

Adrian M. Lister
University College London

The Pliocene deer of the Red Crag Nodule Bed (UK)

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Deer remains from the Pliocene Red Crag Nodule Bed comprise a series of antler bases and teeth. The antlers were given the name *Cervus suttonensis* by Dawkins (1878). On the basis of re-examination and biometric study of the teeth and antlers, it is suggested that Dawkins's species may be a composite of the cervid taxa *Cervus perrieri* CROIZET & JOBERT 1828 and *Cervus pardinensis* CROIZET & JOBERT 1828; and that the species *Procapreolus cusanus* (CROIZET & JOBERT 1828) may also be present in the assemblage. This suggests a broad correlation to the Etouaires fauna (Early Villafranchian) of France.

Correspondence: A.M. Lister, Department of Biology, University College London, London WC1E 6BT, UK

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INTRODUCTION

The Red Crag Formation, comprising shelly marine sands of Pliocene age, outcrops in Essex and Suffolk, in the southern part of East Anglia, England. At its base is the 'Red Crag Nodule Bed' or 'Basement Bed'. Relatively sparse mammalian fossils from both deposits have been collected over an extended period. Those from the Red Crag proper are relatively unmineralised and include such species as *Mammuthus meridionalis*, *Equus* cf. *bressanus* and *Eucladoceros falconeri* (Spencer 1964, Stuart 1982, Lister 1998). Surface exposures largely correlate to the Pre-Ludhamian Stage of the British sequence (Gibbard *et al.* 1998), and on the basis of foraminifera are dated to c. 2.5 My (Funnell 1998).

The fossils of the Red Crag Nodule Bed are, by contrast, heavily mineralised and of a dark, polished appearance. They include reworked material of Eocene and possibly

Miocene age (Spencer 1971), but the majority of the mammalian assemblage appears to be of broadly Early Villafranchian complexion, and includes *Mammuth borsoni*, *Tapirus arver-nensis*, *Hipparion* sp. and *Leptobos* sp. (Stuart 1982). Cervid remains from the Red Crag Nodule Bed largely comprise a series of antler bases and teeth, conserved at the Natural History Museum (London), Ipswich Museum, The British Geological Survey (Keyworth) and York Museum.

This cervid assemblage was first given serious consideration by Dawkins (1878), who created the species *Cervus suttonensis* on the basis of four antler bases from the 'Crag' of Sutton and Woodbridge, Suffolk. The antlers are polished and mineralised, and clearly originated in the Nodule Bed. The syntypes were figured by Dawkins (1878) and De Vos *et al.* (1995); two of them are illustrated here (Figs. 1 and 2).

ANTLER MORPHOLOGY

The '*C. suttonensis*' antler material is fragmentary, none of the available antlers preserving more than the basal part, usually the rose, first tine, and lower part of the beam. Given the number of known cervid taxa with a single basal tine, this renders the Nodule Bed material close to being indeterminable (Azzaroli & Mazza, 1992; De Vos *et al.* 1995). Cautious examination of the antler bases and dental remains in the collections does, however, allow tentative taxonomic conclusions to be drawn.

Dawkins (1878) indicated for his *C. suttonensis* that the antlers were characterised by an acute (<90 degree) angle of the first tine to the beam, and a marked 'webbing' in the fork of the first tine. Already at that time he drew attention to the similarity of the British antlers to those of the continental species *Cervus pardinensis* CROIZET & JOBERT, stating that 'The *Cervus suttonensis* is, in its general form, closely allied to *C. pardinensis*, of which it may be a small breed or variety'. This view has persisted, Spencer (1971) and

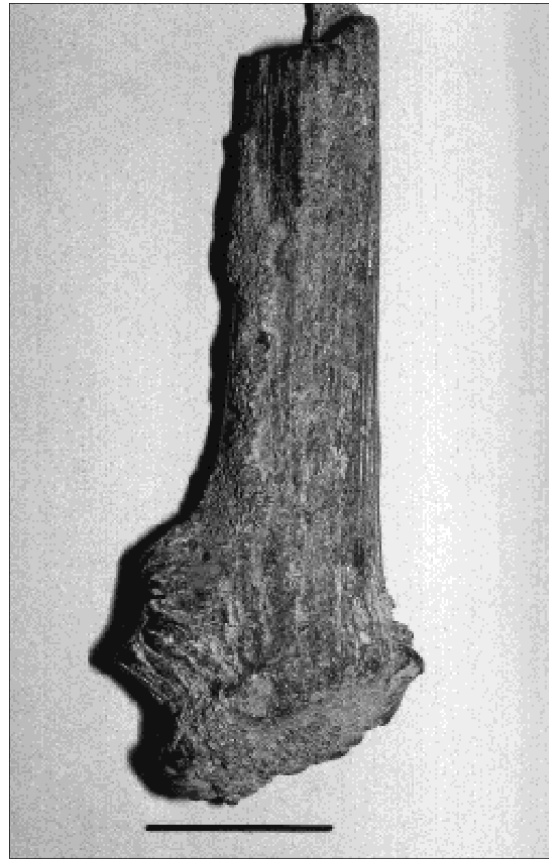


Figure 2 Left shed antler NHM 27515, Sutton. Syntype of *Cervus suttonensis* DAWKINS, here referred to *C. perrieri*. Scale bar 5 cm.

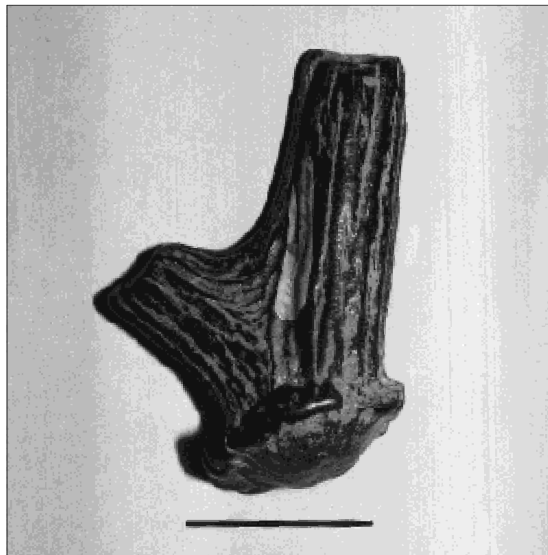


Figure 1 Left shed antler NHM 27858, Felixstowe. Syntype of *Cervus suttonensis* DAWKINS, here referred to *C. pardinensis*. Scale bar 5 cm.

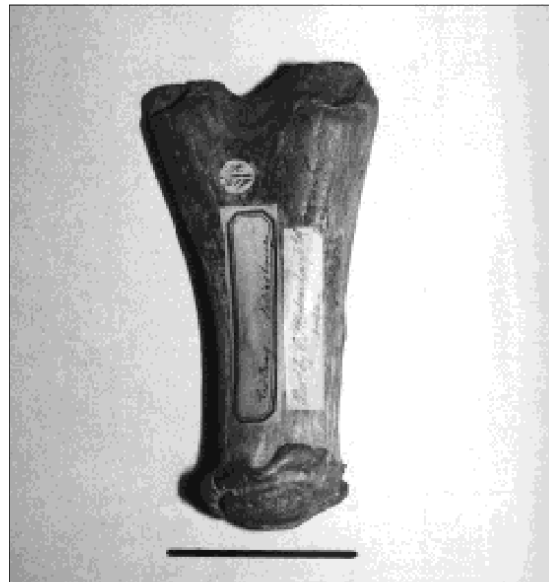


Figure 3 Shed antler NHM 1617, Felixstowe, here referred to *Procapreolus cusanus*. Scale bar 5 cm.

Stuart (1974), for example, recording '*Axis pardinensis*' from the Nodule Bed. The attribution to '*Axis*' was based on the similarity of the antler base to that of the living *Axis* deer or Chital of south-east Asia, *Cervus (*Axis*) axis*.

The majority of the antler bases are of a consistent size and form, corresponding to Dawkins's description of his species given above. Moreover, in comparison with the illustrations and descriptions given by Heintz (1970), the attribution to *C. pardinensis* seems justified, particularly in the acute fork, sometimes rather high above the rose, and the

peculiar 'webbing' in its axis. Antlers of this type include one of Dawkins's syntypes, NHM 27858 (Dawkins 1878, fig. 7; here Fig. 1).

A few antlers in the Nodule Bed sample, however, differ in being markedly larger, with an oblique angle of the first tine (>90 degrees), and less marked 'webbing' in the fork. One of these specimens is another of Dawkins's *C. suttonensis* syntypes, NHM specimen 27515 (Dawkins 1878, fig. 8; here Fig. 2). Another is the specimen in York Museum figured by Newton (1891, fig. 13) and measured during this study. It is sugge-

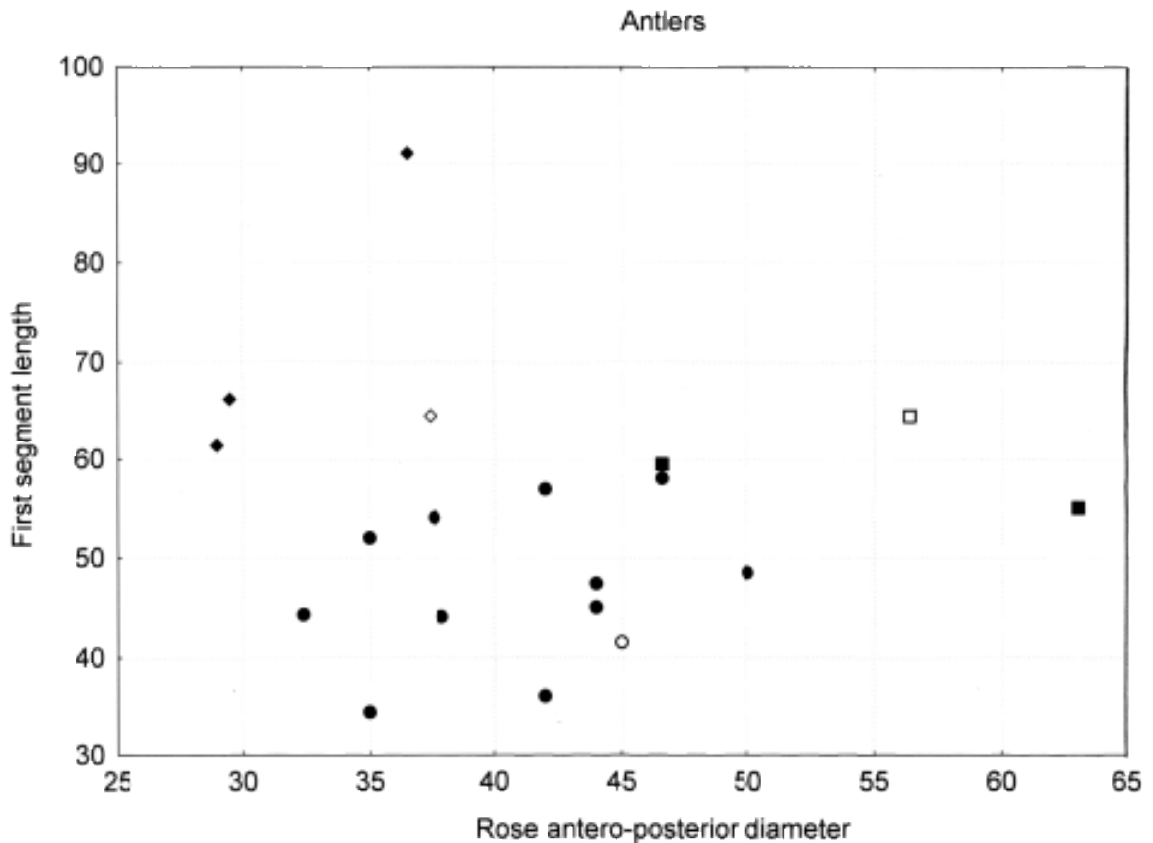


Figure 4 Scatterplot of antler bases from the Red Crag Nodule Bed. **Closed diamonds:** specimens referred to *Procacpreolus cusanus*. **Open diamond:** specimen of uncertain attribution, *P. cusanus* or *C. pardinensis*. **Closed circles:** specimens referred to *Cervus pardinensis*. **Open circle:** specimen of uncertain attribution, *C. pardinensis* or *C. perrieri*. **Closed squares:** specimens referred to *Cervus perrieri*. **Open square:** specimen of uncertain attribution, probably *C. perrieri*, possibly *C. pardinensis*.

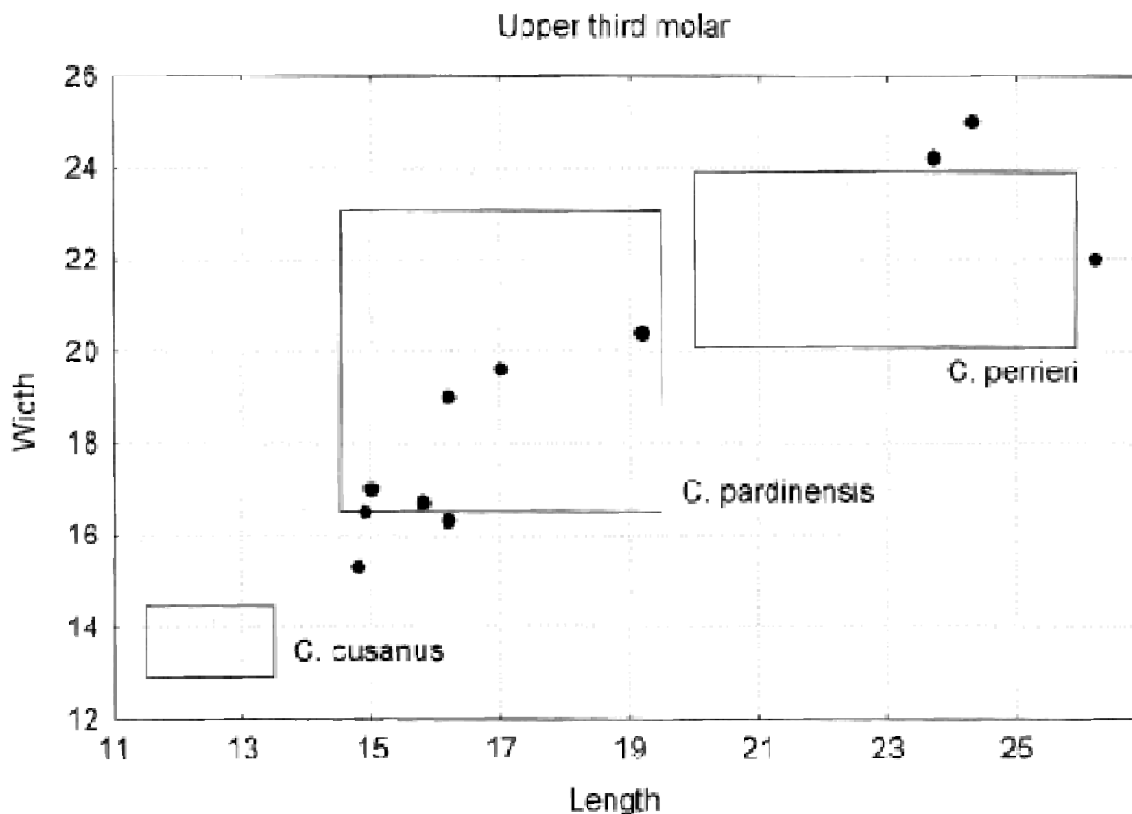


Figure 5 Scatterplot of cervid upper third molar dimensions from the Red Crag Nodule Bed. Rectangles are ranges of the named species from French and Spanish localities, taken from Heintz (1970): *Cervus* (= *Procapreolus*) *cusanus* (n= 9) from Etouaires; *C. pardinensis* (n=36) from Etouaires and Vialette; *C. perrieri* (n=24) from Villaroya and Etouaires. Dimensions in millimetres.

sted, by comparison with Heintz (1970), that these specimens may be attributable to the species *Cervus perrieri* CROIZET & JOBERT. In addition to the large size and oblique angle, one of the British specimens (Ipswich Museum, no number) has a swelling in the axis of the first fork which corresponds to the tubercle indicated by Heintz (1970) as characteristic of this species. Relative to the size of the antler base, the first tine tends to originate closer to the base than in the specimens referred to *C. pardinensis*. The remaining two *C. suttonensis* syntypes figured by Dawkins are clearly juvenile and their specific attribution is impossible to determine.

A few other antler bases do not fit into either

of these two categories. These are of small size but with laterally flattened beam and a remarkably high first tine. One of them (NHM 1617) is illustrated in Figure 3. This morphology suggests the early roe deer *Procapreolus cusanus* (CROIZET & JOBERT 1828), an identification supported by Dr I. Vislobokova (pers. comm.), who has extensive experience with this genus. Reviews of the taxonomy, morphology and distribution of *Procapreolus* are given by Vislobokova & Kalmykov (1994) and Lister *et al.* (1998).

In Figure 4, antero-posterior rose diameter (an index of size and age) is plotted against the height of the first tine (first segment length), according to the method described by Heintz

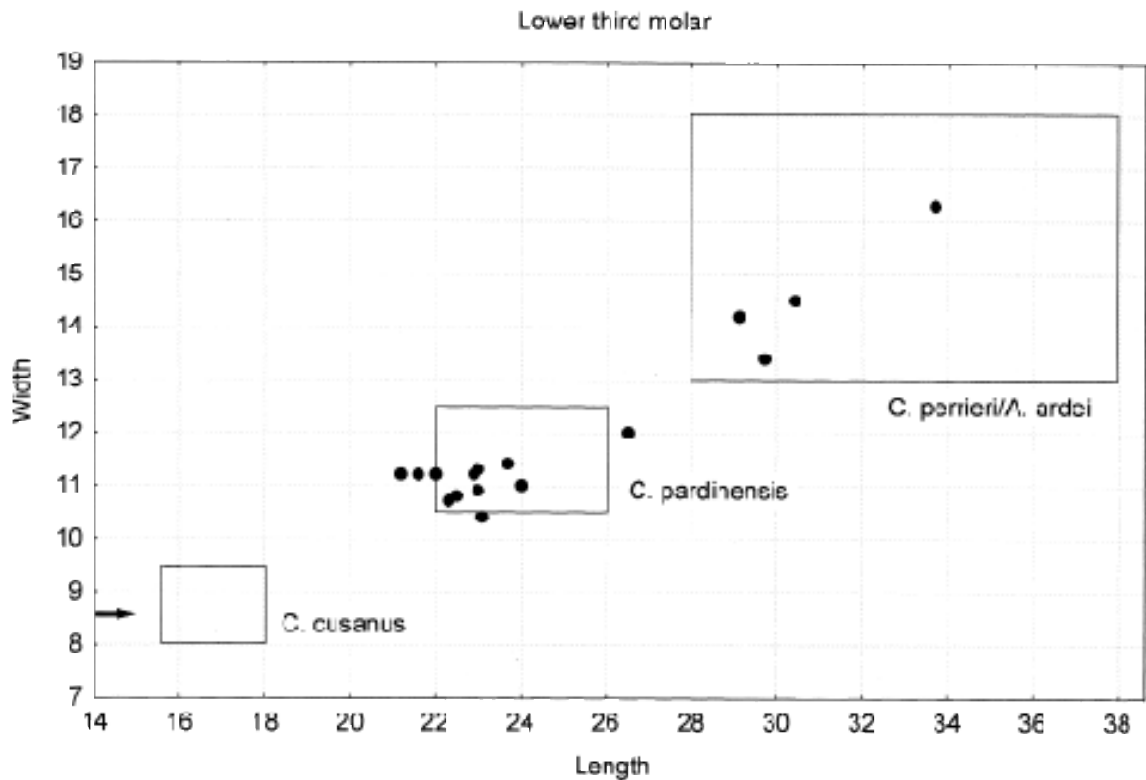


Figure 6 Scatterplot of cervid lower third molar dimensions from the Red Crag Nodule Bed. One British specimen, on which only width could be measured (8.6 mm), is indicated by an arrow. Rectangles are ranges of the named species from French and Spanish localities, taken from Heintz (1970): '*Cervus*' (= *Procapreolus*) *cusanus* (n= 19) from Etouaires; *C. pardinensis* (n=28) from Etouaires and Vialette; *C. perrieri/Arvernoceros ardei* (n=53) from Villaroya and Etouaires. Heintz was unable to separate the teeth of *C. perrieri* and *A. ardei*, so a combined range is given. Dimensions in millimetres.

(1970). First segment length is measured from the upper edge of the rose to the lowest point of the fork, on the medial side. The specimens referred to the three species on overall morphology are indicated on the graph. In general, the measurements are close to the ranges for *C. pardinensis*, *C. perrieri* and *P. cusanus* given by Heintz (1970) from French material, although I have found that for all species my first tine heights tend to be somewhat lower than his. This may reflect a systematic measuring error which needs to be checked on Heintz's original material.

DENTAL MATERIAL

The taxonomic composition of the Nodule Bed assemblage is supported by a biometric study of the dental remains. In Figures 5 and 6, upper and lower third molar sizes are plotted, with ranges given by Heintz for *P. cusanus*, *C. pardinensis* and *C. perrieri* superimposed. A considerable range of dental size is indicated for the British sample, and the scatter is consistent with attribution of most specimens to *C. pardinensis*, a few to *C. perrieri*, and one (a lower third molar on which only width is measurable) to *P. cusanus* (cf. Fig. 7). This relative abundance corresponds to that observed in the antlers. The identification of *C. pardinensis* is supported by the occurrence on several (though

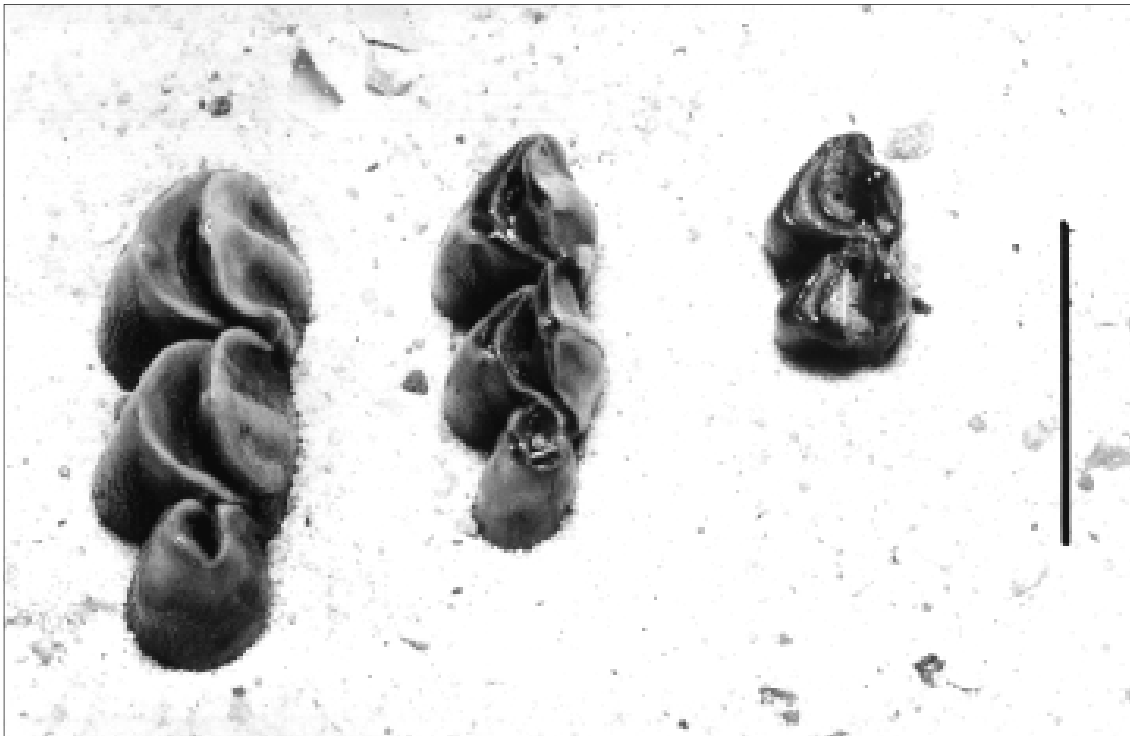


Figure 7 Cervid left lower third molars from the Red Crag Nodule Bed. From left to right: cf. *Cervus perrieri* NHM 9159; cf. *Cervus pardinensis* NHM 9154; cf. *Procapreolus cusanus* NHM 9155. Scale bar 2cm.

not all) of the upper molars of a very strong lingual cingulum (Fig. 8), a species-diagnostic character noted by Heintz (1970). Molars of *C. perrieri* do not possess any particularly diagnostic features (Heintz, 1970), and the single specimen referred to *P. cusanus* on size is unfortunately too fragmentary to observe diagnostic morphology.

DISCUSSION

Some of the conclusions of this study have been hinted at in the writings of earlier authors. As indicated above, Dawkins (1878) suggested a close link between his 'suttonensis' material and *C. pardinensis*. He also (1878, p. 409) indicated that some other antlers, in a private collection from Beccles (Suffolk), might pertain to the species *C. perrieri*. The morphology and whereabouts of the latter material (if it still exists) are unknown, but the locality suggests the Red Crag Nodule Bed.



Figure 8 Cervid left upper first or second molar from the Red Crag Nodule Bed of Woodbridge, NHM 46706, referred to *Cervus pardinensis*.

Spencer (1963, 1970) went further. He believed that the '*C. suttonensis*' antler material comprised two species, corresponding exactly to the morphological categories here designated *C. pardinensis* and *C. perrieri*. Spencer applied the name *C. pardinensis* to the former group, and decided to retain '*C. suttonensis*' for the larger antlers here referred to *C. perrieri*.

In Heintz's (1970) stratigraphic scheme, all three species *Cervus perrieri*, *C. pardinensis* and *Procapreolus cusanus* are restricted to the Early Villafranchian, chiefly at the sites of Etouaires and Vialette, France. There they are accompanied by the cervids *Croizetoceros ramosus* and *Arvernoceros ardei*, taxa for which there is currently no evidence in Britain. Stefaniak (1995) has recently described a cervid fauna from the Late Pliocene of Poland (referred to zone MN16), which comprises *P. cf. cusanus*, *C. pardinensis*, *C. ramosus* and *cf. A. ardei* (two teeth only). The absence of *A. ardei* and *C. ramosus* in the Nodule Bed does not negate the implied broad correlation with Etouaires. It is impossible to say if this reflects sampling error, a minor chronological difference, or possibly a geographical range restriction of the species.

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