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Pollen reveals the diet and environment of an extinct Pleistocene giant deer from the Netherlands

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ABSTRACT

Pollen analysis of five teeth (two premolars, three molars) from a single maxilla of a giant deer (*Megaloceros giganteus*) found in Pleistocene deposits in The Netherlands reflects the diet and the landscape of the specimen that lived in eastern Doggerland. Apiaceae (among which *Anthriscus sylvestris*, *Heracleum* and *Hydrocotyle*), Asteraceae (among which *Anthemis*-type, *Senecio*-type and Cichorioideae), *Filipendula*, Poaceae and *Symphytum* were among the ingested plants. The landscape had dense, species-rich tall-herb vegetation and an open tree layer of *Alnus* and *Betula*, whereas thermophilous tree taxa were absent. Climate was probably cool-temperate, semi-dry, sub-continental. A radiocarbon date of the maxilla is beyond the ^{14}C detection limit. We conclude that our giant deer most likely lived during the early Eemian or during an early Weichselian interstadial.

1. Introduction

The Marker Wadden (MW) is a newly created nature reserve in the lake Markermeer (part of the IJsselmeer), owned and managed by the Dutch nature conservancy organization Natuurmonumenten (Fig. 1). Dikes and islands were built in the period 2016 to 2022 by the Boskalis company, using mostly sandy sediments dredged from deep local late Pleistocene deposits. With the sand also bones of large Pleistocene mammals became exposed, which were eagerly collected by citizen scientists. Van Geel et al. (2019) published the results of pollen extracted from the contents of molar or premolar folds of eight large herbivore species found in various localities in The Netherlands but mostly in Doggerland, among which were ten molars/premolars of the now-extinct giant deer, *Megaloceros giganteus* (Blumenbach, 1799). These molars/premolars derived from different animals from unknown, but potentially different time periods and vegetational settings, and thus, not amazingly, contained a range of different pollen assemblages. The recent finding of a giant deer maxilla in MW that still contained several molars and pre-molars attracted therefore our immediate attention, and we decided to subject this to a more thorough investigation of the pollen that we hoped to find hidden in the molar folds. Questions were: Do the different molars/premolars in this single fossil yield similar pollen assemblages? What do the pollen assemblages tell us about the feeding habits of this individual giant deer? What can we learn from the pollen about the vegetation and environmental settings in which the animal was living? When did our giant deer live?

2. Material and methods

Faunal elements recovered from the Marker Wadden (MW) dredging operations include the cold-adapted (Weichselian) wooly mammoth (*Mammuthus primigenius* (Blumenbach 1799)), wooly rhinoceros (*Coelodonta antiquitatis* (Blumenbach 1799)), horse (*Equus caballus* Linnaeus 1758), steppe bison (*Bison priscus* Bojanus 1827), musk-ox (*Ovibos moschatus* (Zimmermann 1780)), giant deer (*Megaloceros giganteus* (Blumenbach 1799)), reindeer (*Rangifer tarandus* (Linnaeus 1758)), cave lion (*Panthera leo spelaea* (Goldfuss 1810)) and cave hyena (*Crocuta crocuta spelaea* (Goldfuss 1832)), and also taxa adapted to a more temperate climate (Eemian or early Holocene), such as the straight-tusked elephant (*Elephas antiquus* Falconer & Cautley 1847), aurochs (*Bos primigenius* Bojanus 1827), elk (named 'moose' in North America; *Alces alces* (Linnaeus 1758)), red deer (*Cervus elaphus* Linnaeus 1758), roe deer (*Capreolus capreolus* (Linnaeus 1758)), beaver (*Castor fiber* Linnaeus 1758) and brown bear (*Ursus arctos* Linnaeus 1758).

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In August 2022, one half of a maxilla (jaw) of a giant deer was dredged up together with sand from pit-2 near the south of the MW harbor entrance (Lat. 52° 34.29′ N, Long. 5° 22.2146′ E). The jaw had been embedded in Pleistocene sandy deposits at a depth between 26 and 40 m. It contained the premolars P3 and P4 and the molars M1, M2 and M3 (Fig. 2). The maxilla fragment was handed over to Natuurmonumenten, and after that became part of the palaeontological collection of the fourth author (FR), where it is registered as MW1177. A compact bone fragment (*materia compacta*) of the jaw, registered by the fifth author (DM) under number CM-DM 189, was submitted for radiocarbon dating to the Centre for Isotope Research, University of Groningen. Here we present the pollen analysis of material obtained from folds in the molars/premolars of the jaw and we discuss the possible environment and time period in which our giant deer lived.

2.1. Pollen sampling, preparation and analysis

The pollen-bearing material was firmly attached to the inner part of the molar/premolar folds. We stirred with preparation needles to detach the material from the walls of the folds, resulting in small amounts of fine, dust-like material collected in glass beakers (cf. van Geel et al., 2018, 2019). We collected nine samples, including one from premolar P3 and two from each of the premolar P4 and molars M1, M2 and M3, one rather shallow, the other from deep in the fold. The shallow samples were taken to detect possible contamination with younger, possibly even modern pollen in this more exposed position in the fold. The preparation of microfossils followed Faegri and Iversen (1989). For pollen identifications we used Punt (1976, 1984), Punt and Clarke (1980, 1981, 1984), Punt et al. (1988, 1995), Punt and Blackmore (1991), Punt and Hoen (2009) and Beug (2004). The amount of material was too small and too fragmented for macrofossil analysis.

3. Results

3.1. Description and identification of the MW maxillary fragment

The brown-beige colored maxillary fragment derives from the upper right jaw in which the permanent dental elements P3 to M3 have been preserved, whereas P2 may have been lost during dredging. Measured anterior–posterior, the total length of the fragment is 268 mm, and the length of the tooth row is 131 mm, which corresponds to a giant deer of average size (Breda, 2005; Geist, 1998; Monaghan, 2019; Reynolds, 1929). The measurements of the individual dental elements are given in Table 1. The alveoli of the premolars are well preserved, which indicates that the animal had already replaced its milk dentition when it died. In M3, the occlusal surface is slightly more worn than in the corresponding right upper M3 of another giant deer individual described by van Geel et al. (2018), but it is slightly smaller, which indicates a somewhat younger age at the time of death.

3.1.1. Identification

The premolars and molars are low-crowned, which is typical for a mixed feeder. The cinculum at the crown base is very weakly developed in P3, P4 and M1. An accessory pillar is present at the base of molars M1–M3 but is somewhat worn in M1, probably caused by use. The surface enamel of the protocone and hypocone on the lingual side and of the paracone and metacone on the buccal side of M1–M3 is strongly ribbed, which is characteristic of giant deer but not well developed in other cervids of similar size. The weakly oblique position of the paracone and metacone at the base of the molars points to giant deer as it excludes an attribution to moose in which they are considerably more obliquely developed.

3.1.2. Health and age at death

The appearance sequence and duration of molars/premolars of giant deer is unknown. It takes a few years in other, present-day cervids, before the milk dentition of premolars (P2 to P4) are replaced. In the MW maxilla, M1 and M2 are the most worn, so that their dentin is clearly visible (Fig. 2). The dentin is up to 4 mm thick. M3 is the least worn and was therefore the last to break through and become in use. Premolar P3 is more worn than P4, which indicates that it broke through earlier and was used longer. We could not determine whether the animal was male or female. Based on the morphological features, we conclude that the animal was an adult individual in the prime of his or her life.

3.2. Radiocarbon dating of the molar

A compact bone fragment was taken for radiocarbon dating. In view

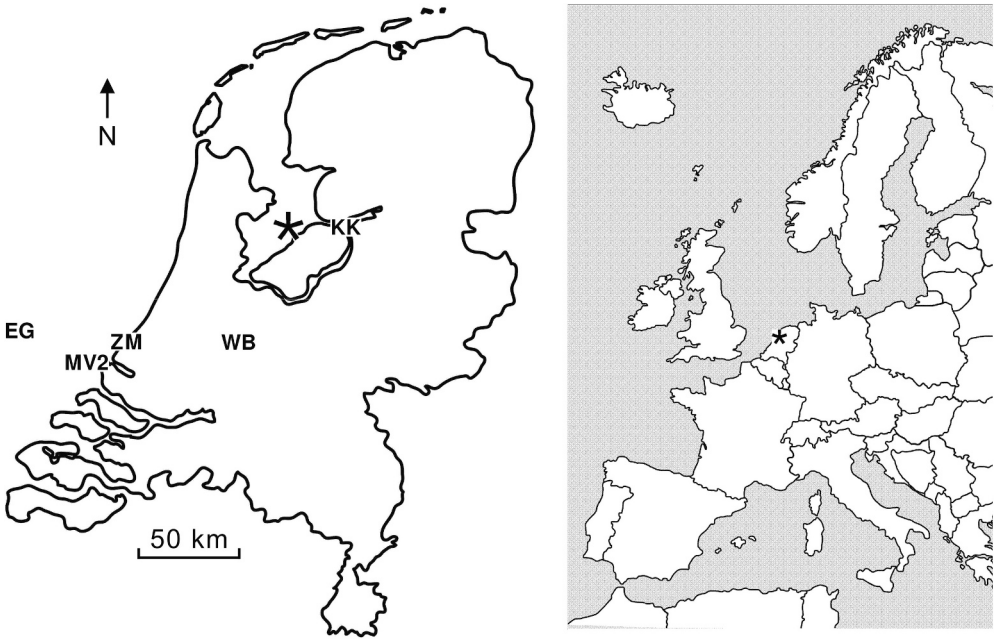

Fig. 1. The IJsselmeer region in the central Netherlands showing the position of the Marker Wadden with a star. Locations of earlier pollen studies on giant-deer molars are indicated with abbreviations according to Table 2.

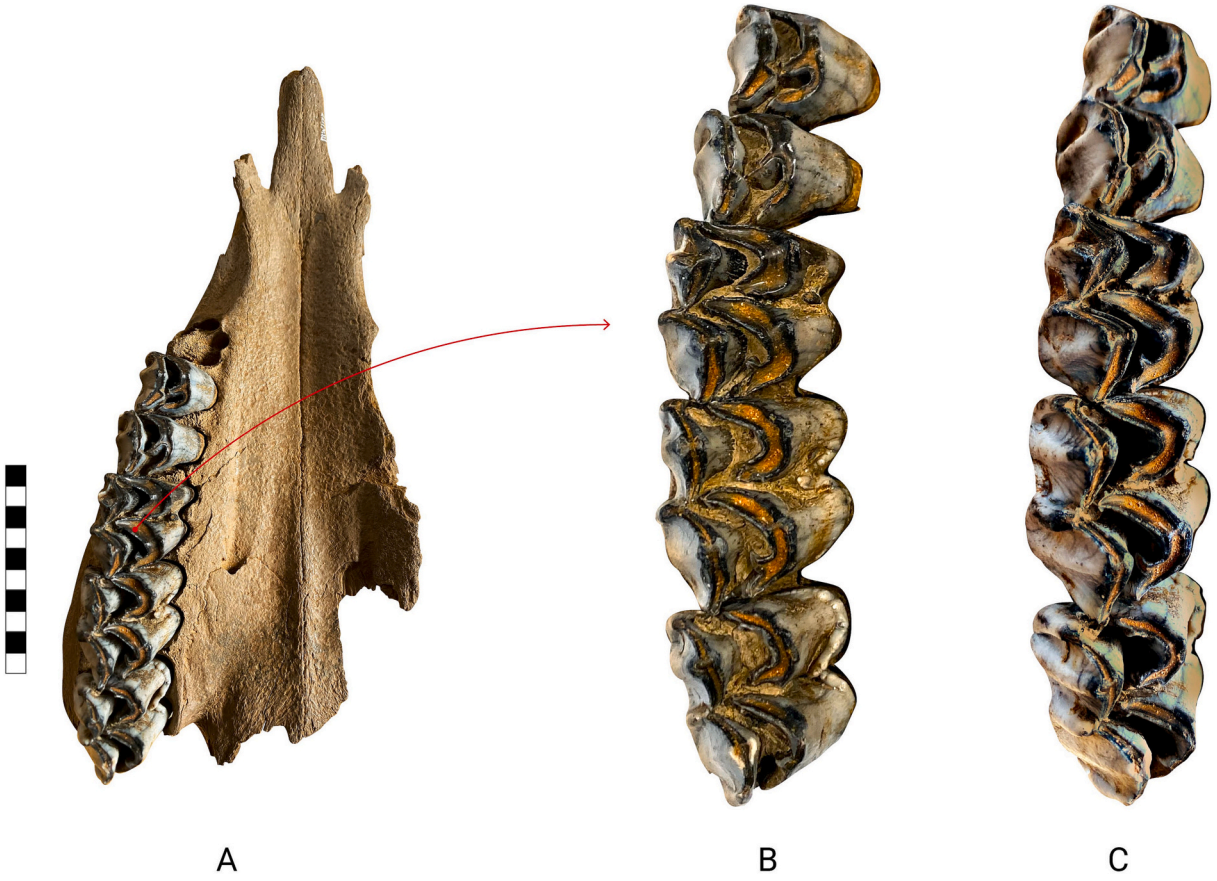

Fig. 2. Upper right jaw (maxilla) of *Megaloceros giganteus* (giant deer) from the Marker Wadden (The Netherlands) containing five teeth: from top to bottom the premolars P3 and P4 and the molars M1, M2 and M3. Cm-scale at left. A – the complete fossil; B – the teeth with its infillings; C – the teeth with infillings removed.

Table 1
MW maxilla of *Megaloceros giganteus*: Premolar and molar measurements in mm at the base of the crown.

Type of tooth	Premolar		Molar		
Code for the position in the jaw	P3	P4	M1	M2	M3
Maximum length, anterior–posterior	23	21	31	35	31
Maximum width	24	27	28	31	29
Maximum height, lingual	22	23	15	19	23
Maximum height, buccal	22	23	24	27	22
Maximum depth of the molar fold	18	17	17	23	22

of the possibility that the bone would be younger than the detection limit, the sample was included in a batch financed by the project "Resurfacing Doggerland" which is led by the University of Groningen. The material yielded an age beyond the radiocarbon detection limit (Groningen laboratory number GrM-33060), which implies an age older than 45,000 yr BP.

3.3. Pollen analysis

The result of the analysis of pollen and spores is shown in Fig. 3. Percentages are based on the sum of total pollen (100% by definition). Two aspects are notable: the low proportion of tree and shrub pollen, and the high pollen diversity of Apiaceae, Asteraceae and other herbs.

4. Interpretation

4.1. Origin of the encountered pollen

The infill of the molar/premolar folds and thus the pollen in it might have different origins:

Contamination with modern material, entering the folds in the period between the dredging and the laboratory preparations;

Sediment entering the folds between the death of the animal and the dredging up of the jaw;

Ingestion by the animal while feeding, pressed into the folds during chewing.

4.1.1. Contamination

We do not observe any pollen types or features that can be associated with human activity, such as (a) higher abundance of a pollen type in a few samples contrasting with absence in others, (b) pollen types indicative of cultural practices (like human impact indicators and crop plants), and (c) pollen types indicative of plants that were introduced to The Netherlands from elsewhere. The pollen record does thus not indicate contamination of any kind.

4.1.2. Sediment

Pollen assemblages ingested by herbivores as part of the food may show characteristics that differ from assemblages encountered in lacustrine sediments or peat deposits. The latter are mainly biased towards (1) wind-pollinated plant taxa, as such taxa produce considerably more pollen and (2) tall-growing taxa whose pollen disperses easier by wind, both of which suppresses the proportions of pollen of (1) insect-dispersed taxa, which produce much less pollen and (2) low-growing

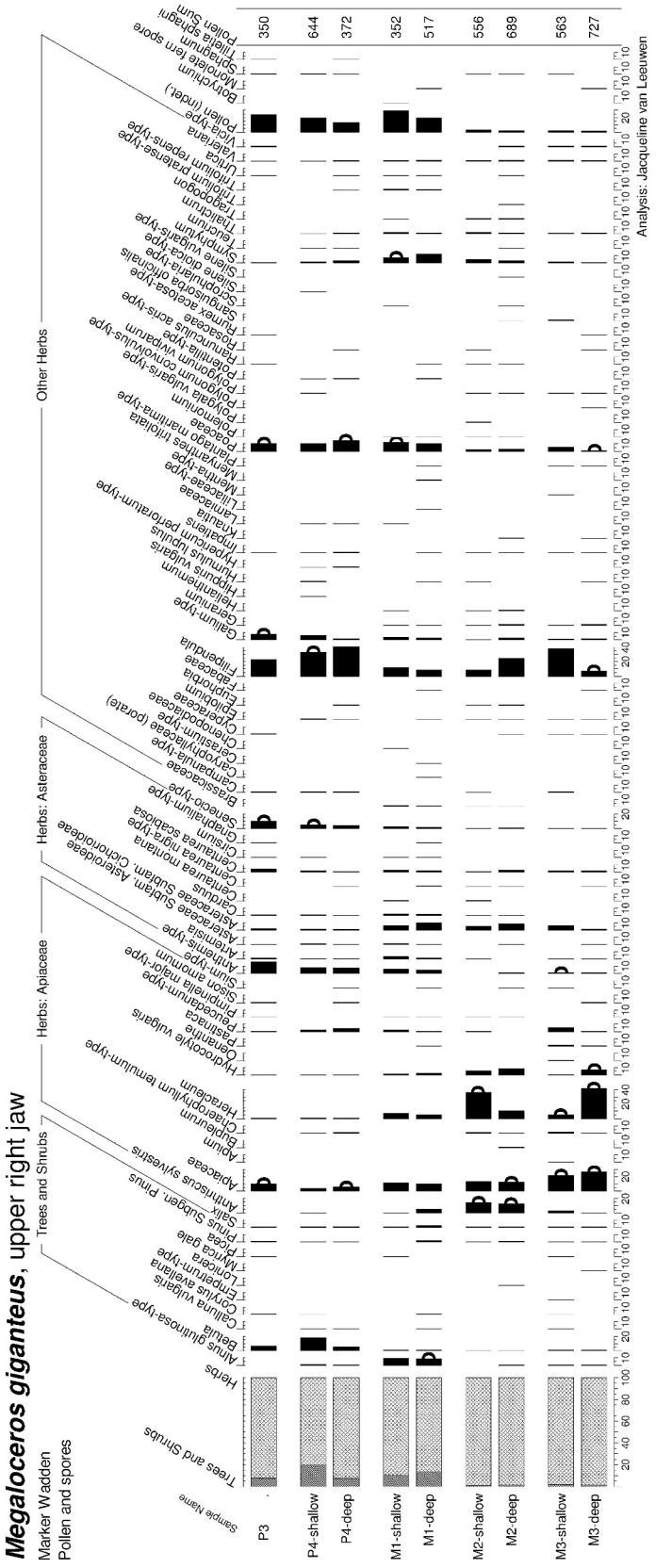

Fig. 3. Pollen percentage diagram of material from molar/premolar folds of a giant deer (*Megaloceros giganteus*) jaw from the Marker Wadden, The Netherlands. Clumps of pollen are indicated with nose-rings. In the text, pollen-type names are shortened where this does not give rise to confusion with other names (e.g., *Alnus* and *Calluna* in the text for *Alnus glutinosa*-type and *Calluna vulgaris* in the diagram).

taxa, whose pollen spreads little. Ingested pollen assemblages, on the other hand, are strongly biased by the food choice of the animals, which tends to include insect-pollinated flowers of herbs (in red deer at least; van de Veen, 1979; van Geel et al., 2022a). The pollen assemblages of our molar data have pollen proportions of several herbs that are higher than usually encountered in lacustrine sediments or peat deposits (*Anthemis*-type, *Senecio*-type, *Centaurea scabiosa*, *Anthriscus sylvestris*-type, *Heracleum*, *Hydrocotyle*, *Filipendula*, and *Symphytum*) and have relatively low pollen proportions of wind-pollinated trees and Poaceae, which suggests ingestion with food.

4.1.3. Ingestion

Another characteristic of assemblages of pollen ingested by animals with food is the occurrence of single-taxon clumps of not-fully-ripe pollen, which derive from complete flowers consumed by the animal (van Geel, 2022). Such clumps are rare in lake sediments and peat deposits but abundant in our molar samples. As shown in Fig. 3, clumps were encountered in all samples, and comprise nine different pollen types. This high frequency of clumps and their diversity suggest ingestion of the pollen with the food.

Our conclusion is that at least an appreciable part (if not all) of the pollen encountered in the single-jaw giant-deer molars has been taken up by the animal during feeding.

4.2. Molar/Premolar pollen comparisons

It may be useful to evaluate together all giant-deer molar/premolar pollen data that we now possess. These comprise pollen from ten disconnected (i.e. separately-found) molars/premolars published by van Geel et al. (2019) and the nine samples from the single-jaw molars/premolars of this study (Table 2, Fig. 4). We harmonized the pollen types between the two pollen subsets, which was needed because of different pollen analysts. PCA was carried out on the harmonized dataset, using standardization and square-root transformation (Fig. 5). Sample Mg-03 was omitted from the analysis because it contains insufficient pollen, but its position as a passive sample is shown in Fig. 5. The following observations on the PCA plot may be useful for the interpretation in terms of past vegetation and environment:

First, the group of ten disconnected molars/premolars (G.) are on the first axis in PCA well separated from the nine single-jaw molar/premolar samples of this study (P. and M.), the one group on the right side, the other on the left. This indicates that the diet of the animals of the disconnected molars differed markedly from the diet of the animal of the present study.

Second, pollination type, by wind versus insects, dominates the first PCA axis, as shown by the long, oppositely directed arrows labeled WIND versus INSECT. The group of disconnected molars/premolars (G.) is associated with wind pollination, the group of the MW single-jaw samples (P. and M.) with insect pollination.

Third, the single-jaw molars/premolars are in the PCA plot approximately arranged according to their position in the jaw: P3 and P4 in the jaw front, M1 in the jaw middle, M2 and M3 back in the jaw. It is tempting to search for a relation between this trend in pollen assemblages and a supposed gradual appearance of molars/premolars from front to back. The sequence of molar/premolar appearance is for giant deer unknown, but the traces of wear (as described above) do indeed suggest that P3 appeared before P4 and that M1 and M2 appeared before M3. Further, for such a relation to be of any significance, we have to infer that the infilling of each molar/premolar fold started with its appearance and that at least some of the early infill remained in place. However, more studies of a similar kind are needed to explore this further.

4.3. Past vegetation and environment

Based on the analysis of pollen and spores of intestinal material (Birks et al., 2018; Gravendeel et al., 2014; Langeveld et al., 2017; Polling et al., 2021; van Geel et al., 2022b; Welker et al., 2014; Zhang et al., 2019) and of molar folds (van Geel et al., 2018, 2019), reconstructions of the diet and habitats of Weichselian mammals have been obtained. Care is needed with such interpretations, as the pollen assemblages depend not only on factors that we want to reconstruct, like the local flora where the animals lived and the relative abundance of the plants. The pollen assemblages also depend on the relative pollen production of the involved taxa, the food choice by the animals, and the season of ingestion. The relative pollen production of many plant taxa is approximately known and differs markedly among species. As a general rule it is high in wind-pollinated, low in insect-pollinated plants. The animals will preferentially consume parts of plants that are tasty to them, within their reach, and sufficiently abundant, of which we hardly know a thing.

All encountered pollen types in the MW maxilla can be related to plant taxa that are native in The Netherlands today. The pollen data show a low diversity of trees and a strikingly high diversity of herbs in all molars/premolars (Fig. 3). This indicates that pollen-bearing food was ingested during the flowering season. A signal of early- versus late-flowering plants is not obvious in the data, unless it is hidden in the parallel arrangement of the molars/premolars in the jaw and of the samples in the PCA plot. Trees (*Alnus*, *Betula* and possibly *Pinus*) grew in the landscape in unknown quantities, but the high diversity of light-demanding herbs indicates that the landscape was not fully forested. Pollen indicators for open, dry, treeless vegetation include modest amounts of *Artemisia* and *Helianthemum* and a single occurrence of Chenopodiaceae (in M1d). Pollen indicators for moist environments such as stream-sides are much more abundant, especially *Filipendula* and *Hydrocotyle* and also *Alnus*, low amounts of Cyperaceae, *Sium*-type, *Humulus*, *Impatiens*, *Polemonium*, *Sanguisorba*, *Valeriana* and spores of *Sphagnum*, and several single occurrences (*Hippuris* in P4s, *Botrychium* in M1s, *Menyanthes* in M1d, and *Myrica*, *Apium*-type, *Oenanthe* and *Mentha*-type in M3s). Several other pollen types are less informative on soil moisture as they each potentially represent a range of plant taxa growing from moist to moderately dry (*Betula*, *Peucedanum*-type, Cichorioideae, Brassicaceae, Caryophyllaceae, *Epilobium*, *Galium*, *Geranium*, *Hypericum*, Lamiaceae, Poaceae, *Polygonum convolvulus*-type, *Potentilla*-type, *Scrophularia*-type, *Thalictrum*), but the great bulk of pollen types represent

Table 2
Available pollen data from molars of *Megaloceros giganteus* (giant deer) found in The Netherlands and the North Sea. Locations of the separate molars are shown in Fig. 2: ZM – Zandmotor; MV2 – Maasvlakte site 2; EG – Eurogeul; WB – Woerden–Breeveld; KK – Kampen–Kattendiep.

Sample name	Location	Code
Separate molars (van Geel et al., 2019)		
Mg01, Mg02	ZM	G1 + 2
Mg03	ZM	G3
Mg04	MV2	G4
Mg05	MV2	G5
Mg06	MV2	G6
Mg07	MV2	G7
Mg08	MV2	G8
Mg09	EG	G9
Mg10	WB	G10
Mg11	KK	G11
MW (pre-) molar pollen from single jaw (upper right maxilla) (this study)		
P3		P3
P4 shallow		P4s
P4 deep		P4d
M1 shallow		M1s
M1 deep		M1d
M2 shallow		M2s
M2 deep		M2d
M3 shallow		M3s
M3 deep		M3d

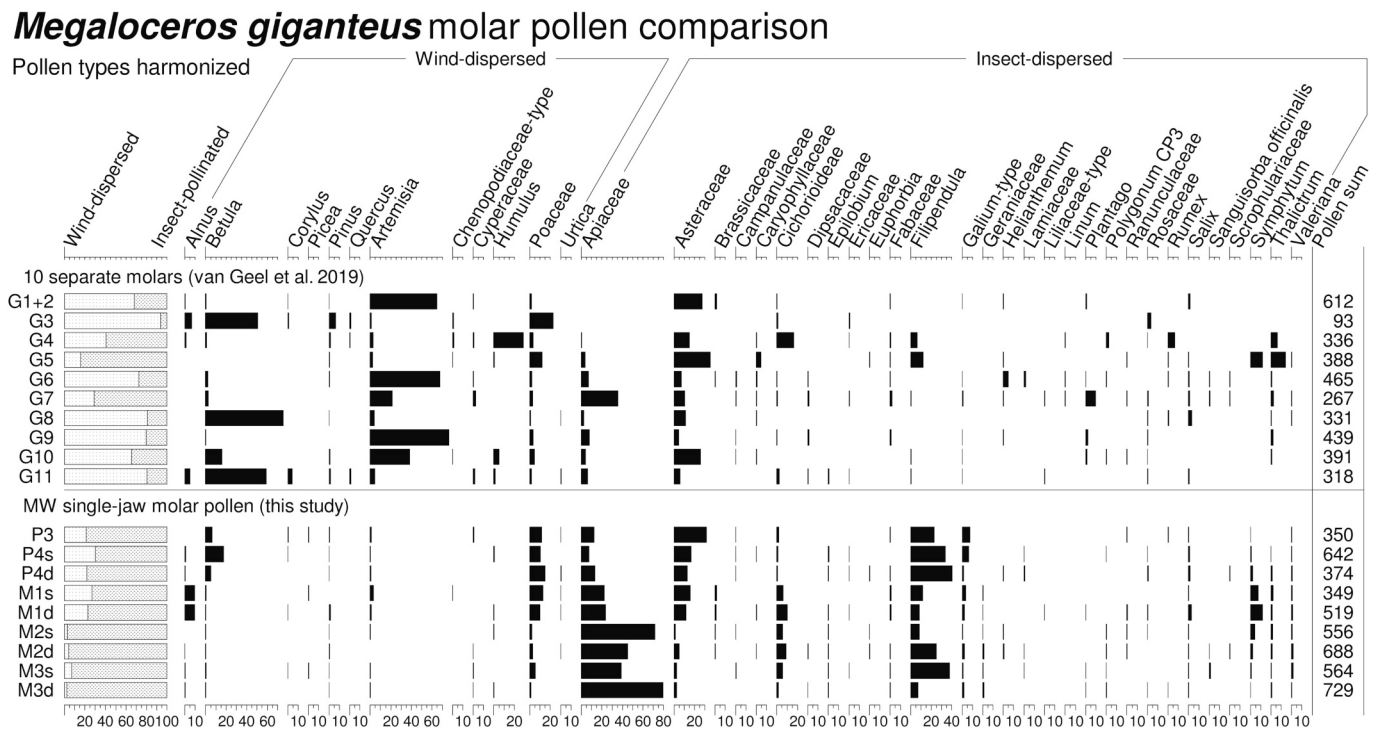

Fig. 4. Comparison of pollen in giant-deer molars/premolars of different origins. Sample codes as in Table 2. Pollen types are harmonized between the two datasets. Types with one or two occurrences are not shown, including the wind-dispersed *Picea*, *Sparganium*-type and *Typha latifolia*-type, and further *Hedera*, *Hypericum*, *Lonicera*, *Lysimachia*, *Lythrum*, Malvaceae, *Menyanthes*, *Myrica*, *Rhamnus*, *Ulmus* and *Viburnum*.

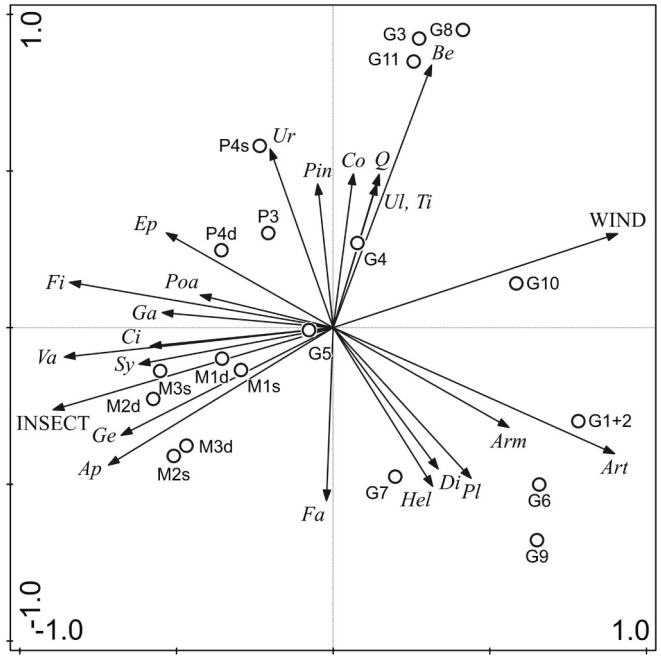

Fig. 5. PCA of the giant-deer pollen data listed in Table 2 and shown in Fig. 4; G3 is excluded from the analysis but added to the plot as a passive sample. Pollen data are square-root transformed and standardized per sample to sum = 1 and centered per pollen type to mean = 0. The horizontal axis explains 40.0%, the vertical axis 20.0%, so the plot explains a total of 60% variance. The sum of wind-dispersed pollen (WIND) and that of insect-dispersed pollen (INSECT) are added to the plot as passive variables. The attribution of pollen types to wind-dispersed or insect-dispersed is shown in Fig. 4. Sample codes (see Table 2) are in roman print. Pollen-type abbreviations are in italic print and comprise the first few letters of the full name (listed in Fig. 4). The 22 pollen types with the strongest contribution to explained variance are shown.

plants that predominantly grow in intermediate moisture conditions, from rather moist to rather dry but less so in the extremes. Pollen types indicative of low-growing plants are scarce (*Calluna*, *Gnaphalium*-type, *Helianthemum*, *Cerastium*-type), whereas types indicative of taller-growing plants are abundant. This may in part reflect the giant deer's feeding strategies, but it also indicates that taller-growing herbal vegetation played a role in the landscape, not only along streams but also on less wet soils, whereas pollen indicators of open, dry patches are scarce. The inferred scarcity of low-growing plants and open vegetation indicates that the grazing pressure on the landscape had not created a predominance of large over-grazed stretches, which suggests that the openness of the tree layer was not the result of (over-) grazing. But this has an uncertainty: if stretches of low open vegetation had been present, they may have been unattractive to a hungry herbivore and thus escaped the record.

Which plant taxa were ingested by the MW giant deer individual? Pollen grains of wind-pollinated plant taxa can be deposited on another plant taxon, and thus can become ingested by the giant deer without ingesting the pollen producer. This may have been the case with all wind-pollinated trees, since their pollen proportions are rather low (*Alnus*, *Betula*, *Corylus*, *Pinus*, etc.) (Fig. 3), but also pollen types that are classified as insect-dispersed can fall on top of other plants. Single pollen grains of a certain taxon found in few samples only are therefore no proof that the taxon has been consumed. Though it is difficult to estimate a pollen threshold above which we can assume ingestion, we infer that at least several Apiaceae (among which *Anthriscus sylvestris*, *Heracleum* and *Hydrocotyle*), Asteraceae (among which *Anthemis*-type, *Senecio*-type and Cichorioideae), *Filipendula*, Poaceae and *Symphytum* were among the ingested plants.

The PCA plot shows that the nine pollen assemblages from the MW jaw fall outside the range of assemblages in all ten previously studied, separately collected giant-deer molars/premolars (Fig. 5). This may in part be caused by different feeding habits of individual animals and by different grazing seasons, but differences in available plants and their abundances in the landscape must also have played a role. The

landscapes associated with the separate molars had in general more wind-pollinated plants such as *Betula*, *Pinus*, *Artemisia*, Poaceae and *Urtica* (Fig. 4) and, in some molars, abundant indicator pollen of open pioneer vegetation (*Artemisia*), contrasting with the closed, herb-rich vegetation reconstructed from the MW jaw pollen.

In summary, the pollen data suggest that the studied giant deer individual foraged in a savannah-like landscape scarce in trees and dominated by closed, mainly tall-herb vegetation in which the openness of the tree layer was not the result of over-grazing.

4.4. Past climate

The reconstructed past vegetation and environment provide a few hints concerning the climate of that period. However, our climate reconstruction on the basis of past vegetation will be done in general terms only, as it is tentative and any uncertainty in the vegetation reconstruction may propagate in the climate reconstruction. The inferred absence of thermophilous tree taxa in the vegetation and the openness of the tree layer agree with a climate that was distinctly cooler than during an interglacial such as the Eemian. This assumes that the vegetation is in equilibrium with the climate; a point of uncertainty is the possibility of migrational lags of thermophilous tree taxa during the beginning of a warm period. The apparently closed tall-herb vegetation suggests that moisture availability was higher than in steppe or desert climates, but apparently insufficient for closed forest. In summary, the pollen assemblage in the MW giant-deer jaw provides indications for a cool but not cold, dry but not arid, sub-continental climate.

4.5. Age of the MW giant deer

The radiocarbon date of the studied MW giant deer indicates an age older than 45,000 yr BP. Additional information on the possible age may be deduced from the surface weathering of the jaw. Two types of surface weathering exist in late Pleistocene skeletal elements which are associated with different climatic settings. The surface of the *materia compacta* is usually smooth in animals from the late-Pleistocene cold, dry and almost treeless mammoth steppe, such as wooly mammoth, steppe bison and wild horse. In contrast, the surface of the *materia compacta* is usually irregular, as it were heavily pockmarked, in skeletal elements of animals from the IJsselmeer region such as wild boar, hippo, forest elephant, aurochs, red deer and giant deer. This surface structure is also seen in the studied MW giant-deer maxilla fragment. We have also observed this characteristic weathering on skeletal elements from other sites in Western Europe: Germany (von Koenigswald, 1988; Rosendahl and Döppes, 2011), Berlare in Belgium (unpublished data), North Sea (Mol and Bakker, 2022) and the British Isles (Reynolds, 1929; Stuart, 1982). Such an irregular surface indicates corrosion, possibly caused by etching through acids, and thus suggests relatively warm and moist conditions. This may indicate that the studied MW giant deer lived (and died) in an interstadial or an interglacial, older than 45,000 yr BP. However, the relative abundance of pollen of the trees *Alnus*, *Betula* and *Salix* combined with the absence or scarcity of pollen of more thermophilous tree taxa (*Abies*, *Corylus*, *Quercus*, *Carpinus*, *Tilia*, *Ulmus*) excludes a full Eemian age (see Lang et al., 2023). The pollen record suggests a period with cool (but not cold) climatic conditions, which could be early Eemian or an early Weichselian interstadial, which is in agreement with the surface weathering.

5. Discussion and conclusions

The studied MW giant-deer maxilla is the first from the IJsselmeer region that has been radiocarbon dated. Pollen studies on infills of molar/premolar folds have been published before, but this is the first pollen study on multiple molars/premolars from the same individual animal and the first in high taxonomic resolution. Several of our findings depend on this high resolution, including a fairly detailed picture of the plants consumed by the animal and a good impression of the past vegetation diversity and structure. The following reasoning (a–d) would not have been possible without the high pollen-taxonomic diversity: (a) Pollen indicates that the animal foraged both in moist terrain with alder and birch trees and in drier terrain. (b) The grazed vegetation consisted in both situations of light-demanding tall-herbs of high diversity, which indicates that tree growth was scarce or locally absent, as in a savannah. (c) Pollen of low-growing, open herb vegetation, on the other hand, is scarce, which suggests that the openness of the tree layer is not the result of over-grazing. (d) The predominance of not over-grazed savannah suggests a semi-arid climate. Independent of the high pollen-taxonomic resolution is the inference that the presence of alder and birch but absence of thermophilous tree taxa indicates a cool climate. Combined with the radiocarbon date (older than 45,000 yr BP), the reconstructed environment suggests that the studied giant deer lived shortly after the start of the Eemian or during an early Weichselian interstadial.

A small study like this brings a wealth of new insights on the behavior and environment of a now-extinct animal. The deductions in terms of past vegetation and especially climate, are still rather coarse. We therefore expect much progress in knowledge and insight from future thorough, detailed pollen studies on additional mammal fossils.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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