



25 mesowear analysis, these reconstructions of *Stephanorhinus* diets indicate that habitat  
26 diversity and interspecific competition with closely related rhinoceros species induced  
27 variation in feeding behaviour. Although anatomical features of both species suggest  
28 significantly higher dietary specializations compared to the Early to early Middle Pleistocene  
29 *S. hundsheimensis*, their mesowear signals are characteristic of a mixed feeder diet, similar to  
30 that of extant mammal species in relatively open habitats. Both species retained a degree of  
31 dietary flexibility, enabling them to survive in a range of environments. Although each of  
32 these rhinoceroses preferred different habitats, species identity alone is not sufficient to  
33 establish the real dietary traits of a *Stephanorhinus* palaeopopulation. As a consequence, their  
34 occurrence in a faunal assemblage alone cannot be taken to indicate a specific habitat.  
35 *S. kirchbergensis* and *S. hemitoechus* were embedded in a dynamic process of temporo-spatial  
36 replacements and interspecific differentiation of rhinoceroses in the western Palaearctic.  
37 However, dietary specialization in these Middle to Late Pleistocene European rhinoceroses  
38 was not the result of a directed time-transgressive evolution. Rather, within the range of each  
39 species' ecological tolerance, it was controlled by environmental parameters, with habitat  
40 variability as the main factor.

41

## 42 **1. Introduction**

43 The reconstruction of fossil faunal assemblages can significantly contribute to our  
44 understanding of the natural variability and evolution of past ecosystems and climates. In  
45 particular, assessments of dietary requirements for each species and inferences to their  
46 corresponding subsistence strategies have proved to be valuable methods for reconstructing  
47 palaeoenvironmental parameters. In the case of herbivores, reconstructions of the vegetational  
48 character of associated palaeoenvironments based on dietary signals may provide detailed  
49 insights into the behaviour of different species, when corresponding palaeobotanical records  
50 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 Palaeartic (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 Palaeartic  
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 Palaeartic  
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 Palaeartic 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

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

105 During the early Middle Pleistocene two new rhinoceros species, *S. kirchbergensis* and *S.*  
106 *hemitoechus*, with different and more specialised feeding strategies, appeared in Europe to  
107 compete with the previously unchallenged generalist *Stephanorhinus hundsheimensis*. After a  
108 period of sympatry between 0.7 and 0.6 Ma BP, documented in the faunal assemblages of  
109 several early Middle Pleistocene sites, such as Kolkotova Balka and Sukleya near Tiraspol  
110 (Moldova), Mauer and Mosbach 2 (Germany), as well as Soleilhac (France), *S. kirchbergensis*  
111 started to replace *S. hundsheimensis* in temperate faunas (Beljaeva and David, 1975; Guérin,  
112 1980; Fortelius et al., 1993; Schreiber, 2005). *S. kirchbergensis*, an immigrant of Asian origin  
113 (Guérin, 1980; Van der Made, 2000), was a very large animal with long legs, a high head  
114 posture, and moderately hypsodont molars (Fortelius et al., 1993), indicating a diet with  
115 significant portions of browsing.

116 Between 0.6 and 0.5 Ma, a second rhinoceros species, *S. hemitoechus*, appeared in Europe, as  
117 recorded in the Mosbach 2 gravels (Fortelius et al., 1993; Hemmer et al., 2003). Its anatomy,  
118 especially its relatively short limbs, the low-slung cranium, more hypsodont molars and  
119 reduced premolar segment of the tooth rows compared to those of *S. kirchbergensis*, indicate  
120 affinities to less forested landscapes or open grasslands (Guérin, 1980; Janis, 1990; Mazza,  
121 1993; Fortelius et al., 1993). This is corroborated by the fact that it was especially widespread  
122 in Europe under dryer and/or moderate to cooler conditions. The origins of both rhinoceroses,  
123 *S. kirchbergensis* and *S. hemitoechus*, seem to ultimately derive from the development of the  
124 100 ka periodicity in the global climatic record, which led to a longer lasting environmental  
125 continuity in the resulting biomes compared to the preceding 41 ka span of time (Kahlke et  
126 al., 2011).

127 Alternating stages of prolonged colder and temperate climatic conditions resulted in mutual  
128 alternations of *Coelodonta tologojensis* / *C. antiquitatis* and *S. hemitoechus* populations from  
129 the Middle Pleistocene onwards. When *C. tologojensis* 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 Palaeartic 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  $42.542 \pm 1.068$  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

### 153 3. Material and methods

#### 154 3.1. Material

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

170 In Central Germany, the rhinoceros remains from Bilzingsleben, Weimar-Ehringsdorf and  
171 Weimar-Taubach (all in Thüringen; Table 1), were included in our study. The rhinoceros  
172 remains of these sites originate from travertine layers. Bilzingsleben II (hominin site) is  
173 related to one of the warm stages of the late Middle Pleistocene “Holstein-Komplex” (Mania,  
174 1997, 2006; Heinrich, 2003), assigned by most authors to MIS 11 (Nitychoruk et al., 2006).  
175 Schreve and Bridgland (2002) correlate Bilzingsleben II with the younger of two temperate  
176 warm substages documented in the MIS 11 sequence of the Thames valley (UK). The fossil  
177 layer of Bilzingsleben II formed within a very short and hence biostratigraphically  
178 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 19<sup>th</sup> 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

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; Carrant, 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 Lacomat, 2005, 2009). Measurements were taken and qualitative characteristics were  
293 recorded for the upper and lower teeth following Lacomat (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

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-Odenaal 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

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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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

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 ( $\chi^2=13.023$ ,  $p=0.011$ ). 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. hundsheimensis* (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

## 636 **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 Palearctic. 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).

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

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

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

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

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!”

699

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