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Pollen and spores from molar folds reflect food choice of late Pleistocene and Early Holocene herbivores in The Netherlands and the adjacent North Sea area

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ABSTRACT

Molars of eight large herbivore species (*Megaloceros giganteus, Cervus elaphus*, *Rangifer tarandus, Alces alces, Bison priscus, Ovibos moschatus, Coelodonta antiquitatis* and *Stephanorhinus kirchbergensis*) were collected *ex situ* from Pleistocene and Holocene sands dredged in the North Sea, and from Dutch inland sites. Folds in many molars contained compacted masticated plant remains, and also microfossils. We identified pollen, spores, and non-pollen palynomorphs and discuss and interpret food preferences, represented flowering seasons, or parts of flowering seasons, and we discuss effects of changing vegetation composition in relation to climate and age of the molars, based on the pollen spectra. Various confounding factors have contributed to the recorded pollen composition, but nevertheless the pollen spectra show valuable aspects of vegetation composition, food choice, age, and landscapes, from subarctic open areas to interglacial forest. Ecological and statistical analysis of the results shows dietary differences between the mammal species analyzed.

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1. Introduction

The mammoth steppe ecosystem contained a combination of plant and animal species that does not occur anywhere today. It was characterized by diverse megafauna of mostly herbivorous species (Guthrie, 1990). Food choice is an interesting and crucial part of a species' ecology, and understanding the diet of animals within an ecosystem helps to better understand the system (Owen-Smith, 2002). Hofmann (1989) classified extant ruminants, based on extensive dietary work on fresh specimens into concentrate selectors (selecting high quality food, rich in plant cell contents), grass/roughage eaters (selecting low quality food, rich in plant cell wall, cellulose) and intermediate, or mixed feeder types. There is a link with body size: the bigger the ruminant, the more suited is its digestive tract to process large volumes of low quality diet. Most large ruminants (e.g. bison) are classified as grass/roughage eaters, while most medium sized species of deer (including reindeer and red deer) are intermediate types. The moose is an exception, as it can be clearly classified as a concentrate selector, despite its large body size (Hofmann, 1989). Herbivores actively select certain plants from a given area based on their physiological needs and past experiences. Even large grazing animals, classified as roughage eaters, do not indiscriminately graze all plants (e.g. Villalba and Provenza, 2009; Kleynhans et al., 2011). Here, we use observations on fossil molar contents of ruminants and non-ruminants to assess fossil mammal diets in the mammoth steppe ecosystem and during the Early Holocene.

In 2011 an artificial peninsula called 'Zandmotor' was created along the shoreline of The Netherlands south of The Hague. For that purpose late Pleistocene and Early Holocene sediments were dredged from the relatively shallow North Sea bed. The new land

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functions as a coastal reinforcement. 'Maasvlakte 2' is a westward extension of the port of Rotterdam and it was also built from dredged sandy North Sea deposits. Three sediment units were dredged: from marine Holocene/recent sandbars, from Early Holocene deposits, and from underlying (predominantly) Late Pleistocene sandy sediments. The dredged sediments were originally deposited in ancient Rhine and Meuse deltas (Laban and Rijsdijk, 2002; van der Valk et al., 2011; Langeveld, 2013; Kuitems et al., 2015) when, worldwide, sea levels were much lower than today and therefore the southern part of the North Sea area was dry land.

Maasvlakte 2 and Zandmotor became localities for collecting fossils by citizen scientists, including mammal bones from Pleistocene (Weichselian) and Early Holocene sediments (Mol et al., 2006, 2008; van der Valk et al., 2011). The fauna was dominated by large herbivores, such as woolly mammoth, woolly rhinoceros, steppe bison, giant deer and wild horse. Radiocarbon dated material shows that representatives of this fauna lived between c. 50,000 and 25,000 BP when North West Europe was part of the mammoth steppe ecosystem (Mol et al., 2006, 2008).

A study of the botanical infill of folds (infundibula) in a molar of a mid-Weichselian giant deer from Zandmotor yielded well-preserved pollen and shed light on the diet of giant deer (van Geel et al., 2018). For the present study we selected a number of species to study the pollen contents of molar infundibula. The selected species were the ruminants *Megaloceros giganteus* (giant deer), *Cervus elaphus* (red deer), *Rangifer tarandus* (reindeer), *Alces alces* (moose), *Bison priscus* (steppe bison) and *Ovibos moschatus* (muskox), and the non-ruminants *Coelodonta antiquitatis* (woolly rhinoceros) and *Stephanorhinus kirchbergensis* (forest rhinoceros; the fossil record of this species ended shortly after the Eemian interglacial). We borrowed molars of these species from various private collections and museums in The Netherlands. Most molars were from North Sea deposits but some of the molars were recovered from dredged inland river deposits (Table 1). The molars were identified to species level through comparison with molars of identified skeletons in the reference collection of the Natural History Museum Rotterdam (NMR). Botanical material present in infundibula was sampled for the analysis of pollen and non-pollen palynomorphs (NPP). Quantities of organic material were not sufficient for macrofossil analysis and radiocarbon dating.

Pollen and spore records from cored lake sediments and peat deposits show regional trends of vegetation changes. The vegetation composition in The Netherlands during mid-Weichselian interstadials is recorded in detailed pollen records (Brinkkemper et al., 1987; Ran, 1990). For the vegetation history of the Lateglacial period in The Netherlands we refer to Hoek (1997) and for the Holocene to van Geel et al. (1981).

Palynologists are accustomed to the fact that wind-pollinated taxa produce high amounts of pollen, and that such taxa therefore are over-represented compared to the relative abundance of the source plants in the vegetation. In contrast, insect-pollinated taxa produce relatively low amounts of pollen and are thus underrepresented. A sediment sample or a peat sample normally represents a multi-annual mixture of pollen deposition. The interpretation of the presence and frequencies of pollen and spore taxa from molar infundibula in terms of past vegetation cover is different, and the pollen records will be biased for several reasons. For the interpretation of our results we have to keep in mind that there remain some basal, still unsolved questions about the indicative value of such samples (chronology, vegetation composition, phenology, food choice, age of the material).

2. Ecology of selected species

2.1. *Megaloceros giganteus (Blumenbach, 1799)* - giant deer

The extinct *M. giganteus* could attain a maximum body weight of 600–700 kg (Moen et al., 1999); this matches modern moose. The fossil record can be traced back to at least the early Late Pleistocene in Europe (Kahlke, 1999). The North Sea has yielded numerous specimens, some of which were radiocarbon dated. The youngest is 36,300 ± 1100 BP and the oldest is >45,000 BP. The species is known from both glacial and interglacial (or interstadial) deposits (Lister and Stuart, 2019). Chritz et al. (2009) studied stable isotopes in dentition and concluded a grass- and forb-based diet, supplemented by browsing. Rivals and Lister (2016) and Saarinen et al. (2016) studied meso- and microwear and concluded that *M. giganteus* had a wide range of dietary behaviour including grazing, leaf browsing and mixed feeding, but generally tending towards mixed feeding and grazing. The diet of one specimen, based on pollen in molar folds, was reviewed by van Geel et al. (2018): it was completely dominated by *Artemisia*, indicating that the animal foraged in a steppe environment and may have preferred to eat *Artemisia*, which contain a high level of mineral nutrients such as calcium and phosphorous (Klein, 1965; Ashraf et al., 2010; van Geel et al., 2018).

2.2. *Cervus elaphus Linnaeus, 1758* - red deer

C. elaphus is very flexible in its choice of habitat and diet. Hofmann (1989) classifies it as a mixed feeder. This large deer (75–340 kg; Nowak, 1991) is known from both glacial and interglacial fossil deposits since at least the Middle Pleistocene (Rivals et al., 2009). The Dutch and North Sea fossil record includes many Early Holocene occurrences, especially worked antlers from the Mesolithic (e.g. Louwe Kooijmans, 1970; Mol et al., 2008). There are no Late Pleistocene radiocarbon dates, but the state of fossilisation of some of the red deer material suggests that the species was part of the Late Pleistocene fauna as well (Mol et al., 2008). *C. elaphus* currently has a very extensive range, including much of Europe, Asia and North America. It occurs in various habitats, ranging from coniferous and deciduous forests to open grasslands, heathlands, moorlands and even semi-arid environments. Its diet reflects its broad habitat range and varies from grass to sedges, ferns, mosses, lichens, fungi, twigs, nuts, shoots and bark of trees. It usually varies from season to season and whenever possible includes both herbaceous and browsed material (Straus, 1981; Nowak, 1991; Chen et al., 1998; Clutton-Brock and McIntyre, 1999; Gebert and Verheyden-Tixier, 2001; Suter et al., 2004; Augustyniak, 2010; Ligi and Randveer, 2012; Berlioz et al., 2017). A similar flexibility in the diet of *C. elaphus* was found through isotopic and dental wear analyses for Pleistocene populations (Drucker et al., 2003; Rivals et al., 2009, 2010; Saarinen et al., 2016).

2.3. *Rangifer tarandus (Linnaeus, 1758)* - reindeer

R. tarandus is one of the large mammals that lived on the mammoth steppe and it survived into the Holocene. Hofmann (1989) classifies it as a mixed feeder. This moderately sized deer (body weight 60–318 kg; Nowak, 1991) has a fossil record that starts at least in the Early Pleistocene. It was common in the European Weichselian, especially during the Magdalenian period. Its range extended from northern Spain into North America (Kahlke, 1999). Radiocarbon dates from The Netherlands and the North Sea range from >45,000 BP till 39,000 + 700, −600 BP and an isolated date at 29,460 ± 250 BP (Glimmerveen et al., 2006). Today, reindeer populations may migrate for up to 1000 km between

Table 1
Code and numbering of samples, collection codes, location of sites, and molar positions in jaws.

Molar list

Code	Collection	Location	Molar
Mg01	NMR999100013942	ZM	M3 sup. dex.
Mg02	NMR999100013942	ZM	M3 sup. dex.
Mg03	HM0017	ZM	premolar indet.
Mg04	BKO2866	MV2	M1 sup. sin.
Mg05	MKR AH9	MV2	M2 sup. sin.
Mg06	16MV037	MV2	m2 inf. sin.
Mg07	18MV013	MV2	m2 inf. sin.
Mg08	HTSM00806	MV2	m3 inf. Dex.
Mg09	BDW001	EG	complete maxilla
Mg10	RCEWB2	WB	M3 sup. sin.
Mg11	NMR99900008893	KK	mand. p4 m3
Ce01	RVB185	ZM	M2 sup.sin.
Ce02	RVB256	ZM	m1 inf.dex.
Ce03	WVW003	ZM	p4 sub. Dex
Ce04	IVM205	ZM	M1 sup. dex.
Ce05	IVM190	ZM	P4 sup. dex.
Ce06	HM0018	ZM	m3 inf. sin.
Ce07	DDU005	ZM	M2 sup. sin.
Ce08	RVB291	MV1	m3 inf. dex.
Ce09	WPE002	MV2	M1 sup. dex.
Ce10	HKV694	MV2	m3 inf. dex.
Ce11	DB2566	MV2	M2 sup. sin.
Ce12	HKV498bi	MV2	M2 sup. sin.
Ce13	HKV498bu	MV2	M2 sup. sin.
Ce14	DB1456	MV2	M1 sup. sin.
Ce15	17MV047	MV2	m1 or m2
Ce16	HVK549	MV2	p4 inf. sin.
Ce17	HVK176A	HvH	p2 sup. dex.
Rt01	IVM450	ZM	M3 sup. dex.
Rt02	IVM172	ZM	M3 sup. dex.
Rt03	DDU006	ZM	M2 sup. sin.
Rt04	WVW002	ZM	p4 inf. sin.
Rt05	HVK369	ZM	M3 sup. sin.
Rt06	HM0006	ZM	P3 sup. dext.
Rt07	HM0008	ZM	M2 sup. dext.
Rt08	HVK176	HvH	m2 inf. sin.
Rt09	NMR999100000500	WE	mandibula m1-m2 sin.
Rt10	BHO001/1	HV	Mandibula sin. with p2/p3/p4/m1/m2/m3
Rt11	BHO001/2	HV	Mandibula sin. with p2/p3/p4/m1/m2/m3
Aa01	HVK183	ZM	M2 sup. sin.
Aa02	NatMusBrabant42638	OS	mandibula p2-m3 dex.
Aa03	NMR999100008377	PH	mandibula p2-m3 dex.
Bp01	NMR999100009684	ZH	mandibula m1-m3
Om01	DDU004	ZM	m3 inf. dex.
Ca01	DDU003	ZM	P3 sup. dex.
Ca02	DDU002	ZM	M1 sup. dex.
Ca03	DDU001	ZM	DP4 sup. dex.
Ca04	RVB300	ZM	M2 sup. dex.
Ca05	NMR999100007608	MV2	M3
Ca06	NMR999100000487	WE	P2 dex.
Ca07	NMR999100008760	ZR	M3 sin.
Sk01	NMR999100008752	ZH	M3 dex.

Location	Location name	Latitude	Longitude
ZM	Zandmotor	52°03′19″N	4°11′05″E
MV1	Maasvlakte-1	51°57′24″N	4°01′25″E
MV2	Maasvlakte-2	51°57′24″N	4°01′25″E
HvH	Hoek van Holland	51°59′25″N	4°06′45″E
EG	Eurogeul	52°10′28″N	3°23′16″E
OS	Oosterschelde	51°34′26″N	3°56′54″E
WE	Westerschelde-Ellewoutsdijk	51°23′10″N	3°48′42″E
WB	Woerden-Breeveld	52°06′11″N	4°55′24″E
ZH	Zwolle-Haerst	52°33′40″N	6°08′54″E
KK	Kampen-Kattendiep	52°35′11″N	5°48′31″E
HV	Heelweg-Varsseveld	51°59′15″N	6°29′04″E
ZR	Zevenaar-Rhederlaag	51°59′24″N	6°01′47″E
PH	Punthorst	52°35′22″N	6°16′23″E

summer grounds in the tundra and winter grounds in forested areas. They feed on a variety of plants, including lichens and leaves of shrubs and fine twigs (Nowak, 1991; Augustyniak, 2010). Using dental mesowear analysis, Saarinen et al. (2016) found that Pleistocene reindeer browsed for soft forage even in more open vegetation of the mammoth steppe. Using carbon and nitrogen isotopes, Fox-Dobbs et al. (2008) reconstructed Pleistocene reindeer diet in eastern Beringia as consisting mostly of lichens, mosses and fungi. Utilizing both meso- and microwear, Rivals et al. (2010) and Rivals and Semprebon (2017) concluded that reindeer from the Brown Bank in the North Sea were mixed feeders, possibly with a more abrasive diet than modern populations.

2.4. *Alces alces (Linnaeus, 1758) - moose*

A. alces is the largest extant deer species with a body weight of 200–825 kg. Hofmann (1989) classifies it as a concentrate selector. It occurs in the northern parts of Eurasia and North America (Nowak, 1991). Fossil moose are known from The Netherlands and the North Sea deposits. They date from the Early Holocene until late medieval time (Walch, 2000; van Geel and van Wijngaarden-Bakker, 2002; Mol et al., 2006; Spinney, 2018), but there is one date of 44,560 + 1840/-1490 BP (Mol et al., 2008). Moose are rather specialized feeders that live in forested areas. They mainly feed on willow (*Salix* spp.), but they also forage on water plants and can swallow with their head submerged (Dungan and Wright, 2005; Shipley, 2010). Rivals et al. (2010) studied meso- and microwear of *A. alces* from the North Sea (Brown Bank) and reconstructed a strictly non-abrasive browsing diet, comparable to the modern diet. Saarinen et al. (2016) reached the same conclusion.

2.5. *Bison priscus Bojanus, 1827 - steppe bison*

B. priscus was a characteristic component of the *Mammuthus-Coelodonta* Faunal Complex (Kahlke, 1999). Recent genetic evidence showed that there were two distinct types of *Bison* in the Late Pleistocene of Europe, including the North Sea plain (Soubrier et al., 2016; Grange et al., 2018), but they appeared to be morphologically indistinguishable and therefore we here use *B. priscus*. They were large animals, with a body weight of around 1000 kg (Boeskorov et al., 2014). A radiocarbon date of 45,350 + 2400/-1850 BP (Mol et al., 2008) places *B. priscus* in the Late Pleistocene of the North Sea area. *Bison* has a very rich fossil record across all of its geographical range. It appears to be the most common taxon from the North Sea, but paleoecological data on the diet are scarce. Guthrie (1990) provided data on North American *B. priscus*. Using cuticle analysis of plant material obtained from molar infills and mesowear analysis, he concluded that these animals were grazers, with grasses making up 80–90% of their diet (followed by other herbs). Rivals et al. (2010) studied microwear of *B. priscus* from the North Sea (Brown Bank) and concluded that they were primarily grazers, or mixed feeders with a grass-dominated diet. Saarinen et al. (2016) studied mesowear of fossils from the United Kingdom and Germany and reconstructed mixed feeding diets with a significant component of grass.

2.6. *Ovibos moschatus (Zimmermann, 1780) - muskox*

O. moschatus weigh 200–410 kg. Hofmann (1989) classifies it as a mixed feeder. Their fossil record in Europe starts in the late Middle Pleistocene (Kahlke, 1999). Together with reindeer, muskox is one of the few large mammals of the mammoth steppe that survived the end of the Pleistocene in Eurasia with the youngest radiocarbon date from the Taimyr Peninsula at 2900 ± 60 BP (MacPhee et al., 2002). Today they occur only on arctic tundra, with a preference for moist habitats in summer and windy higher areas (thus with little snow cover) in winter. Currently they occur in parts of the far north of Eurasia, where they were reintroduced in the 20th century, e.g. in Norway, the Taimyr Peninsula, Yakutia, North America and Greenland (Nowak, 1991). Remains of *O. moschatus* are rare in The Netherlands and the North Sea area; they have been dated to the Late Pleistocene (Mol et al., 2006). Modern *O. moschatus* feed primarily on grasses, sedges and dwarf willows. They are not very selective feeders and in winter they do not travel extensively to suitable foraging grounds (Klein, 1991; Oakes et al., 1992; Klein and Bay, 1994; Kristensen et al., 2011). Carbon and nitrogen isotopic analysis of fossil *O. moschatus* from the Holarctic suggests a diet flexibility that followed changes in precipitation (Raghavan et al., 2014).

2.7. *Coelodonta antiquitatis (Blumenbach, 1799) - woolly rhinoceros*

C. antiquitatis was a characteristic component of the *Mammuthus-Coelodonta* Faunal Complex (Kahlke, 1999). It was a large animal (over 2000 kg) and it occurred over a large range, stretching from Great Britain and Spain across Europe to northeast Siberia, northern China and Mongolia; it never reached North America (Stuart and Lister, 2012). It is a common species in Late Pleistocene fossil assemblages, though never as common as woolly mammoth, steppe bison and wild horse. Its fossil record extends at least back to the late Middle Pleistocene (Kahlke, 1999). Its range contracted eastwards from 35 ka and it went extinct ca. 14 ka (Stuart and Lister, 2012). A radiocarbon date from the North Sea places the species in the Late Pleistocene at 39,910 + 1070/-950 BP (Mol et al., 2006). Much of its ecology has been studied from permafrost and natural paraffin wax preserved carcasses, including stomach contents and molar infills. Both skeletal and soft tissue morphology (Stuart and Lister, 2012) as well as these food remains (Boeskorov et al., 2011) characterize *C. antiquitatis* as a true grazer, well adapted to the tough and dry mammoth steppe vegetation. While mesowear analysis from the North Sea (Brown Bank) and adjacent areas supports this, microwear analysis of North Sea material suggests periodical inclusion of some woody components in its diet (Rivals et al., 2010; Saarinen et al., 2016).

2.8. *Stephanorhinus kirchbergensis (Jäger, 1839) - forest (or Merck's) rhinoceros*

S. kirchbergensis was a large animal with relatively long legs (Fortelius et al., 1993). It is considered an interglacial species with a fossil record in Europe starting in the Middle Pleistocene at 0.6 Ma and ending shortly after the Eemian interglacial (van der Made, 2010; Mol and van der Plicht, 2012). Analysis of plant macroremains trapped in molar folds and mesowear from specimens recovered from Germany and Russia indicates that the species was a mixed feeder that tended to browse on foliage of trees or shrubs, but also included grasses and herbs in its diet (van der Made and Grube, 2010; van Asperen and Kahlke, 2015; Kirillova et al., 2017). Based on mesowear analysis, Saarinen et al. (2016) reconstructed a browsing diet for this species.

3. Material and methods

The molar folds of about half of the screened specimens appeared to be empty or too poor in pollen to get sufficient microfossil spectra, while some other molar samples contained badly preserved microfossils. Such samples had to be discarded. Molar folds of *Megaloceros giganteus* (Mg), *Cervus elaphus* (Ce), *Rangifer tarandus* (Rt), *Alces alces* (Aa), *Bison priscus* (Bp), *Ovibos*

moschatus (Om), *Coelodonta antiquitatis* (Ca) and *Stephanorhinus kirchbergensis* (Sk) contained plant remains and microfossils were successfully retrieved. Fifty-two samples were analyzed for pollen, spores and non-pollen palynomorphs (NPP; van Geel, 2001); the microscope slides are stored in the collection of the Natural History Museum Rotterdam, accession number 19–112. For practical reasons we abbreviate the zoological species names in Table 1, in the plotted DCA, and in the text below. Table 1 shows the numbering of samples, the collection codes, the location of the sites, and the molar positions in the jaws.

Sampling of the botanical material occurred by using clean preparation needles in order to separate the plant remains from the molar folds. The obtained palynological 'mini-samples' were collected in small beakers and a standard pollen preparation method was applied (Faegri and Iversen, 1989). Microscopic analysis was applied using Beug (2004) and Punt et al. (1976–2009) for difficult pollen identifications. Detrended Correspondence Analysis (DCA; Hill and Gauch, 1980) was applied in PAST 3.16 (Hammer et al., 2001) as an addition to a conventional ecological interpretation.

4. Results

In most cases more than three hundred pollen grains and spores were counted per sample, but for some molars that sum could not be reached. Calculation of percentages, as shown in Fig. 1A–D, was based on sums of pollen grains and spores of vascular cryptogams. NPP frequencies were also calculated as percentages of those sums. The diagrams show the percentages of pollen grains, spores and NPP. Observations of monospecific aggregates of pollen grains (each aggregate was recorded as 1 pollen grain) are shown in the diagram with a black square. Such aggregates (Fig. 2A–D) may indicate that flowering plants with unripe pollen grains were consumed, thus providing extra information about the herbivore diets.

5. Interpretation

5.1. Megaloceros giganteus

Mg03, Mg08, Mg10 and Mg11 show relatively high *Betula* percentages. In Mg08 and Mg11 aggregates of *Betula* pollen show that flowering birch was consumed. *Alnus* and *Corylus* with some *Tilia* and *Ulmus* pollen in Mg11 suggest that the sample may represent post-depositional Holocene contamination, but an upper Eemian or an early Weichselian interstadial age cannot be excluded. *Artemisia* and Asteraceae sf. Asteroideae are common in most of the Mg-samples. Other light-demanding taxa (Poaceae and a variety of herbaceous taxa, like Caryophyllaceae, Chenopodiaceae, *Filipendula*, *Linum, Plantago, Thalictrum* and *Helianthemum*) are of regular occurrence. *Humulus* was also consumed, considering the presence of aggregated *Humulus* pollen in Mg04. *Equisetum* shows high values in Mg07 and *Osmunda* was very common in Mg03, but the absence in other *Megaloceros* samples shows that they were not regular components of the giant deer food choice. Pollen of Poaceae is present in all samples analyzed, but always in low percentages; only in Mg05 a slightly higher percentage and an aggregate of unripe grass pollen was observed. This matches work based on isotopes and tooth wear that suggests mixed feeding for *M. giganteus*. The dominance of *Artemisia,* that was observed by van Geel et al. (2018) for one giant deer molar, was found here in other molars as well, also with aggregates of unripe *Artemisia* pollen. This provides further evidence of *M. giganteus* selecting *Artemisia* as a food plant. Saarinen et al. (2016) found that *M. giganteus* was commonly associated with rather open vegetation, but also occurred in localities relatively rich in arboreal pollen.

5.2. Cervus elaphus

Based on the relatively high numbers of *Corylus* and *Alnus* and ferns, samples Ce07, Ce11, Ce 12, Ce13, and Ce14 may point to a Holocene (but pre-inundation) age. The other Ce-samples are probably of Pleistocene age. Remarkable are Ce04 and Ce10 with high *Betula* values. A *Betula* aggregate in Ce04 points to consumption of flowering birch. Ce05 contained a very large number of *Helianthemum* and aggregates show that *Helianthemum* was consumed. The quantity of *Humulus* and *Impatiens* in Ce06 probably points to consumption, while the pollen record of Ce06, Ce15 and Ce16 may point to *Urtica* as a food plant. We suppose that Ce08 and Ce12 point to *Filipendula* as a food plant, while Ce11 may indicate that *Equisetum* was eaten. Ce08 and Ce14 point to consumption of *Symphytum*. Asteroideae, Apiaceae, Poaceae and Cyperaceae were common in many samples. Saarinen et al. (2016) found that *Cervus elaphus* was clearly associated with both open and closed forest environments.

5.3. Rangifer tarandus

Most samples show relatively low tree pollen values, pointing to a sub-arctic open landscape. In Rt08 only few individual *Betula* pollen grains were recorded, but an aggregate of *B. nana* shows consumption of dwarf birch.

Rt05 and Rt07 show rather high *Salix* pollen values and, considering the composition of the pollen spectra of those two samples this *Salix* pollen may well have been produced by dwarf willows. *Artemisia* is common in most samples; Rt03 and Rt08 yielded aggregates of *Artemisia*. Aggregates in the two samples with high values of Cyperaceae (Rt02 and Rt06) point to a bias (consumption and over-representation in the pollen spectra) of flowering Cyperaceae. Several samples show rather high records of *Helianthemum*, and three even show aggregates, indicating a preference for *Helianthemum* as a food source. According to Milotic et al. (2017) herbivores in the landscape even stimulate the growth and expansion of *Helianthemum*.

The frequencies of *Pedicularis palustris*-type in the Rt-samples (absent in almost all other samples) point to *Pedicularis* (*P. lapponica*?) as a preferred species for consumption. Some other taxa worth to be mentioned are *Centaurium*, *Papaver rhoeas*-type and *Polemonium* in Rt09, *Triglochin* in Rt11 and *Silene dioica*-type in Rt07. Poaceae pollen generally is slightly more common in *R. tarandus* than in *M. giganteus*, but lower than in *C. elaphus*, suggesting that grasses were part of the reindeer diet, but not to a very large extent. The pollen data match studies on meso- and microwear of reindeer specimens from the North Sea. Based on pollen records Saarinen et al. (2016) found that *Rangifer tarandus* was evidently associated with open environments.

5.4. Alces alces

Considering the amount of tree and shrub pollen (*Betula*, *Pinus*, *Corylus*, *Alnus, Taxus, Tilia, Ulmus, Frangula alnus*) and fern spores, and taking into account the geological information of the dredged deposits, Aa01 and Aa02 are of Early to mid-Holocene age. An aggregate of *Alnus* pollen in Aa02 probably points to consumption of *Alnus*. Aa03 is older than the other two samples (maybe Allerød interstadial, or a Preboreal age), because *Alnus* and *Corylus* are almost absent, while it shows high *Pinus* pollen percentages and even a *Pinus* tracheid pit.

Aa03 shows indicators of open water (*Nymphaea*, including

Microfossils from molars, part 1

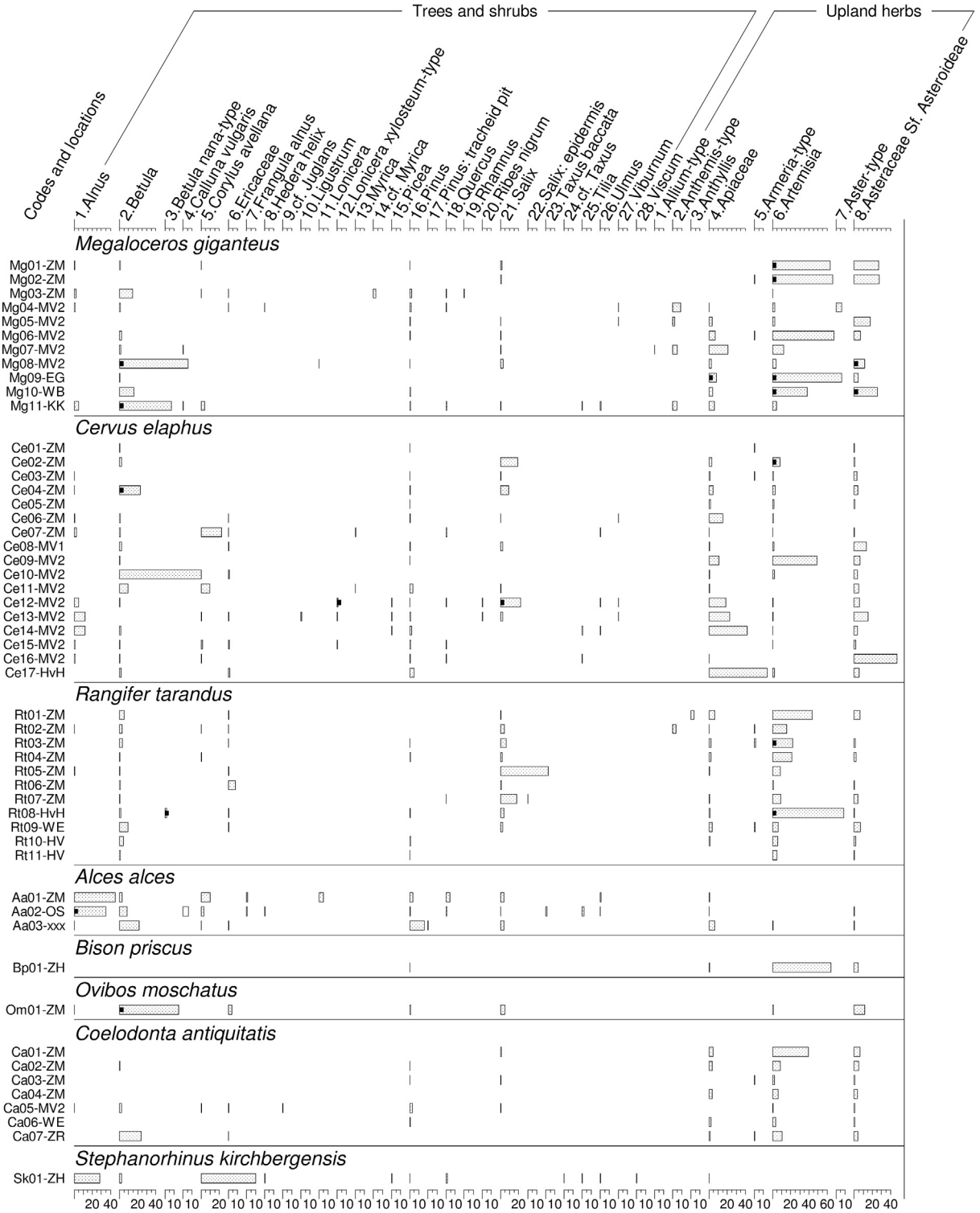


Fig. 1. A: Microfossils from molars, part 1, B: Microfossils from molars, part 2, C: Microfossils from molars, part 3, D: Microfossils from molars, part 4.

Microfossils from molars, part 2

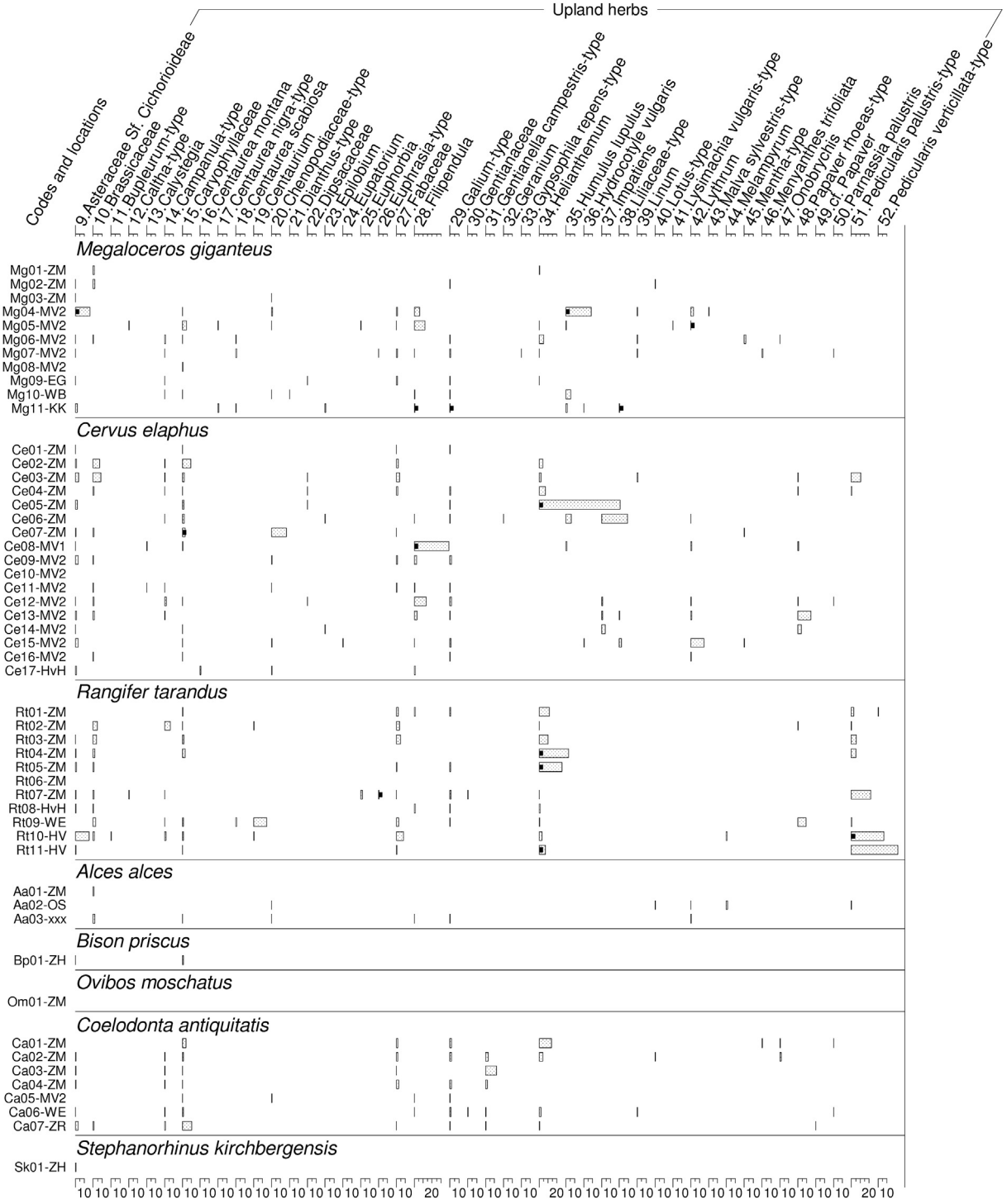
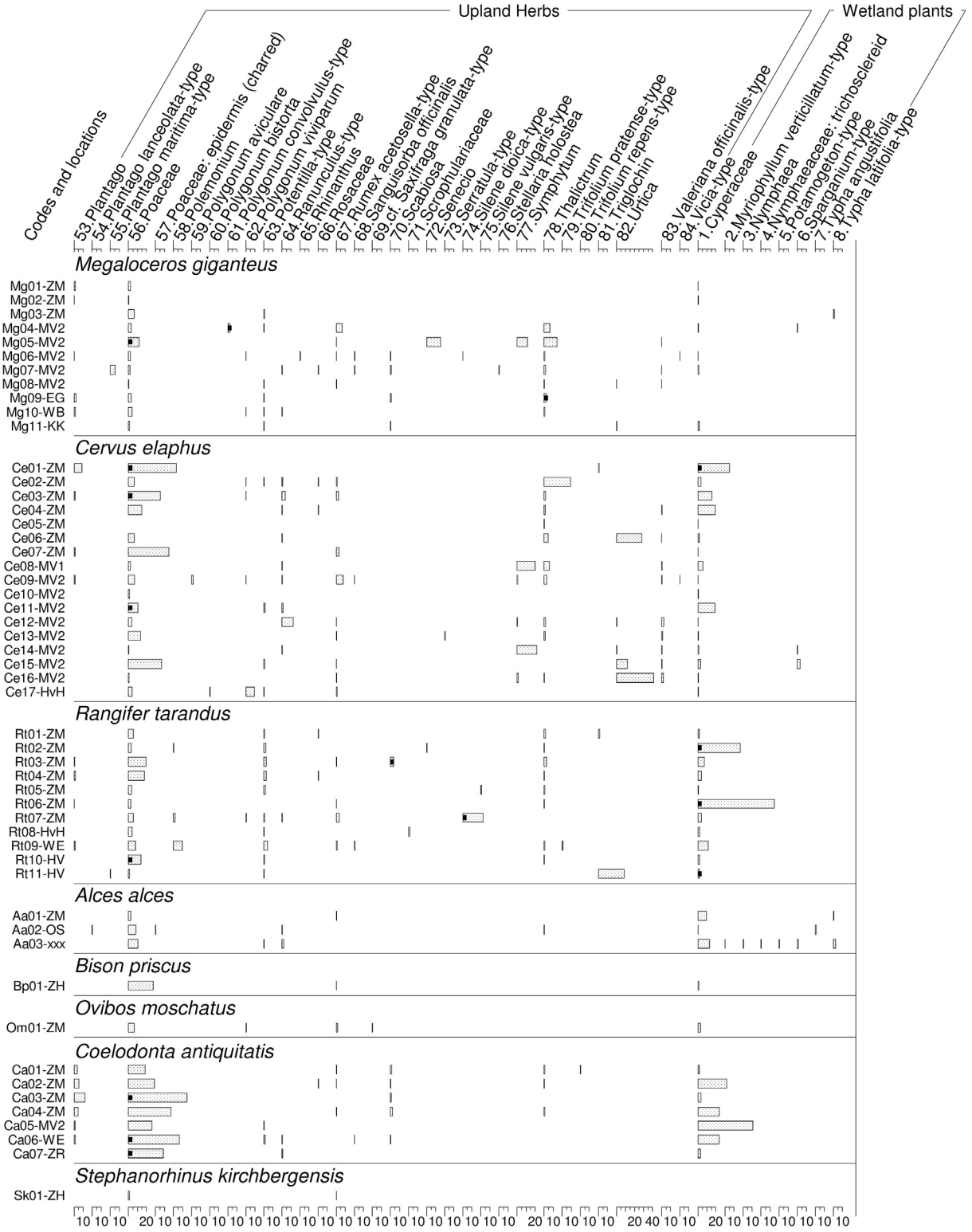


Fig. 1. (*continued*).



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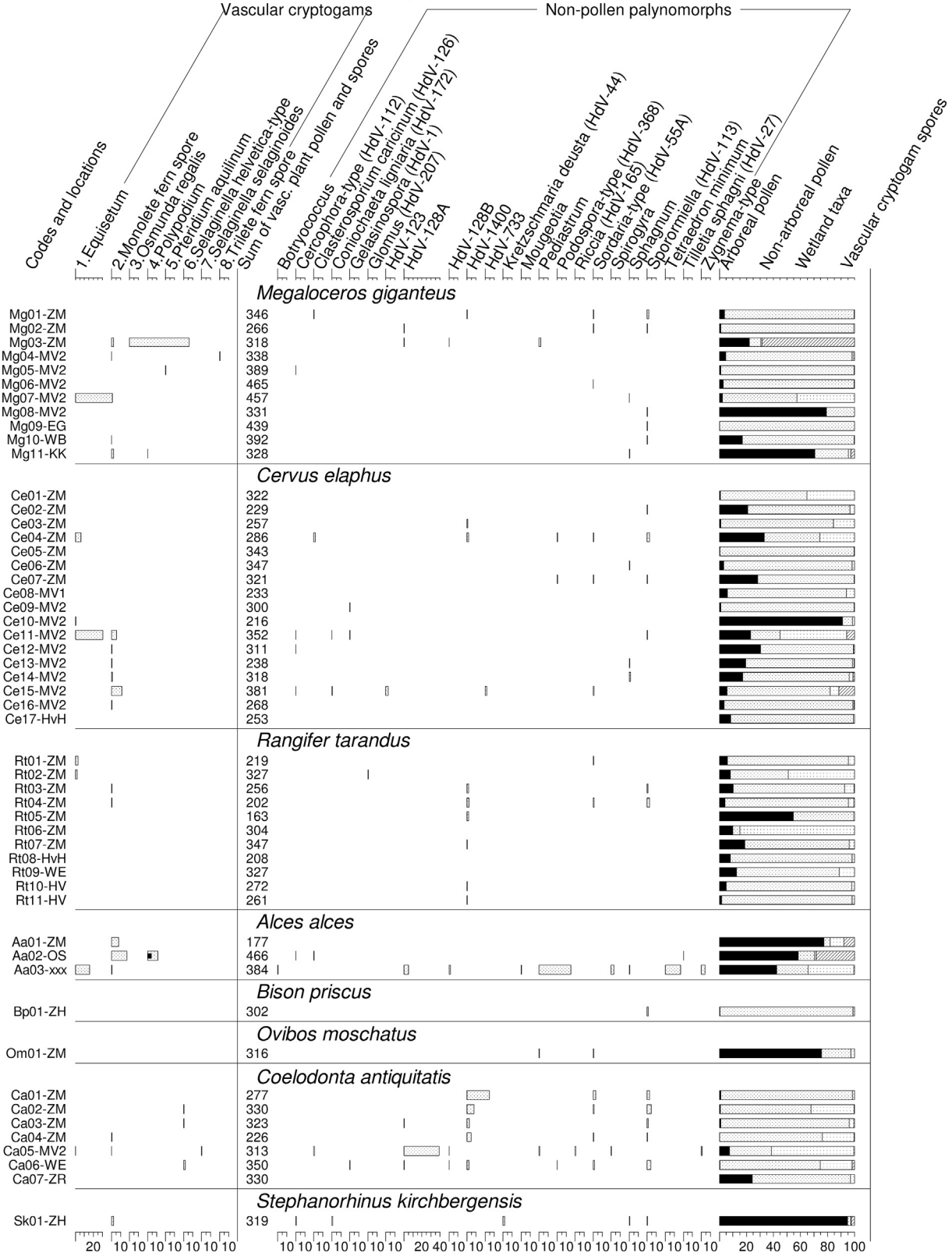

Fig. 1. (*continued*).

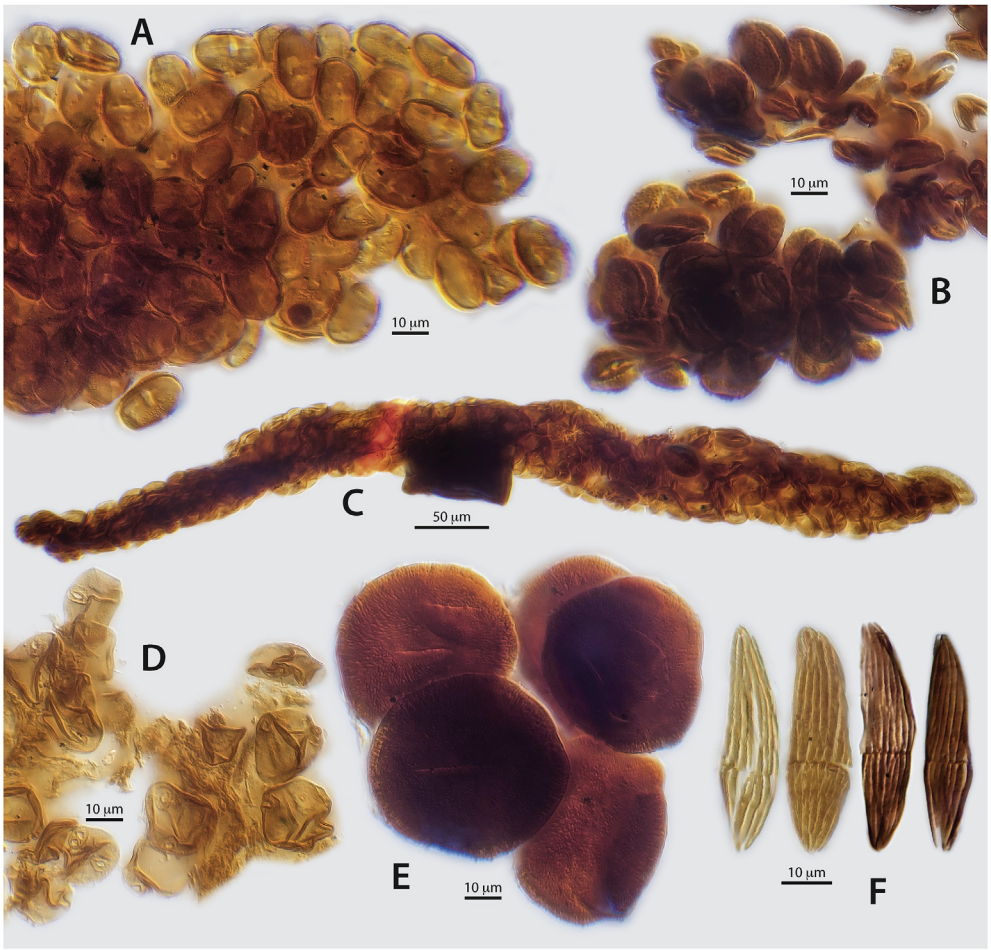

Fig. 2. A–E: aggregates of pollen from molar fold samples. A: part of an aggregate of Apiaceae (cf. *Sium*) from *Megaloceros giganteus* (Mg09); B: *Artemisia* pollen from *Megaloceros giganteus* (Mg09); C: cf. *Artemisia* from *Megaloceros giganteus* (Mg09); D: *Humulus* pollen from *Megaloceros giganteus* (Mg04); E: *Scabiosa* pollen from *Rangifer tarandus* (Rt03); F: HdV-1400 ascospores from *Coelodonta antiquitatis* (Ca06).

trichosclereid, *Myriophyllum*, *Potamogeton*, *Sparganium*, *Typha*, and various algae (*Botryococcus*, *Pediastrum*, *Spirogyra*, *Tetraedron*, *Zygnema*-type, *Mougeotia*, HdV-128A and HdV-128B)). The *Equisetum* spores may well have been produced by the wet growing species *E. fluviatile*.

Aa01 and Aa02 represent relatively 'dry' environments with, among others, *Calluna*, *Lonicera* and ferns. Aa02 contains *Salix* epidermis: a clear indication of consumption of *Salix*. Willows are very important food plants for modern moose. In concert with our results, Saarinen et al. (2016) found that *Alces alces* - with low mesowear values - was linked with low non-arboreal pollen percentages, which supports the status as a forest-adapted browser.

5.5. Bison priscus

The only pollen spectrum that could be obtained is completely dominated by pollen of *Artemisia,* Asteroideae and Poaceae. Tree pollen is absent, pointing to Weichselian subarctic steppe conditions and a grazing diet. This is in accordance with the scarce previous work done on the palaeobiology of steppe bison. Saarinen et al. (2016) found that *Bison priscus* was commonly associated with rather open vegetation, but also occurred in environments relatively rich in arboreal pollen.

5.6. Ovibos moschatus

Aggregates of *Betula* pollen, present in the only available molar point to browsing of flowering birches, but the landscape was rather open, considering the representation of Asteraceae, Ericaceae and Poaceae. *Polygonum viviparum* is an arctic-alpine species and its presence fits in the open landscape under subarctic conditions.

5.7. Coelodonta antiquitatis

Tree pollen values are low, and the vegetation was dominated by Poaceae, Cyperaceae, *Plantago*, *Galium*-type, *Gentianella campestris*, *Scabiosa*, *Helianthemum*, *Artemisia* and other Asteraceae. Aggregates of pollen of Poaceae in three samples point to consumption of flowering grasses and therefore Poaceae are probably overrepresented in the pollen spectra. The data clearly point to a grazing diet, which matches previous work done on molar wear and stomach contents.

Ca05 shows a spectrum pointing to a moist habitat: the aquatic HdV-128A is very common and also some other algal spores point to wet conditions. Fungal spores HdV-1400 (unequally 2-celled, longitudinally ribbed; Fig. 2F) that were only known from a Weichselian interstadial deposit (van Geel et al. 2010) now appear to be linked to the habitat of *C. antiquitatis* (cold, dry climatic

conditions). The presence of spores of the coprophilous fungi *Podospora*, *Sordaria* and *Sporormiella* may well point to HdV-1400 as another coprophilous fungus.

5.8. *Stephanorhinus kirchbergensis*

The single molar spectrum shows a dominance of tree pollen (mainly *Alnus* and *Corylus,* with some *Betula, Quercus, Tilia, Ulmus*). In combination with *Viscum album*, *Hedera helix*, ferns and *Kretzschmaria deusta* (a fungal parasite on a variety of tree species; van Geel and Aptroot, 2006; van Geel et al., 2013) the sample represents a predominantly forested environment and supposedly it has an Eemian interglacial, or an early Weichselian interstadial age. We can exclude a Holocene age as *S. kirchbergensis* became extinct shortly after the Eemian interglacial (van der Made, 2010; Mol et al., 2012).

5.9. DCA

Fig. 3 shows the DCA plot of the plant taxa. There are three poorly defined clusters. The cluster on the right contains mostly thermophilous interglacial taxa like *Alnus*, *Betula*, *Corylus*, ferns, *Frangula*, *Hedera*, *Lonicera*, *Myrica*, *Quercus*, *Rhamnus*, *Tilia*, *Typha*, *Ulmus* and *Viscum* and most of the wetland taxa. Most taxa on the left represent species of tree-less landscapes.

Fig. 4 shows the DCA of the zoological taxa, as based on the pollen spectra recorded from the molars. There is clustering of the various species and variation between those species. The samples from *C. antiquitatis* cluster strongly together (except sample Ca01). This is in sharp contrast to the *C. elaphus* samples that are spread through most of the plot. This may be explained by the extreme dietary flexibility of *C. elaphus* compared to the strictly grazing diet of *C. antiquitatis*. *R. tarandus* samples cluster close to both *M. giganteus* and *B. priscus* and some of the *R. tarandus* samples are also similar to *C. antiquitatis*. *M. giganteus* samples show a rather large variation along Axis 1, but not so much along Axis 2. This suggests a more specialized diet than that of *C. elaphus*. *A. alces* and *S. kirchbergensis* cluster close together; the abundance of arboreal (interglacial) pollen in those samples explains this. The dominance of *Betula* pollen in the *O. moschatus* sample explains its clustering close to these temperate taxa, but *Betula* may be strongly over-represented (pollen aggregate).

The three outliers have unique microfossil compositions. Mg03 is the only sample rich in *Osmunda regalis*. Rt11 has abundant *Triglochin* and *Pedicularis palustris*-type, which may be caused by grazing of flowers. Ce05 contains a remarkably high abundance of *Helianthemum*, including an aggregate.

R. tarandus and *C. elaphus* are both large mammals that survived into the Holocene. It is worth noting that both species show a larger variation in the DCA plot than the extinct *M. giganteus* and *C. antiquitatis*. Species with low diet diversity are most vulnerable for extinction. After abrupt climate change, sudden vegetation changes could cause a population crash and possibly extinction (Augustyniak, 2010; van Geel et al., 2018).

6. Discussion

6.1. Chronology and phenology

How much time (days, weeks, months, years?) does a pollen sample from an infundibulum represent? In other words: how much time did it take to fill an infundibulum? If different very short periods are represented in the pollen records from infundibula then different parts of the flowering season (and therefore different plant taxa) may be represented in the pollen and spore samples even if the same area was foraged. Infundibula that were filled with compacted plant fragments when less or no flowering took place (late autumn and winter) will show low amounts, or may even be devoid of pollen. Probably the infill of infundibula directly followed the eruption of molars into the oral cavity. This eruption has a set order and a rather narrow timing in the ontogeny of many mammals (Hillson, 2005). However, variation in timing within a species of only a couple of weeks may lead to significantly different parts of the flowering season being represented in the infundibulum. Can we expect further compression and therefore additional, later infill of an infundibulum when decomposition of the plant remains, and related additional compaction in the infundibulum takes place? In other words: may such samples represent large time intervals, or even complete flowering seasons? Our questions remain unanswered by our data and require experimental investigations.

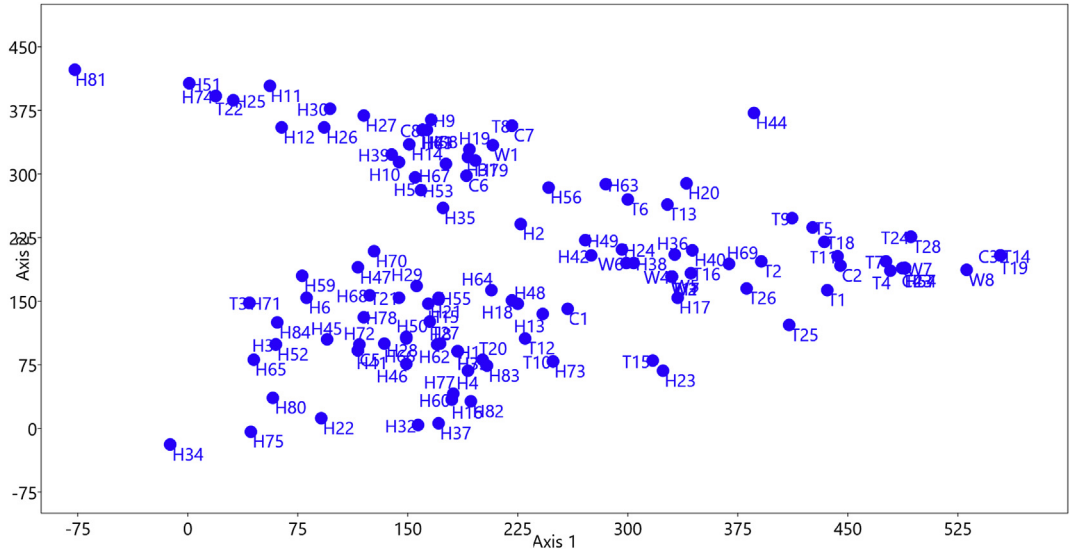

Fig. 3. Detrended Corresponence Analysis of botanical taxa. T: trees and shrubs; H: upland herbs; W: wetland plants; C: vascular cryptogams. Numbering corresponds with numbered names of taxa as indicated in Fig. 1A–D.

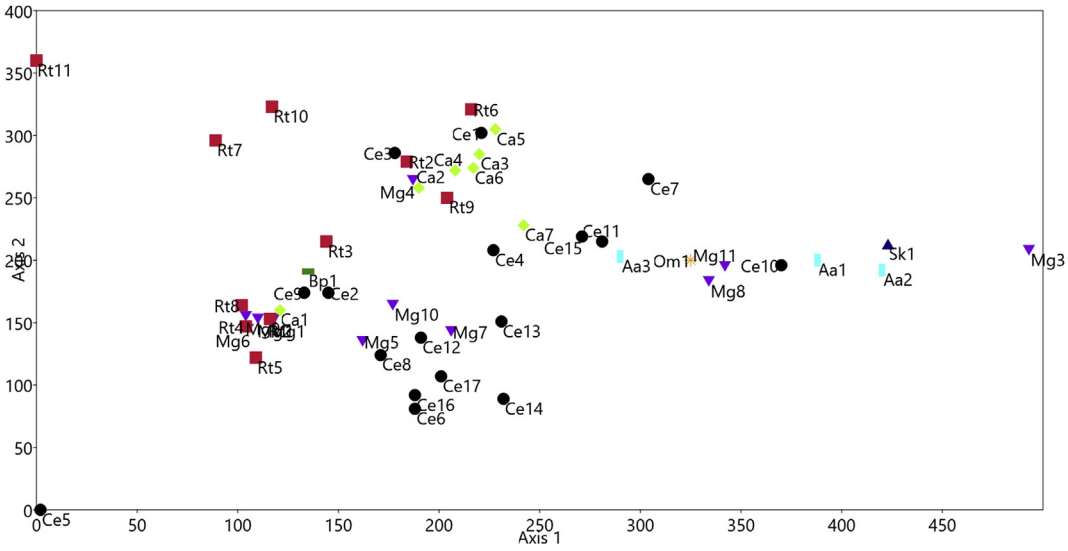

Fig. 4. Detrended Corresponence Analysis of zoological taxa. Purple inverted triangle: *M. giganteus*; black dot: *C. elaphus*; red square: *R. tarandus*; light blue bar: *A. alces*; dark green dash: B. *priscus*; orange star: *O. moschatus*; light green diamond: *C. antiquitatis*; dark blue triangle: *S. kirchbergensis*. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

6.2. Food choice and age of the molars

What were random effects of individual food choices of herbivores on our pollen records from molars, and can we anyhow expect that we can derive preferences in the food choice based on pollen and spores? The differences between pollen records from the same species do show that there are factors that must cause these differences. The abundance of Poaceae pollen in *Coelodonta*, a known grazer, is a striking example of a link between our pollen records and the animal's diet. Furthermore, the clustering of our samples in the DCA does point to some structure in the dataset that may well be explained by food preferences and selectivity of the species.

Flowers often are the most sun-exposed (highest) parts of plants and therefore flowers with not yet dispersed pollen may have been consumed. We observed that not yet released, unripe pollen grains appeared as pollen aggregates in the microscope slides. Consumption of flowers could lead to a strong overrepresentation of some plant species, but an advantage of the presence of pollen aggregates is that direct information on consumption of certain plant species becomes available.

Individual herbivore specimens lived during a relatively short period, while climatic conditions were not at all stable over longer time intervals (interglacials, glacial stadials, interstadials and periods of transitional climatic conditions). Migration of plant species will have taken place after climate change and different successive climatic conditions were linked to the existence of different vegetation types. Therefore differences between pollen spectra may occur that are not only influenced by the season and the food choice of the herbivores but also by the age of the molar in relation to changing climatic conditions and related changes in the vegetation composition. We also should be aware that the pollen rain - especially pollen of wind-pollinated taxa - will have landed on plants that were consumed by the herbivores and thus various pollen taxa will be represented, independent from the individual food choice of the animal.

Taking into account the limitations in the interpretations of our pollen and spore record, we nevertheless obtained new information about the food choice of giant deer, red deer, reindeer, moose, steppe bison, muskox, woolly rhino, and forest rhino.

7. Conclusions

Based on molar-embedded pollen grains and spores we gained insight into the diet of eight herbivore species that lived during the Eemian interglacial, the Weichselian, and the Early to mid-Holocene (until inundation because of sea level rise), respectively. Food plants were represented as relatively high percentages of their pollen or spores, and monospecific pollen aggregates in the microfossil slides gave valuable additional information about food choice. Compared to pollen records from stratigraphic sequences, our pollen spectra were strongly biased. Some of our questions about the pollen sources (pollen rain *versus* active food selection) remained unanswered by our data and require experimental investigation.

By combining ecological data of the recovered plant taxa with statistical analysis, we showed variations in diet between the various sympatric large herbivores of the mammoth steppe ecosystem. Although resource partitioning through competition over food is still hotly debated in large herbivores (Owen-Smith, 2002), we conclude that the dietary differences we found may have allowed different herbivore species to coexist.

Author contributions

B.v.G. took the botanical samples, analyzed the microfossils, led the discussion and wrote part of the manuscript. B.W.L. and D.M. identified the molars, wrote the general text about the mammal species and contributed to the discussion and the interpretation of the data. B.W.L. executed the DCA of the zoological and botanical data. J.F.N.v.L. and P.W.O.v.d.K. identified problematic pollen taxa, made the microfossil diagram and were involved in discussions and interpretation of both zoological and botanical data.

Declaration of competing interest

None.

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