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Article

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2 ***kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat**

3 **diversity**

4

5 *You'll have to take pot luck!*

6 (proverb)

7

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19

20 **Abstract**

21 To trace the dietary evolution of the two abundant Middle to Late Pleistocene rhinoceros

22 species *Stephanorhinus kirchbergensis* and *S. hemitoechus* in Europe over several climatic

23 cycles, we examined comprehensive material of stratigraphically well-defined

24 palaeopopulations from different regions and interglacials. Using morphometrics and

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mesowear analysis, these reconstructions of *Stephanorhinus* diets indicate that habitat

diversity and interspecific competition with closely related rhinoceros species induced

variation in feeding behaviour. Although anatomical features of both species suggest

significantly higher dietary specializations compared to the Early to early Middle Pleistocene

S. hundsheimensis, their mesowear signals are characteristic of a mixed feeder diet, similar to

that of extant mammal species in relatively open habitats. Both species retained a degree of

dietary flexibility, enabling them to survive in a range of environments. Although each of

these rhinoceroses preferred different habitats, species identity alone is not sufficient to

establish the real dietary traits of a *Stephanorhinus* palaeopopulation. As a consequence, their

occurrence in a faunal assemblage alone cannot be taken to indicate a specific habitat.

S. kirchbergensis and *S. hemitoechus* were embedded in a dynamic process of temporo-spatial

replacements and interspecific differentiation of rhinoceroses in the western Palaearctic.

However, dietary specialization in these Middle to Late Pleistocene European rhinoceroses

was not the result of a directed time-transgressive evolution. Rather, within the range of each

species' ecological tolerance, it was controlled by environmental parameters, with habitat

variability as the main factor.

1. Introduction

The reconstruction of fossil faunal assemblages can significantly contribute to our

understanding of the natural variability and evolution of past ecosystems and climates. In

particular, assessments of dietary requirements for each species and inferences to their

corresponding subsistence strategies have proved to be valuable methods for reconstructing

palaeoenvironmental parameters. In the case of herbivores, reconstructions of the vegetational

character of associated palaeoenvironments based on dietary signals may provide detailed

insights into the behaviour of different species, when corresponding palaeobotanical records

are not available.

51 Pleistocene herbivore communities clearly reflect fluctuations in global climate and resulting

52 environmental changes (e.g. Lister, 2004; Kahlke et al., 2011). Rhinocerotids in particular are

53 among the most significant ecological trace species of the Palaearctic (Zeuner, 1934; Loose,

54 1975; Guérin, 1980; Fortelius, 1982; Fortelius et al., 1993; Lacombat, 2006; Hernesniemi et

55 al., 2011; Kahlke, 2014). Recent investigations have revealed that Pleistocene rhinoceroses

56 show an individualistic response to changes in the periodicity of environmental variation

57 (Raymo and Nisancioglu, 2003, Figure 1; Lisiecki and Raymo, 2005, Figure 4), resulting in

58 different evolutionary patterns between species. Thus, the subsistence strategy of

59 *Stephanorhinus hundsheimensis*, as the only rhinocerotid species of western Palaearctic

60 mammal faunas between 1.4/1.2 and 0.6/0.5 Ma BP, was that of a generalist. Its lifestyle

61 evolved under the influence of the relatively stable 41 ka climatic periodicity and proved to be

62 very successful also during the more unsteady climate course of the transitional interval

63 linking with the following 100 ka regime (Kahlke et al., 2011, p. 1388). The dietary

64 variability of *S. hundsheimensis* ranged from grazing regimes to predominantly browsing

65 ones, characterising the species as the ecologically most tolerant rhinoceros of the Palaearctic

66 Plio-Pleistocene (Kahlke and Kaiser, 2011).

67 A different path of evolution can be traced in the genus *Coelodonta*. From the Late Pliocene

68 onwards (Deng et al., 2011), its range was for more than three million years restricted to open

69 landscapes in Central Asia. Strictly progressive adaptation to efficient grazing enabled woolly

70 rhinoceroses to inhabit the pan-Eurasian tundra-steppe for the first time around 460 ka BP

71 (Kahlke and Lacombat, 2008). This new type of biome originated during marine isotope stage

72 (MIS) 12, a long-lasting and pronounced cold interval within the 100 ka periodicity span.

73 During most of the subsequent warm and humid stages *Coelodonta* populations retreated from

74 western Palaearctic areas, only to re-occupy extended Eurasian territories as increasingly

75 more specialized grazers during the succeeding cold and continental periods (Kahlke, 2014).

76   Over substantial periods of the Pleistocene *Stephanorhinus hundsheimensis* and *Coelodonta*

77   species occupied huge territories of the Palaearctic. Members of both groups predominantly

78   occurred as the only rhinoceros species of corresponding faunas, and their subsistence

79   strategies were principally different. However, at present it is not well understood whether a

80   co-occurrence of t w o species of Pleistocene rhinoceros might have affected their dietary

81   specialization, and whether rhinoceros dietary flexibility interacts with environmental

82   conditions. Sympatries of closely related species are not uncommon in mammalian

83   communities (e.g. Jacoby et al., 1999; Hayward and Kerley, 2008; Li et al., 2008; Dammhahn

84   et al., 2013). Such co-occurrences of closely related species are durable only if intraspecific

85   competition is stronger than interspecific competition (Elton, 1927). Sympatric species tend to

86   reduce competition through differences in their use of resources, whether by focusing on

87   different resources, by using these resources at different times or at different intensities, or by

88   exploiting different habitats within the same landscape (e.g. Chase and Leibold, 2003).

89   Several extant rhinoceros species occur sympatrically. Specialised grazer *Ceratotherium*

90   *simum* and the co-occurring browsing species *Diceros bicornis* have little overlap in diet

91   (Groves, 1972; Owen-Smith, 1988; Hillman-Smith and Groves, 1994; Codron et al., 2007;

92   Steuer et al., 2010). The browsing species *Dicerorhinus sumatrensis* and *Rhinoceros*

93   *sondaicus*, whose ranges overlapped in the past, avoided competitive interactions by using

94   upland resp. lowland habitats (Groves and Kurt, 1972; Groves and Leslie, 2011).

95   Here we investigate the subsistence strategy of two closely related rhinoceros species,

96   *Stephanorhinus kirchbergensis* (Jäger, 1839), the so-called forest rhinoceros, and *S.*

97   *hemitoechus* (Falconer, 1868), the slightly smaller-bodied steppe rhinoceros. Both species

98   occurred in most regions of the western Palaearctic during temperate periods of the Middle

99   and Late Pleistocene, sometimes allopatrically, at other times sympatrically. To trace their

100   dietary evolution in Europe over several climatic cycles we examined *Stephanorhinus*

101   material from palaeopopulations of different regions and interglacials.

102

2. Appearance and spread of *Stephanorhinus kirchbergensis* and *S. hemitoechus* in Europe

During the early Middle Pleistocene two new rhinoceros species, *S. kirchbergensis* and *S. hemitoechus*, with different and more specialised feeding strategies, appeared in Europe to compete with the previously unchallenged generalist *Stephanorhinus hundsheimensis*. After a period of sympatry between 0.7 and 0.6 Ma BP, documented in the faunal assemblages of several early Middle Pleistocene sites, such as Kolkotova Balka and Sukleya near Tiraspol (Moldova), Mauer and Mosbach 2 (Germany), as well as Soleilhac (France), *S. kirchbergensis* started to replace *S. hundsheimensis* in temperate faunas (Beljaeva and David, 1975; Guérin, 1980; Fortelius et al., 1993; Schreiber, 2005). *S. kirchbergensis*, an immigrant of Asian origin (Guérin, 1980; Van der Made, 2000), was a very large animal with long legs, a high head posture, and moderately hypsodont molars (Fortelius et al., 1993), indicating a diet with significant portions of browsing.

Between 0.6 and 0.5 Ma, a second rhinoceros species, *S. hemitoechus*, appeared in Europe, as recorded in the Mosbach 2 gravels (Fortelius et al., 1993; Hemmer et al., 2003). Its anatomy, especially its relatively short limbs, the low-slung cranium, more hypsodont molars and reduced premolar segment of the tooth rows compared to those of *S. kirchbergensis*, indicate affinities to less forested landscapes or open grasslands (Guérin, 1980; Janis, 1990; Mazza, 1993; Fortelius et al., 1993). This is corroborated by the fact that it was especially widespread in Europe under dryer and/or moderate to cooler conditions. The origins of both rhinoceroses, *S. kirchbergensis* and *S. hemitoechus*, seem to ultimately derive from the development of the 100 ka periodicity in the global climatic record, which led to a longer lasting environmental continuity in the resulting biomes compared to the preceding 41 ka span of time (Kahlke et al., 2011).

127 Alternating stages of prolonged colder and temperate climatic conditions resulted in mutual

128 alternations of *Coelodonta tologoijensis* / *C. antiquitatis* and *S. hemitoechus* populations from

129 the Middle Pleistocene onwards. When *C. tologoijensis* spread into Eastern and Central

130 Europe during MIS 12, *S. hemitoechus* retreated to Western Europe and survived there, as it is

131 recorded e.g. from Tautavel (Ensemble III) in France (Moigne et al., 2006). Both species co-

132 occurred at the sites of La Fage (layer 5) in France during MIS 10 or 8 (Guérin, 1973) and

133 Weimar-Ehringsdorf (Upper Travertines) in Germany during MIS 7 and/or 5 (Kahlke, 1975;

134 Kahlke et al., 2002). Stratigraphic sequences at the latter site indicate that *S. hemitoechus* was

135 replaced successively by *Coelodonta*. A similar alternation has been observed in areas of

136 Great Britain (Schreve, 2001a) and in the northern part of the Iberian Peninsula (Álvarez-Lao

137 and García, 2011). During interstadials and especially during periods of interglacial warming

138 the opposite happened: *S. hemitoechus* prevailed and *Coelodonta* disappeared from large

139 areas of Europe. However, under optimal interglacial conditions with extensive afforestation,

140 the steppe rhino was successively replaced by the ecologically more demanding *S.*

141 *kirchbergensis*, as far as the latter had access to corresponding areas.

142 During the Last Glacial *Stephanorhinus* withdrew from most areas of Europe to - probably

143 several - southern refugia. Both *S. kirchbergensis* and *S. hemitoechus* became extinct in the

144 Western Palaearctic well before the Last Glacial Maximum (LGM). Youngest finds of *S.*

145 *kirchbergensis* from the Grotte des Enfants and the Grotte du Prince (Grimaldi Caves) in Italy

146 are assigned to MIS 4 to 3 (Lacombat, 2005, 2006). The latest occurrence of *S. hemitoechus*

147 reported so far, from the Bulgarian Bacho Kiro Cave, approximately 42.542 ± 1.068 cal. ka in

148 age (Stuart and Lister, 2007), may correlate with Greenland Interstadial (GI) 10 of MIS 3

149 (Van Meerbeeck et al., 2011). Supposedly younger *Stephanorhinus* finds of Azilian or

150 Neolithic age from Spain are dubious (Cerdeño, 1990; Sánchez et al., 2005; D.J. Álvarez-Lao,

151 pers. comm.).

152

3. Material and methods

3.1. Material

To achieve a reliable dataset documenting the history of dietary specialization of *S. kirchbergensis* and *S. hemitoechus*, rhinoceros palaeopopulations from two European regions of different biogeographic location were selected. The inclusion of fossil rhino remains from different geographic areas provides control over the effect that regional differences, such as a reported geographic gradient in body size (Lacombat, 2009), may have on the results. We chose Central Germany and the British Isles representing Central and Northwest Europe respectively, because in both of these regions extensive fossil material of the two species from a range of more or less well-dated faunal assemblages is available (Figure 1; Table 1). Moreover, the dietary signals obtained here should not have been overprinted by the influence of competing species, because all assemblages considered here have a similar fauna of co-occurring herbivores feeding on the same levels of vegetation as the two rhinoceroses, often even at similar abundances (see references below). While episodes of co-occurrence of the two *Stephanorhinus* species have been documented for earlier interglacials (MIS 11, 7), during some parts of the Last Interglacial (MIS 5e) the species had a largely disjunct distribution in the studied area.

In Central Germany, the rhinoceros remains from Bilzingsleben, Weimar-Ehringsdorf and Weimar-Taubach (all in Thüringen; Table 1), were included in our study. The rhinoceros remains of these sites originate from travertine layers. Bilzingsleben II (hominin site) is related to one of the warm stages of the late Middle Pleistocene "Holstein-Komplex" (Mania, 1997, 2006; Heinrich, 2003), assigned by most authors to MIS 11 (Nitychoruk et al., 2006). Schreve and Bridgland (2002) correlate Bilzingsleben II with the younger of two temperate warm substages documented in the MIS 11 sequence of the Thames valley (UK). The fossil layer of Bilzingsleben II formed within a very short and hence biostratigraphically instantaneous time span, and produced a considerable number of individuals of both *S.*

179   *kirchbergensis* and *S. hemitoechus* (Figures 2a-b and 3a-b; Table 1; Van der Made, 2000), so

180   that sympatry has to be concluded.

181   The very complex Pleistocene sequence of Weimar-Ehringsdorf contains remains of at least

182   12 biochronologically distinguishable mammal faunas (Kahlke et al., 2002 and references

183   therein). The abundant *S. kirchbergensis* finds of Weimar-Ehringsdorf were recovered

184   exclusively from the lower and middle parts of the Lower Travertin (hominin layers, Mammal

185   Fauna 2), which reflect fully developed interglacial conditions (Kahlke, 1975: p. 385). The

186   stratigraphic distribution of Ehringsdorf's rhinoceros fossils (Figures 2c-d and 3c-d), as far as

187   accurate data on their discovery horizons are available (Kahlke, 1975: Figure 32), clearly

188   indicate the co-occurrence of *S. kirchbergensis* and *S. hemitoechus* during the accumulation of

189   the middle part of the Lower Travertine (Fauna 2). Such sympatry is not repeated during the

190   later part of the Ehringsdorf faunal sequence. With the deposition of the upper part of the

191   Lower Travertine (Mammal Fauna 3) the *kirchbergensis*-population has been completely

192   replaced by *hemitoechus*-rhinos. Low numbers of *S. hemitoechus* fossils were also recorded in

193   Ehringsdorf's Pariser horizon above the Lower Travertine (Mammal Fauna 5) and more

194   frequently in the Upper Travertines (Mammal Faunas 7-8), here either as the only rhinoceros

195   species or jointly with *Coelodonta antiquitatis* (Kahlke, 1975: p. 383). The stratigraphic

196   classification of the individual fossiliferous horizons of Weimar-Ehringsdorf is still debated.

197   The majority of biostratigraphic arguments (compiled in Kahlke et al., 2002; Katzschmann,

198   2007) assign the Lower Travertine with its Mammal Faunas 2 und 3 to MIS 7, without,

199   however, ultimate clarity. The correlation of the *S. hemitoechus* bearing Upper Travertines

200   either with MIS 7 or with 5e is also uncertain (Kahlke et al., 2002; Katzschmann, 2007).

201   The travertines of Weimar-Taubach inclusive of the Lower Travertine Sands, which produced

202   the extended series of *S. kirchbergensis* finds (Table 1, Figure 2e-f), are confidently assigned

203   to the Eemian, i.e. to the MIS 5e interglacial (Kahlke, 1977; Heinrich, 2003). Since the

204   majority of Weimar-Taubach's rhinoceros remains are the result of Middle Palaeolithic

205 killing and butchering activities (Bratlund, 1999 and references therein), they represent not

206 just the immediate vicinity of the site within the water-rich floodplain of the river Ilm, but the

207 more extended range of the human hunters. *S. kirchbergensis* therefore appears to have been

208 the only rhino species present fully developed interglacial conditions in the Taubach area. The

209 origin of a single *hemitoechus*-p4 from Weimar-Taubach is unclear; it probably derives from

210 younger layers (Kahlke, 1977).

211 A range of rhinoceros fossils from the British Isles dated to MIS 7 and MIS 5e were studied

212 (Table 1). Three rhinoceros species are recorded from the temperate deposits at Ilford (Uphall

213 Pit; West et al., 1964) in the Lower Thames Valley: *S. hemitoechus*, *S. kirchbergensis* and a

214 few specimens of *C. antiquitatis* (Schreve, 1997). The faunal material was collected from the

215 Taplow-Mucking Formation in specific brickearth pits during the 19th century, although their

216 exact provenance is largely unknown.

217 The sequence at Crayford (Scott, 2009), also in the Lower Thames Valley, shows great

218 similarities to the Ilford sequence and has a similar research history (Bridgland, 1994;

219 Gibbard, 1994). As at Ilford, the exact provenance of most specimens is unclear. The fauna

220 from the Crayford Gravel underlying the brickearth includes *S. hemitoechus* and *C.*

221 *antiquitatis*. The Lower Brickearth contained specimens of *S. kirchbergensis* and *C.*

222 *antiquitatis* (Schreve, 1997). Amino acid ratios are indicative of an MIS 7 age for the

223 temperate sediments at both sites (Penkman et al., 2008).

224 A temperate fauna, including a virtually complete skeleton of *S. hemitoechus*, was recovered

225 from Bed 2 of the Lifeboat Station channel near Selsey, West Sussex (West et al., 1960). The

226 channel is dated to MIS 7 based mainly on the composition of the mammalian fauna (Parfitt,

227 1998).

228 All three faunas are correlated with the late MIS 7 Sandy Lane Mammal Assemblage Zone

229 (MAZ), which is thought to reflect relatively continental climatic conditions (Schreve, 2001a,

230 b). Co-occurrence of *S. hemitoechus* and *S. kirchbergensis* can only tentatively be asserted for

9

231 Ilford, whilst at Crayford and Selsey only a single *Stephanorhinus* species is documented in

232 each assemblage. However, these sites date from the same temperate stage, and both species

233 have been found co-occurring at other Sandy Lane MAZ sites (e.g. West Thurrock,

234 Pontnewydd; Green, 1984; Schreve et al., 2006). Both species were therefore present during

235 MIS 7 and may have interacted. Below, these samples are collectively referred to as the

236 'British MIS 7 *S. hemitoechus*' or 'British MIS 7 *S. kirchbergensis*' sample.

237 For MIS 5e, six sites were chosen based on the reported presence of rhinoceros material in

238 good condition. The Last Interglacial faunal assemblage from Victoria Cave was collected

239 from the Hyaena Bone Bed within the Lower Cave Earth (Lord et al., 2007). Inside the cave,

240 it is overlain by a thin flowstone, which started forming relatively late in the interglacial

241 (Lundberg et al., 2010). The flowstone and calcite encasing a red deer antler from the Hyaena

242 Bone Bed was dated directly by U-series and TIMS to the Last Interglacial (Gascoyne et al.,

243 1981: p. 654; Gilmour et al., 2007: p. 795; Lundberg et al., 2010). In Kirkdale Cave the

244 fossiliferous deposit is reported to have been of homogeneous character, with a depth of about

245 30 cm (Dawkins, 1874; Boylan, 1981). A flowstone on top of this bone bed was dated by U-

246 series to the Last Interglacial (McFarlane and Ford, 1998). A number of specimens that are

247 labelled as coming from Kirkdale Cave have very different preservation characteristics from

248 the main collections. These specimens are excluded here. Based on faunal composition, the

249 site is correlated with the climatic optimum of the Ipswichian (MIS 5e). The fossiliferous

250 layer at Raygill Fissure (Davis, 1880) was correlated with *Hippopotamus*-bearing Ipswichian

251 clay in the Leeds area (Earp, 1961). The fossiliferous deposit in Joint Mitnor Cave (Figure 3e-

252 f) is dated to the Ipswichian based on faunal content (Sutcliffe, 1960). The Great Bone Bed in

253 Tornewton Cave can be correlated to the Hyaena Stratum of later excavations (Sutcliffe and

254 Zeuner, 1962; Currant, 1998). The age of the Hyaena Stratum is bracketed by two TIMS dates

255 of ca. 134 and 98 ka BP on stalagmite, although some authors regard the fauna as dating from

256 a later part of MIS 5 based on pollen and faunal composition (Gilmour et al., 2007).

257   A single fluvial site, Barrington, was included (Figure 3g-h). Channel infills, known as the

258   Barrington Beds, were exposed in quarries, and produced mammalian remains (Sparks, 1952).

259   Based on the composition of the mammal fauna, the Barrington Beds are ascribed to the

260   Ipswichian (Gibbard and Stuart, 1975).

261   All six Ipswichian sites considered produced remains of a single rhinoceros species,

262   *Stephanorhinus hemitoechus*. No *S. kirchbergensis* remains have been recovered from any

263   Last Interglacial sites in the British Isles even though rich faunal assemblages are available

264   from a range of depositional contexts dated to different phases of the interglacial. We

265   therefore here assume that *S. kirchbergensis* was absent from or extremely rare in the British

266   Isles during MIS 5e (Van Asperen, in prep.). Since all the above-mentioned British MIS 5e

267   sites, except for the lowland site of Barrington, come from upland areas, they are collectively

268   referred to as the 'British MIS 5e upland' sample in the DFA. The lowland sample from

269   Barrington is analyzed separately. In all other analyses, all British MIS 5e sites are collated

270   into a single sample.

271

272   [Insert here: Figure 1. Sites with remains of late Middle to Late Pleistocene *Stephanorhinus*

273   palaeopopulations studied for dietary signature (in the order of appearance in the text, see

274   section 3.1.): 1 - Bilzingsleben II; 2 - Weimar-Ehringsdorf; 3 - Weimar-Taubach; 4 - Ilford; 5

275   – Crayford; 6 - Selsey; 7 - Victoria Cave; 8 - Kirkdale Cave; 9 - Raygill Fissure; 10 - Joint

276   Mitnor Cave; 11 - Tornewton Cave; 12 - Barrington.

277   Figure 2. Tooth rows of *Stephanorhinus kirchbergensis*, occlusal and buccal views; a and b.

278   Bilzingsleben (no. 388-163, P2-M3 sin); c and d. Weimar-Ehringsdorf (IQW 1965-3440 (Ehr.

279   4089) and IQW 1965-3377 (Ehr. 10072), P2-M2 dex); e and f. Taubach (IQW 1968-10692

280   (Taub. 2632…2639), P3-M3 dex).

281   Figure 3. Teeth of *Stephanorhinus hemitoechus*, occlusal and buccal views; a and b.

282   Bilzingsleben (no. 663-4; M2 sin); c-d. Weimar-Ehringsdorf (IQW 1965-318 (Ehr. 3410), M2

283 dex); e-f. Joint Mitnor Cave (P36774, M1 sin; courtesy of Torquay Museum); g-h. Barrington

284 (BGS GSM779, M2 sin; courtesy of the Geological Survey Museum, Keyworth).]

285 [Insert here: Table 1. Minimum number of individuals (MNI) represented by the material of

286 *Stephanorhinus* studied; abbreviations in [] used in Figures]

287

288 **3.2. Morphometrics**

289 Due to differences in size and morphology, it is usually relatively straightforward to

290 distinguish skeletal elements of *S. kirchbergensis* and *S. hemitoechus*, although a degree of

291 overlap occurs (Staesche, 1941; Fortelius et al., 1993; Mazza, 1993; Van der Made, 2000;

292 Lacombat, 2005, 2009). Measurements were taken and qualitative characteristics were

293 recorded for the upper and lower teeth following Lacombat (2009), who provides a system of

294 measurements that is modified and expanded from the work of Guérin (1980), Mazza (1988)

295 and Fortelius et al. (1993).

296 Overall levels of sexual dimorphism appear to be low in extant rhinoceroses (Loose, 1975).

297 Dimorphism in cranial measurements has been documented in free-ranging *Ceratotherium*

298 *simum* (Owen-Smith, 1988; Berger, 1994; Rachlow and Berger, 1997). Although several

299 cranial measurements are significantly different between the sexes in *Rhinoceros unicornis*,

300 and to a lesser degree in *Rhinoceros sondaicus* and *Dicerorhinus sumatrensis*, dental

301 measurements are not (Groves, 1982; Dinerstein, 1991). To assess the impact of sexual

302 dimorphism on dental characters in Pleistocene *Stephanorhinus*, coefficients of variation

303 (CVs, standard deviation/mean*100) were calculated for the different samples, as well as

304 overall CVs for the two species. These were compared with CVs for the same measurements

305 on extant rhinoceros teeth. CVs provide a means of comparing the degree of variation

306 between measurements of different absolute sizes. CVs for the same measurements for

307 closely related extant species gives some indication of how much variability can be expected

308 to occur in fossil species (Cope and Lacy, 1995). Although CVs should be used with caution

12

309 as indicators of biologically meaningful variables such as number of species and sexual

310 dimorphism (Carrasco, 1998, 2004), some trends can be discerned. Linear measurements of

311 mammalian dentitions tend to show little sexual dimorphism and have CVs between 5 and 10

312 (Gingerich, 1974; Yablokov, 1974; Gingerich and Schoeninger, 1979; Gingerich and Winkler,

313 1979). Sexually dimorphic variables tend to have coefficients of variation greater than 10

314 (Mihlbachler, 2007). Summary statistics for extant species and the Pleistocene samples can be

315 found in the Supplementary Data.

316 To examine the extent of the size differentiation between the two species, t-tests were carried

317 out for lengths and widths of the teeth. Results for the tests were considered significant if $p \leq$

318 0.05. Only samples where $n \geq 10$ were included in the tests since these tests are relatively

319 sensitive to small sample size.

320

321 **3.3. Mesowear analysis**

322 Mesowear analysis is a well-validated method that indicates wear patterns over a large part of

323 the lifespan of an individual animal (Fortelius and Solounias, 2000; Rivals et al., 2007). Tooth

324 wear in browsers, which consume mainly low-abrasive foodstuffs, is dominated by sharp

325 cusps and high relief. In contrast, grazers consume more grasses, often with a higher amount

326 of grit, both of which contribute to an abrasion-dominated wear pattern with round or blunt

327 cusps with low relief (Williams and Kay, 2001). Relatively small samples (n>10) give reliable

328 and significant results (Fortelius and Solounias, 2000).

329 The upper first and second molars were scored for mesowear on the buccal side of the tooth

330 (Franz-Odendaal and Kaiser, 2003). The occlusal relief was scored as either high or low.

331 Cusp shape was scored on the sharpest cusp as sharp, round or blunt. Teeth of very young

332 (more sharp cusps) and very old (more blunt cusps) individuals were excluded to prevent any

333 influence extreme wear stages may have on the classification (Fortelius and Solounias, 2000;

334 Rivals et al., 2007). The rhinoceros assemblage from Weimar-Taubach reflects selective

335 hunting of young individuals (Bratlund, 1999), leading to a reduced MNI for mesowear

336 analysis compared to total MNI (Table 1).

337 Scores for relief and cusp shape were combined into an overall mesowear score (0 = high and

338 sharp, 1 = high and round, 2 = low and sharp, 3 = low and round, 4 = low and blunt; Louys et

339 al., 2012). The Kruskal-Wallis test was used to analyse differences in mesowear scores

340 between the samples. For those analyses where the Kruskal-Wallis test showed a significant

341 difference, Mann-Whitney U-tests were used to investigate which samples had significantly

342 different mesowear scores. An overall Mann-Whitney U-test between the scores for *S.*

343 *hemitoechus* and *S. kirchbergensis* was also carried out.

344 Using the comparative dataset for 64 extant ungulates, compiled by Fortelius & Solounias

345 (2000), as a training set, a stepwise discriminant function analysis using Wilk's lambda was

346 carried out with the Pleistocene rhinoceros samples as ungrouped specimens. Mesowear data

347 for M1/2 of the *Stephanorhinus hundsheimensis* samples from the Central German sites of

348 Süßenborn [SUE] and Voigtstedt [VOI] (Kaiser and Kahlke, 2005; Kahlke and Kaiser, 2011)

349 were also included as ungrouped specimens. Mesowear scores for the fossil assemblages can

350 be found in Table 2. Because the mesowear scores are not independent (teeth with blunt cusps

351 have low relief), variables entered in the analysis were % of teeth with high relief, % of teeth

352 with sharp cusps and % of teeth with round cusps. Species with problematic dietary data (the

353 'mabra' species of Fortelius and Solounias, 2000) were left out of further analyses (cf. Kaiser

354 and Solounias, 2003), and the conservative dietary classification of Fortelius and Solounias

355 (2000) was used. The accuracy and robusticity of the differentiation between the dietary

356 categories was investigated with jackknifed cross-validation models, using a single species as

357 ungrouped case while using the other species in the original dataset as a generator set for

358 calculating discriminant functions. Hierarchical cluster analysis with complete linkage

359 (furthest neighbour, squared Euclidean distance) was carried out on the same dataset to

360 investigate which extant species are the most similar in their mesowear signature to the

14

361   Pleistocene rhinoceroses. All statistical analyses were performed with the Statistical Package

362   for the Social Sciences (SPSS) version 21.

363

364   [Insert here: Table 2. Mesowear scores for the fossil assemblages.]

365

366   Recently, there has been considerable discussion about the value of mesowear in determining

367   diets of past herbivore populations. The question has been raised whether mesowear provides

368   a dietary signal or whether environmental factors, in particular the amount of dust or grit on

369   the foodstuffs consumed, influence the mesowear value. Kaiser et al. (2013) suggested that

370   mesowear is primarily related to diet, whilst the presence of dust particles on the food may

371   contribute to overall wear of the tooth (and thus exerts selective pressure towards

372   hypsodonty), but does not impact on the morphology of tooth wear facets due to the small

373   size of the particles and the relatively uniform distribution of this wear. Kaiser et al. (2013)

374   also showed that mesowear is not related to habitat. Loffredo and DeSantis (2014) found that

375   teeth with similar mesowear values can display a wide range of δ^{13}C values. Therefore they

376   state that mesowear values should not be taken as indicative of individual diets, although they

377   regard the method as moderately reliable for assessing diet at population level. Like Loffredo

378   and DeSantis (2014), Ecker et al. (2013) found that there was no correlation between

379   mesowear, microwear (Rivals et al., 2009) and δ^{13}C values for a range of herbivore species

380   from the site of Payre in southeast France, dated to MIS 8-5. However, Ecker et al. (2013)

381   inferred that these herbivore species maintain their browsing or grazing diet across different

382   habitats, with δ^{13}C values reflecting differences in vegetation openness between e.g. river

383   valley and plateau. Differences between mesowear and microwear signatures can be

384   explained by the different timescales recorded by these two methods: while mesowear reflects

385   diet over a longer period of time (months to years), microwear records the diet over the last

386   days to weeks of an animal's life (Fortelius and Solounias, 2000; Rivals et al., 2007). In the

15

387   light of this discussion and the clear correlation of mesowear with diet in extant species

388   (Fortelius and Solounias, 2000), we here conclude that mesowear provides valid information

389   on a species' diet, especially at population level.

390   The diet of extant rhinoceros species varies from grazing via mixed feeding to browsing

391   (Owen-Smith, 1988). The diet of Pleistocene rhinoceroses was equally diverse. Hernesniemi

392   et al. (2011) compared mesowear scores for the extant species *Diceros bicornis,*

393   *Ceratotherium simum, Dicerorhinus sumatrensis, Rhinoceros sondaicus* and *R. unicornis* with

394   scores for the Pleistocene species *Stephanorhinus kirchbergensis, S. hemitoechus, S.*

395   *hundsheimensis* and *Coelodonta antiquitatis* from the British Isles. Cluster analysis for the

396   scores on M1 and M2 grouped *Stephanorhinus kirchbergensis* with *Dicerorhinus sumatrensis*

397   and *S. hundsheimensis* with *Rhinoceros sondaicus*. Together with the somewhat more distant

398   *Stephanorhinus hemitoechus*, these browsing species were clearly distinct from the mixed

399   feeder *Rhinoceros unicornis*, which grouped closely with British *Coelodonta antiquitatis* in a

400   cluster which also contains the grazer *Ceratotherium simum*. Within-species variation can be

401   almost equally large. Mesowear analysis of two samples of early Middle Pleistocene *S.*

402   *hundsheimensis* from the Central German sites of Süßenborn and Voigtstedt showed this

403   species had a wide dietary range (Kaiser and Kahlke, 2005; Kahlke and Kaiser, 2011) varying

404   from moderate grazing to non-specialised browsing with a high diversity of food items.

405

406   **4. Results**

407   **4.1. Absolute size**

408   The teeth of the two *Stephanorhinus* species are similar in shape but differ in size. T-tests are

409   significant for all upper and lower lengths and widths (Table 3). Scatterplots of width versus

410   length show two clusters, with varying but small degrees of overlap (Figure 4). Overall, the

411   metric characteristics are congruent with qualitative traits; teeth with traits characteristic for *S.*

412   *kirchbergensis* are mostly larger than teeth with *S. hemitoechus* traits. The teeth of *S.*

413   *kirchbergensis* from Bilzingsleben II are relatively small and overlap in size with the *S.*

414   *hemitoechus* teeth from the same location, although qualitative characteristics of the teeth, as

415   well as qualitative and quantitative data for the postcranial remains, clearly indicate the

416   presence of two species.

417   Van der Made (2000) documented a linear size increase of the lower third molars within the

418   *kirchbergensis*-group from Bilzingsleben II via Weimar-Ehringsdorf to Weimar-Taubach.

419   Our data, which includes the British MIS 7 *S. kirchbergensis* teeth and larger samples for the

420   German sites, confirm this trend (Figure 5).

421

422   [Insert here: Table 3. Table 3. Results of t-tests for dental measurements of *S. hemitoechus*

423   and *S. kirchbergensis*.

424   Figure 4. Scatterplots of width (L10/L9) vs. length (L2) for a. M2; b. m2; abbreviations: see

425   Table 1.

426   Figure 5. Mean values for the width of the posterior lobe of m1, m2 and m3 of *S.*

427   *kirchbergensis* from German late Middle Pleistocene sites.]

428

429   **4.2. Coefficient of variation**

430   73% of measurements of the upper and lower dentition of both extant and Pleistocene

431   rhinoceroses have CVs below 10. In the upper dentitions, some measurements for extant

432   *Ceratotherium simum* are relatively high, particularly on M2. The maximum length of the

433   crochet (L6) in the upper teeth is a highly variable qualitative characteristic, which is also

434   small in absolute size. Similarly, the two measurements in the lower teeth that are small in

435   absolute size (minimum height of the anterior and posterior valleys, L6 and L5) range widely,

436   more than half having a CV higher than 15. It is a well-known phenomenon for measurements

437   of small absolute size to have relatively high coefficients of variation (Yablokov, 1974;

438   MacFadden, 1989). Partly this is caused by the stronger impact of measurement error on

439   smaller variables, although in the case of L6 in the upper dentition it reflects a high level of

440   natural variation in this characteristic. CVs for measurements with small sample sizes are

441   somewhat higher than those for larger samples.

442

443   **4.3. Mesowear**

444   An overall Mann-Whitney U-test for differences between the mesowear scores for the two

445   *Stephanorhinus* species is significant (U=3184, p=0.035). A Kruskal-Wallis test for all

446   samples is significant (χ^2=13.023, p=0.011). Mann-Whitney U-tests reveal that the Weimar-

447   Ehringsdorf *S. kirchbergensis* sample is significantly different from the British MIS 5e *S.*

448   *hemitoechus* sample (U=879, p=0.016) and the Bilzingsleben II *S. kirchbergensis* sample

449   ($U=1012,$ p=0.005), whilst the Weimar-Taubach *S. kirchbergensis* sample is also different

450   from these two samples (British MIS 5e *S. hemitoechus*: U=256.5, p=0.050; Bilzingsleben II

451   *S. kirchbergensis*: U= 296.5, p=0.027).

452   The DFA has an overall correct reclassification rate of 72.2% (cross-validation: 64.8%). 7 out

453   of the 11 studied Pleistocene rhinoceros samples are classified as mixed feeders (Table 4).

454   The *S. hemitoechus* samples from the British MIS 7 sites and the MIS 5e lowland site fall

455   along the grazer axis (Figure 6). The other samples fall along a straight line, with the Weimar-

456   Ehringsdorf *S. hemitoechus* identified as a grazer and with early Middle Pleistocene *S.*

457   *hundsheimensis* from Voigtstedt located at the extreme browser end of the spectrum. The *S.*

458   *kirchbergensis* samples align more closely with the browsers and mixed feeders, and the *S.*

459   *hemitoechus* samples cluster toward the mixed feeder-grazer end of the spectrum.

460

461   [Insert here: Table 4. Dietary classification of Pleistocene *Stephanorhinus* samples using

462   DFA]

463

464 The patterns found in the DFA are born out in the cluster analysis (Figure 7). The main

465 distinction is between a browser cluster, a number of mixed feeder clusters and a grazer

466 cluster. The three browsing and one mixed feeding extant rhinoceros species are included in a

467 browser-dominated cluster, while the grazing *Ceratotherium simum* falls within the cluster of

468 the extreme grazers.

469 The British MIS 7 *S. hemitoechus* sample is the only fossil assemblage that clusters with the

470 extreme grazers. The remaining *S. hemitoechus* samples, as well as the *S. kirchbergensis*

471 samples from Bilzingsleben II and early Middle Pleistocene *S. hundsheimensis* from

472 Süßenborn, are linked most closely with a mixed feeder-grazer group of Artiodactyla with a

473 mesowear signature is characterised by a high percentage of teeth with high relief and round

474 cusps. The mixed feeder cluster that includes the *S. kirchbergensis* samples from the British

475 MIS 7 sites, Weimar-Ehringsdorf and Weimar-Taubach consists of cervids, bovids and

476 camelids with a high percentage of teeth with high relief, while a higher percentage of teeth

477 with sharp cusps is present than in the *S. hemitoechus* cluster. The Voigtstedt *S.*

478 *hundsheimensis* remains are in the same group as the browsing extant rhinoceros species (cf.

479 Kahlke and Kaiser, 2011).

480

481 [Insert here: Figure 6. Plot of scores on DF2 vs. DF1 for a range of extant herbivore species

482 and Pleistocene rhinoceros assemblages; abbreviations: see Table 1.

483 Figure 7. Cluster diagram using mesowear variables for extant herbivores and European

484 Pleistocene rhinoceros assemblages; dots: extant rhinoceros species; arrows: Pleistocene

485 samples.]

486

487 **5. Discussion**

488 The overall mesowear signature of the studied samples of European Pleistocene

489 *Stephanorhinus* indicates a predominantly mixed feeder diet (Table 4). Interestingly, the only

490   fossil sample that clusters closely with any of the extant rhinoceros species, at the browser

491   end of the spectrum, is the Voigtstedt *S. hundsheimensis* sample (see Kahlke and Kaiser,

492   2011). In comparison with the extant Asian and African rhinoceroses, most European late

493   Middle Pleistocene *Stephanorhinus* had a diet that was shifted more towards the mixed

494   feeder-grazer end of the dietary spectrum (Figure 6). Extant rhinoceros species therefore do

495   not provide the most suitable dietary analogues for European Pleistocene rhinoceroses

496   (compare Hernesniemi et al., 2011; Taylor et al., 2013). The British MIS 7 *S. hemitoechus*

497   sample falls in the same group of grazers as *Ceratotherium simum*, characterised by a high

498   percentage of teeth with low relief. These grazers feed primarily on grasses, particularly short

499   grasses, in open environments, apart from *Saiga tatarica*, a mixed feeder that today lives in

500   the Central Asian dry steppe and semi-desert (Bannikow, 1963; Bekenov et al., 1998; Sokolov

501   and Zhirnov, 1998).

502   The remaining *S. hemitoechus* samples from Central Europe, as well as the *S. kirchbergensis*

503   sample from Bilzingsleben II and the *S. hundsheimensis* sample from Süßenborn, align with

504   the extant bovids *Alcelaphus lichtensteinii*, *Boselaphus tragocamelus*, *Hippotragus equinus*,

505   *Hippotragus niger*, *Kobus ellipsiprymnus*, *Redunca fulvorufula*, *Redunca redunca*, *Syncerus*

506   *caffer* and *Tragelaphus strepsiceros*, and the cervid *Axis porcinus* (Figure 7). This cluster

507   consists of grazers and mixed feeders living in a variety of environments ranging from

508   floodplains and savannahs to open woodlands. The *S. kirchbergensis* samples from the British

509   MIS 7 sites, Weimar-Ehringsdorf and Weimar-Taubach fall most closely to the extant cervids

510   *Axis axis* and *Cervus unicolor*, the bovids *Aepyceros melampus*, *Ammodorcas clarkei*,

511   *Litocranius walleri*, *Ourebia ourebi, Tetracerus quadricornis* and *Tragelaphus angasii*, and

512   the camelids *Camelus dromedarius* and *Lama glama*. This cluster is dominated by mixed

513   feeders which incorporate a larger amount of browse in their diet. Most of these species live

514   in relatively dry areas of open woodland and grassland.

515   When comparing the dietary flexibility of *S. hundsheimensis* with that of the other two

516   *Stephanorhinus* species, it is clear that the former had a broader dietary range than either *S.*

517   *kirchbergensis* or *S. hemitoechus*, ranging from an extreme browser to a mixed feeder with a

518   considerable amount of grass in the diet. Our results therefore illustrate how the generalist

519   subsistence strategy of *S. hundheimensis* (cf. Kahlke and Kaiser, 2011) contrasts with the

520   more specialised strategies of *S. kirchbergensis* and *S. hemitoechus*. There is a clear indication

521   of more browse in the diet of *S. kirchbergensis* compared to that of *S. hemitoechus*, whilst *S.*

522   *hemitoechus* had the ability to subsist on a diet rich in grasses. However, it is too simplistic to

523   describe *S. kirchbergensis* as a 'forest' rhinoceros and *S. hemitoechus* as a 'steppe'

524   rhinoceros, assuming a browsing resp. grazing diet and taking these species as indicative of

525   forested versus open landscapes. The 'forest' rhinoceros did not feed exclusively in forest

526   areas, and likewise the 'steppe' rhinoceros was not exclusively a steppe grazer. The analysis

527   of the dietary signature of these rhinoceros species in cases of sympatry and allopatry clearly

528   demonstrates that their feeding traits, within a certain range of variation, relate to the

529   characteristics of available food resources, which in turn reflect the range of habitats present

530   in the regions considered during the Middle and Late Pleistocene interglacials.

531   The *S. hemitoechus* samples studied here do not appear in stratigraphic order in the DFA and

532   the dendrogram (Figures 6 and 7). In the *S. kirchbergensis* samples, there is an increase in the

533   size of the dentition, especially the m3 (Figure 5), and a weak trend towards a larger

534   proportion of browse in the diet (Figure 6). The increased size of the dentition in *S.*

535   *kirchbergensis* could find an explanation in the fact that in herbivores the dimensions of the

536   teeth are related to the quantity and quality of the food. Larger occlusal surfaces enable more

537   effective mastication of food (e.g. Janis, 1976, 1988; Van der Made, 2010; Anders and Von

538   Koenigswald, 2013), providing a selective advantage when the proportion of low quality food

539   resources in the diet increases. For the hindgut fermenter *S. kirchbergensis*, an increasing

540   proportion of less-digestible browse in the diet may have necessitated a higher food intake (cf.

541 Steuer et al., 2010). However, dietary differences between the MIS 7 and MIS 5e *S.*

542 *kirchbergensis* specimens are limited (Figure 6). Thus, there is little indication for a

543 directional evolutionary process of increasing specialization of the two species as grazer resp.

544 browser during the timespan considered. Instead, the individuals of the considered

545 palaeopopulations reacted to changing environmental conditions within the limits of their

546 feeding abilities.

547 The Bilzingsleben II samples present a suitable starting point for deciphering the relationships

548 between the *Stephanorhinus* mesowear record, environmental factors and competitive

549 interactions between the two species. The great similarity of the dietary traits of co-occurring

550 *S. kirchbergensis* and *S. hemitoechus* individuals from this site must be explained by a high

551 degree of spatial and temporal uniformity of food resources available to both species.

552 Although the botanical evidence from the fossil layer of the *Stephanorhinus* remains is not

553 sufficient for a detailed reconstruction of the contemporaneous vegetation (Erd, 1997), the

554 geographic position of the site explains the apparent low habitat diversity of the region under

555 fully developed interglacial (MIS 11) conditions. Bilzingsleben II lies within an area known

556 as the 'Zirkumherzynes Trockengebiet', a relatively dry region in the rain shadow of the Harz

557 Mountains (Figure 1). As is presently the case, during the Middle and Late Pleistocene

558 interglacials Atlantic low-pressure systems controlled precipitation levels in Northwest and

559 Central Europe (Kaspar and Cubasch, 2007). The mountains immediately northwest of

560 Bilzingsleben protected the region against the prevailing winds from the west. As a

561 mesoclimatic result, the area east and southeast of the Harz had a subcontinental climate,

562 which in combination with the uniform morphological and edaphic characteristics of the

563 region resulted in a relatively uniform vegetation pattern (T. Litt, pers. comm.). Based on

564 these geomorphological considerations and the interglacial character of the mammalian fauna

565 recovered from the site, which includes an abundance of large herbivores (Mania, 1991), the

566 inferred vegetation consisted of subcontinental thermophilous woodland with rich

567 undergrowth (T. Litt, pers. comm.). Such a habitat has a relatively high biomass and

568 productivity in vegetation layers available to the rhinoceroses and other large herbivores.

569 Both rhinoceros species are present in nearly equal numbers, indicating that *S. kirchbergensis*,

570 which later appears to be a strong competitor, did not outcompete *S. hemitoechus* at this time.

571 This may be due to the fact that its teeth were still small relative to its body size, while *S.*

572 *hemitoechus* benefited from its smaller body size.

573 Compared to Bilzingsleben II, the dietary signals of the two *Stephanorhinus* species from

574 Weimar-Ehringsdorf (MIS 7/5e) are significantly more differentiated (Figure 6). The latter

575 fossil site is located in a wetter region of the central German Thuringian Basin, on the flank of

576 a tectonic graben forming the valley of the River Ilm. The abundant floral remains from the

577 find layers of the Ehringsdorf *S. kirchbergensis* (Mammal Fauna 2) and *S. hemitoechus*

578 (Mammal Faunas 2-3, 7-8) specimens reveal a generally high diversity of habitats in the

579 vicinity of the site (Vent, 1974). However, in comparison with the lower and middle parts of

580 the Lower Travertine (Mammal Fauna 2; see section 3.1.), the Upper Travertines (Mammal

581 Faunas 7-8) experienced intensified subcontinental climatic influences. Due to this

582 environmental trend and the time-transgressive nature of the Ehringsdorf *S. hemitoechus*

583 sample (Table 1), a wide diversity of rhinoceros habitats is represented in the divergence of

584 the dietary signal. In particular, the relatively grazer-like signature of the *S. hemitoechus*

585 sample reflects the influence of the more subcontinental climate of the Upper Travertine.

586 The three British MIS 7 sites are all of fluvial origin, although the Selsey channel was of a

587 smaller scale than the Thames River (Ilford and Crayford). The latter part of MIS 7, from

588 which these sites date, is known to have been relatively dry and continental in northwest

589 Europe, with somewhat lower temperatures than in most other late Middle Pleistocene

590 interglacials (Ruddiman and McIntyre, 1982; Petit et al., 1999; Desprat et al. 2006). This part

591 of the interglacial witnessed an influx of animals adapted to open environments into

592 northwest Europe, whilst forest-adapted animals withdrew (Schreve, 2001a, 2004; Auguste,

593   2009). The British MIS 7 samples display the largest dietary difference between the two

594   *Stephanorhinus* species within the time span considered. In comparison with the Weimar-

595   Ehringsdorf specimens, the British MIS 7 *S. kirchbergensis* sample is shifted towards the

596   mixed feeder end of the spectrum (Figure 6), whilst *S. hemitoechus* has the dietary signature

597   of a grazer. This indicates that the availability of browse was limited, in accordance with

598   other environmental proxies which are indicative of open environments in the British Isles

599   (Schreve, 2001a). Even though its optimal diet seems to have incorporated more browse (see

600   below), *S. kirchbergensis* was able to increase the grazing component in its diet, and be a

601   strong enough competitor to force *S. hemitoechus* to consume greater proportions of abrasive

602   foodstuffs.

603   During at least part of MIS 5e, the *Stephanorhinus* species show a mostly disjunct

604   distribution, with *S. kirchbergensis* occurring in Central Europe, whilst *S. hemitoechus* is

605   common in western parts of the continent and in the British Isles. Under these conditions, *S.*

606   *kirchbergensis* at Weimar-Taubach consumed a significantly higher percentage of browse

607   than *S. hemitoechus*. The geomorphological characteristics of this site are similar to those at

608   Weimar-Ehringsdorf, situated only 2 kilometres northwest of Taubach, providing a similar

609   diversity of habitats. Nevertheless, the absence of the only other temperate-adapted rhinoceros

610   species and the diverse range of available foodstuffs ameliorated the environmental

611   conditions for *S. kirchbergensis*.

612   Of the British MIS 5e sites with *S. hemitoechus* fossils, Victoria Cave, Kirkdale Cave and

613   Joint Mitnor Cave are all located on the boundary between an upland area and a lowland area,

614   providing a diverse habitat of plateaus, slopes, valleys and floodplains. Raygill Fissure, and to

615   a lesser degree Tornewton Cave are situated in a diverse upland landscape with plateaus,

616   valleys and streams. In contrast, the site of Barrington lies in a lowland area with lower

617   habitat diversity, with open environments along the river and possibly woodland further away

618   from the active stream (Gibbard and Stuart, 1975). Although we studied only a single lowland

619 site and we cannot exclude that other lowland sites show a different pattern, interestingly,

620 these different levels of habitat diversity can be traced in the mesowear scores for these sites:

621 the upland samples are classified as mixed feeder, whereas the lowland sample is classified as

622 grazer, although it is not displaced towards the grazer end of the spectrum as much as the

623 British MIS 7 *S. hemitoechus* sample (Figure 6).

624 Since further environmental proxies are only available for the Barrington site, we cannot

625 exclude the possibility that these sites date from different phases of the same interglacial.

626 However, this scenario seems unlikely based on the fully developed interglacial character of

627 the faunal assemblages: the ecologically demanding *Hippopotamus amphibius* is recorded

628 from all sites, and other 'temperate indicators' such as *Palaeoloxodon antiquus*, *Sus scrofa,*

629 *Dama dama* and *Capreolus capreolus* are also present in the upland sites. Since the large

630 herbivore faunas from the upland and lowland sites are very similar, the difference in the

631 mesowear scores could reflect the availability of foodstuffs in the environment. A more

632 diverse habitat would have provided a wider range of resources, enabling *S. hemitoechus* to

633 subsist on a mixed feeder diet, whilst a more homogeneous environment with open grassland

634 forced the species to graze.

635

6. Conclusions

637 *Stephanorhinus kirchbergensis* and *S. hemitoechus* were embedded in a dynamic process of

638 temporo-spatial replacements and interspecific differentiation of Middle to Late Pleistocene

639 rhinoceroses in the western Palaearctic. Both their anatomical features (see section 2) and the

640 obtained mesowear scores show significantly higher dietary specializations compared to the

641 Early to early Middle Pleistocene *S. hundsheimensis*. This is consistent with the idea that the

642 100 ka periodicity in the global climatic record caused a sustained environmental continuity

643 compared to the preceding 41 ka regime and thus promoted the development of more

644 specialized subsistence strategies (Kahlke and Kaiser, 2011).

The presence of the rhinoceros species considered here is often taken as a first indication of the character of the vegetation prevailing in their respective habitats. However, our studies demonstrate that species identity alone is not sufficient to establish the real dietary traits of a *Stephanorhinus* palaeopopulation. The occurrence of the 'forest' rhinoceros *S. kirchbergensis* in a faunal assemblage by no means indicates exclusively forested habitats. Similarly, the 'steppe' rhinoceros *S. hemitoechus* did not occupy steppe landscapes only. Instead, the reconstruction of past rhinoceros diets on the level of extended samples from stratigraphically well-defined palaeopopulations of different European regions sheds light on the impact of habitat diversity and the effect of interspecific competition with closely related rhinoceros species on feeding behaviour.

Whilst both *S. kirchbergensis* and *S. hemitoechus* had already developed advanced dietary specializations compared to that of the "indigenous" *S. hundsheimensis* when they first entered Europe, there is little evidence of progressing dietary specialization of the two newcomers over the late Middle and Late Pleistocene. A moderate size increase of the molar row in *S. kirchbergensis* over this period may have provided some advantage. The mesowear signals of both species indicate a mixed feeder diet, similar to that of extant mammal species in relatively open habitats. In comparison with *S. hemitoechus*, *S. kirchbergensis* generally consumed more browse. Nevertheless, both species maintained a level of dietary flexibility, with *S. kirchbergensis* including more or less browse in its diet depending on the quality of the habitat, and *S. hemitoechus* shifting from mixed feeder to consuming more grass when necessary. Although this indicates they preferred different habitats, clearly both species were capable of surviving on a range of diets in a range of environments.

Low habitat variability forced *S. kirchbergensis* and *S. hemitoechus* to consume very similar diets, as is evidenced by the sympatric Bilzingsleben II populations. Increasing habitat variability correlates with an increasing degree of divergence in feeding traits both within and between *Stephanorhinus* species. At Weimar-Ehringsdorf, Weimar-Taubach, and the British

26

671   MIS 5e upland sites, high habitat variability was combined with relatively high precipitation,

672   allowing *S. hemitoechus* to consume its optimal mixed feeder diet, and *S. kirchbergensis* to

673   incorporate more browse. Low habitat variability pushed *S. hemitoechus* towards consuming

674   more grass even in the absence of *S. kirchbergensis,* as reflected by the British MIS 5e

675   lowland sites. This pattern therefore holds regardless of whether both species were co-

676   occurring or only one species was present, although the disjunct distribution pattern during

677   MIS 5e appears to have presented optimum conditions for both species. However, in some

678   cases the impact of habitat variability on dietary composition was modified by the presence of

679   a closely related competitor. Thus, *S. kirchbergensis* from British MIS 7 sites, with low

680   precipitation levels, was able to survive on less browse, thereby displacing co-occurring *S.*

681   *hemitoechus* towards a grass-dominated diet.

682   Similar patterns of dietary variation related to habitat characteristics and competitive

683   interactions have been observed in a range of other fossil species, such as Neogene equids

684   (Kaiser, 2003) and bovids (Solounias and Hayek, 1993; Merceron et al., 2004, 2006;

685   Kostopoulos and Karakütük, in press), Early and Middle Pleistocene Proboscidea (Rivals et

686   al., 2012; Rivals et al., in prep.) and Late Pleistocene cervids (Rivals and Solounias, 2007;

687   Rivals et al., 2010). As in the rhinoceros species with highly specialised feeding traits studied

688   here, these animals had a considerable dietary flexibility and adapted their diet according to

689   the availability of food resources in different habitats (Kaiser, 2003; Rivals and Solounias,

690   2007; Tütken et al., 2013).

691   For Middle to Late Pleistocene *S. kirchbergensis* and *S. hemitoechus* of Central and

692   Northwest Europe, it appears likely that the diet consumed was not simply the result of a

693   directed time-transgressive evolution. Even as specialists they retained a certain amount of

694   ecological flexibility as part of their subsistence strategy. Rather, within the range of each

695   species' ecological tolerance, diet was controlled by environmental parameters, with a

696   particular role for habitat variability. Whilst these rhinos obviously had a preferred optimal

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697   diet, in most cases they had to make do with what was available in their environment,

698   following the timeless proverb "You'll have to take pot luck!"

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