captions

664

665   **Fig. 1** Map of Europe showing the location of Kůlna cave (yellow circle) and other Neandertal sites with an insert

666   showing the position of Kůlna cave of Moravia (shaded gray) in the Czech Republic

667   **Fig. 2** The top diagrams represent high anisotropy (A) and high complexity (B); note that (A) has many features in

668   parallel and (B) has several large features; the remaining images are representative photomicrographs of high

669   anisotropy (C), low anisotropy (D), high complexity (E), and low complexity (F)

670   **Fig. 3** Two-dimensional photosimulations (left) and three-dimensional surface reconstructions (right) of Kůlna 1

671   **Fig. 4** Complexity (*Asfc*) versus anisotropy *(epLsar)* in Kůlna 1 compared to the Hortus assemblage (n = 6) coupled

672   with a convex hull, which includes 100% of the variation of the sample as well as three isolated Neandertal sites

673   **Fig. 5** Comparison of complexity (*Asfc*) for Kůlna 1 compared to Hortus, Krapina and Vindija assemblages, isolated

674   Neandertal sites and nine human groups; yellow circles = Neandertals; red squares = hunter-gatherers; green

675   triangles = farmers; blue diamond = pastoralists. Horizontal bars = one standard deviation

676   **Fig. 6** Comparison of anisotropy (*epLsar*) for Kůlna 1 compared to Hortus, Krapina and Vindija assemblages,

677   isolated Neandertal sites and nine human groups; yellow circles = Neandertals; red squares = hunter-gatherers; green

678   triangles = farmers; blue diamond = pastoralists. Horizontal bars = one standard deviation

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List of tables

681   **Table 1** Locality, dating and paleoecology of Kůlna 1 compared to the other Neandertal sites examined

682   **Table 2** Microwear texture means and standard deviations (SD) for nine comparative human samples (n = 181)

683   **Table 3** Neandertal microwear results

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687   Table 1

	MIS	Paleoecology / climate type
Kůlna 1	3	Temperate interstitial period; continental[1]
Hortus III, V, VIII (Phase Vb)	3	Intense cold and extreme aridity; Mediterranean[2]
Hortus XI (Phase Va)	3	Less cold and arid compared to Phase Vb; Mediterranean[2]
Hortus IV (Phase IVb)	3	Less cold and arid compared to Phases Va and Vb; Mediterranean[2]
Hortus VI	3	Found in excavated infill of Horus cave; Mediterranean[2]
La Quina 5	3	Cold and arid; open-steppe; continental[3]
Malarnaud	5	Interglacial with warmer temperatures; continental[4]
Krapina (isolated molars, n = 19)	5	Interglacial with warmer temperatures; continental[5]
Spy I	3	Cold and wet; open-steppe; continental[6]
Vindija (isolated molars, n = 4)	3	Temperate with mixed forest and open grassland; continental[7]

688

689   [1]Neruda & Nerudová 2014; Nerudová et al. 2014; Rink et al. 1996; Svoboda 2005

690   [2]de Lumley, 1972; de Lumley & Licht, 1972; de Lumley, 1973; Lebègue et al., 2010; Pillard, 1972

691   [3]Discamps & Royer 2017; Petite-Marie et al. 1971

692   [4]Petite-Marie et al. 1971; [5]Rink et al. 1995; [6]Semal et al. 2009, 2011, 2013; Toussaint et al. 2011;

693   [7]Miracle et al., 2010; Wild et al., 2001

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696   Table 2

		Complexity (*Asfc*)		Anisotropy (*epLsar*)	
	n	Mean	SD	Mean	SD
Epipaleolithic foragers, Natufians, Israel[1]	15	1.41	0.645	0.0038	0.0017
Early Holocene foragers, Lagoa Santa, Brazil[2]	23	2.45	1.020	0.0029	0.0015
Early Holocene subadult foragers, Lagoa Santa, Brazil[2]	14	2.64	1.150	0.0028	0.0014
Indiana Archaic (Middle/Late) foragers/some farming[3]	34	1.26	0.471	0.0026	0.0011
Kentucky Archaic (Middle/Late) foragers/some farming[1]	13	1.04	0.158	0.0029	0.0013
Indiana Woodland (Middle/Late) foragers/some farming[3]	30	1.62	0.606	0.0023	0.0094
Early Neolithic farmers, Israel[1]	16	1.34	0.811	0.0034	0.0017
Early Bronze Age farmers, England[1]	21	1.34	0.443	0.0041	0.0016
Neolithic Xiongnu pastoralists, Mongolia[1]	29	0.92	0.311	0.0034	0.0017

697   [1]Karriger et al. (2016); [2]Da-Gloria & Schmidt (2020), the total of 23 includes 14 subadults; [3]Schmidt et al. (2020)

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700 Table 3

	Microwear results	Complexity (*Asfc*)	Anisotropy (*epLsar*)
Kůlna 1	Very high complexity; low anisotropy	1.83	0.0021
Hortus III, V, VIII, Phase Vb	Low complexity; very high anisotropy in Hortus V and VIII and low anisotropy in Hortus III	Mean = 1.13 SD = 0.12	Mean = 0.0031 SD = 0.0020
Hortus XI, Phase Va	High complexity; low anisotropy	1.54	0.0021
Hortus IV, Phase IVb	High complexity; very high anisotropy	1.36	0.0051
Hortus VI	High complexity; very high anisotropy	1.50	0.0041
La Quina 5	Very low complexity; low anisotropy	0.75	0.0024
Malarnaud	Low complexity; very low anisotropy	1.01	0.0011
Krapina (n = 19)	Low complexity; very high anisotropy	Mean = 1.12 SD = 0.58	Mean = 0.0043 SD = 0.0020
Spy I	Very high complexity; high anisotropy	2.22	0.0032
Vindija (n = 4)	Very low complexity; low anisotropy	Mean = 0.84 SD = 0.21	Mean = 0.0027 SD = 0.0031

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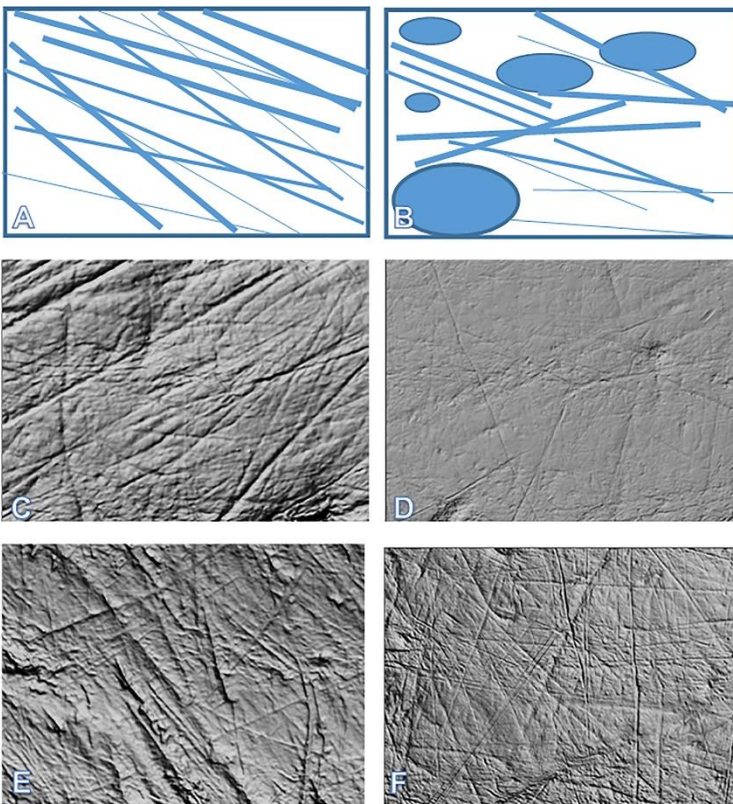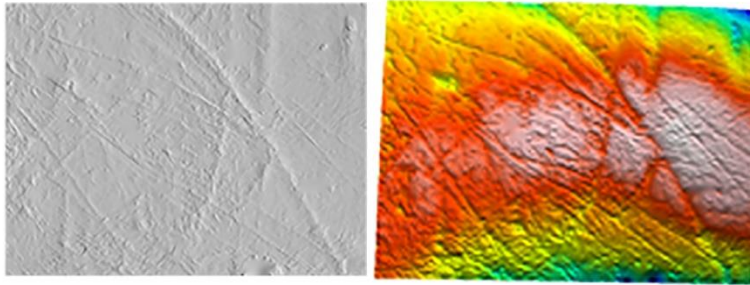704
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708 **Figure 1**
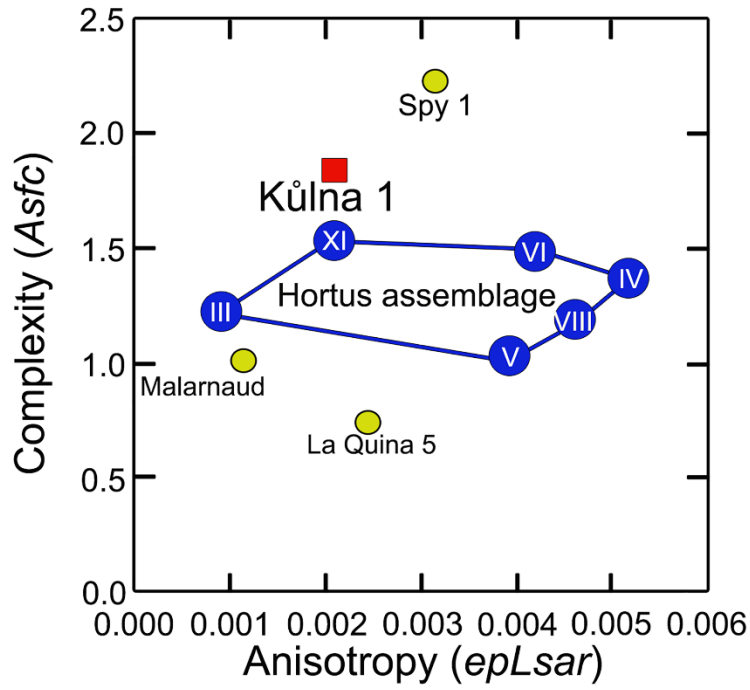

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712 **Figure 2**

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Figure 3
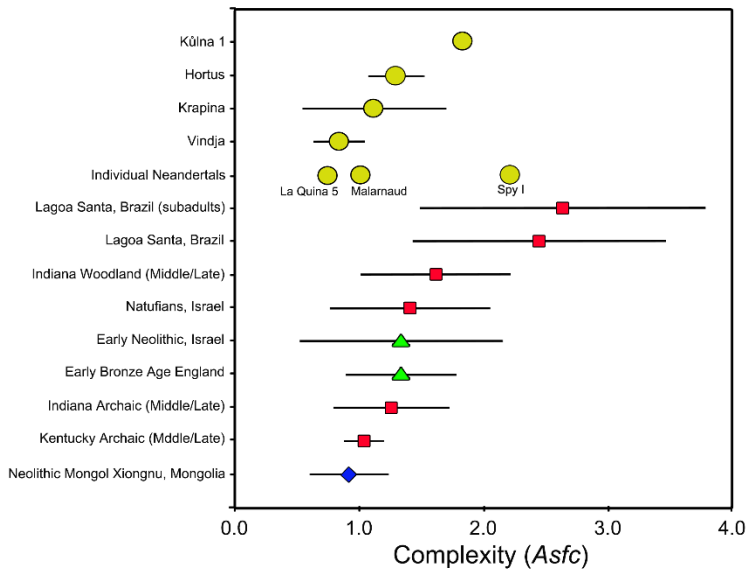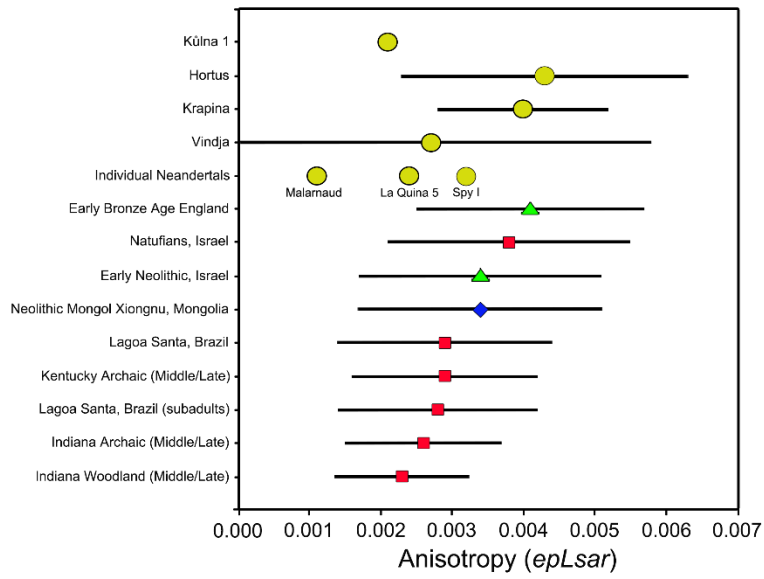
Figure 4

Figure 5

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722   **Figure 6**
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