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Analysis of Late Pleistocene megafauna and puparia from the Lent dredging site, province of Gelderland (the Netherlands)

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Abstract

More than 900 vertebrate bones, ranging from Late Pleistocene to Holocene in age, have been identified in a collection that was recovered by a single dredging operation for the construction of artificial lakes near Lent (Nijmegen, province of Gelderland, the Netherlands). The Late Pleistocene assemblage comprises mainly Weichselian glacial fauna such as mammoths, reindeer and bison. Some Eemian fauna is represented as well, e.g. straight-tusked elephant. The abundance of certain species over others suggests that preservation bias had a considerable impact on this assemblage, while its time-averaged nature resulted in overrepresentation of certain species. A case study is here conducted on a fragmentary skull of a subadult woolly mammoth bull with embedded blowfly puparia. Some of these puparia are fully developed, indicating prolonged exposure of the mammoth carcass.

Introduction

Skeletal remains of Late Pleistocene mammals can be found across the Netherlands as they were preserved by fluvial sediments which now surface across the country (Doppert et al., 1975; Van Kolfschoten & Laban, 1995; De Mulder et al., 2003; Gouw & Erkens, 2007; Laban & Van der Meer, 2011; DINOloket, 2020). At dredging sites, large numbers of such fossils have been collected and subsequently published (Mol et al., 1999; Van Kolfschoten, 2001; Van der Jagt, 2005; Van Kolfschoten et al., 2011).

Thousands of specimens have been collected during dredging operations at Lent near Nijmegen (51°52'38.6"N, 5°51'57.5"E; Fig. 1A). In total, 909 bones in this collection were considered suitable for identification. The faunal remains comprise 732 Holocene and 177 Late Pleistocene mammals. The Late Pleistocene fauna is analysed, with particular attention paid to fly puparia found embedded in skull fragments of the woolly mammoth, *Mammuthus primigenius* (Blumenbach, 1799), contained in the collections of the Oertijdmuseum at Boxtel (MAB10673).

Late Pleistocene faunal abundance

One of the most common mammals found in Late Pleistocene deposits throughout the Netherlands is the woolly mammoth (Mol et al., 1999), and Lent is no exception (Fig. 2F further below). Mammoth remains make up 50.3% of the Late Pleistocene assemblage from this locality (Fig. 1B) and are represented mainly as fragmentary skulls, mandibles and pelvises. This high percentage is due in part to their colossal size, which increases the chances of preservation. Additionally, this taxon was abundant and widely distributed during the Late Pleistocene, having been well adapted to grazing and cold temperatures.

Wild horse *Equus ferus* Boddaert, 1785 is also common (25.1%) at Lent, followed by steppe bison *Bison priscus* Bojanus, 1827 (11.7%) and reindeer *Rangifer tarandus* (Linnaeus, 1758) (5.6%). Horse remains are abundant, likely because their ecological niche was relatively large compared to that of reindeer or steppe bison. Horses were able to cope with open steppe conditions as well as with more forested environments, while bison and reindeer were restricted to open steppe environments. This flexibility explains why horses are represented not only in interstadial and stadial faunas, but possibly even in interglacial ones (Von Koenigswald, 2003; Saarinen et al., 2016). Furthermore, reindeer material is less likely to be preserved compared to other herbivores in the present collection, as their thin-walled humeri and radii were easily eroded or gnawed away by predators and scavengers (Van der Jagt, 2005; Zimov et al., 2012).

This collection contains only a few remains of the woolly rhinoceros, *Coelodonta antiquitatis* (Blumenbach, 1799), accounting for 2.8%. This low percentage likely represents the true number

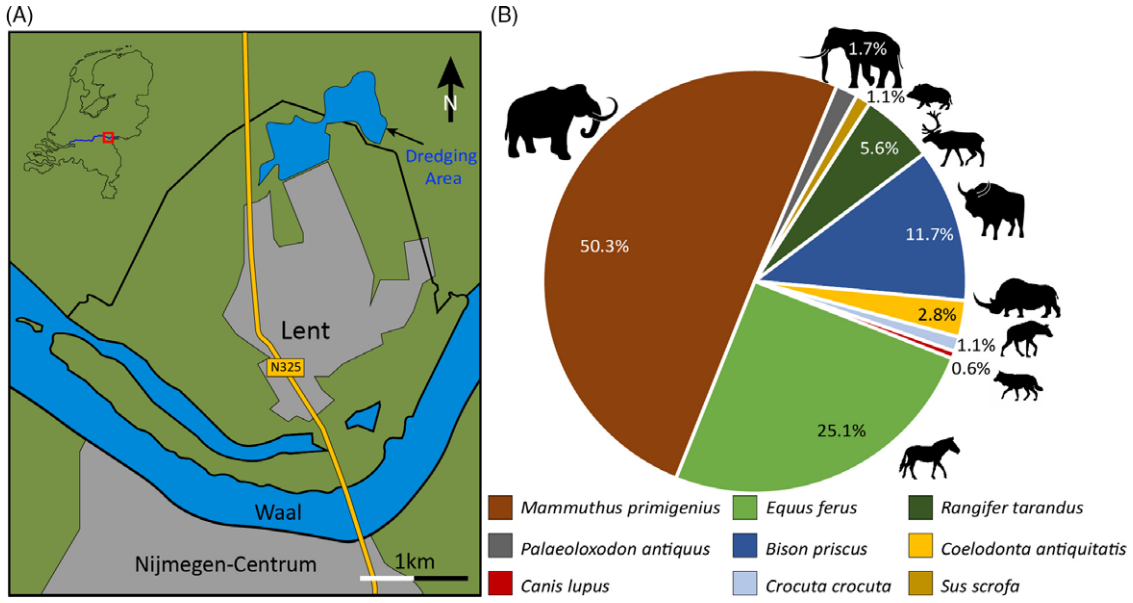

Figure 1. Location of the dredging site and the abundance of Pleistocene megafauna fossils.

Figure 2. Late Pleistocene fossils found at the Lent site: A. dextral radius of a cave hyena (*Crocuta crocuta spelaea*); B. dextral humerus of a cave hyena; C. atlas of a wild boar (*Sus scrofa*); D. pelvic fragment of a wolf (*Canis lupus lupus*); E. dextral lower M3 fragment of a straight-tusked elephant (*Palaeoloxodon antiquus*); and F. sinistral upper M1 molar of a woolly mammoth (*Mammuthus primigenius*). Black bar represents 5 cm.

of individuals of this species that lived during the Late Pleistocene. Woolly rhinos are thought to have been solitary, with males having territories similar to extant forms (Garutt, 1999; Diedrich, 2008; Becker et al., 2014). By contrast, mammoths, horses, steppe bison and reindeer lived in herds, and thus had considerably higher population densities compared to the woolly rhinoceros.

The geology at the site suggests these herbivores are to be associated with cold climatic conditions during the Late Pleistocene, and in particular with the Weichselian Glacial (DINOloket, 2020). They were occupants of the 'mammoth steppe', the cold, dry grass steppe that extended over much of the Northern Hemisphere during the Late Pleistocene (Zimov et al., 2012).

Predators are not well represented in this assemblage. Of the three bones recovered, two belong to the cave hyena (*Crocuta crocuta spelaea* Goldfuss, 1823; Fig. 2A–B). The third is a heavily mineralised pelvic fragment of a wolf (*Canis lupus*, Linnaeus, 1758; Fig. 2D). Fossils of cave hyenas are not particularly rare in the Netherlands (Reumer et al., 2010), while the absence of skeletal remains of other predators suggests that these were too rare in the ecosystem for them to be represented in this assemblage, as predators often are. It is difficult to connect the presence of predators with a particular climatic condition as they can be found both in warm and cold periods of the Late Pleistocene (Von Koenigswald, 2003). Other predators missing from the present assemblage are notably cave lions, brown bears and cave bears (cf. Bocherens, 2015).

Species associated with warmer climatic conditions are few in the assemblage. Three molars of the straight-tusked elephant *Palaeoloxodon antiquus* (Falconer & Cautley, 1846; Fig. 2E) and two heavily mineralised bones of wild boar (*Sus scrofa* Linnaeus, 1758; Fig. 2C) have been identified. The geology at the dredging site suggests that the remains of these animals date back to the Eemian and are possibly reworked (Laban & Van der Meer, 2011; DINOloket, 2020).

Fly puparia

In Pleistocene mammalian bones, blowfly puparia, typically the species *Protophormia terraenovae* Robineau-Desvoidy, 1830, are occasionally found (Gautier & Schumann, 1973; Vervoenen, 1991; Gautier, 1995; Verhagen & Mol, 2009; Van der Plicht et al., 2012; Mähler et al., 2016). This Holarctic species of the Calliphoridae family is absent from the Netherlands at present (Erzinçlioğlu, 2009; Vanin et al., 2009; Verhagen & Mol, 2009). This species breeds on the carcasses of vertebrates, on which their larvae feed and pupate (Roux et al., 2006; Erzinçlioğlu, 2009). Until the 1970s, remains of puparia in Pleistocene mammalian fossils

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Table 1. Length, width and shape factor of the Lent puparia, compared with the data from Erzinçlioğlu (1988)

	Length (mm)	Maximum width (mm)	Shape factor	Empty (E) or unopened (U)	Reference
Puparium 1	8.4	3.9	0.46	U	This study
Puparium 2	8.9	3.1	0.35	U	This study
Puparium 3	9.5*	5.0	0.53	E	This study
Puparium 4	8.5	4.1	0.48	E	This study
Puparium 5	8.7*	4.3	0.49	E	This study
P. terraenovae	8.37–9.13	2.50–3.38	0.30–0.37		Erzinçlioğlu (1988)

*Estimated length because these puparia were incomplete. Shape factor calculated by dividing the greatest width by overall length.

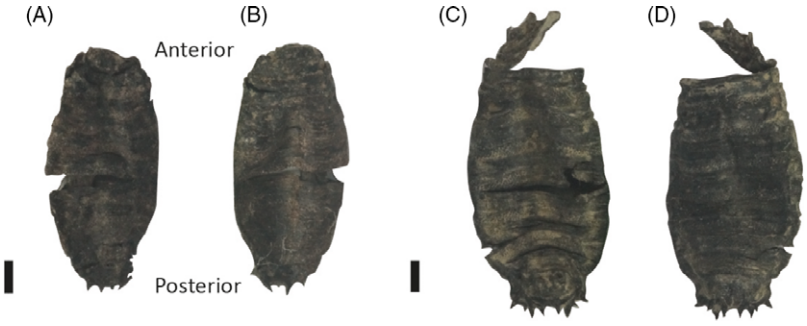

Figure 3. MAB11313 Puparium 1 (unopened) ventral (A) and dorsal (B) view; Puparium 3 (opened) ventral (C) and dorsal (D) view. Black bar represents 1 mm.

were thought to be rare; subsequently, there have been more observed (Gautier & Schumann, 1973; Vervoenen, 1991; Gautier, 1995; Verhagen & Mol, 2009; Van der Plicht et al., 2012; Mähler et al., 2016).

A skull of a woolly mammoth (MAB10673) from Lent comprises 43 separate fragments (e.g. Fig. 2F), 15 of which contained puparia. Only five puparia (MAB11313; Table 1) were deemed to be sufficiently preserved for identification in accordance with criteria presented in the relevant literature (Gautier & Schumann, 1973; Erzinçlioğlu, 2009; see Fig. 3). All five have been identified as *P. terraenovae* on the basis of length and morphology. Two of these have larger widths than is typical of this species (Erzinçlioğlu, 1988), but this is likely due to infilling sediment having flattened the puparia inside the skull fragments.

These puparia were recovered from skull fragments close to natural body orifices such as the eyes (zygomatic arch), which are used by blowflies to enter the body, as has been documented for colonisation of human carcasses (Haskell et al., 1997). The larvae likely travelled further into the carcass to feed (Roux et al., 2006).

The mammoth host was likely a subadult bull, as the wear patterns observed on the lower dextral M2 suggest that it had reached the age of 24.5 ± 2 African Equivalent Years (Laws, 1966), an estimate based on the procedure outlined by Haynes (1993) for extinct proboscideans. Sex was determined by comparing the dimensions of the isolated occipital *pars basalis* to those of the analogous bone in the complete skull of an adult female (MAB11628; Van der Merwe et al., 1995; Averianov, 1996).

By applying modern forensic methods to the analysis of puparia, one can approximate the minimum temperature at the time of the mammoth's death (Gilbert & Bass, 1967; Vanin et al., 2009). *Protophormia terraenovae* can develop its eggs only in temperatures higher than 9°C (Nuorteva, 1987; Grassberger & Reiter, 2002). Reconstructions by Caspers & Freund (2001) suggest that mean July temperatures during the Weichselian ranged from approximately 17°C during the early Weichselian to 3°C during the Late High Glacial stadials. This suggests that this mammoth died either during the early Weichselian or during an interstadial of the High Glacial when temperatures were high enough for egg development.

Three of the five puparia analysed were empty, suggesting that the flies fully developed and left their puparium (Nuorteva, 1987). Hence, the carcass was likely exposed to the surface long enough for them to become fully developed. Studies on the periods of development of extant *P. terraenovae* suggest that full development takes between 35 and 39 days (Marchenko, 2001; Grassberger & Reiter, 2002). However, this varies according to region and temperature (Grassberger & Reiter, 2002). Other heat sources, such as the carcass itself (Henssge, 1988) and 'maggot mass heating', should be taken into account, as they can cause development times to be considerably shorter (Haskell et al., 1997; Erzinçlioğlu, 2009).

Conclusions

Late Pleistocene megafaunal remains from Lent document a considerable preservational bias in favour of mammoths and against species such as reindeer, while accurately representing the abundance of horses, steppe bison and woolly rhinoceros throughout climatic changes during the Late Pleistocene. The presence of *Protophormia terraenovae* puparia in the woolly mammoth bull skull MAB10763 suggests carcass colonisation occurred during the early Weichselian, or during an interstadial of the High Glacial, during which temperatures met the minimum requirement for egg development.

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