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Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity

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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 ± 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 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

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

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 Palaeartic. 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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