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Generalism as a subsistence strategy: advantages and limitations of the highly flexible feeding traits of Pleistocene *Stephanorhinus hundsheimensis* (Rhinocerotidae, Mammalia)[☆]

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ABSTRACT

The so-called Hundsheim rhinoceros, *Stephanorhinus hundsheimensis*, was a very common faunal element of the Early to early Middle Pleistocene period in the western Palaearctic. In this study, individuals from two different central European populations of the Hundsheim rhinoceros were analysed in order to determine whether their local dietary signals could reflect differing food availability between the two populations, and whether such information could provide a better understanding of the ecological role of *S. hundsheimensis* within corresponding faunal assemblages, and of its principal subsistence strategy in the western Palaearctic. The mesowear traits observed in the studied *S. hundsheimensis* populations have been interpreted as representing biome-specific signals, indicating grassland vegetation at the site of Süßenborn, and dense to open forests at Voigtstedt (both localities in Germany). The analyses performed on the fossil rhino material demonstrate the most pronounced dietary variability ever established for a single herbivorous ungulate species by mesowear studies. This variability ranges from an attrition dominated grazing regime, to a one of predominantly browsing, and characterises *S. hundsheimensis* as the most ecologically tolerant rhinoceros of the Palaearctic Plio-Pleistocene. Although such dietary flexibility proved an effective enough subsistence strategy over a period of 600–900 ka (1.4/1.2–0.6/0.5 Myr) in the western Palaearctic, the situation changed dramatically after 0.6 Myr BP, when the new species of rhinoceroses, *Stephanorhinus hemitoechus* and *Stephanorhinus kirchbergensis*, appeared and started to compete for both the grass and the browse. For the generalist *S. hundsheimensis*, this bilateral interference was detrimental to its success in all of its habitats. The successful competition of specialised forms of rhinoceroses, which might have originated as a result of the development of 100 ka periodicity in the global climatic record, is proposed as the main reason for the extinction of *S. hundsheimensis* during the early Middle Pleistocene.

1. Introduction

Fossil vertebrate remains can be useful tools for reconstructing palaeoenvironmental parameters and improving knowledge on the natural variability and evolution of palaeoecosystems and -climates. However, accurate reconstruction of fossil faunal assemblages requires the establishment of the food resources available for each species, and conclusions on their corresponding subsistence strategies. In the case of herbivores, reconstructions of the vegetational character of associated palaeobiomes,

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[☆] In memoriam Dr. Andrei V. Sher († 11th August 2008). From 1971 until his death, Andrei Sher was a regular research partner of the Institute of Quaternary Palaeontology in Weimar (Germany). He became a close friend of the founder and first director of the Weimar institute, Hans-Dietrich Kahlke (Sher, 2004), and for more than two decades he also worked closely with one of the authors (RDK), studying fossil material recovered from different Thuringian sites. During this time, Andrei's research interests were mainly focused on fossil bison and early members of the mammoth evolutionary line. Due to his extended research stays during the study program on the late Early Pleistocene site of Untermaßfeld, he became a valued member of the Weimar team, and played an intrinsic role. As a result, he published a detailed description of the earliest Eurasian bison s. str. (member of the subgenus *Bison*), which he named *Bison menneri* (Sher, 1997). The results of his studies on early Middle Pleistocene *Mammuthus meridionalis* and *M. trogontherii*, from Voigtstedt and Süßenborn respectively, are mirrored in transregional studies on mammoth evolution (Lister and Sher, 2001; Lister et al., 2005). With this present study we follow Andrei to the early Middle Pleistocene sites. Whereas this period saw two distinct mammoth species in the western Palaearctic, for a long time only one rhino species roamed in corresponding habitats. This first study of its remarkable subsistence strategy we dedicate to our colleague and friend Andrei V. Sher.

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using the dietary interface as a pathway, may provide subtle insights into the behaviour of different species based on dietary signals only, even when no palaeobotanical record is available.

For this study, we selected a species of rhinoceros, *Stephanorhinus hundsheimensis*, which was very common during the Early to early Middle Pleistocene period in the western Palaearctic. Since taxonomic work in fossil rhinoceroses is strongly based on dental morphology, a tooth related method of dietary evaluation, the mesowear method (Fortelius and Solounias, 2000; Kaiser and Fortelius, 2003; Kaiser and Solounias, 2003; Kaiser and Rössner, 2007), has been chosen. This method provides a long-term signal of the overall abrasiveness of the forage, covering a considerable part of an individual's life span. In contrast to the dental microwear method (e.g., Hayek et al., 1992; Solounias and Semprebon, 2002; Rivals et al., 2008), it is not affected by seasonal fluctuation.

Mesowear evaluation has been rather frequently applied as a community based approach to palaeoecology (e.g. Schubert et al., 2006), however, studies of intraspecific variability of closely related populations within a time series are rare so far (e.g. Rivals et al., 2007; Semprebon and Rivals, 2007). As an approach to intraspecific variability of contemporaneous populations of a single species and as a measure of the degree of generalism the method has yet been applied only by Kaiser (2003), making the approach attempted here a rather novel one.

2. Hypothesis

Just a few extant herbivore species are known to be nearly monophageous, such as the koala (*Phascolarctus cinereus*), which has developed a trophic dependence on the foliage and bark of only around 20 *Eucalyptus* species (Zoidis and Markowitz, 1992; Ellis et al., 2002). The majority of today's herbivores have a much more opportunistic feeding strategy, reflected by a broader spectrum of food resources (Ansell, 1960; Darling, 1960; Lamprey, 1963; Skinner and Smithers, 1990; Estes, 1991). If conspecific populations from different habitats are investigated, the dietary signal of a given species should not only provide information on the availability of food items within these habitats, but could also reveal the corresponding dietary spectra considered by the studied vertebrate species. In turn, such information would provide a tool with which the flexibility of the feeding behaviour of the studied herbivores could be determined.

The hypothesis tested here is, whether the individuals from two different fossil populations of the so-called Hundsheim rhinoceros, *S. hundsheimensis* (Toula, 1902), reflect different food availability in their local dietary signals. If so, we would expect to recover general information on the subsistence strategy of this species, and, in addition, obtain further information on its evolutionary history within the Early to Middle Pleistocene faunal assemblages of the western Palaearctic. The samples chosen for this study originate from two well studied European early Middle Pleistocene sites with very different habitats.

The applied mesowear method (Fortelius and Solounias, 2000) involves measuring the abrasiveness of a typical diet. Many angiosperms, both monocotyledons and dicotyledons (Piperno et al., 2002), may heavily impregnate their vegetative and reproductive organs with phytoliths. Besides lignifications, phytoliths are considered to constitute an important system of mechanical defence in angiosperms. The evolution of hypsodont dentitions during the upper Miocene (Fortelius et al., 2002), when open woodlands and savannas expanded globally at the expense of forests, has been hypothesised to be linked to the high phytolith content of grass leaves in particular (Cerling et al., 1998). Since opalines were long considered to be the only substance hard enough to grind and abrade the tooth enamel of herbivorous mammals (e.g. Baker et al., 1959), this paradigm has recently been challenged (Sanson et al., 2007).

In addition to phytoliths, exogenous grit makes up the second major source of abrasives eaten by herbivorous mammals, where higher levels of grit are broadly associated with less water availability to the existing plant cover (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007). Differences in habitat structure should, therefore, be indicated by the mesowear signature, as a simple measure of overall abrasiveness of foods averaged over a considerable part of an individual's life span. Variation observed in mesowear signatures of a species at different locations, should thus not only reflect habitat conditions, but also indicate the magnitude of variability in the feeding trait of the studied species. A third source of abrasiveness could arise from excessive fruit or seed consumption, as suggested by Fortelius and Solounias (2000).

3. Material and methods

3.1. Investigated rhinoceros species

The fossil genus *Stephanorhinus* Kretzoi, 1942 comprises dolichocephalic, two-horned rhinos with strongly molarised premolars without functional incisors (Fortelius et al., 1993). Its temporo-spatial distribution is restricted to the Palaearctic Neogene and Quaternary. The phylogenetic relationship of Plio-Pleistocene species of *Stephanorhinus* is still under debate. Whereas the classical evolution model (e.g. Guérin, 1982; H.-D. Kahlke, 2001) sees a single Plio- to early Middle Pleistocene evolutionary line of *Stephanorhinus etruscus*, comprising the Early to Late Villafranchian nominate form *S. etruscus etruscus* and the late Early to early Middle Pleistocene *S. etruscus brachycephalus* sensu Guérin (1980) (including *S.* cf. *hundsheimensis* of several authors; see H.-D. Kahlke, 2001), Fortelius et al. (1993) and Lacombat (2007, 2009) link the Early to early Middle Pleistocene *S. hundsheimensis* with the Early Villafranchian species *S. jeanvireti*, which has, so far, only been recorded in Europe. For the latter authors, the *S. jeanvireti*/*hundsheimensis* group of rhinos form a separate Eurasian evolutionary branch different from that of Villafranchian *S. etruscus*.

Independent from the current debate, the studied early Middle Pleistocene rhinocerotid fossil populations from Süßenborn and Voigtstedt (Fig. 1) belong to a single species (H.-D. Kahlke, 1965b, 1969b). Following the model of Lacombat (2006a, 2006b, 2007), we have assigned the material from both sites to *S. hundsheimensis*, which appeared in Europe for the first time between 1.4 and 1.2 Myr (Pirro Nord and Pietrafitta in Italy, Mazza et al., 1993; Venta-Micena, Fuente Nueva 3 and Barranco Léon 5 in Spain, Lacombat and Martinez-Navarro, in press), and survived until 0.6–0.5 Myr (Mauer and Mosbach 2 in Germany, Fortelius et al., 1993; Schreiber, 2005). *S. hundsheimensis* was a long-legged rhinoceros with cursorial limb-proportions and a head posture that presumably allowed the animal to feed both as a grazer and browser on vegetation of intermediate height (Fig. 2).

3.2. Investigated rhinoceros populations

3.2.1. Süßenborn (SH-SUESS)

The extended fossil mammal material from the Ilm river gravels of Weimar-Süßenborn (50°59′16″N, 11°23′58″E) in central Thuringia (Germany) was collected more or less systematically during the second half of the 19th century up to the 1980s – especially during periods of hand quarrying. The resulting Süßenborn collection comprises approximately 3200 finds (stored in the Senckenberg Research Station of Quaternary Palaeontology Weimar; abbreviated as IQW). Süßenborn's, up to 15 m thick, fluviatile

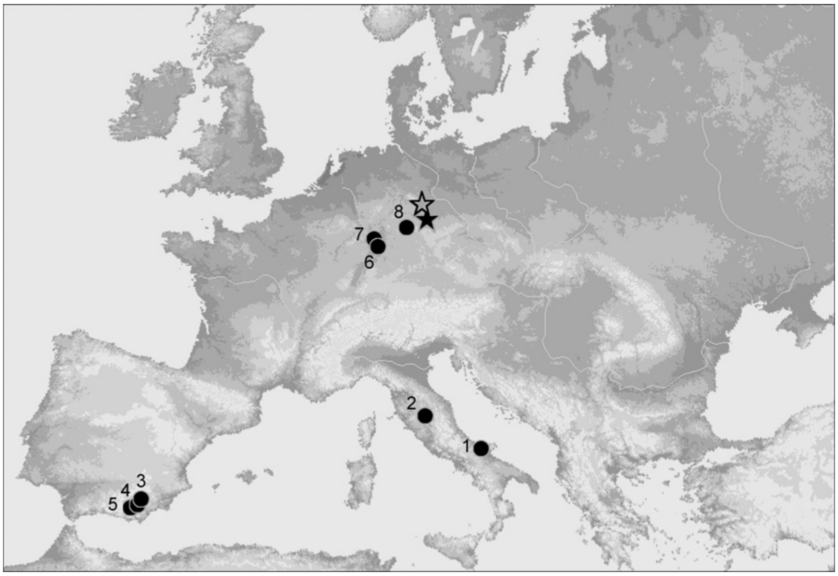

Fig. 1. Locality map of European Plio-Pleistocene sites of *Stephanorhinus hundsheimensis* in order of appearance in the text: star – Süßenborn; open star – Voigtstedt; 1 – Pirro Nord; 2 – Pietrafitta; 3 – Venta Micena; 4 – Fuente Nueva 3; 5 – Barranco Léon 5; 6 – Mauer; 7 – Mosbach 2; 8 – Untermaβfeld.

horizons represent a relatively long time interval of the early Brunhes magnetochrone (with *Mimomys savini* as a biostratigraphic marker). Its mammal fauna includes characteristic early Middle Pleistocene elements, such as *Soergelia elisabethae*, *Bison schoetensacki*, *Capreolus suessenbornensis*, *Alces latifrons*, *Praemegaceros verticornis*, *Megaloceros savini*, *Equus suessenbornensis*, *Equus altidens*, and an extended series of *Mammuthus trogontherii* remains (monograph: H.-D. Kahlke, 1969a). Although several climatic oscillations are represented in the sequence, the faunal inventory does not indicate periglacial conditions, or the formation of a steppe-tundra (R.-D. Kahlke, 1999). Single occurrences of the earliest Eurasian reindeer (*Rangifer tarandus stadelmanni*) and musk-ox (*Ovibos moschatus suessenbornensis*) at Süßenborn have been assigned as sporadic appearances from winter visitors from sub-Arctic or Arctic regions (Soergel, 1939; R.-D. Kahlke, 1999).

According to the fluviatile character of the site, most of the 465 remains of *S. hundsheimensis*, among them one calvarium, were found disarticulated. In addition, some of the finds show strong traces of pre-depositional transportation. In rare cases, individually found dental or skeletal elements were later assigned to each other; however complete mandibles were more common. The varying stages of preservation of the fossils possibly reflect the variability of water currents within the riverine system. For this study, only well-preserved dental elements were used.

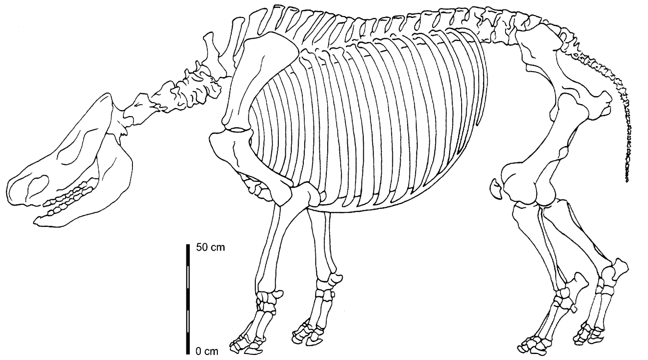

Fig. 2. Skeletal reconstruction of *Stephanorhinus hundsheimensis*, based on elements of a single, relatively large sized male individual from the late Early Pleistocene site of Untermaβfeld (Thuringia, Germany), dated at 1.05 Myr (after R.-D. Kahlke, 2006).

3.2.2. Voigtstedt (SH-VOI)

The fossil vertebrate fauna from the former clay pit immediately east of Voigtstedt (51°23′49″N, 11°20′01″E) near Sangerhausen (northern Thuringia, Germany) was systematically excavated (in total 2650 m^2) during the years 1954–1966 (H.-D. Kahlke, 1965a). The entire c. 2500 fossil mammal finds (stored in the IQW) originate from the so-called “Lehmzone” (“loam layer”), which was deposited during an early period of the Brunhes magnetochron. The occurrence of the biostragraphically indicative arvicolid *Mimomys savini* assigns the fauna to the Late Biharian, most probably to MIS 17 (Maul et al., 2007), an age that fits with the large mammal record. The Voigtstedt fauna includes, amongst others, *B. schoetensacki*, *A. latifrons*, *P. verticornis*, and *E. altidens*; species which clearly reflect warm climatic conditions. According to the MIS 17 correlation, the age of the Voigtstedt fauna is believed to be around 0.7 Myr (absolute data from Bassinot et al., 1994).

Among the 273 rhinocerotid finds recovered at the site were two, more or less complete, skeletons of a juvenile and a subadult individual (Fig. 3). Their carcasses were deposited in stagnant waters, low in oxygen, and were effectively unavailable to large scavengers. Additional material was found in more or less disarticulated states.

3.3. Mesowear analysis

The mesowear method applied to the fossil *S. hundsheimensis* populations from Süßenborn and Voigtstedt (Fig. 4), was developed by Fortelius and Solounias (2000). Mesowear is based on facet development on the occlusal surfaces of the ungulate upper molar teeth. The degree of facet development reflects the relative proportions of tooth-to-tooth contact (attrition) and food to tooth contact (abrasion). Attrition creates facets and abrasion obliterates them. Mesowear analysis defines ungulate tooth mesowear by two variables: 1. Occlusal relief (OR) and 2. Cusp shape (CS). The occlusal relief is classified as high (h) or low (l), depending on how high the

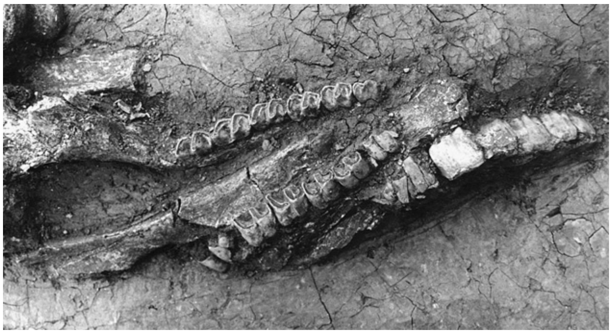

Fig. 3. Lower jaw and skull of a subadult female *Stephanorhinus hundsheimensis* in situ (IQW Voi. 3280, included in this study), part of a nearly complete skeleton, Voigtstedt excavation 1959 (Photograph: H. Wöllner).

cusps rise above the valley between them (Table 1). Data from this analysis is given as percentages: % high and % low (Table 2). The second mesowear variable, cusp shape, is comprised of three scored attributes: sharp (s), round (r), and blunt (b), according to the degree of facet development (see Fortelius and Solounias, 2000). Cusp shape is also given as a percentage in Table 2, as are the three variables % sharp, % round, and % blunt. Where both cusp apices (paracone and metacone) are preserved, the sharper of the two was selected for analysis as proposed by Fortelius and Solounias (2000) (Table 2, Fig. 5A–C). Cusp shape variables were evaluated for both cusp apices of each tooth independently (Table 2, Fig. 5D).

Fortelius and Solounias (2000) restricted their study on ungulate mesowear to the labial wall of the upper M2. Their methodology was modified for this study by selecting all upper M1-M3 of *S. hundsheimensis*, following the ''extended'' mesowear method introduced by Kaiser and Solounias (2003). This methodology was chosen in order to include lesser-extended samples of fossil teeth, such as the Voigtstedt material. The mesowear principle has been proven to allow consistent inter- and intraspecific comparison in extant rhinocerotids (Fortelius and Solounias, 2000).

For this study, only upper cheek teeth from wear stages 2 and 3 (sensu Kaiser et al., 2003) were used. Unworn teeth, specimens in very early wear, and very worn teeth were excluded. In total, 44 dental specimens from the Süßenborn population (SH-SUESS), which most likely represent 39 individuals, and seven dental specimens from six individuals from Voigtstedt (SH-VOI), were available for study (Table 1). 52 extant species, as reported by Fortelius and Solounias (2000), were used as comparative data for dietary classification; however, here, their original dataset was modified slightly by excluding the two domestic species, *Camelus dromedarius* and *Lama guanicoe* f. *glama*.

The set of fossil populations in our study was plotted within a nested set of extant ungulate species. Extant species were classified into the three broad dietary categories: browsers, mixed

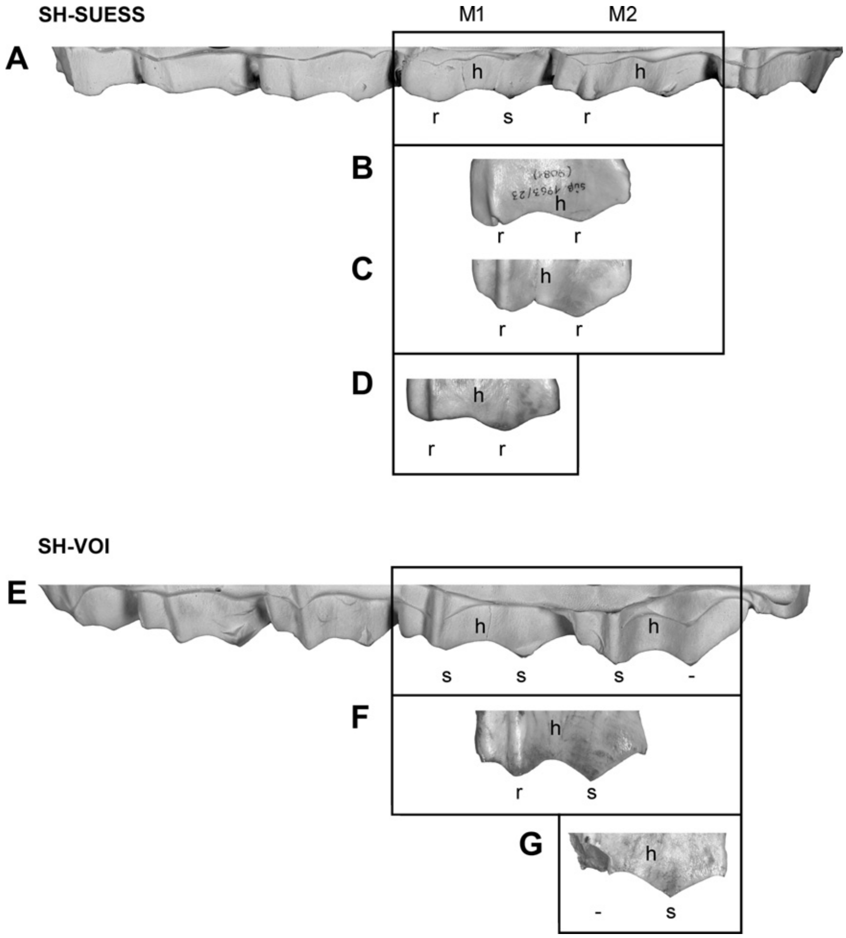

Fig. 4. Dental elements of early Middle Pleistocene *Stephanorhinus hundsheimensis* (labial views) from Süßenborn (A–D) and Voigtstedt (E–G). A: IQW Suess. 1964 680/7143, upper right tooth row (P2-M3), mirror imaged; B: IQW Suess. 1963 23/9081, upper left M1 or M2; C: IQW Suess. 1963 39/9083, upper right M1 or M2, mirror imaged; D: IQW Suess. 1963 29/7150, upper left M1; E: IQW Voi. 3280I/1–1966 74/15, upper left tooth row (P2-M2, M3 erupting); F: IQW Voi. 1965 3700/1003, upper right M1 or M2, mirror imaged; G: IQW Voi. 1965 3727/981, upper left M2. Note that cusp apices are rounded in many Süßenborn specimens and sharp in most of Voigtstedt specimens. Given mesowear scorings correspond to Table 1.

Table 1
Maxillary cheek teeth of fossil *Stephanorhinus hundsheimensis* investigated: SPEC ID = specimen identification number; LOC = locality (SUESS = Süßenborn, VOI = Voigtstedt); TOOTH = tooth position (txM1 = first upper molar, txM2 = second upper molar, txM12 = first or second upper molar, txM3 = third upper molar); SIDE = body side (r = right, l = left); OR = occlusal relief mesowear variables scoring (h = high, l = low); CS = cusp shape mesowear scores, anterior (distal) cusp (s = sharp, r = round, b = blunt, dash = cusp broken or not preserved); A = anterior cusp; P = posterior cusp; WEAR = wear stage.

SPEC ID	LOC	TOOTH	SIDE	OR	CS-A	CS-P	WEAR
IQW Suess. 1963 1/5045	SUESS	txM12	l	l	b	r	3
IQW Suess. 1963 1/5045	SUESS	txM12	l	l	b	r	3
IQW Suess. 1963 13/463	SUESS	txM12	r	h	r	r	3
IQW Suess. 1963 2/7154	SUESS	txM3	r	h	r	–	3
IQW Suess. 1963 21/6982	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 23/9081	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 24/6847	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 27/4133	SUESS	txM12	r	h	–	r	3
IQW Suess. 1963 28/5981	SUESS	txM3	l	h	r	–	3
IQW Suess. 1963 29/7150	SUESS	txM1	l	h	r	r	3
IQW Suess. 1963 30/9082	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 31/7175	SUESS	txM3	r	h	s	–	3
IQW Suess. 1963 32/7993	SUESS	txM12	l	h	–	r	3
IQW Suess. 1963 33/7157	SUESS	txM2	r	h	r	r	3
IQW Suess. 1963 36/42?69	SUESS	txM12	l	h	–	–	3
IQW Suess. 1963 38/260	SUESS	txM1	l	h	r	r	3
IQW Suess. 1963 39/9083	SUESS	txM12	r	h	r	r	2
IQW Suess. 1963 40	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 42/7165	SUESS	txM12	r	h	r	r	3
IQW Suess. 1963 43/7459	SUESS	txM3	r	l	r	–	3
IQW Suess. 1963 44	SUESS	txM12	r	h	r	r	3
IQW Suess. 1963 47/7469	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 5	SUESS	txM12	r	h	r	r	2
IQW Suess. 1963 50/7153	SUESS	txM12	r	h	–	r	3
IQW Suess. 1963 51	SUESS	txM12	l	h	r	r	3
IQW Suess. 1963 53/7164	SUESS	txM12	l	h	–	r	3
IQW Suess. 1963 54/6919	SUESS	txM12	r	h	–	r	3
IQW Suess. 1963 55/4270	SUESS	txM12	l	h	r	–	2
IQW Suess. 1963 56/464	SUESS	txM12	r	h	–	r	3
IQW Suess. 1963 57/5272	SUESS	txM12	r	h	r	r	3
IQW Suess. 1963 58/369	SUESS	txM12	r	h	r	r	3
IQW Suess. 1963 7/9076	SUESS	txM1	l	h	r	r	3
IQW Suess. 1963 9/9077	SUESS	txM12	r	h	r	r	3
IQW Suess. 1964 315/9128	SUESS	txM12	l	h	r	r	3
IQW Suess. 1964 316/9129	SUESS	txM12	l	h	s	b	3
IQW Suess. 1964 317/9130	SUESS	txM3	l	h	r	–	3
IQW Suess. 1964 319/9132	SUESS	txM12	r	h	–	r	3
IQW Suess. 1964 666	SUESS	txM1	l	l	r	r	3
IQW Suess. 1964 666	SUESS	txM2	l	h	–	r	3
IQW Suess. 1964 680/7143	SUESS	txM1	r	h	r	s	3
IQW Suess. 1964 680/7143	SUESS	txM2	r	h	r	–	3
IQW Suess. 1964 680/7143	SUESS	txM2	l	h	–	–	3
IQW Suess. 1964 680/7143	SUESS	txM3	r	h	–	–	3
IQW Suess. 1964 680/7143	SUESS	txM3	l	h	–	–	3
IQW Voi. 1965 3700/1003	VOI	txM12	r	h	r	s	3
IQW Voi. 1965 3725/3233	VOI	txM3	l	h	–	–	3
IQW Voi. 1965 3727/981	VOI	txM2	l	h	–	s	3
IQW Voi. 1966 5850/653	VOI	txM1	l	h	r	s	3
IQW Voi. 1966 5916	VOI	txM1	r	h	s	s	3
IQW Voi. 3280I/1 1966/74 15	VOI	txM1	l	h	s	s	3
IQW Voi. 3280I/1 1966/74 15	VOI	txM2	l	h	s	–	3

feeders, and grazers, following the "conservative" (CONS) classification of Fortelius and Solounias (2000). All statistics were computed using Systat 9.0 and Axum 6 software. Hierarchical cluster analysis with complete linkage (furthest neighbour) was applied following the standard hierarchical amalgamation method of Hartigan (1975). According to the default settings of Systat 9.0, the algorithm of Gruvaeus and Wainer (1972) was used to order the trees. The three mesowear variables, % high, % sharp and % blunt were analysed by cluster statistics. We performed three cluster analyses using three different sets of extant reference species. In Fig. 5A we have included all 52 extant species classified as "normal" and "typical" by Fortelius and Solounias (2000) (52 species model). Fig. 5B is based on the reduced set of 27 "typical" species (27 species model), and in Fig. 5C we have used the 5 extant rhinoceroses as reference species (5 species model). Chi-square corresponding probabilities were computed for each dataset, giving the probability that the null hypotheses of independence should be rejected (at an error probability of 0.05). The absolute frequencies of mesowear variables ("high", "sharp", and "round") were tested.

4. Results

In both of the studied fossil *S. hundsheimensis* (SH) populations, occlusal relief is close to 100% high. If only the sharpest cusp is evaluated following the original mesowear technique by Fortelius and Solounias (2000) (one cusp model), cusp shape scorings range between 7% (SH-SUESS) and 100% (SH-VOI) sharp, and 93% (SH-SUESS) and 0% (SH-VOI) round. No blunt cusps were identified in either sample (Table 2). Applying the two cusps model results in a slight decrease of sharp cusps in both the Süßenborn (4.5%) and Voigtstedt populations (80%) (Fig. 6A, E). Percentages of round cusps remain almost unchanged in the SH-SUESS population (93/91%), but increase substantially in the SH-VOI population (0.0/20%). When applying the two cusps model, 4.5% blunt cusps can be identified in the SH-SUESS population (Fig. 6A).

A chi-square test of combined variables of occlusal relief and cusp shape (h, s, and *r*) indicates the high probabilities of different mesowear signatures of the two studied populations ($p < 0.001$ in both of the cusp models). Similarly, high probabilities are obtained for cusp shape variables sharp and round ($p < 0.001$). If the one cusp model is tested against the two cusps model, *p*-values are typically high ($p > 0.3 < 0.9$). These data indicate the low likelihood of the models differing significantly with 0.05 error probability (Table 2).

The cluster diagrams (Fig. 5A–C) illustrate the relationships between the datasets: the closer the data, the smaller the Euclidean distance (ED) at the branching point. The dendrogram in Fig. 5A shows four main clusters: cluster 1 contains only grazers; cluster 2 comprises several mixed feeders, in addition to some grazers and one browser; cluster 3 contains the majority of the mixed feeders, three browsers, and no grazers; cluster 4 corresponds to the attrition-dominated end of the dietary spectrum and contains most of the browsers, only two attrition-dominated mixed feeders, and no grazers.

Data from the *S. hundsheimensis* samples from Süßenborn (SH-SUESS) fall into cluster 2, together with several grazers and the abrasion dominated mixed feeders. The Süßenborn rhino is linked most closely to the extant reedbuck (*Redunca redunca*, rr), a grazing African bovid that inhabits flood plains, and requires reed beds and grasses alongside a steady supply of water. The most distinctive feature in the mesowear signature that the SH-SUESS population shares with *R. redunca*, is the high percentage of high relief and round cusps (Fig. 6A, B, 7).

The SH-VOI population is classified in cluster 4, where it shares a close sub-cluster with two of the three extant Asian rhinocerotids; the Sumatran rhino (*Dicerorhinus sumatrensis*, DS) and the Indian rhino (*Rhinoceros unicornis*, Ru) (Fig. 6F, K). Close proximity with the giraffe (*Giraffa camelopardalis*, GC; Fig. 6H) and the mule deer (*Odocoileus hemionus*, OH; Fig. 6G) is also evident.

If cluster analysis is restricted to those extant comparison species recognized to represent "typical" dietary categories by Fortelius and Solounias (2000: 27 species model), the pattern becomes more distinct (Fig. 5B). Clusters 1 and 2 contain only grazers, and cluster 3 all of the mixed feeders. The fossil SH-SUESS population falls into cluster 2, where it shares a sub-cluster with the reedbuck (*R. redunca*, rr), the Roan antelope (*Hippotragus equinus*, he; Fig. 6D) and the waterbuck (*Kobus ellipsiprymnus*, ke;

Table 2
Distribution of mesowear variables in the populations of *Stephanorhinus hundsheimensis*: LOC = locality (SUESS = Süßenborn, VOI = Voigtstedt); OR = occlusal relief variables (l = absolute scorings low, h = absolute scorings high, %h = percent high occlusal relief); CS = cusp shape variables (n1 = number of specimens available in the one cusp model [original convention after Fortelius and Solounias (2000), only the sharpest cusp is included in the mesowear model], n2 = number of specimens available in the two cusps model [all cusp apices preserved are included in the mesowear model], s = sharp, r = round, b = blunt, %s = percent sharp cusps, %r = percent rounded cusps, %b = percent blunt cusps).

SPECIES	LOC	OR			CS (one cusp model)							CS (two cusps model)						
		l	h	%h	n1	s	r	b	%s	%r	%b	n2	s	r	b	%s	%r	%b
Stephanorhinus hundsheimensis	SUESS	4	41	91.1	41	3	38	0	7.3	92.7	0.0	66	3	60	3	4.5	90.9	4.5
S. hundsheimensis	VOI	0	7	100	6	6	0	0	100	0	0	10	8	2	0	80	20	0

SUESS/VOI, one cusp model: h, s, *r*	χ-square = 27.4465, df = 2, *p*-value <0.0001
SUESS/VOI, two cusps model: h, s, *r*	χ-square = 37.39, df = 2, *p*-value <0.0001
SUESS/VOI, one cusp model: s, *r*	χ-square = 23.3627, df = 1, *p*-value <0.0001
SUESS/VOI, two cusps model: s, *r*	χ-square = 32.5203, df = 1, *p*-value <0.0001
SUESS, one cusp model/SUESS, two cusps model: h, s, *r*	χ-square = 2.3698, df = 2, *p*-value = 0.3058
VOI, one cusp model/VOI, two cusps model: h, s, *r*	χ-square = 1.7841, df = 2, *p*-value = 0.4098
SUESS, one cusp model/SUESS, two cusps model: s, *r*	χ-square = 0.0134, df = 1, *p*-value = 0.9078
VOI, one cusp model/VOI, two cusps model: s, *r*	χ-square = 0.1524, df = 1, *p*-value = 0.6963

Fig. 6C). The SH-VOI population falls into cluster 4, together with the browsing only extant species. As seen in Fig. 5A, *S. hundsheimensis* is most closely linked to *D. sumatrensis* (DS), *G. camelopardalis* (GC), and *O. hemionus* (OH).

Further reducing the set of extant species to rhinocerotids (5 species model) results in only two major clusters (Fig. 5C). Cluster 1 comprises the African White rhinoceros (*Ceratotherium simum*, cs; Fig. 6I), which is the only modern grazing rhino (Janis, 1988, 1990; Janis and Ehrhardt, 1988; Estes, 1991), and the SH-SUESS fossil population. Cluster 2 comprises the four remaining extant rhinocerotids, i.e. the African Black rhino (*Diceros bicornis*, DB; Fig. 6L), the Sumatran, the Indian, and the Javan rhinoceroses (*D. sumatrensis*, DS; *Rhinoceros unicornis*, Ru; *R. sondaicus*, RS; Fig. 6M). Whereas the Indian rhinoceros can be considered as a mixed feeder, the remaining three species are browsers (Janis, 1988, 1990; Janis and Ehrhardt, 1988; Fortelius and Solounias, 2000). Furthermore, it should be noted that the two extant rhinoceroses that cluster closest to the SH-VOI population are both Asian forms.

5. Discussion

The fossil remains of the investigated *Stephanorhinus* populations originate from two fundamentally different depositional environments. The Süßenborn faunal remains have been

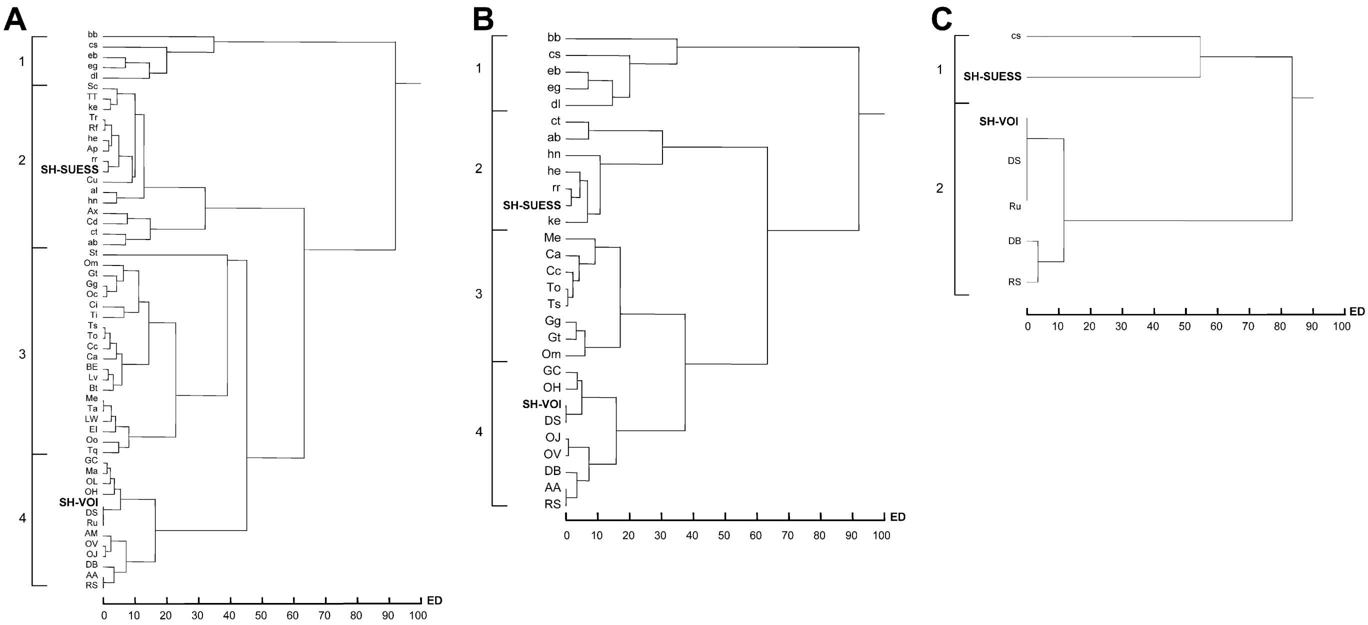

Fig. 5. Hierarchical cluster diagrams based on the reference tooth positions of upper M1-M3 according to the "extended" mesowear method (Kaiser and Solounias, 2003). ED = Euclidean distance (root-mean-squared difference). Clusters base on a set of 52 "normal" and "typical" extant species. Classification follows the conservative (CONS) scheme of Fortelius and Solounias (2000): Browsers (CONS): AA = *Alces alces*, AM = *Antilocapra americana*, BE = *Boocercus eurycerus*, DB = *Diceros bicornis*, DS = *Dicerorhinus sumatrensis*, El = *Ammodorcas clarkei*, GC = *Giraffa camelopardalis*, LW = *Litocranius walleri*, OH = *Odocoileus hemionus*, OJ = *Okapia johnstoni*, OL = *Capreolus capreolus*, OV = *Odocoileus virginianus*, RS = *Rhinoceros sondaicus*, TT = *Tragelaphus strepsiceros*; Grazers (CONS): ab = *Alcelaphus buselaphus*, al = *Alcelaphus lichtensteinii*, bb = *Bison bison*, cs = *Ceratotherium simum*, ct = *Connochaetes taurinus*, dl = *Damaliscus lunatus*, eb = *Equus burchelli*, eg = *Equus grevyi*, he = *Hippotragus equinus*, hn = *Hippotragus niger*, ke = *Kobus ellipsiprymnus*, rr = *Redunca redunca*; Mixed feeders (CONS): Ap = *Axis porcinus*, Ax = *Axis axis*, Bt = *Budorcas taxicolor*, Ca = *Capricornis sumatraensis*, Cc = *Cervus elaphus* canadensis, Cd = *Cervus duvauceli*, Ci = *Capra ibex*, Cu = *Cervus unicolor*, Gg = *Gazella granti*, Gt = *Gazella thomsoni*, Lv = *Lama vicugna*, Ma = *Antidorcas marsupialis*, Me = *Aepyceros melampus*, Oc = *Ovis canadensis*, Om = *Ovibos moschatus*, Oo = *Ourebia ourebi*, Rf = *Redunca fulvorufula*, Ru = *Rhinoceros unicornis*, Sc = *Syncerus caffer*, St = *Saiga tatarica*, Ta = *Tragelaphus angasi*, Ti = *Tragelaphus imberbis*, To = *Taurotragus oryx*, Tq = *Tetracerus quadricornis*, Tr = *Boselaphus tragocamelus*, Ts = *Tragelaphus scriptus*. Fossil populations of *Stephanorhinus hundsheimensis*: SH-SUESS = Süßenborn; SH-VOI = Voigtstedt. (A) 52 species model: Clusters based on a set of 52 "normal" and "typical" extant species; (B) 27 species model: Clusters based on a set of 27 "typical" extant species; (C) 5 species model: Clusters based on a set of 5 rhinocerotid species. All models after Fortelius and Solounias (2000).

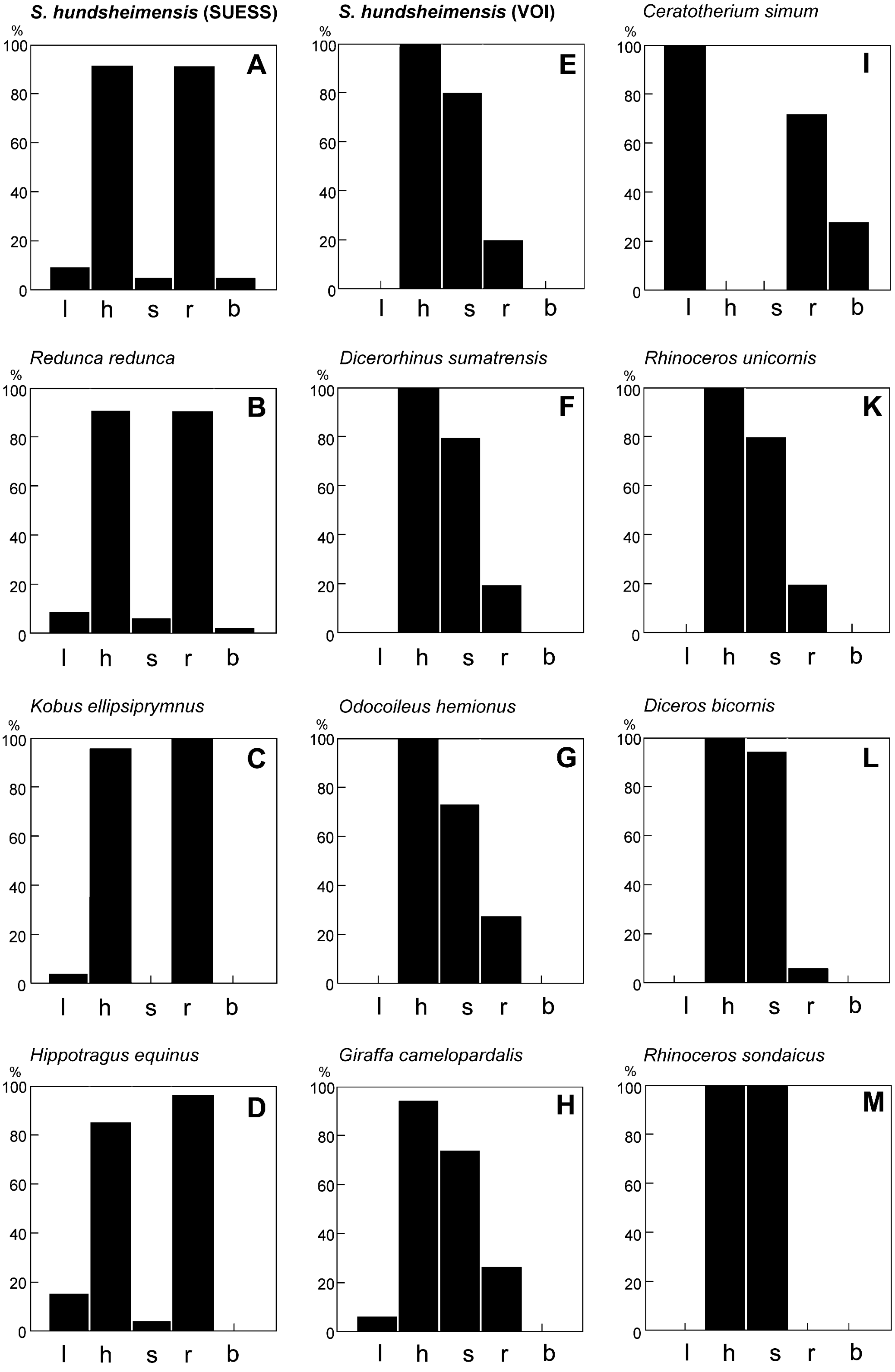
S. hundsheimensis (SUESS)
S. hundsheimensis (VOI)
Ceratotherium simum
Redunca redunca
Dicerorhinus sumatrensis
Rhinoceros unicornis
Kobus ellipsiprymnus
Odocoileus hemionus
Diceros bicornis
Hippotragus equinus
Giraffa camelopardalis
Rhinoceros sondaicus

Fig. 6. Histograms of mesowear variables % low (l), % high (h), % sharp (s), % round (r) and % blunt (b). The histograms of *Stephanorhinus hundsheimensis* (A, E) based on the two cusps model, values are given in Table 2. Comparative histograms based on data by Fortelius and Solounias (2000).

embedded in riverine gravels accumulated during a rather long, geochronologically relevant span of time. The majority of faunal elements indicate a continental type climate, with cool to cold conditions (see above). Most of the recorded species of large mammals (e.g., *Alces latifrons*, *M. savini*, *E. suessenbornensis*, *M. trogontherii*), as well as several of the micromammals (Maul, 2002), primarily inhabited open landscapes, which were prevailing in the immediate and broader environs of the site. The Voigtstedt fauna, on the other hand, lived in predominantly forested areas, rich in stagnant water bodies. Here, the fossil remains became deposited during a relatively short span of time in limnic sediments. The Voigtstedt fauna lived under warm-humid (Atlantic influenced) climatic conditions, as is indicated by several thermophilous mammal species, such as *Sus scrofa* ssp., *Mammuthus meridionalis* "*voigtstedtensis*" (= a late evolutionary stage), *Trogontherium cuvieri*, and *Petauria voigtstedtensis*.

The two palaeoenvironments are believed to have maintained a distinct composition of food resources for the corresponding ungulate faunas. The diversity in species representing a certain dietary trait should allow inference on the availability, abundance, and overall abrasiveness of the related dietary sources in the habitat under consideration. In order to resolve the dietary regimes of the studied *Stephanorhinus* populations, we used the following determined extant dietary analogues:

The SH-SUESS population is referenced by the reedbuck (*R. redunca*), which according to Gagnon and Chew (2000) is an obligate grazer with a monocot/dicot ratio of 95/5% in its diet, which does not include fruit (Fig. 7A). Cerling et al. (2003) identify the species as a "hypergrazer" with >95% grass in its diet, consisting of a variety of grass species (Skinner and Smithers, 1990), including common reed (*Phragmites communis*), foraged close to water bodies, as a major component. Estes (1991) notes that the reedbuck may also eat forbs and the leaves of woody plants in dry seasons. The mesowear signature of *R. redunca* (Fig. 5) is never linked to bulk or roughage feeders, but indicates a grazer situated at the more attrition-dominated end of the grazing spectrum. This position matches Hofmann and Stewart's (1972) classification, which characterises the species as being a fresh grass grazer.

Among the rhinocerotids, *C. simum* shares most similarities with the Süßenborn population of *S. hundsheimensis* (Fig. 5C). The African White rhinoceros lives in bush-covered, flat, short grass areas and is thus adapted to open country environments (Player and Feely, 1960). The species is recognized as a selective grazer (Janis, 1988, 1990; Janis and Ehrhardt, 1988) with a preference for short grass (Owen-Smith, 1988). Among the extant rhinocerotids, *C. simum* is the most specialised form, as it is adapted to subsist from highly abrasive and less nutritious roughage. The mesowear signature of SH-SUESS differs from that of *C. simum*, as indicated by the prevalence of low relief and the comparably high percentage of blunt cusps in the latter species (Figs. 4 and 6I). The Süßenborn *S. hundsheimensis* probably had a less abrasive feeding regime compared to that of the modern White rhino. With its brachydont teeth fresh grass grazing may have been temporarily viable for the Süßenborn *S. hundsheimensis* without wearing out teeth before reproductive age was reached. We consider the reedbuck, therefore, the more likely dietary analogue for the SH-SUESS fossil population.

The extant dietary analogue of the SH-VOI population is *D. sumatrensis*. Unfortunately, little is known about the biology of the Sumatran rhinoceros, owing to its near extinctiction in present times. The species inhabits hilly country covered with tropical rain forest and mountain moss forests. According to Van Strien (1974), *D. sumatrensis* is very flexible and can live in a wide variety of

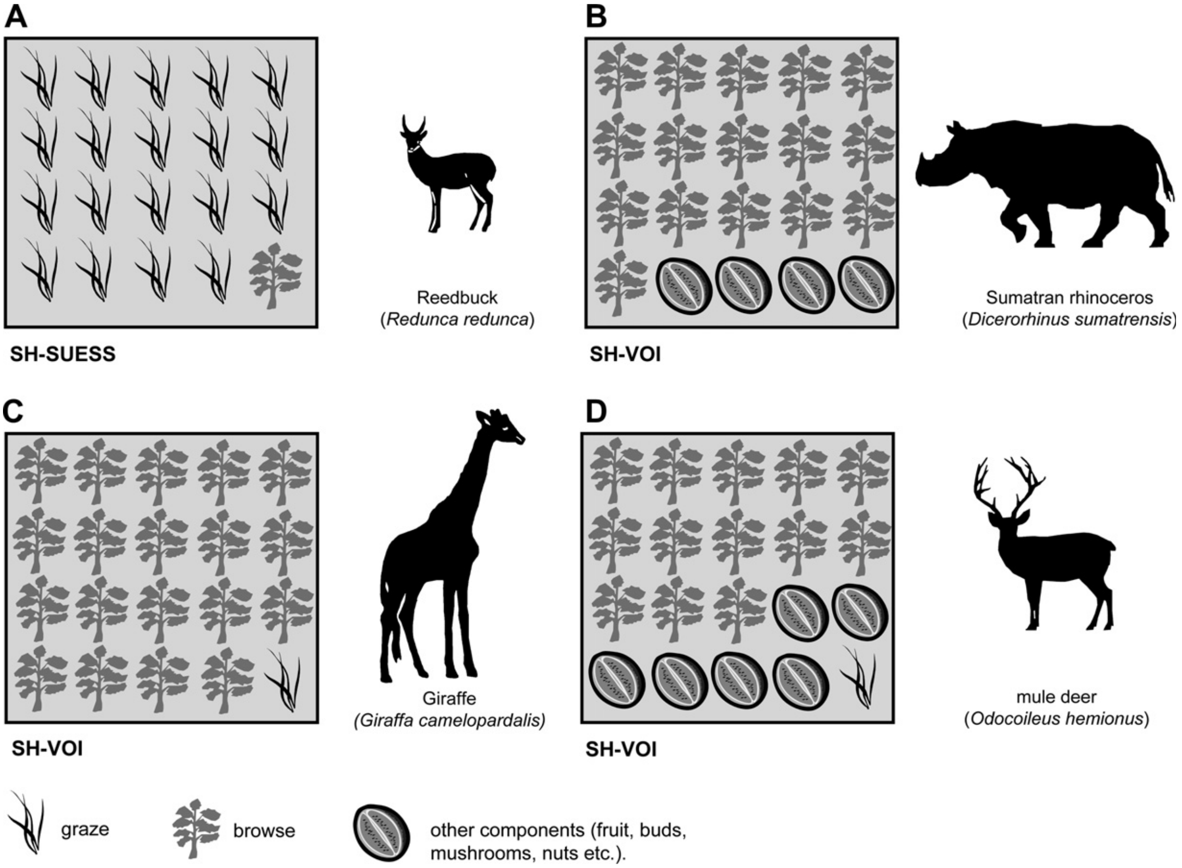

Fig. 7. Dietary regimes of the extant reference taxa. (A) The reedbuck (*Redunca redunca*) is the extant dietary analogue species of the *Stephanorhinus hundsheimensis* fossil population from Süßenborn (SH-SUESS). (B) The Voigtstedt population of *S. hundsheimensis* (SH-VOI) is referenced by the Sumatran rhinoceros (*Dicerorhinus sumatrensis*), a browser. (C) Its closest non-rhinocerotids dietary analogues are the giraffe (*Giraffa camelopardalis*) and (D) mule deer (*Odocoileus hemionus*) (see text). Dietary proportions from: Gagnon and Chew (2000) for *R. redunca*; Van Strien (1974) and Dierenfeld et al. (2000) for *D. sumatrensis*; Codron et al. (2005) for *G. camelopardalis*; Kufeld et al. (1973), Van Wieren (1996) and Nicholson et al. (2006) for *Odocoileus hemionus*. Pictograms of *D. sumatraensis* and *Odocoileus hemionus* after Mochi and Carter (1971).

habitats, from swamps at sea level to high altitudes in the mountains. However, it is never found far from sources of water and salt. The Sumatran rhino is consistently recognized as a browser (Janis, 1988, 1990; Janis and Ehrhardt, 1988; Nowak, 1999) and saplings probably form its major food source. Fruit, such as wild mangoes and figs, alongside leaves, twigs, bark, and all kinds of foods in secondary growth, including cultivated crops, are eaten (Nowak, 1999). Compared to other extant rhinos, the dietary diversity, as well as the variety of habitats, indicate that *D. sumatrensis* is a highly adaptive species.

Another rhinocerotid in the 5 species model closely linked to the SH-VOI population, is *R. unicornis* (Fig. 5C). The Indian rhino predominantly lives in alluvial plain grasslands with grass of up to 8 m tall, in addition to adjacent swamps and forests (Nowak, 1999). The dietary traits of *R. unicornis* seem to lie between the browsing rhinos and the African White rhinoceros. Tall grass makes up a large portion of the Indian rhino's diet, but, fruit, leaves, and branches are also eaten. Fortelius and Solounias (2000) classify the Indian rhinoceros as a mixed feeder in both of their extant species' classification schemes. These authors assign *R. unicornis* the status of a "no particular class species", where mesowear does not necessarily reflect the dietary classification. Subsequently, we have not used this species as an extant dietary analogue for the SH-VOI fossil rhinos.

The remaining browsers among the extant rhino species also share many similarities in their mesowear signature with the SH-VOI fossil population (Fig. 6L, M). *D. bicornis* inhabits the transitional zones between grassland and forest, where it favours the edges of thickets and extended areas of short woody growth (Schenkel and Schenkel-Hullinger, 1969). The African Black rhino is considered a browser (Janis, 1988, 1990; Janis and Ehrhardt, 1988; Estes, 1991), which feeds on twigs with woody growth in a great variety of plant species, though acacias seem to be a favourite (Nowak, 1999). A certain degree of flexibility is demonstrated by the observation that the species occasionally grazes heavily on short grasses (Skinner and Smithers, 1990, p. 573). The Javan rhinoceros (*R. sondaicus*) is found mostly in dense rain forests of low-lying areas, and is also consistently classified as a browser (Janis, 1988, 1990; Janis and Ehrhardt, 1988). Nowak (1999) identifies shoots, twigs, young foliage, and fallen fruit as major food items.

The similarities that the SH-VOI rhino population shares with all extant browsing rhinoceroses, identifies the fossil *S. hundsheimensis* from Voigtstedt as having also been a browser. As characterised by its mesowear signature, which possesses high percentages of high relief and sharp cusps (Fig. 6F), the Sumatran rhinoceros is the likeliest dietary analogue for the Voigtstedt rhino population. The closest non-rhinocerotids that are dietary analogues for the SH-VOI, *G. camelopardalis* (Fig. 7C) and *O. hemionus* (Fig. 6G), are also C3 browsers. The giraffe has up to 5% C4 (grass) intake according to Codron et al. (2007). However, Codron et al. (2005) have also recorded up to 10% C4 grass in the isotope signatures of giraffe faeces from the Kruger National Park. *O. hemionus* is a more diverse feeder, and its diet consists of more then 788 species of plants, including 202 species of trees and shrub, 484 species of forbs, and 84 species of grass, rush and sedges (Kufeld et al., 1973; Nicholson et al., 2006). The majority of its diet is browse (57% according to Van Wieren, 1996), and at least 20% is composed from fruit, lichens, mushrooms and nuts, similar to the Sumatran rhinoceros (Van Strien, 1974; Dierenfeld et al., 2000).

To summarise, the two investigated early Middle Pleistocene populations of *S. hundsheimensis* subsisted from significantly different dietary spectra. Whereas the SH-VOI population was characterised by a predominantly less abrasive browsing strategy, the SH-SUESS rhinos were feeding on much more abrasive plant resources.

6. Conclusions

The SH-VOI population reflects a particularly high diversity of dietary sources, as concluded from the feeding strategy of its dietary analogue, *D. sumatrensis*. The abrasive components eaten by the individuals of the SH-SUESS population do not appear to have occurred in large amounts in the dietary spectrum of the SH-VOI rhinos. Two possible explanations may shed light on this phenomenon: 1. The early Middle Pleistocene Süßenborn biome supported more abrasive food components, such as e.g., grass, dicots rich in phytoliths, grit loaded foliage, fruit with hard seeds, or 2. The Süßenborn *S. hundsheimensis* had to compete for a predominantly browsing dietary niche with at least one other large herbivorous species, and was therefore likely to incorporate a greater amount of less nutritious (Owen-Smith, 1997), and more abrasive, components in its diet.

The latter scenario can be discarded as the Süßenborn fauna did not comprise another rhinoceros species more adapted to browsing than *S. hundsheimensis*. Moreover, if the diet of *M. trogontherii*, whose remains have been regularly found at Süßenborn, had included a significant amount of browse, these animals, with shoulder heights of up to 4.5 m, would have exploited a different storey of the vegetation than that of the rhinos. Furthermore, the group of large sized cervids frequently recorded at Süßenborn (*A. latifrons*, *P. verticornis*, *M. savini*), can also not be taken as serious competitors for the browsing niche of the rhinos, since all of them (or in the case of *M. savini* a closely related form) were similarly abundant in the Voigtstedt fauna, but did not prevent the browsing strategy of the SH-VOI population.

In summary, the mesowear traits of both of the SH-SUESS und the SH-VOI populations must be interpreted as biome-specific signals of food availability. As such, they reflect dry and predominantly open environmental conditions with grassland vegetation at the site of Süßenborn, and extended dense to open forests in the case of Voigtstedt. This mesowear study has produced the most pronounced dietary variability ever established for a single herbivorous ungulate species, which ranges from an attrition dominated grazing regime at Süßenborn, to a pronounced browsing one at Voigtstedt. Based on these data, we have determined that the European early Middle Pleistocene rhinoceros *S. hundsheimensis* was not specific in its dietary traits, but rather a highly flexible feeder.

For the majority of the period that *S. hundsheimensis* was present in the western Palaearctic (c. 1.4/1.2–0.6/0.5 Myr; see 3.1.), it was the only rhinocerotid species in corresponding mammal faunas. Throughout most of the given time span, contemporaneous members of the mammoth evolutionary line were represented in corresponding faunas by two different species (late forms of *M. meridionalis* and *M. trogontherii*), which replaced each other by paralleling the changes of habitat conditions (detailed discussion in Lister et al., 2005). In contrast, the Hundsheim rhinoceros, as an ecological generalist, was adapted to the whole range of habitats occupied by both of the aforementioned mammoth species. Thus, *S. hundsheimensis* was undoubtedly the most ecologically tolerant rhinoceros of the Palaearctic Plio-Pleistocene. For more than half a million years it ranged from the Mediterranean coast to Northwest Europe, and from the Iberian peninsula to Transcaucasia, the Levant, the Caspian lowlands, and beyond (sketch map in H.-D. Kahlke, 1969b: p. 706). Due to the lack of any sympatric rhino, or other species seriously competing for the available food resources, the generalistic feeding behaviour of *S. hundsheimensis* proved to be the most successful subsistence strategy under the given faunistic circumstances.

The retreat of *S. hundsheimensis* only began when more specialised rhino species appeared in the western Palaearctic. After a period of sympatry, documented in the faunal spectra of several early Middle Pleistocene sites, such as Soleilhac (France), Mauer and Mosbach 2 (Germany), as well as Kolkotova Balka and Sukleya near Tiraspol (Moldova), the so-called forest rhinoceros, *Stephanorhinus kirchbergensis*, started to replace *S. hundsheimensis* in temperate environment faunas (Beljaeva and David, 1975; Guérin, 1980, p. 972; Fortelius et al., 1993, p. 118; Schreiber, 2005). Its migration into the western Palaearctic was paralleled by the appearance of a new proboscidean in Europe, the straight-tusked elephant *Elephas* (*Palaeoloxodon*) *antiquus* (detailed data in Lister, 2004), which roamed as a specialised browser in the same type of habitats as *S. kirchbergensis*. The *kirchbergensis*-rhino was a very large animal with long legs, a high head posture, and moderately hypsodont molars (Fortelius et al., 1993), and was, therefore, also clearly adapted to a browsing lifestyle. It exploited a different storey of vegetation than the straight-tusked elephant, but browsed at the same level as *S. hundsheimensis*. Thus the specialised *S. kirchbergensis*, with its more effective browsing abilities, became a serious food competitor of *S. hundsheimensis* in forested habitats, which formed an important part of the Hundsheim rhino's ecological range.

During cooler to colder periods, *S. hundsheimensis* was replaced by *Stephanorhinus hemitoechus*, another highly specialised rhino, over wide areas of the western Palaearctic. The latter species, which probably originated in Asia, appeared for the first time between 0.6 and 0.5 Myr, as recorded by the Mosbach 2 gravels (Fortelius et al., 1993, p. 118f.; faunal list in Hemmer et al., 2003). Its anatomy, especially its relatively short limbs, hypsodont molars, and its low-slung cranium (Fortelius et al., 1993), indicate its closer affinities to open grasslands and abrasive food resources. The origins of such specialised forms of rhinoceroses might have been ultimately caused by the development of the 100 ka periodicity in the global climatic record (Lisiecki and Raymo, 2005: Fig. 4), which led to a longer lasting stability in the resulting biomes compared to the preceding 41 kyr span of time. *S. hemitoechus*, also called the steppe rhino, appeared to successfully compete for food resources in open landscapes, which over hundreds of millennia had formed an essential part of the Hundsheim rhino's ecological range.

Whereas the described flexible feeding style of western Palaearctic *S. hundsheimensis* was an effective enough subsistence strategy when no specialised food competitors were around, the situation changed dramatically after 0.6 Myr BP with the appearance of the new species of rhinoceroses, *S. hemitoechus* and *S. kirchbergensis*. For the generalist *S. hundsheimensis*, such bilateral interference produced detrimental effects in practically all of its habitats, owing to the superiority of both the recently arrived rhinoceros species due to their specialised feeding strategies. At present, it is not well understood whether or not this interference actually led to morphological or ecological character displacement (Dayan and Simberloff, 2005) in western Palaearctic *Stephanorhinus*-populations of early Middle Pleistocene age. Body size changes in *S. hundsheimensis*, *S. kirchbergensis*, and *S. hemitoechus*, as recently described by Lacombat (2006a, 2006b) from Mediterranean Europe and the French Massif Central, might be linked to this kind of evolutionary process.

To conclude, we propose that the successful competition of the two forms of advanced rhinoceroses (*S. hemitoechus*, *S. kirchbergensis*), i.e. the bilateral interference of their ecological ranges with that of *S. hundsheimensis*, was the main reason for the extinction of the latter during the early Middle Pleistocene. The invasion of these new rhinoceroses, specialised as grazers and browsers, turned the advantage of the Hundsheim rhino's generalism into a major disadvantage. Although the impact of only one single highly specialised species might have been compensated for by a generalist feeding strategy, several competing specialists increased the disadvantages of such a feeding strategy dramatically. In the described case of western Palaearctic rhinoceroses, the appearance of two phylogenetically closely related rhinos with different but specialised feeding strategies, ended the long period of existence of an impressive ecological generalist with unique flexible feeding traits.

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