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MACAQUE MOLAR FROM THE RED CRAG FORMATION, WALDRINGFIELD, ENGLAND

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Abstract: Fossil monkeys are rare in the British palaeontological record, a few specimens having been reported from the Pleistocene, and a single specimen from the Red Crag, possibly of Late Miocene or Pliocene age. An undescribed monkey tooth from the Red Crag at Waldringfield collected circa 1908 that has remained unidentified in the collections of the Sedgwick Museum, Cambridge, is described herein. The fossil was associated with dental remains of a suid, a tapir and a deer which, taken as an assemblage, are best correlated to the Early Pliocene, being similar to specimens from Perrier, France. Because of the high latitudinal position of Waldringfield (52°N) and indications for a tropical to sub-tropical palaeoenvironment during the Late Miocene – Early Pliocene, the monkey tooth from there is of great interest.

Key words: Mio-Pliocene, Cercopithecidae, Palaeoenvironment, Palaeoclimate, Taphonomy, East Anglia

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Introduction

Until recently, the only known cercopithecid fossils from Britain were from West Runton, Hoxne, Cudmore Grove, Grays Thurrock, Purfleet, Swanscombe, Ebbsfleet and the Norfolk Forest Bed (Hinton 1908, Delson 1973, 1974, Ardito and Mottura 1987, Stuart 1996, Schreve et al. 2002, Roe et al. 2009, Alba et al. 2011, Parfitt 2013) most of which are of Pleistocene age (Schreve 2001), with only one specimen from the Red Crag being potentially of Pliocene or Miocene age (the specimen thought by Delson (1973) to be of Early Pleistocene age, is possibly Late Miocene (this paper)).

It is therefore of interest to place on record the identification of a macaque tooth (right upper molar, M1/ or M2/) recovered from Waldringfield, Suffolk, circa 1908, and presented to the Sedgwick Museum, Cambridge, by Dr Lloyd Jones. The preservation characters of the fossil indicate that it was redeposited into the Red Crag after derivation from a pre-existing body of sediment along with similarly preserved remains of tapirs, pigs, mastodonts, deer and carnivorans that indicate a Late Miocene to Early Pliocene age for the fossils, more or less equivalent to the palaeofauna from Les Etouaires, Perrier, France (MN 16: 3.9–3.4 Ma (Bout 1968), 3.6–2.4 Ma (Steininger et al. 1990)) from which a similar suite of mammalian species was described by Croizet and Jobert (1828).

Interestingly, while Delson (1980) noted that all macaque fossils from the Mediterranean Basin from the Miocene up to the Late Pleistocene look alike, most of the described fossil taxa included in the genus *Macaca* Lacépède, 1799 were erected on the basis of specimens collected north of 48°N latitude. This was the case for *Macaca pliocena* Owen, 1846 from Grays Thurrock, England (Owen 1845, 1846) and *Macaca suevica* from the Gutenberger Höhle, Heppenloch, Germany (48°32′34″N : 31°19′03″E; Hedinger 1891). However, except for the small island endemic species *Macaca majori* Azzaroli, 1946 from Sardinia, Italy (Azzaroli 1946) most of the fossil macaque "nominal species" are either indistinguishable from each other or may, at most, be separated at the subspecific rank, with the result that several recent authors retain *Macaca sylvanus florentina* (Cocchi, 1872) first described from the Upper Valdarno, Italy (Cocchi 1872) as the only valid subspecies, even though *M. s. pliocena* Owen, 1846 has priority according to the International Code of Zoological Nomenclature (ICZN 1999). The subspecies *M. sylvanus prisca* Gervais, 1859 from the Pliocene (type locality: Montpellier, France; Ruscinian) that is of comparable age to the Waldringfield molar, has been retained as valid by Alba et al. (2011, 2019) along with *M. s. pliocena*. *M. s. florentina* is distinguished from the extant Barbary macaque, *M. s. sylvanus* (Linnaeus,

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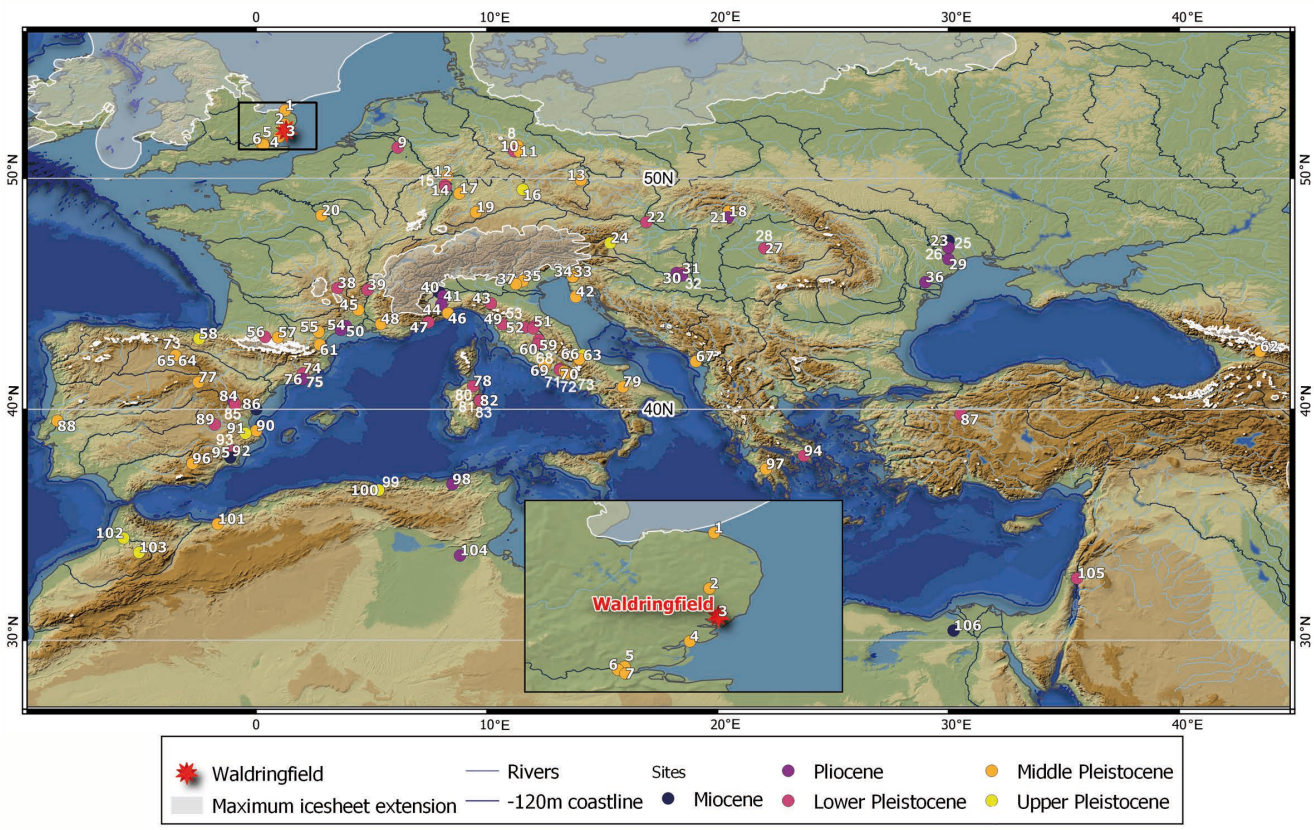


Text-fig. 1. Distribution of fossil macaques in Europe and Northern Africa. Waldringfield is the red star. Data from Ardito and Mottura (1987), Alba et al. (2008, 2011, 2016, 2019, 2021), Elton and O'Regan (2014) and Mecozzi et al. (2021). The inlay at the bottom of the map shows the English localities in greater detail. Numbers correspond to localities listed in Table 1. The maximum icesheet extension refers to the last glacial.

1758) by its longer and broader upper molars and its narrower lower third molars (Alba et al. 2011).

Abbreviations

BGSK	British Geological Survey, Keyworth
CAMSM	Cambridge Sedgwick Museum of Earth Science, Cambridge
NHMUK	Natural History Museum of the United Kingdom, London

Geological setting

Historical background and context

Newton (1891) reported that no monkey fossils had been found in the Red Crag, the only cercopithecid known from Britain at the time being the specimen called *Macacus pliocenus* by Owen (1846) from Grays in Essex ("Newer Pliocene" Brickearth) listed as Grays Thurrock by Delson (1973, 1974) and subsequent authors (Text-fig. 1). The type locality of *M. sylvanus pliocena* Owen, 1846, is correlated to Marine Isotope Stage (MIS) 9 (Middle Pleistocene; Schreve 2001).

In part 5 of his series of papers on Suffolk geology, Spencer (1971e) reported that the "[Red Crag] …. at Newbourne and Waldringfield …. has produced a suspicious number of Pliocene species which have been accepted as indigenous Red Crag fossils, species which are poorly represented in the newer Crag". In the section on Mammalia from the Red Crag, however, Spencer (1953) stressed the important point that the mammal fossils from the Red Crag are of two classes, echoing the observations of previous researchers (Owen 1843, 1845, 1846, 1856, Wood 1859, Lankester 1865, Lydekker 1886). The first category comprises material of diverse pre-Crag ages that were reworked from older deposits and redeposited in the Crag, including *Hipparion gracile*, *Mastodon borsoni*, *Mastodon longirostris* and *Mastodon arvernensis*, a tapir, various species of pigs, an axis deer (*Axis pardinensis*) and *Cervus suttonensis*, along with diverse whale and shark bones and teeth. The second class of mammal fossils comprises species that lived and died at the time of accumulation of the Red Crag. In particular Spencer (1953) mentioned the presence of *Equus robustus* at Waldringfield which, if correctly identified, means that the Red Crag is of Pleistocene age. Hand-written labels in the Cambridge palaeontology collections reveal that Spencer was aware of the presence of tapirs, deer, fish and suids from the Red Crag at Waldringfield. The box with these labels also contains the upper molar of a cercopithecid, which is the subject of this paper (Text-fig. 2).

Delson (1973, 1974) recorded ?*Mesopithecus monspessulanus* (Gervais, 1849) from the Red Crag on the basis of an isolated upper third molar, but no details were available concerning the precise locality from which the fossil (NHMUK M9171) was obtained. It was purchased by

Table 1. Late Miocene to Late Pleistocene localities in Europe, the Near East and North Africa that have yielded fossil macaques corresponding to locations in Text-fig. 1.

1	West Runton
2	Hoxne
3	Waldringfield Red Crag
4	Cudmore Grove
5	Gray‘s Thurrock
6	Purfleet
7	Swanscombe
8	Voigtstedt
9	Steyl (Tegelen)
10	Untermassfeld
11	Bilzingsleben II
12	Mosbach 2
13	Cave C 718
14	Gundersheim
15	Hohensülzen
16	Hunas
17	Mauer
18	Gombasek
19	Heppenloch
20	La Celle
21	Osztramos 1
22	Deutsch-Altenburg 2C1, 4B
23	Zhovten
24	Kugelsteinhöhle 2
25	Novopetrovka
26	Voinichevo
27	Betfia 9
28	Betfia 13
29	Grebeniki 2
30	Csarnóta 2
31	Somssich Hill N° 2
32	Beremend 4
33	Bristie 2 Sgonico Trieste
34	Visogliano
35	S. Vito de Leguzzano 2
36	Moldavian Roussillon
37	Zoppega 2
38	Senèze
39	St. Vallier
40	Moncucco Torinese
41	RDB Quarry Triversa
42	Šandalja 1 near Pula
43	Mugello
44	Villafranca d‘Asti
45	Orgnac 3
46	Valdemino (Borgio)
47	Vallonnet Cave
48	La Grotte de l‘Escale
49	Casa Sgherri
50	Montpellier (terrestrial)
51	Strette
52	Valdarno
53	Val di Chiana
54	Balaruc 2
55	Grotte d‘Aldene
56	Montousse 5
57	Montsaunes
58	Lezetxiki II
59	Pietrafitta Perugia
60	Monte Peglia Orvieto
61	Caune de l‘Arago (Tautavel)
62	Kudaro 1 Cave
63	Grotta degli Orsi Volanto
64	Sima del Elefante
65	Gran Dolina TD8
66	Fontana Ranuccio
67	Gajtan
68	Monte Sacro
69	Torre in Pietra
70	Colle Marino
71	Coste San Giacomo
72	Cava Pompi Frosinone
73	Pofi
74	Cal Guardiola
75	Vallpardís
76	Cova Bonica
77	Ambrona
78	Capo Figari
79	Notachirico
80	Fissure 10, 3 Uccelli Quarry
81	Fissue 10, Ghiro Quarry
82	Fissure 6, Quarry 3
83	Fissure 7, Mustelide Quarry
84	Orrios 7
85	La Puebla de Valverde
86	Casablanca Almenara
87	Eskisehir
88	Torres Novas (Galeria Pesadas)
89	Cueva Negra
90	Cova del Bolomor
91	Cova Negra
92	Suibas
93	Sierra de Quibas
94	Tourkovounia 2
95	Puerto de la Cadena
96	La Solana di Zamborino
97	Marathousa 1
98	Ain Brimba
99	Afalou bou Rhummel
100	Tamar Hat
101	Traras Monts des Nedroma
102	Es Zarka
103	Chrafate
104	Garaet Ichkeul
105	‘Ubeidiya
106	Wadi Natrun

Text-fig. 2. Assemblage of fossils and their labels curated in a tray at the Sedgwick Museum of Earth Sciences, Cambridge. Note the slip of paper with identifications by H.E.P.S. (Harold Spencer). a: CAMSM C.13378, mammalian first phalanx; b: CAMSM X.50379, *Tapirus* upper cheek tooth; c: CAMSM X.50378, *Dasychoerus arvernensis* m/3 distal portion; d: CAMSM X.50381, cervid upper molar; e–f: CAMSM X.50376 and X 50377, wolffish teeth (*Anarhicas lupus*); g: CAMSM X.50380, *Macaca* sp. upper molar (Photo credit – Matt Riley, Sedgwick Museum of Earth Science).

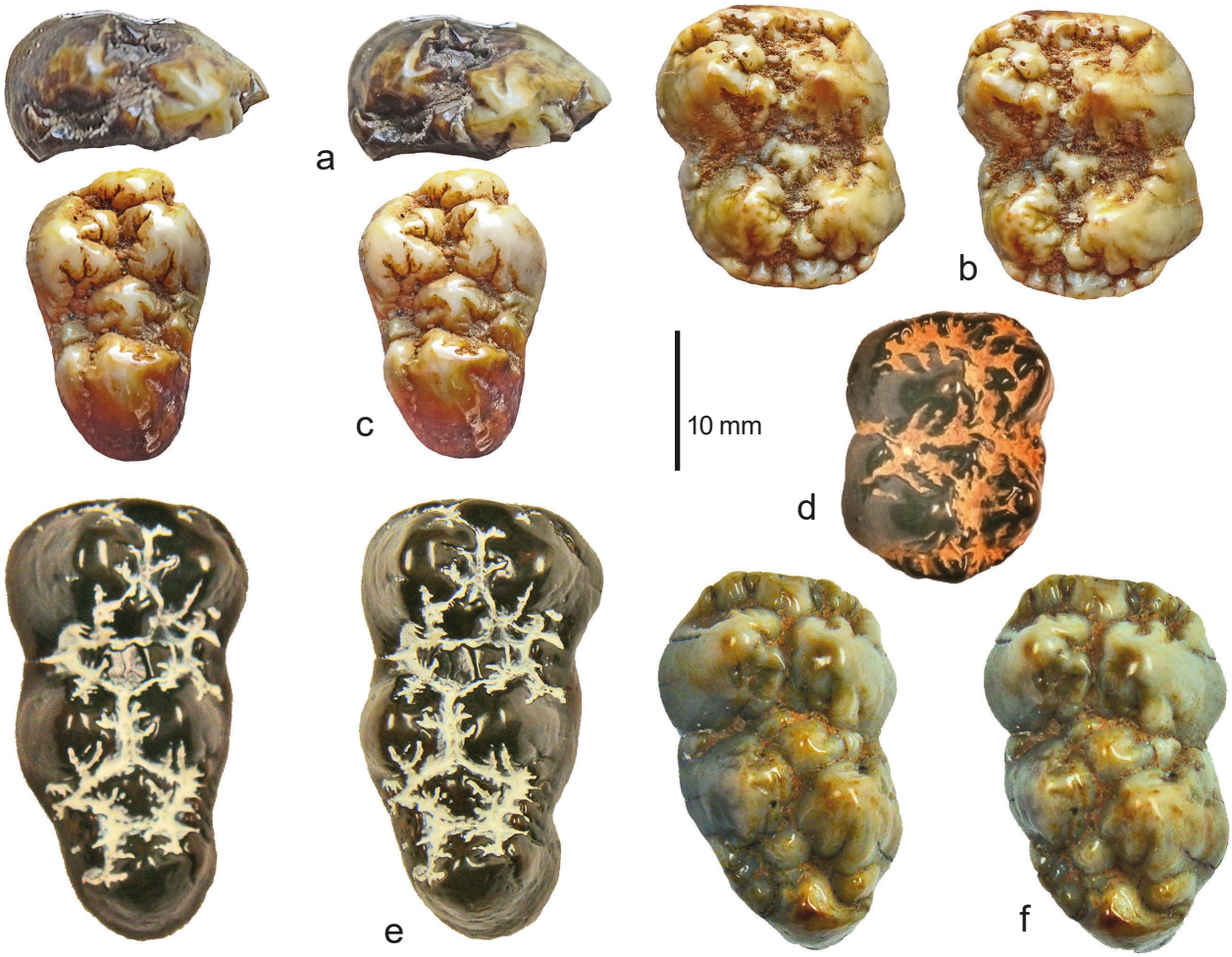
the museum in January, 1905, from F. H. Butler and was included in the Pinder collection.

Taphonomy

As was discussed by Spencer (1953, 1964, 1971a–e, 1972) vertebrate fossils collected from the Red Crag, but derived from older deposits, are usually dark brown with glossy surfaces. The monkey tooth from Waldringfield is varicoloured but predominantly dark brown with a highly polished surface, agreeing in preservation characters with teeth of a tapir, some suids and a deer from the same deposits (Text-figs 2, 3). There can be little doubt that the monkey molar discussed herein was originally fossilised in a pre-Crag deposit, then eroded from it and redeposited as a clast within the Red Crag. The specimen was most likely collected from the so-called Nodule Bed or Coprolite Bed, which yielded many well-preserved, highly polished vertebrate bones and teeth (Newton 1891).

Geological age

The Red Crag is generally considered to have been deposited during the Pleistocene (Spencer 1953, 1964, 1971a–e, 1972, Stuart 1996, Schreve et al. 2002, Roe et al. 2009, King 2016, Davies et al. 2019) but, as has been pointed out on several occasions (see above) many of the fossil mammals found in it are reworked from older



Text-fig. 3. Occlusal views of upper and lower molars of *Dasychoerus arvernensis* from the Red Crag, Waldringfield, England. a: CAMSM C.48973, left upper molar fragment (coprolite bed); b: CAMSM drawer 392, right M2/; c: CAMSM Display Vi 2, distal portion of right m/3; d: BGSK 21716, left M2/; e: BGSK 7311, right m/3; f: BGSK 2171, right M3/. a, b, c, e, f are stereo images.

deposits (Wood 1859, Prestwich 1871a, b). An examination of the proboscideans and suids reveals that there are some Late Miocene and Early Pliocene taxa in the Red Crag ranging in age from ca. 10 Ma to 3 Ma (corresponding to MN 10 to MN 16 in the European land mammal zonation; Steininger et al. 1990, Pickford 2013a, b). Some of the suid fossils, in particular, were considered in the older literature to belong to *Sus palaeochoerus* (= *Propotamochoerus palaeochoerus* in more recent literature) and *Sus antiquus* (= *Hippopotamodon antiquus* in recent literature) which would suggest correlation to MN 9 and MN 10, but most of them are in fact closer in dimensions and morphology to material of *Dasychoerus arvernensis*, upon which basis Pickford (2013a, b) and Pickford and Obada (2016) correlated the Red Crag mammals to MN 16. The Red Crag has also yielded a few specimens of *Hippopotamodon erymanthius* or *Hippopotamodon major* (MN 11 – MN 12) (Pickford 2015).

There is thus a degree of uncertainty about the age of the monkey tooth from Waldringfield, but its association (albeit secondary) with specimens of *Dasychoerus arvernensis*, *Anancus arvernensis*, and *Tapirus* sp. indicate that it is most likely to be of latest Miocene to Early Pliocene age. It is certainly older than the period of deposition of the Red Crag itself, which accumulated during the Pleistocene (Davies et al. 2019).

Palaeoenvironment

The presence in the Red Crag faunas of mammals with close relatives that today occur in tropical and sub-tropical forested environments, such as tapirs (Owen 1856, Newton 1891, Spencer 1953), red pandas (*Parailurus anglicus*) (Boyd-Dawkins 1888, Newton 1890), rhinoceroses and warty pigs (*Dasychoerus*) (Pickford and Obada 2016) suggests that for a time, East Anglia was warmer and more densely vegetated than it is today, likely being sub-tropical rather than fully tropical (Gibson et al. 2022). The macaque fossil described herein does not contradict this inference, even though extant macaques can survive in regions with severe winters (Alba et al. 2011). Nowadays in the Maghreb, Barbary macaques occur in the cedar forests of the High and Middle Atlas in Morocco and in the coastal regions of the Rif (Fooden 2007). They feed on fruits during the summer and on seeds and bark during the winter (El Alami and Chait 2015). Thanks to this dietary flexibility (Ménard and Vallet 1997) they easily survive in high altitude zones during the winter and in the presence of snow (Kowalski and Rzebik-Kowalska 1991). The relatively common occurrence of the

proboscidean *Anancus arvernensis* in Red Crag deposits also suggests that the palaeoclimate was of sub-tropical affinities at the time that they lived in the region, although on the basis of mesowear angle analysis, Saarinen and Lister (2016) suggested that this genus had a browse-dominated diet in a more wooded environment, opening the possibility that it could also inhabit a more boreal palaeoenvironment.

Systematic palaeontolgy

Order Primates Linnaeus, 1758
Superfamily Cercopithecoidea Gray, 1821
Family Cercopithecidae Gray, 1821
Subfamily Cercopithecinae Gray, 1821
Tribe Papionini Burnett, 1828

Genus *Macaca* Lacépède, 1799

***Macaca* sp.**
Text-fig. 4

Material. CAMSM X.50380, right upper molar, M1/ or M2/.

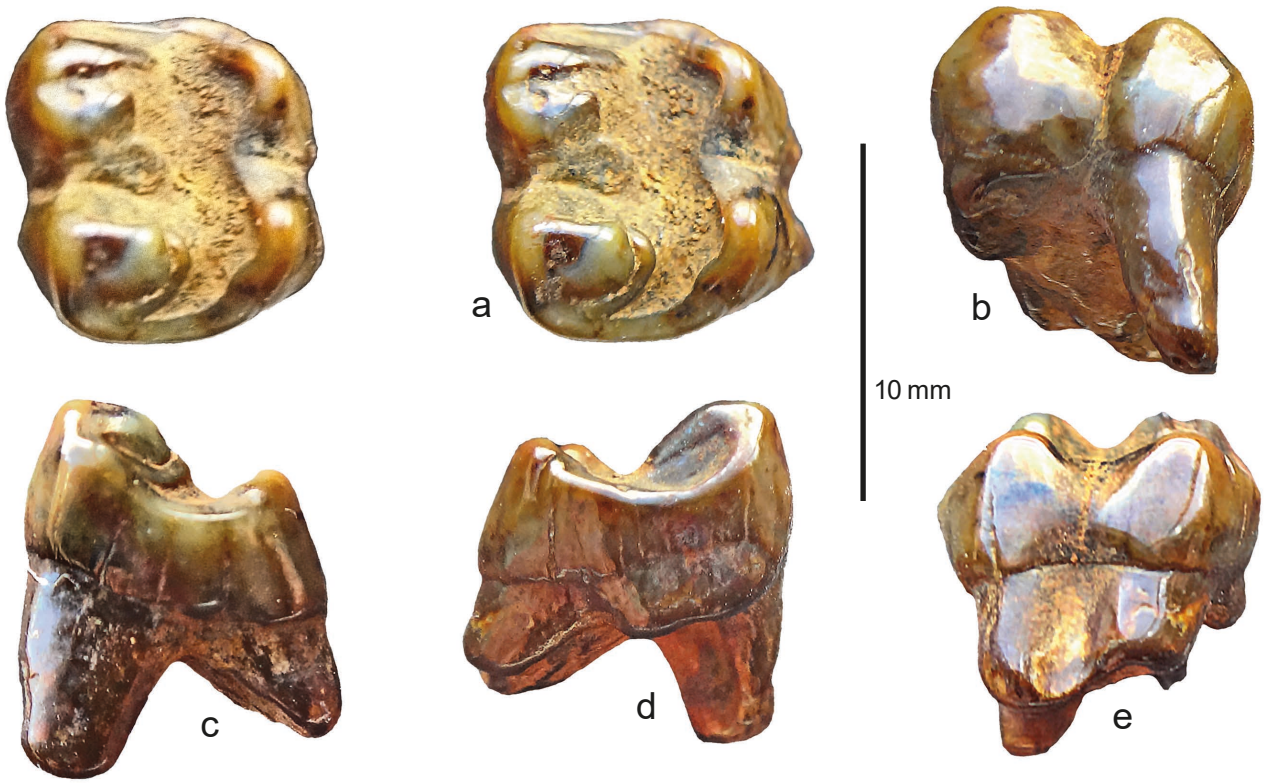
Locality and geological context. Waldringfield, Suffolk, United Kingdom (52°03'10"N : 01°19'39"E). Reworked into the Red Crag Formation from a pre-existing deposit.

Description. The isolated cercopithecoid tooth from Waldringfield has a glossy surface and the roots are polished and somewhat abraded indicating that it has been reworked into the Red Crag from a pre-existing deposit. The occlusal surface is deeply worn, indicating adult status, up to stage A4 of Ingicco's ageing system (Ingicco et al. 2012) but the crown is otherwise well preserved (Text-fig. 4).

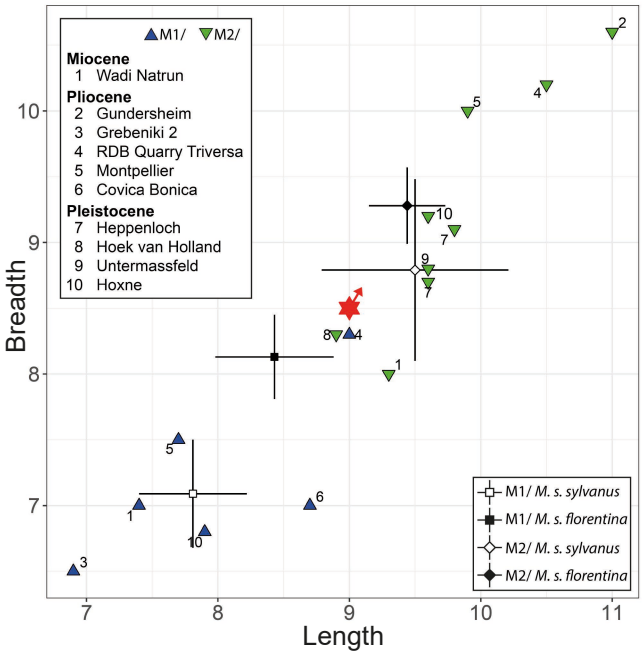
The tooth is quadricuspidate and bilophodont with shallow buccal and lingual notches and the floor of the median transverse valley is elevated well above cervical level. The two lingual roots are coalescent; the buccal ones separated from each other. The occlusal surface is heavily worn, to the extent that dentine lakes on the protocone and hypocone have coalesced across the median transverse valley. The dentine exposures on the paracone and metacone are smaller, the one on the paracone has joined the one developed on the protocone, the one on the hypocone is isolated at the apex of the cusp. The preprotocrista runs mesio-buccally, almost reaching the mesio-buccal corner of the crown. The posthypocrista is directed disto-buccally stopping short of the disto-buccal corner of the tooth.

The mesio-distal length of the tooth is 9.0 mm and its bucco-lingual breadth is 8.5 mm.

Discussion. Based on its dimensions, the Waldringfield tooth is more likely to be an M2/ than an M1/ although in the bivariate diagram (Text-fig. 5) it plots close to the zone of overlap between M1/ and M2/. Given that its measurements may be slightly underestimated due to the abrasion and polishing that the tooth has undergone (red arrow in Text-fig. 5) the unabraded position would have been closer to the mean of M2/ of the two subspecies in the plot (*M. s. florentina* and *M. s. sylvanus*) suggesting that the Waldringfield tooth is more likely to be an M2/ than an M1/.



Text-fig. 4. CAMSM X.50380, right M1/ or M2/ of *Macaca* sp. from Waldringfield, Suffolk, England. a: stereo occlusal view; b: buccal view; c: distal view; d: mesial view; e: lingual view.



Text-fig. 5. Length / breadth dimensions (in mm) of first and second upper molars of fossil and extant macaques. The red star with arrow represents the Waldringfield fossil. The white square represents *M. s. sylvanus*, and the black one *M. s. florentina*. Bars indicate the standard deviations around the mean. Blue and green triangles depict European fossils selected for their old age and their geographic position north of latitude 48°N. Miocene fossils are: 1. Wadi Natrun; Pliocene fossils are: 2. Gundersheim, 3. Grebeniki 2, 4. RDB Quarry Triversa, 5. Montpellier, 6. Cova Bonica; Pleistocene fossils from latitudes higher than 48°N are: 7. Heppenloch, 8. Hoek van Holland, 9. Untermassfeld and 10. Hoxne (data from Alba et al. 2011).

The presence of a distoconule disto-lingual to the hypocone on the M3/ is the main character mentioned by Cocchi (1872) for erecting the taxon *M. s. florentina*. This small additional cusp is present in most of the fossils attributed to the species and occurs in two-thirds of the specimens from Quibas, Spain (Alba et al. 2011). However, because the Waldringfield specimen is not an M3/, it is not possible to confirm its subspecies attribution on the basis of this character. Furthermore, the tooth has morphometric similarities to *Macaca libyca* (Stromer, 1920). Given the scarcity of material, it is preferable to leave it in open nomencature, and to refer to it as *Macaca* sp.

Subfamily Colobinae Blyth, 1863

Genus *Mesopithecus* Wagner, 1839

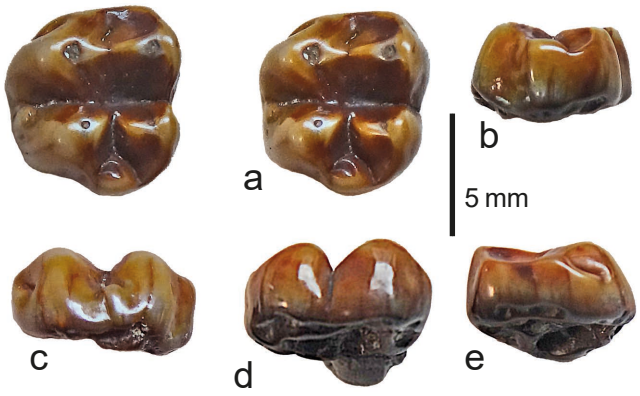
***Mesopithecus* sp.**

Text-fig. 6

Material. NHMUK PV M9171, left M3/ in light wear.

Geological context and age. Redeposited into the Red Crag, England, from a pre-existing deposit (precise locality unknown). The age is uncertain but possibly Late Miocene or Early Pliocene.

Description. The colobine upper molar from the Red Crag is dark brown, with a glossy surface and has been



Text-fig. 6. NHMUK PV M 9171, left M3/ of *Mesopithecus* sp. from the Red Crag, East Anglia, England. a: stereo occlusal view; b: distal view; c: lingual view; d: buccal view; e: mesial view.

rolled and polished, like most of the mammalian teeth from the deposit. The tooth is quadricuspidate, with the four main cusps arranged in two transverse lophs. There is a small low basal pillar at the lingual end of the median transverse valley and a low talon cusp (distoconule) at the distal end, in the midline of the tooth, indicating that the specimen is an M3/. The buccal and lingual notches are mesiodistally wide and occlusally deep, and the floor of the median transverse valley is slightly above the cervix. The roots have been abraded off.

Wear has advanced to the stage where small dentine lakes are exposed at the apices of the four main cusps, as well as the apex of the distoconule. This signifies a fully adult status, but not an aged individual.

The mesio-distal length of the tooth is 7.7 mm, the breadth of the mesial loph is 7.2 mm and that of the distal loph is 6.4 mm (the original measurements prior to abrasion and polishing would have been slightly greater than these figures).

Discussion. This upper third molar from the Red Crag (Text-fig. 6) was attributed to ?*Mesopithecus monspessulanus* by Delson (1973) but we prefer to leave it in open nomenclature as *Mesopithecus* sp.

General discussion

The Waldringfield macaque molar (Text-fig. 4) differs from those of colobine monkeys (Text-fig. 6) by the shallow buccal and lingual notches and by the floor of the median transverse valley being elevated well above the cervix. For these reasons it is attributed to the Cercopithecinae. Among cercopithecines, the tooth most closely resembles those of papionins, especially members of the genus *Macaca*.

The dimensions of the fossil agree with a diversity of Late Miocene to Pleistocene and Recent monkeys, both colobines and cercopithecines. If the specimen is an M1/, then its dimensions accord with those of *Macaca sylvanus florentina* from Quibas, Spain (Pleistocene ca. 1.8–1.1 Ma) (Alba et al. 2011) and *M. s. prisca*/*M. s.* cf. *prisca* from Montpellier, RDB quarry, Cova Bonica and Gundersheim. If it is an M2/, then it is slightly smaller than teeth of these

species. However, comparison of the Waldringfield fossil with specimens from latitudes higher than 48°N suggests that it is more likely to be an M2/ than an M1/. The tooth is compatible in dimensions with specimens of *Macaca libyca* from Sahabi, Libya (Late Miocene) (Benefit et al. 2003) and Wadi Natrun, Egypt (Late Miocene to Early Pliocene) (Stromer 1913, Pickford et al. 2022). Macaques of similar dimensions are known from many localities in the Circum-Mediterranean region (Delson 1973) as well as further afield in Asia in deposits ranging in age from the Late Miocene to Recent (Ardito and Mottura 1987).

Under the circumstances and given that the tooth could be either a first or second molar, the most appropriate decision is to leave the specimen in open nomenclature as *Macaca* sp. while recognising that it has morphometric affinities to molars of the species *Macaca libyca* and *Macaca sylvanus*.

The recognition of this fossil monkey tooth in the Sedgwick Museum, Cambridge, highlights the value of re-examining old collections of fossils, in this case more than a century after the material was donated to the institution. Similar research in the old collections of the University of Tübingen, Germany, resulted in the recognition of a Miocene monkey tooth from Melchingen. The Melchingen karst infillings (Bohnerz deposits) correlate to MN 9, MN 10 and MN 13, with the monkey tooth most likely being of Turolian age. It had lain misidentified as a carnivoran in the collections since about 1902 (Schlosser 1902, Pickford 2016). Each such specimen has augmented knowledge about the distribution of the species concerned, as well as yielding information about the palaeoenvironment and palaeoclimate of the locations and geological time periods concerned.

Conclusion

The recognition of a macaque upper molar from the Red Crag Formation at Waldringfield, England, is of interest for several reasons. Firstly, it is from 52°N latitude, and thus one of the most northerly occurrences of the genus in Europe. Secondly, it and the associated fauna indicate that the palaeoclimate was likely to have been of sub-tropical affinities. Thirdly, it increases the known diversity of monkeys from pre-Pleistocene contexts in the country. Macaques have long been known to occur in English Pleistocene deposits (Owen 1845) but this paper reports the first record of the genus *Macaca* in the Pliocene or Late Miocene, where it joins the record of *Mesopithecus* sp. from an unknown locality in the Red Crag (Delson 1973).

Konidaris et al. (2022) pointed out that the oldest macaque fossil thus far recorded from Europe is considered to date from the Late Miocene, ca. 5.5 Ma (Köhler et al. 2000, Alba et al. 2014). Even though there is doubt about the precise age of the Waldringfield specimen, it is potentially one of the older specimens from Europe, possibly somewhat older than the site of Les Etouaires, France (MN 16: 3.9– 3.4 Ma – Bout 1968; 3.6–2.4 Ma – Steininger et al. 1990).

Few sites in Europe have yielded fossils of both *Mesopithecus* and *Macaca* (Alba et al. 2014). Even though the precise locality of the ?*Mesopithecus monspessulanus* tooth from the Red Crag described by Delson (1973) is not recorded, the possibility exists that these two genera may have co-existed in East Anglia, England during the latest Miocene or Early Pliocene.

The Waldringfield macaque forms part of a small collection of vertebrate fossils donated to the Sedgwick Museum in 1908. In the same box are teeth of a tapir (*Tapirus*) a warty pig (*Dasychoerus arvernensis*) as well as a deer and there are two fish teeth and a first phalanx of an unidentified mammal. As an assemblage these fossils suggest that the palaeoenvironment was warm and humid, possibly tropical forest, and that the most likely age of the ensemble is Early Pliocene. If this interpretation is correct then it supports the results of previous researchers such as Newton (1891) who concluded that the Red Crag mammals indicated that tropical forest-like conditions prevailed in East Anglia at the time that the mammals lived there, contrasting with its present day boreal environment with marked winter-summer cycles.

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