Quaternary Science Reviews 69 (2013) 155–167

Contents lists available at SciVerse ScienceDirect

Quaternary Science Reviews

journal homepage: www.elsevier.com/locate/quascirev

Dama roberti, a new species of deer from the early Middle Pleistocene of Europe, and the origins of modern fallow deer

Marzia Breda [a,b,*], Adrian M. Lister [a]

[a] Department of Earth Sciences, The Natural History Museum, Cromwell Road, London SW7 5BD, UK
[b] Department of Human Studies, University of Ferrara, Corso Ercole I D'Este, 32, Ferrara 44100, Italy

ARTICLE INFO

Article history:
Received 27 October 2012
Received in revised form
23 January 2013
Accepted 26 January 2013
Available online 15 April 2013

Keywords:
Dama roberti n. sp.
Fallow deer
Early Middle Pleistocene
Pakefield (UK)
Soleilhac (FR)

ABSTRACT

The ancestry of the modern fallow deer, *Dama dama*, has been tentatively traced back to Pliocene/Early Pleistocene forms referred to '*Pseudodama*', characterized by unpalmated three- or four-point antlers. By the late Middle Pleistocene, *Dama* with palmated antlers appears, as *Dama dama clactoniana*. However, fallow deer from the interim period, the early Middle Pleistocene, are poorly-known. A new specimen from Pakefield (Suffolk, UK), represented by a portion of cranium with a substantial part of both antlers plus a mandible and scapula, is the most complete medium-sized deer specimen from the British early Middle Pleistocene (ca 700 ka). The position and orientation of the basal tine, together with dental characters and mandibular morphology, are typical of fallow deer. The narrow palmation is reminiscent of *D. dama clactoniana*, but the lack of palmation tines is unique. Moreover, the lack of second (and third) tines in an adult specimen differs from both *D. dama dama* and *D. d. clactoniana*, being a primitive character shared with the last representatives of '*Pseudodama*' which, on the other hand, has a circular beam lacking any palmation. This combination of features justifies the erection of a new species provisionally placed within the genus *Dama*, *Dama roberti* n. sp. Another specimen, from Soleilhac (Auvergne, France), represented by portions of the two antlers, a mandible and a tibia, shares antler morphology with the Pakefield specimen and can be ascribed to the same new species. Isolated antler and dental remains from coeval British sites are tentatively ascribed to *D. roberti* n. sp. The new species has implications for the ancestry of modern fallow deer.

1. Introduction

Most living mammal species had their origin in the Quaternary (Lister, 2004). While the rich fossil record of the Quaternary provides the opportunity in principle to trace the evolutionary origin and ecological history of the living fauna, in practice only for relatively few modern species do we yet have a convincing series of fossils illustrating their ancestry. We here describe a new species within a widespread large mammal lineage of the European and Near Eastern Quaternary: the fallow deer *Dama*. The genus today comprises the European *D. dama dama* and endangered *D. d. mesopotamica* of the Near East. In Europe, late Middle to Late Pleistocene fossils are clearly close to modern European fallow, while a distinct series of Pliocene to Early Pleistocene species has been implicated in their ancestry. However, fallow deer from the early Middle Pleistocene, a critical period in the origin of many modern mammal species, have until now been poorly represented and their taxonomy unclear. The new and reinterpreted early Middle Pleistocene material presented here is strikingly distinct from previously described species and is of likely significance in understanding the origins of modern fallow.

Several of the medium-sized deer species from the European Pliocene and Early Pleistocene were united by Azzaroli (1992) in the genus *Pseudodama*. They share with modern fallow antler features such an obliquely-oriented basal portion of the antler beam, a single basal tine set at an oblique angle to the beam, and lack of surface pearling on beam and tines (Lister, 1996a). The main feature distinguishing the '*Pseudodama*' species from later *Dama* is the complete lack of palmation of their three- or four-pointed antlers; this is a primitive feature so '*Pseudodama*' probably has the status of a paraphyletic stem-group. The name will, however, be retained here for ease of reference to this group of species.

In the late Middle Pleistocene, a fallow deer with palmated antlers appears in Italy, France, Spain and Britain, where its first occurrence is in Marine Isotope Stage (MIS) 11. This is *Dama dama*

* Corresponding author. Department of Human Studies, University of Ferrara, Corso Ercole I D'Este, 32, Ferrara, 44100, Italy. Tel.: +39 347 9449940.
E-mail addresses: marziabreda@hotmail.com, marzia.breda@unife.it (M. Breda).

0277-3791/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.quascirev.2013.01.029

clactoniana, differing from living *D. d. dama* in the narrower palmation, the presence of three tines on the anterior side of the beam (rather than two as usually occurs in *D. d. dama*), and the distribution and size of the palmation tines (large and mainly on the distal edge rather than small and on the palmation caudal edge in *D. d. dama*). According to Di Stefano and Petronio (2003), the subspecies *D. d. tiberina* and *D. d. geiseliana* occur in the late Middle Pleistocene (MIS 7), while the living *D. dama dama* appears only in the early Late Pleistocene (MIS 5e). In the Middle East, characteristic Mesopotamian fallow deer, *D. d. mesopotamica*, is first known in MIS 5 (Di Stefano and Petronio, 1996, who call it *D. clactoniana mesopotamica*); earlier *Dama* from the region are less well known and of uncertain affinity (Di Stefano and Petronio, 1996; Rabinovich et al., 2008).

However, fallow deer from the early Middle Pleistocene (eMP) – the period between '*Pseudodama*' and the earliest well-represented *Dama* – have until now been poorly-known and fragmentary. Azzaroli (1953) tentatively referred eMP remains from the Cromer Forest-bed Formation (CF-bF) to *D. d. clactoniana*, but Lister (1993, 1996b) and Lister et al. (2010) pointed out that, since the diagnostic upper part of the antler is lacking, specific attribution is problematic.

Here we report a recently-discovered specimen from Pakefield, represented by a portion of cranium with substantial parts of each antler plus a mandible and scapula. It is the only fallow deer specimen from the British eMP represented by associated elements, and was found *in situ* in a deposit dated to ca 700 ka (Stuart and Lister, 2010). A second specimen, from Soleilhac (Auvergne, France), closely matches the morphology of the Pakefield antler. This specimen, of similar age to Pakefield, also consists of associated elements, namely the right antler, fragments of the left antler, a mandible and tibia.

The peculiarities of the antlers from Pakefield and Soleilhac, as well as dental characters shared in other eMP fallow, justify the description of a new species. This species fills the temporal, and to some extent morphological, gap in the fallow deer record between Pliocene to Early Pleistocene '*Pseudodama*' and late Middle Pleistocene to Recent *Dama*.

2. Materials and methods

Our approach to species recognition is inevitably morphological, with the degree of differentiation observed among living species a guide to taxonomic distinction. Among deer, the recognition of extinct species has rested heavily on antlers, since they are the most distinctive bony elements across living deer, and are abundantly preserved as fossils. We accept the taxonomic value of antlers, while noting that their ontogenetic and individual variation has led to unjustified multiplication of fossil species in the past, and needs to be carefully taken into account when delimiting new species. Teeth and bones are more conservative among deer species, but do contain taxon-specific variation (e.g. Lister, 1996a; Breda, 2005).

The nomenclature of modern fallow deer has itself been the subject of debate, some authorities (e.g. Rabiei and Saltz, 2011) regarding the European and Mesopotamian forms as separate species *D. dama* and *D. mesopotamica*, others (e.g. Fernández-García, 2012) treating them as subspecies *D. dama dama* and *D. d. mesopotamica*. The situation is complicated further by the inclusion of fossil forms such as *clactoniana*, and we here adopt the convention of retaining all these forms as subspecies of *D. dama* (Lister, 1986).

We studied all available British eMP *Dama*-sized deer in the Natural History Museum, London (NHM – including the major collections of A.C. Savin from West Runton and Pakefield, and R. Mutch from Pakefield), and in the Castle Museum, Norwich (NCM – including new material from the West Runton Freshwater Bed recently collected *in situ*; Stuart and Lister, 2010). The NHM also houses remains from the Calcareous Member at Westbury-sub-Mendip, Somerset (Bishop, 1982; Andrews et al., 1999), and from Boxgrove, West Sussex (Roberts and Parfitt, 1999). The West Runton Freshwater Bed falls in the early part of the early Middle Pleistocene at ca 700–600 ka, possibly in MIS 17 (Stuart and Lister, 2010). The Pakefield and Kessingland deposits form a single stratigraphic unit (Stuart and Lister, 2001), of similar age to West Runton or possibly slightly older (Preece and Parfitt, 2008; see below). Boxgrove and Westbury are placed in the later part of the early Middle Pleistocene, ca 500 ka (Preece and Parfitt, 2000). Location of sites is shown in Fig. 1.

We also studied all the *Dama*-sized deer material from Soleilhac (Haute-Loire, France; Fig. 1) at the Musée Crozatier, Le-Puy-en-Velay (MC) and reviewed the literature of coeval *Dama*-sized deer from other European localities.

Comparative data on *Dama dama* subspecies is taken from Lister (1996a), Lister et al. (2005), and new observations on *D. d. clactoniana* from Swanscombe, Kent and Clacton, Essex, and on the *D. d. mesopotamica* paratype plus fossil material from Tabun, Israel (NHM collections). For '*Pseudodama*' species we studied material of '*P.*' *lyra*, '*P.*' *nestii*, '*P.*' *eurygonos*, '*P.*' *farnetensis* from localities in central Italy (Museo di Geologia e Paleontologia of the University of Florence), '*P.*' *philisi* and '*P.*' *perolensis* from the Massif Central, France (Musée Géologique Université Claud Bernard, Lyon 1), and drew information on teeth and antlers of '*P.*' *vallonnetensis* from Kahlke (1997, 2001, 2009).

For the antler material, measurements are described in Table 1. For the teeth (Table 2), length is measured at the crown base to avoid wear-related modifications, while the crown width is the maximum perpendicular to the tooth's antero-posterior axis. For limb bone measurements we followed von den Driesich (1976).

Fig. 1. Map of (A) southern Britain, and (B) Western Europe with Pakefield (UK), Soleilhac (France) and other eMP localities quoted in the text, plus Swanscombe (late Middle Pleistocene).