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Resource partitioning and niche separation between mammoths (*Mammuthus rumanus* and *Mammuthus meridionalis*) and gomphotheres (*Anancus arvernensis*) in the Early Pleistocene of Europe

Florent Rivals [a, b, c, *], Dick Mol [d], Frédéric Lacombat [e], Adrian M. Lister [f], Gina M. Semprebon [g]

[a] Institució Catalana de Recerca i Estudis Avançats (ICREA), Barcelona, Spain
[b] Institut Català de Paleoecologia Humana i Evolució Social (IPHES), C. Marcellí Domingo s/n, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain
[c] Area de Prehistoria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain
[d] Natural History Museum Rotterdam, Westzeedijk 345, 3015 AA Rotterdam, The Netherlands
[e] Musée de Paléontologie de Chilhac, Place de l'Eglise, 43380 Chilhac, France
[f] Earth Sciences Department, Natural History Museum, Cromwell Road, London SW7 5BD, UK
[g] Bay Path University, 588 Longmeadow Street, Longmeadow, MA 01106, USA

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ABSTRACT

This paper presents the results from a tooth microwear analysis of three proboscideans (*Mammuthus rumanus*, *Mammuthus meridionalis*, and *Anancus arvernensis*) from four Early Pleistocene localities in Europe (Red Crag, Norwich Crag, Chilhac, and Eastern Scheldt). The particularity of these four localities is that mammoths and gomphotheres co-occur. The quantitative microwear data (numbers of pits and scratches) were informative about the broad feeding traits in each species. For both genera studied, diets range from strict browsing (including leaf and fruit browsing) to grass-dominated mixed feeding. These data reveal highly variable dietary traits in the mammoths and gomphotheres studied, but the qualitative results provide evidence of differences between the two sympatric genera. We were able to identify the consumption of fruits, seeds, bark and twigs in *A. arvernensis*, and the ingestion of high quantities of grit in *M. rumanus* and *M. meridionalis* which is most likely related to open or semi-open habitats. The data also support the hypothesis that resource partitioning existed between mammoths and gomphotheres when they co-occurred at a locality.

1. Introduction

Niche separation is a mechanism frequently observed in related extant taxa, and is thought to reduce competition for food resources among species with broadly similar nutritional requirements (Pianka, 1974; Schoener, 1983; Walter, 1991). Niche separation is also evidenced in fossil mammals through various proxies such as stable isotopes or tooth wear analyses (Stewart et al., 2003; Bibi, 2007; Calandra et al., 2008; Rivals et al., 2010; Bocherens et al., 2011; Kaiser, 2011). Among proboscideans, this phenomenon has been reported in deinotheres and gomphotheres, and has helped to explain the coexistence of sympatric megaherbivores during the Miocene (Calandra et al., 2008). Sympatric species of proboscideans also occur during the Quaternary, such as the Early Pleistocene *Mammuthus rumanus* (Stefanescu, 1924) or *Mammuthus meridionalis* (Nesti, 1825) which are found associated with *Anancus arvernensis* (Croizet and Jobert, 1828) in some localities of Europe.

Morphologically, the mandibles of *A. arvernensis* were short and the molars had nipple-shaped cusps arranged in transverse rows. These bunodont molars are generally taken to imply a soft diet of leaves, fruit and twigs. The feet were adapted to walk on soft soil, suggesting that *Anancus* was an inhabitant of moist woodlands (Braber et al., 1999; Mol et al., 1999). In the fossil record of *A. arvernensis*, the molar crown became higher, the valleys between the cusps and rows were filled with cement and the transverse

Abbreviations: IPSMG, Ipswich Museum, Ipswich, United Kingdom; MPC, Musée de Paléontologie de Chilhac, Chilhac, France; NCB Naturalis, Netherlands Center for Biodiversity Naturalis, Leiden, The Netherlands; NHM, Natural History Museum, London, United Kingdom.

* Corresponding author. Institut Català de Paleoecologia Humana i Evolució Social (IPHES), C. Marcellí Domingo s/n, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.
E-mail addresses: florent.rivals@gmail.com, florent.rivals@icrea.cat (F. Rivals).

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rows or lophids increased in number. This is believed to imply a trend from soft forest food towards the incorporation of grasses, requiring a grinding component to mastication (MacFadden and Cerling, 1996; de Vos et al., 1998; Zazzo et al., 2000; Lister, 2013).

Mammuthus was an elephantid and, as such, had fused the transverse cusp pairs of gomphotheres into continuous loops of enamel, each filled with dentine and joined to its neighbours by cement. The occlusal faces of the upper and lower molars formed grinding, or more accurately shearing, surfaces (Maglio, 1973). *M. rumanus* is the earliest mammoth known in Europe, with similar number of enamel loops (8–10) as its immediate African progenitors but a somewhat higher tooth crown (Lister and Sher, 2001). In *M. meridionalis* crown height remained similar but the number of enamel loops had increased to typically 12–14 (Lister and Sher, 2001). These represent early stages of the pronounced increase in both variables through the mammoth lineage in the Pleistocene, considered to reflect the transition to a largely open-ground grazing diet, but the dietary composition of the early members, *M. rumanus* and *M. meridionalis*, is poorly-known.

The objectives of this study are (1) to infer the dietary traits of three proboscidean species: *M. rumanus*, *M. meridionalis*, and *A. arvernensis*, and (2) to test the hypothesis that resource partitioning existed between mammoths and gomphotheres when they co-occurred at a locality. For this purpose, samples were collected and analyzed from four European localities or deposits where the two genera were present. We used tooth microwear analysis to study dietary traits of *Mammuthus* and *Anancus*. Tooth microwear patterns reflect the physical properties of food consumed during the last few days or weeks of the animal's life (Walker et al., 1978; Teaford and Oyen, 1989). Tooth microwear studies also provide valuable proxies for demonstrating geographical and/or temporal variability in diet and vegetation structure (Semprebon et al., 2004a; Semprebon and Rivals, 2010; Rivals et al., 2012), as well as niche segregation and resource partitioning (Calandra et al., 2008; Rivals et al., 2008, 2010).

2. Material and methods

2.1. Material sampled

We collected and analyzed samples from four European localities where mammoth and gomphothere species were both present (Fig. 1): Red Crag (UK, 2.6–2.4 Ma), Norwich Crag (UK, ca. 2.3–1.9 Ma), Chilhac (France, ca. 2 Ma) and Eastern Scheldt (The Netherlands, ca. 1.7 Ma).

2.1.1. Red Crag

The Red Crag Formation comprises a series of inshore marine shelly sands. As indicated by Gibbard et al. (1998) and Head (1998), the Red Crag covers the Waltonian, Pre-Ludhamian and Ludhamian Stages of the British Late Pliocene. However, the majority of surface exposures, except those around Walton, are of Pre-Ludhamian age (J. Zalasiewicz, pers. comm.), so it is likely that the bulk of the collected mammalian fauna is of this age. Head (1998) and Funnell (1998), on the basis of dinoflagellates and foraminifera, respectively, concur in placing this part of the Red Crag in the interval 2.6–2.4 Ma. Head (1998) correlates the Pre-Ludhamian with either the cold Praetiglian Stage of The Netherlands (ca. 2.5 Ma), or the preceding Reuverian C Substage (ca. 2.6 Ma), with the latter slightly favoured. The Pre-Ludhamian is a cool interval with regional boreal trees, *Erica* heath and grasses. The mammals include grazing or mixed-feeding species such as the large stenonine horse *Equus bressanus* and early mammoth *M. rumanus* (Lister and van Essen, 2003), as well as woodland elements such as the gomphothere *A. arvernensis* and beaver *Castor* sp. The material studied is housed at the Natural History Museum (London), the British Geological Survey (Keyworth), and Ipswich Museum.

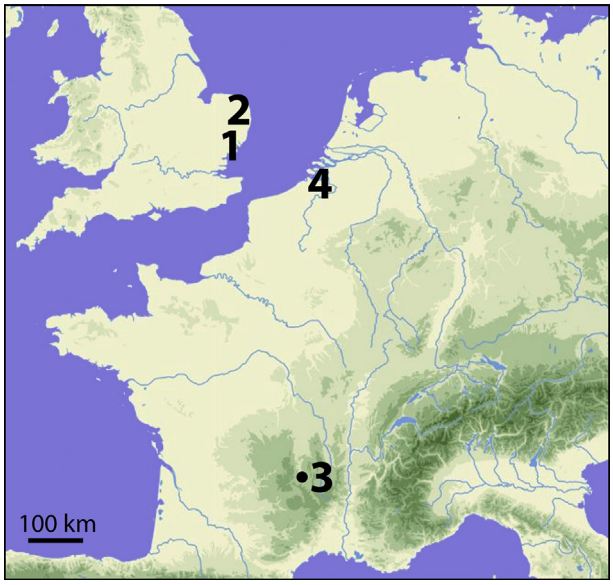

Fig. 1. Geographic position of the localities sampled: (1) Red Crag, (2) Norwich Crag, (3) Chilhac, and (4) Eastern Scheldt.

2.1.2. Norwich Crag and Wroxham Crag (in part)

The Norwich Crag Formation includes the cool Thurnian and warm Antian (=Bramertonian) stages of the British Early Pleistocene (Funnell, 1998). These deposits are dated to ca. 2.3–1.9 Ma and correlate with Tiglian C1-4b of the Dutch succession. Norwich Crag deposits of Bramertonian age have yielded *E. bressanus*, *M. meridionalis*, *A. arvernensis* and the deer *Eucladoceros* in a mixed temperate forest (Head, 1998), plus cheetah *Acinonyx pardinensis* implying open areas (Turner, 2009). The formerly-named Weybourne Crag of Norfolk is of slightly later, Baventian age (= Pre-Pastonian in part, ca. 1.85 Ma and equivalent to TC4c); it has been reallocated to the Norwich Crag (Gibbard et al., 1998) and more recently to the Wroxham Crag Formation (Rose et al., 2001), so some fossils in the collections labelled 'Norwich Crag' may be of this age. The sample also includes material from the Westleton Beds of northern Suffolk, believed to represent a climatic amelioration towards the end of the Baventian/Pre-Pastonian cold stage (Richards et al., 1999). From the Westleton Beds have come remains of *M. meridionalis* and the early moose *Cervalces gallicus* (Lister, 1998). The material sampled is curated at the Natural History Museum (London), the British Geological Survey (Keyworth), and the Cruickshanks private collection.

2.1.3. Chilhac

Chilhac is a classic and historic paleontological locality (Lacombat et al., 2010) of the French Massif Central. The sites of Chilhac 2 (CH2) and Chilhac 3 (CH3) are located near the valley of the Allier River at the northern edge of the basaltic plateau of the Devès. The extremely well-preserved fossils are discovered on both sides of the small Rabioulet stream in a volcanic context. The two localities do not show any biochronologic difference and the large mammal associations are characteristic of the MN17b biozone (Palombo and Valli, 2004) and of the C.S. Giacomo Faunal Unit (Gliozzi et al., 1997). The site CH2 is covered by a lava flow dated by