
Supplementary information

Genomic history of early dogs in Europe

In the format provided by the
authors and unedited

Supplementary Notes

Archaeological information for specimens and sites

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Supplementary Data

The following are provided as tables in a standalone Excel spreadsheet:

Supplementary Data 1. Ancient genome metadata: Metadata for all ancient canid remains sampled in this study.

Supplementary Data 2. New radiocarbon dates: Results from new radiocarbon dates obtained in this study.

Supplementary Data 3. Previously published genomes: Metadata for previously published modern and ancient canid genomes used in analyses.

Supplementary Data 4. Modern wolf data used for PCA: List of modern wolf individuals used for principal components analysis (PCA) (Fig. 2a).

Supplementary Data 5. Remains possibly same ind.: Sets of sampled remains that potentially could derive from the same biological individual, one set per row.

Supplementary Data 6. Pathogen reference panel: List of microbial genomes used as the pathogen reference panel.

Supplementary Data 7. Dual ancestry qpAdm: Results of all qpAdm models addressing 'dual ancestry' contributions from one or two wolf sources to dogs.

Supplementary Data 8. Mesolithic-Neolithic qpAdm: Results of all qpAdm models addressing Mesolithic and Neolithic contributions to European dogs.

Kesslerloch, Switzerland

Sites: Kesslerloch

Kesslerloch. Kesslerloch is a cave near Thayngen in the canton of Schaffhausen, northern Switzerland. It is located in a narrow valley. The cave is approximately 200 m² in size and is divided by a stone pillar. In prehistoric times, reindeer hunters used the cave as a shelter during the summer months between 17,000 and 11,000 BP (Upper Paleolithic, Magdalenian culture).

The first archaeological excavations in the Kesslerloch cave were carried out by the teacher Konrad Merk in 1873, followed by investigations by Jakob Nüesch and Jakob Heierli in the late 19th and early 20th century. The excavations yielded a large number of animal bones as well as stone, bone and reindeer antler artefacts¹⁻³. Kesslerloch became famous due to naturalistic depictions of animals on bone and antler objects. In addition, it provided small art objects such as pendants made out of shells, animal teeth, snails and jet. During these early excavations, the finds were not systemically recorded and also sold to other collectors. Therefore, the “seeking reindeer”, a naturalistic depiction on a perforated rod, is nowadays exhibited in the Rosgartenmuseum in Konstanz, Germany.

The animal bones could be attributed to 53 different species, among them reindeer, wild horse, mountain hare and snow grouse. Less frequent are bones from woolly rhinoceroses, mammoths, ibexes, and chamois. The distribution indicates the hunting of both large and small game as well as fowling, with a preference for reindeer⁴. A domestic dog maxilla found in the cave in 1874 belongs to an adult individual. It has been dated by radiocarbon dating to around 14,200 calBP⁵.

Gnirshöhle, Germany

Sites: Gnirshöhle

The site of Gnirshöhle is located in the Hegau region, close to Lake Constance, southwestern Germany. Together with the nearby sites of Petersfels and Drexlerhöhle, it forms a Magdalenian site cluster within a narrow contextual area. The first archaeological excavations in Gnirshöhle were carried out by Eduard Peters in 1927⁶. However, he was unable to document any Palaeolithic settlement remains, and only found Holocene material. In 1933, Peters purchased a collection from the owner of the cave, which also contained Magdalenian lithic artefacts, providing a first indication of preserved Palaeolithic sediments⁷. In 1976, activities by a speleological association brought to light finds from the Magdalenian period. Unfortunately, this activity destroyed large quantities of archaeological deposits within the cave. Therefore, the State Office for Cultural Heritage commissioned excavations in 1977 and 1978 under the direction of Gerd Albrecht and Claus-Joachim Kind⁸.

Gnirshöhle has an entrance of 3 m length and 2 m height and opens to the east. About 10 m behind the entrance, the cave branches into two passages, in each of which Magdalenian settlement remains were found. The locations were designated Gnirshöhle 1 and 2, with the latter being closer to the entrance. The small-scale excavations in both places revealed multi-phase Magdalenian horizons. Initial analyses of the fauna and the lithic artefacts indicate short stays of small hunter-gatherer groups. A few objects point towards domestic

activities including the on-site production of ornaments of jet and molluscs as well as organic artefacts such as needles albeit in small numbers. Additionally, sandstone slabs were brought into the cave to plaster settlement areas. Radiocarbon dates frame Magdalenian occupations in Gnrshöhle between 15,500 and 15,000 calBP⁹.

The faunal remains of Gnrshöhle are dominated by typical large game species from the Magdalenian (post-LGM) time period, such as reindeer (*Rangifer tarandus*) and wild horse (*Equus ferus*), both with anthropogenic modifications (cut and impact marks), as well as some cut marks on remains of small game, including foxes, hares, and birds. Another important finding are several canid bones (65 specimens from both chambers), of which one mandible looked 'dog-like' and has been, together with the other canid remains, subject of isotopic and genetic research¹⁰.

Senckenberg, Germany

Sites: Senckenberg swamp

The Senckenberg dog, together with an aurochs (*Bos primigenius*), was excavated in 1914 during building activities at the so-called Senckenberg swamp close to the Senckenberg museum in Frankfurt/Main^{11,12}. Some bones of the aurochs skeleton clearly show bite marks from a dog¹³. Both the dog and the aurochs were first presented in a specially designed reconstruction of Frankfurt's primeval landscape¹⁴ (Richter, 1936). Baas^{15–17} studied sediment samples from the place of discovery palynologically and assessed the dog and the *Bos* to the early post-glacial period (Boreal, approximately 10,000 - 11,000). New ¹⁴C data from the dog and the aurochs indicate a calculated age for the dog of 11,000 years before present (this paper).

Sites in Sweden

Sites: Ageröd, Almeö, Bökeberg, Ljungaviken, Möllehusen, Skateholm, Tågerup

Ageröd I (HC and A). The settlement complex Ageröd I was located adjacent to the former shoreline of Lake Ringsjön, near the outlet of the River Rönne å, approximately 35 kilometres from the coast¹⁸. The site was subjected to investigation during the years 1946–1947¹⁹ and again in 1973–1974¹⁸. The assemblage of bones was recovered from a stratigraphic sequence of peat and gyttja layers, with an additional category termed 'rough excavation' ('grovgävt'), which was not associated with any particular stratigraphic layer. Radiocarbon dating, in conjunction with the typological analysis of the artefacts¹⁸, situated the site within the latest phase of the Maglemose Culture and the earliest part of the Atlantic Chronozone. Ageröd I has been interpreted as a seasonal settlement, potentially serving as a hunting camp occupied during the summer and autumn months. Evidence indicates the hunting of both large and small game, as well as activities related to fishing and fowling²⁰. The dogs are indirectly dated based on charcoal and other animal bones from the same layer²⁰ (7850±85 BP [Ua-19615], 7675±80 BP [Ua-19620], 7530±80 BP [Ua-19616], and 7415±75 BP [Ua-19617]).

Almeö. This is a settlement site attributed to the Early Mesolithic Hensbacka culture²¹, located at the shore of a small island in the Hornborgasjön lake. The dog specimen is one of three dogs found at the site, and comes from a dog burial at the outskirt of the settlement.

The complete skeleton of the dog was laid out on the sandy beach and was sprinkled with red ochre and covered by sand, but not accompanied by artefacts. It has been indirectly dated based on charcoal collected from the cultural layer (9325±120 [St-9236] & 8935±115 BP [St-9235]). As the settlement layer was rapidly covered by peat, it is stratigraphically intact and later intrusions are highly unlikely.

Bökeberg III (Bökebergsslätt 1:1). The site of Bökeberg III was located on a promontory within the former lake Yddingesjön, approximately 15 kilometres from the coast²². The site was subjected to archaeological investigation through research and seminar excavations conducted by students between 1990 and 1995 (Karsten, 2001). It is associated with the Late Kongemose Culture and the Early Ertebølle Culture, with a notable concentration of remains and artefacts from the latter period. The assemblage of bones was retrieved from fen peat and drift gyttja²³. Material recovered from the excavations of 1990–94 has been analysed by students enrolled in the course of Historical Osteology at Lund University²⁴, whilst bones excavated in 1995 were identified by Erikson and Magnell²⁵. The function of the site has been interpreted as a hunting camp utilised by a small group of people. The animal remains suggest that the primary purpose of occupation was hunting red deer, although evidence also points to other subsistence activities, including the gathering of plants, fishing, and hunting of various other animals. The specimen comprises the skull, lower jaw, and cervical vertebrae, which were discovered within a silty deposit that once constituted the lakebed adjacent to the settlement. The lower jaw exhibits cut marks indicative of skinning²⁵.

Ljungaviken. The settlement Ljungaviken was situated in a bay by the Baltic Sea in western Blekinge, Southern Sweden. The site is dated to 7700-5600 cal BC, with a primary phase during 6800-6300 cal BC. The main part of the settlement was excavated in 2020 prior to the construction of a new residential area (Persson, Hammarstrand, Kjällquist, in preparation), while a smaller, less well-preserved part was excavated in 2016²⁶. Within the excavated area, covering 10 000 m², remains of 58 Mesolithic houses, 800 hearths and other features, including a dog burial have been found. The houses investigated are the largest number documented from a Mesolithic settlement in Northern Europe. The site was covered by 0.5 to 4 meters of deposits from the Littorina transgression, consisting of gyttja-clay (decayed anaerobic organic deposits and clay) and sand.

In a small pit near several houses a dog skeleton was found lying on its left side, curled up with crouched legs and head bent over its back. A small stone had been placed on the mandible and by the dog's head and paws eight flints (four microblades, one microlith and three flakes) were found, possibly representing grave gifts. In four soil samples taken by the dog microscopic fibres of barbules have been identified that may indicate that the dog was buried on a bed of feathers. Due to poor preservation of collagen from the dog bones themselves, the burial has been radiocarbon dated by two samples of charred hazel nutshell (Ua-78764 7797±39 BP) and charcoal (Ua-78765 7768±36 BP) from the filling to around 6600 cal BC, and show that the dog burial was contemporary with the settlement²⁷ (Persson, Hammarstrand, Kjällquist, in preparation).

Möllehusen I (Nymölla 12:35). The Nymölla I site (formerly known as Möllehusen), comprising a settlement and burial complex, is situated in north-eastern Scania, Southern Sweden, at the confluence of the Skräbe River and the Baltic Sea²⁸. Excavations were conducted at this location during the years 1938–1939, 1974–1975, and 1980–1985. The

settlement has been typologically attributed to the Pitted Ware Culture. Its economy predominantly centred on hunting and fishing activities. Nymölla I functioned as a coastal occupation site, positioned near the mouth of the river, with particular emphasis on sealing and sea-fishing. Additionally, pig husbandry played a significant role in the settlement's subsistence practices²⁸.

The dog skull examined in the current study was recovered during the excavations carried out in the 1930s. The bones were found within a refuse deposit on the seabed adjacent to the settlement²⁹. The assemblage of bones was initially studied by Herved Berlin³⁰ but was subsequently re-examined by Ola Magnell. The dog is indirectly dated based on charcoal³¹: (Lu-973) 4650±95 BP, (Lu-1110) 4380±60 BP, (Lu-1111) 3850±60 BP, (Lu-1112) 3620±65 BP & (Lu-1113) 4220±110 BP. However, these dates have been suspected to be affected by the "old wood effect", and the association between the radiocarbon-dated material and the settlement has been questioned.

Skateholm II. The Skateholm complex, situated along the southern coast of Scania, Southern Sweden, comprises several archaeological sites that date to various phases of the Mesolithic and Neolithic periods³². The most renowned among these are Skateholm I and Skateholm II, which feature extensive cemeteries from the Late Mesolithic period and adjacent settlement layers located beside a former lagoon. The cemeteries and settlement layers at Skateholm I and II were excavated in the early 1980s³².

Skateholm II, attributed to the Ertebølle Culture based on both radiocarbon dating and the recovered artefacts, is considered the older of the two sites. Although there are currently no definitive dates derived from bones found within the graves at Skateholm II, charcoal samples from the settlement layers predominantly yield dates between 5700 and 4700 cal BC³³.

Dog Grave XXI constitutes the most richly furnished burial within the entire cemetery. As grave goods, the dog was accompanied by a red deer antler, which was positioned along its back, an antler hammer decorated with carved motifs, and three flintknives. The dog is indirectly dated based on charcoal from other graves and objects³¹: (Lu-2443) 5460±110 BP, (Lu-2444) 5900±140 BP, (Lu-2445) 5660±110 BP & (Lu-2478) 6300±100 BP.

Tågerup 1:1. The Mesolithic site of Tågerup, situated in western Scania, southern Sweden, is located at the confluence of the small rivers Saxån and Braån, where they join a larger watercourse. The site has been subjected to extensive archaeological investigations between 1995 and 1998³⁴. These investigations uncovered the remains of a hut, several burials, and refuse layers deposited in proximity to the contemporaneous shoreline^{34,35}.

The Mesolithic occupation at Tågerup has been dated to several phases associated with the Kongemose and Ertebølle cultures. The assemblage of bones retrieved from a cultural layer of silty sand, along with a contemporaneous gyttja deposit linked to the earliest phase—principally representing the settlement of the Kongemose Culture—was examined by Mats Eriksson and Ola Magnell³⁶. It is interpreted that the site was occupied throughout the year, with both hunting and fishing playing significant roles in its subsistence economy. The dog bones, predominantly teeth and skulls, with a lesser portion of bones from other parts of the body, were fragmented and recovered intermingled with the other animal bone material from the site³⁶. The dog specimens included in this study have been indirectly dated

based on other dog bones from the same cultural layer (layer 4): Ua-9944, 7810±95 BP, metacarpal 4; Ua-25192, 7440±65 BP, radius; Ua-25194, 7670±75 BP, femur; Ua-25200, 7760±65 BP, radius; Ua-25207, 7470±90 BP, coxae; Ua-25209, 7460±80 BP, mandible.

Sites in Denmark

Sites: Barmosen, Bundsø, East Greenland, Ertebølle, Fannerup, Føllenslev, Gislinge Mose, Gudumlund, Gundsømagle Mose, Halleby Å, Holmegaard, Klintesø, Lindø, Meilgaard, Nivågård, Ramløse Sørog, Sølager, Sværdborg, Syltholm, Åmølle, Ørum Å

Barmosen. The site of Barmosen is considered a Mesolithic site of the Maglemose culture³⁷. The dog mandible sampled here was found in a low lying field (former bog) close to human bones and a “thick butted axe”, an axe type known from the middle and late Neolithic period – therefore there is a possibility that the dog could be of Neolithic origin.

The ancestry profile of the dog (Fig. 3a) is not typical of neither Mesolithic nor Neolithic dogs in Denmark, instead displaying a profile more typical of European dogs that lived more recently, in the past few thousand years. This could thus be a case of more recent deposition.

Bundsø. This a well-known Funnel Beaker settlement site, located on the island of Als on the coast of southern Jutland. The actual settlement is on a small island called Flintholm in a former marine inlet called Bundsø. The site was excavated on several occasions, first by German archaeologists 1903-1904 and then 1924-1935 by various Danish archaeologists, including Therkel Mathiassen. The German excavations were published by Hoika³⁸ and the Danish ones by Mathiassen³⁹.

Neolithic finds were found over an area of approximately 200x100 m. Due to partial waterlogging, preservation was excellent and included remains of wooden constructions. The existence of houses was inferred from finds of clay lining with imprints of wooden beams. Typologically, the find material can primarily be classified as Middle Neolithic III, although other periods are also represented, corresponding to ca 3100 – 3000 cal BC⁴⁰.

The faunal material is large and well preserved, but has only been partially published. Bones from the Danish excavations 1924-1935 were analysed by Degerbøl⁴¹ and reanalysed by Nyegaard⁴² (table 9). Almost 5700 bones could be determined to species. The bones were dominated by cattle, followed by pigs and ovicaprids. 197 bones were determined as dog, of which seven were almost complete crania. The dog bones were described in detail by Degerbøl⁴¹.

East Greenland? The wolf cranium (skull and mandibles with teeth in situ) is labelled “*Canis lupus*, (Østgrønland?)” and derives from a study collection 1963 and with no further information on provenance.

Ertebølle. Ertebølle is a well-known Mesolithic site. However, Madsen et al.⁴³ mentions on page 53-56 a wide range of Neolithic objects, including typical polished thin butted flint axes, to a depth of around 30 cm in the kitchen midden, thus clearly documenting a Neolithic horizon in the Ertebølle *locus classicus* site. The stratigraphy is displaying midden layers of up 1.3 m thickness, which is dynamic and different in thickness, showing different kinds of shell depositions over a period of over a 1000 years ranging from the Early Ertebølle Culture (4800 BC) to 3600 BC⁴⁴. But the appearance of the thin butted axes, mentioned by Madsen at page 53-56, also documents a horizon from the later parts of the Early Neolithic (4000-3300 BC).

Fannerup. At Fannerup on Djursland, a series of Mesolithic and Neolithic shell middens were excavated by A. P. Madsen and C. Neergaard from 1888 to 1895⁴³. Further excavations were undertaken in 1956 by Poul Kjaerum, and in 1987-1988 by G. H. Rasmussen^{45,46}. At present a total of 11 shell middens are known from Fannerup. Four sites date to the Neolithic (Fannerup I-III and Ørum Å). Other sites are identified by letters (Fannerup A-G). Fannerup A, C, E and F date to the Ertebølle period, while the remainder are undated. The left mandible (A.8788. F.) excavated in 1888 is according to H. Winges handwritten notes dated 13.12.1889 from kitchen middens not specified any further. The right mandible (65/12) is according to H. Winges handwritten notes dated 25.03.1901 from kitchen middens from the Mesolithikum (ældre stenalder) and thus probably from the Ertebølle period.

Føllenslev Havnsø. Two dog skulls were sent to the Zoological Museum together with domesticated cattle, pig, sheep and horse. There is no information on the provenance or if the bones were found together. The ancestry profile of the dog (Fig. 3a) is not typical of neither Mesolithic nor Neolithic dogs in Denmark, instead displaying a profile more typical of European dogs that lived more recently, in the past few thousand years. This could thus be a case of more recent deposition.

Gislinge mose. The dog remains were sent to the Zoological Museum together with domesticated cattle, pig, sheep and horse. There is no information on the provenance or if the bones were found together. The appearance of a horse in the faunal assemblage could however suggest a date of the whole faunal remains from the Early Bronze Age to the Iron Age.

Gudumlund. In H. Winges handwritten notes he mentions two cattle molars, one phalanx and a lower end of tibia presumed to be from the topsoil based on the appearance. One radius fragment of cattle/aurochs was found, while all other fragments are from wild species. A radiocarbon dated harp seal (*Pagophilus groenlandicus*) suggests Ertebølle culture. However, on this site there is also a Neolithic horizon. It is an old excavation made by Japetus Steenstrup in 1850-1851, so challenging to draw firm conclusions.

Gundsømagle Mose. Bog finds found beneath 2.2 meters of turf. A private landowner sent the finds to the Zoological Museum. Likely to be dated to either the Mesolithic or Neolithic. The ancestry profiles of the two analysed dogs (Fig. 3a) are not typical of neither Mesolithic nor Neolithic dogs in Denmark, instead displaying a profile more typical of European dogs that lived more recently, in the past few thousand years. This could thus be a case of more recent deposition.

Halleby Å. A wolf skull and partial skeleton were found in a bog. Pollen dated to the Subboreal (Zone VIII), contemporaneous with the Neolithic and Bronze Age periods.

Holmegaard I. This is one of at least five Early Mesolithic settlement sites in the Holmegård bog on southern Zealand⁴⁷. Holmegård I was excavated by Broholm⁴⁸ and was typologically dated to the Maglemose culture, ca 9000 – 6000 BC. A calcaneus bone from a dog, not the same bone sampled for DNA here, was C-14 dated: 7980±70 uncal BP (Ka-6998)⁴⁹. With reservoir correction this was calibrated to late Maglemose (8638 cal. BP).

Klintesø. This is an Ertebølle Culture shell midden site. From H. Winges handwritten notes is seen that all fish, bird and mammal species reflect a typical Mesolithic Ertebølle Culture. Apart from one tooth of horse (with too little collagen to be dated), two molars from sheep/goat, and one goat humerus (dated), no other Neolithic indicators were found. In Madsen et al.⁴³, page 123, a find of an *Ovis/Capra* is mentioned, which has been C14 dated to the Middle Neolithic B (ZMK 5): OxA-27065, 3926±33 uncal BP, 2558-2296 cal. BC⁵⁰.

Madsen et al.⁴³, 128 also mention the finds of a polished thick butted axe in the upper layers (first 25 to 30 cm) of the kitchen midden. It is known from later investigations of the kitchen middens that their stratigraphy can be very dynamic, thus showing different kinds of depositions and palimpsests of activities over several habitations over a 1000 years range, and sometimes even longer. Winge also compared the different dog bones with each other, and identified an Ertebølle type and a larger dog-type, which have similarities with dogs he had observed from the Iron Age. It's not clear to which of these two types the specimen sampled for DNA here might belong.

Lindø. On the small island of Lindø in the archipelago south of Fyn, a Middle Neolithic settlement was excavated 1901-1926. It contained large numbers of pits, fireplaces and cultural layers, and some possible small houses⁵¹. The dating, based on pottery typology, is mainly Middle Neolithic IV (ca 3100 – 3000 cal BC), but there are also remains indicating MN I-III, MN V and LN activity^{40,52}.

Winther identified three midden areas, of which no 1 was sampled here. The well preserved bone material was reanalysed by Nyegaard⁴² (table 10). The fauna was dominated by cattle, followed by pigs and ovicaprids. Five specimens of dog were identified from this midden. Wild fauna was marginal, the most common being red deer.

Meilgaard (Mejlgård): This is a Ertebølle culture shell midden site. A few horse and cattle bones were found in the top layers, and radiocarbon dated: *Bos primigenius*: 5115 ± 70 BP (Ua23130); *Monodon* (sample SP1809): 5780 ± 60 BP. The primary publication on the Mejlgård site is Madsen in Aarbøger from 1888, 299 ff⁵³. From the stratigraphy of the site we can see that from the top layer to the fourth layer, pottery is observed in the first and second layers in the different trenches. The pot sherds are described as thick and coarse, which could correspond to either Late Ertebølle or Early Funnel Beaker. Furthermore, Madsen mentions that in the same places in the trenches, there is a transition from oysters to cardium edule/common cockle, which is common when the transition to the Neolithic occurs. Moreover, Winge's handwritten notes mentions several pieces of *Bos taurus*, which indicates a Neolithic horizon at Mejlgård. These possibly occur in different places of the large kitchen midden and at different depths, but most likely in the top layers. It is not known from which layer the dog bone sampled for DNA here comes from, meaning it is difficult to conclude whether it is of Mesolithic or Neolithic age.

Nivågård. This is a Ertebølle culture settlement site. H. Winge found one fragment of an ovicaprid tooth but suspected it to belong to another find. A later excavation in 1992 described by Enghoff⁵⁴ gave the C-14 dates of Late Kongemose Culture, two dates of Lower/middle Ertebølle and one from a pit of Late Ertebølle/Early Funnel Beaker Culture. Enghoff considered the majority of the 1992 excavation to be Late Kongemose to Ertebølle Culture, and did not find any domestic species except for dog.

Ramløse Søkrog Mose. Found at the bottom a bog below two metres of turf. The wolf mandible has been pollen dated to the Boreal (Pollen Zone V), making it contemporaneous with the Maglemose Culture.

Sværdborg I. This is a Maglemose culture settlement site located in southern Zealand, dating to the final part of the Maglemose, ca 7-6000 BC⁵⁵. It was excavated on three occasions, 1917 by Friis Johansen, 1923 by Broholm and 1943-44 by Becker. The excavations revealed a very rich material of flint tools and flint debris but also of animal bones and bone tools, as well as a series of hut floors.

From the excavations in 1923 several dog bones were recorded, while 14 bones were found during the excavations in 1943. An ulna of a dog was retrieved from the find for C-14 dating, however it is not known if it was in fact dated.

Syltholm II. This is a Late Mesolithic-Early Neolithic site, located on the island of Lolland in the south Danish archipelago. It is one of a series of sites excavated 2012-2022 in connection with the Femern Belt project⁵⁶. Datings from Syltholm II span the centuries around 4000 BC, i.e. the Mesolithic-Neolithic transition. Due to waterlogged conditions, a rich organic material was recovered, including bone refuse and tools, macrofossils and wooden artefacts. The bone material comprises at least ca 8200 specimens, of which over 3000 have been determined to species. The documented species include both domestic and wild mammals, in almost equal proportions, but also a large number of fish. 14C dates of three dogs gave Late Mesolithic dates⁵⁶, but the sampled mandible has not been directly dated. Isotopic analyses of 11 dogs indicated significant intake of marine food for all but one of them⁵⁷. No further information is available on the context of the dog bones.

Sølager. This is a shell midden site, located on a peninsula in northern Zealand. It was excavated at several instances from around 1850 up to the early 20th century. Four layers were distinguished with both Ertebølle and Funnel Beaker remains. Layer 1 was attributed to the Ertebølle period while the upper three layers were dated to the Neolithic. This was corroborated by three charcoal dates⁵⁸. Dog remains, 109 pieces in total, were mainly found in layer 1 (75 pieces) but also in layer 2 and 3. It's not clear in which layer the analysed dog was found.

Åmølle. This is an Ertebølle culture shell midden. In H. Wings handwritten notes he mentions that one sheep, one horse and one human were found in the very top layers, while all other species are from the deeper layers of the shell midden. A radiocarbon dated *B. primigenius* indicates Ertebølle Culture. However, in Madsen et al.⁴³, pages 98-99 it is mentioned that polished thin butted axes, dated to the later part of the Early Neolithic (Early Neolithic II: 3700-3300 BC), were found in the marginal zone of the kitchen midden. Furthermore, in the upper layers of the kitchen midden domesticated animals (*Bos taurus* and *Ovis*) were found, thus documenting a Neolithic horizon in this kitchen midden.

Ørum Å (Daugard). This is a Funnel Beaker shell midden belonging to the Fannerup complex on Djursland, see above. It was excavated by A. P. Madsen in 1888-1891 and by C. Neergård in 1895^{43,45}. The rich find material can typologically be placed mainly in the Middle Neolithic II period, although there are examples of both MN I and Ferslev type pottery. The lowest part of the settlement also contained some Ertebølle finds.

Hardinxveld-Giessendam de Bruin and Polderweg, Netherlands

Sites: Hardinxveld-Giessendam de Bruin, Hardinxveld-Giessendam Polderweg

Hardinxveld-Giessendam de Bruin and Hardinxveld-Giessendam Polderweg. These two sites, often together referred to as just 'Hardinxveld', are located ~1 km from each other in the Rhine-Meuse delta in the southwestern Netherlands. They are classified as Late Mesolithic, with inhabitants practicing hunter-gatherer-fisher subsistence strategies, and were inhabited in the period approximately 7500 - 6000 BP⁵⁹.

Sites in Scotland

Sites: Cuween, Tulloch Of Assery, Tulach an t'Sionnaich

Cuween, Orkney. This is a Neolithic passage tomb of Maeshowe type, located on a hillside in the west-central area of Mainland. It was excavated by Malcolm M Charleson in 1901^{60,61}. Evidence for at least eight human bodies was found and Charleson reported that dog and other animal bones were found 'in great abundance' in the filling of the chamber. According to Charleson, in the lowest stratum on the floor of the chamber were 24 dog skulls. Animal bones, including dog bones, had also been found in two of the cells leading off from the chamber in 1888. A few bones and teeth from six of the dogs ended up in the National Museums Scotland collections, and one cranium was subjected to facial reconstruction in 2019 (historicensevironment.scot/about-us/news/forensic-reconstruction-reveals-face-of-man-s-ancient-four-legged-friend/). The C10726 sample that yielded ancient DNA data in the current project is not from that dog, however, coming instead from a selection of disarticulated teeth.

Radiocarbon dating of human and of dog remains from Cuween (as discussed by Sheridan in Knight and Maldonado, 2021)⁶² has demonstrated that the dogs were deposited around 2550-2350 cal BC, several centuries after the passage tomb was in use for the deposition of human remains around the beginning of the third millennium. The presence of so many dogs in the monument may indicate that they were deployed as totemic animals.

Tulloch of Assery B, Highland (formerly Caithness). This is a passage tomb of Orkney-Cromarty type, with a tripartite stalled chamber and a long narrow passage set within the south-eastern part of a round cairn^{63,64}. It is one of three Neolithic chambered cairns (of which Tulach an t'Sionnaich, described below, is another) which are situated around Loch Calder, and were excavated by John Corcoran in advance of the raising of the water level when a dam was constructed nearby in the late 1960s. Tulloch of Assery B was excavated in 1961. The incomplete and disarticulated remains of six people were found in the chamber and passage, mostly on a layer of slabs in the centre of the inner compartment of the chamber. Faunal remains, some found with the human bones on the slab layer and some below it, are those of cattle, red deer, possibly sheep, possibly pig and dogs. In addition, bird bones were found in the chamber and passage, and the remains of a fox were found in the upper parts of the passage and chamber, and in disturbed areas of the cairn; these species are, however, thought to have arrived in the monument naturally, rather than being deposited. The dog remains appear to be dominated by those of young and immature animals.

There is one radiocarbon date for human bone - 4911±32 BP (3768-3638 cal BC at 95.4%, SUERC-68634, OxCal v.4.4.4)⁶⁵ - and five radiocarbon dates for animal bone (species unspecified but most likely to be of cattle or red deer), ranging between 4965±60 BP (3941-3642 cal BC at 95.4%, GU-1332, OxCal v4.4.4) and 3795±60 BP (2456-2039 cal BC at 95.4%, GU-1337, OxCal v4.4.4)⁶⁶. The latest date may well relate to the deliberate infilling of the monument. There is also a date for charcoal (species not given) from an occupation surface underlying the chamber, and this provides a *terminus post quem* for the monument's construction of 4840±65 BP (3775-3382 cal BC at 95.4%, GU-1339, OxCal v4.4.4)⁶⁶. None of the dog remains have been radiocarbon-dated, so it is impossible to tell whether their deposition was contemporary with the main use of the monument at various times over the fourth millennium BC.

Tulach an t'Sionnaich, Highland (formerly Caithness). This is a multi-phase funerary monument that started its existence as a fairly simple passage tomb with a roughly rectangular chamber, short passage and modest round cairn, but was subsequently transformed into a monument with a larger round, then heel-shaped, then long cairn⁶³. It was excavated in 1961 and 1963 by John Corcoran⁶⁴, and unburnt, disarticulated remains originally believed to belong to five people (but recently reassessed as possibly comprising just four) were found in the lowest layer in the chamber, with a secondary (Early Bronze Age) deposit of the cremated remains of a further individual, in a cinerary urn, being found in the cairn slip south of the heel-shaped cairn. Faunal remains, found in the chamber and passage (and in positions in the cairn suggesting that they had been ejected from the chamber or passage), are mainly those of cattle, red deer and dog, the latter comprising the remains of an adult male and a puppy; both of the dogs were sampled for DNA analysis. The disarticulated remains of the adult dog were found in the middle of the main deposit of human remains in the chamber. Its maxillary carnassial length falls within the range recorded by Degerbøl for the Neolithic dogs from Bundsø⁶⁴.

While the Neolithic human remains have produced radiocarbon dates around the middle of the fourth millennium⁶⁷, the radiocarbon date for the adult dog obtained by the current project - 4289±20 BP (2918-2885 cal BC at 95.4%, OxA-43443)⁶⁸ - post-dates these by several centuries. The date is comparable with that of 4210±60 BP (2916-2584 cal BC at 95.4%, GU-1330) obtained for animal (possibly deer) bone in the chamber⁶³. As at Cuween, faunal remains seem to have been deposited in the monument considerably later than the earliest dated human remains. In the chamber, the cattle and deer remains, some burnt, seem to have been deposited, along with a layer of mollusca, as a deliberate act of chamber filling.

Sites in Belgium

Sites: Caverne Marie-Jeanne, Goyet, Trou Magritte, Trou de Chaleux, Trou de Praules, Trou de l'Ours, Trou du Frontal

Goyet: The Third Cave of Goyet. The Goyet caves are located in the Condroz region, south of the Sambre and Meuse valleys in Belgium. The third cave of Goyet is part of a large karstic system situated on the right bank of the Samson River, a tributary of the Meuse River. This cave was first excavated by the geologist E. Dupont in 1868⁶⁹. He recovered numerous Pleistocene mammal bones, human remains, and large quantities of Middle and Upper Palaeolithic artefacts⁶⁹⁻⁷¹. These materials have since been stored in the collections of the Royal Belgian Institute of Natural Science.

In Chamber A, near the entrance of the third cave, Dupont discovered in the three uppermost levels a rich assemblage of bones from various species of Pleistocene mammals, including mammoth, reindeer, horse, canid, and human remains, alongside numerous Middle and Upper Palaeolithic artefacts^{69,70,72-74}. The artifacts can be attributed to the Mousterian, Lincombian-Ranisian-Jerzmanowician, Aurignacian, Gravettian, Magdalenian, Neolithic, and historical periods, indicating that the cave was repeatedly occupied from the Pleniglacial onward^{69,71-73,75,76}. At the rear of Chamber A and in Chamber B, Dupont⁶⁹ identified a fourth and a fifth bone-bearing level, which lacked lithic material but contained remains from cave bear, cave lion, cave hyena, and large canids.

The wide range of AMS dates, as well as the refitting of human bones originating from different bone levels, show clearly the mixed content of the stratigraphic levels recognized by

Dupont, likely due to his excavations methods, which were not as rigorous as today standards^{70,74}. Additional post-depositional mixing may have resulted from the burrowing activities of badgers, whose remains were also found in the faunal assemblages⁷⁰.

In this study, canid remains from bone levels A1, A2 and A3 of the third cave of Goyet were analyzed.

Bone Level A1

As with the other levels, the faunal assemblage from A1 is heterogenous in origin. According to ⁷⁵, the lithic and osseous material from the upper bone level represents several Late Upper Palaeolithic occupations that could correspond to older, middle (similar to the occupation at the nearby Trou de Chaleux cave), and younger (possibly Creswellian) phases of the Magdalenian. The faunal assemblage includes bones showing evidence of human manipulation - such as cut-marks, impact marks, red stains, bone tools, ornaments made of bone, tooth, and ivory - from bear, canids, mammoth, woolly rhino, horse, reindeer, muskox, and ibex ^{77,78}. Recent AMS dates indicate that the bone material from level A1 spans at least from 40,900 BP to 11,785 BP^{78,79}.

C10609 (ulna). Biometric analysis of the canid ulna Vert00-247 (2812-6) indicated that it belonged to a medium-sized Palaeolithic dog, with the greatest breadth across the coronoid process (BPC) of 17.0 mm and a body mass estimate of approximately 20 kg. A direct AMS radiocarbon date (11,785 ± 48 BP, RICH-27945) places the specimen in the Bølling / Allerød interstadial. Modifications on the bone made by both humans and carnivores suggest that the animal was dismembered by a contemporary human, likely to obtain its meat, and subsequently gnawed by a canid-sized carnivore⁷⁸. The genetic data obtained here shows that this individual was a wolf genetically.

Bone Level A2

Like the other levels, bone level A2 contains a mixture of archaeological and faunal material dating from various periods of human occupations. AMS dates on bones, including from this study, range from 41,500 BP to 2,318 BP⁷⁹. Bones showing human modification include those of bear, horse, mammoth, reindeer, bison, and muskox.

2760-3 (upper carnassial). The root of an isolated upper carnassial from level A2 was sampled for DNA analysis. Its large crown length (P4cl: 28.4 mm) falls outside the observed range for Palaeolithic dogs and within the range for Pleistocene wolves⁸⁰, indicating that this specimen is a Pleistocene wolf. Its AMS date (34,024 ± 326 BP, ETH-61241) places it within the Pleniglacial. The genetic data obtained here confirms it was a wolf.

TU96 (ulna). Ulna 2760-17 (TU96), with a BPC of 15.6 mm, is smaller than the smallest recorded value for both the recent northern wolves and Pleistocene wolves⁸⁰, indicating that it is a dog. This is confirmed by the genetic data obtained here. It has a body mass estimate of approximately 16 kg. The AMS date of this specimen (2,318 ± 24 BP, ETH-73411) shows that it is not part of the Pleistocene faunal assemblage but dates to the Iron Age.

Bone Level A3

Bone level A3 also contains a mixed assemblage of faunal remains and lithic material. Human modified bones are identified from bear, mammoth, woolly rhino, horse, red deer, reindeer, and bison. AMS dates range from 37,950 BP to 10,640 BP^{78,79}.

TU94, TU93 (ulnae). Two ulnae were sampled from bone level A3. The smaller specimen, ulna Vert00-248/2240-1 (TU94), has a greatest breadth across the coronoid process (BPC) of 17.3 mm, which falls outside the observed ranges for Pleistocene wolves, Postglacial

wolves, and recent northern dogs⁸⁰, being smaller than all these reference groups. Its small size, with a body mass estimate of approximately 20 kg, suggests it is dog-like. The larger ulna, Vert00-249/2240-2 (TU93), has a BPC of 21.1 mm and a body mass estimate of approximately 29 kg. Its BPC measurement falls just outside the observed range for wolves and within the range for recent northern dogs⁸⁰.

TU95 (tibia). The sampled tibia Vert00-251/2240-4 (TU95) has a distal breadth (Bd) of 25.0 mm and a body mass estimate of approximately 24 kg. The Bd measurement falls within the observed range for both prehistoric and recent northern dogs, and outside the ranges for Pleistocene and Postglacial wolves⁸⁰, suggesting a dog-like size.

Trou de Chaleux. The cave of Trou de Chaleux is located on the right bank of the River Lesse, a tributary of the River Meuse, in a Carboniferous limestone cliff at an altitude of 115 m⁸¹. In 1865, Dupont excavated a major archaeological layer here and recovered numerous skeletal remains of mammals, birds, and fish, along with a large assemblage of Magdalenian artefacts⁶⁹. This makes Trou de Chaleux the richest Late Magdalenian assemblage in Belgium, with large collections of lithic and bone tools as well as figurative art^{69,75,81}. Recent AMS dates indicate that the bone material from the Magdalenian level spans at least from 12,880 to 12,140 BP⁷⁹. However, remains of domestic pig and chicken attest that part of the faunal assemblage is much younger and does not belong to the Pleistocene^{82,83}. Nevertheless, several taxa present, such as arctic fox, reindeer, muskox, ptarmigan and snowy owl⁸²⁻⁸⁴, are typical of glacial environments and consistent with an attribution to the Late Magdalenian. Anthropogenic modifications were observed on remains of horse, reindeer, red deer, muskox, fox and brown bear, swans, goose, ptarmigan, loon, snowy owl, and raven^{82,83,85,86}.

TU97 (metatarsus). A third metatarsus (2602-9) of a large canid was sampled from the Magdalenian assemblage. No metric data are available, as the specimen was too fragmented to be measured.

Trou du Frontal. Just as the nearby caves of Trou de Chaleux and Trou des Nutons, Trou du Frontal is located in a Carboniferous limestone cliff on the right bank of the River Lesse⁷⁵. E. Dupont started the excavations here in 1864. He described several stratigraphic levels. In the second level, he discovered a human burial site, which he thought dated from the Magdalenian⁸⁷, but which proved later to be Neolithic in origin. According to Charles⁸², Dupont⁶⁹ combined a number of separate stratigraphic layers, which then includes a mixture of fauna and artefacts of different ages. Apart from the Neolithic assemblage, at Trou du Frontal, lithic and bone tools dating from the Magdalenian were also discovered. The faunal assemblage consists of a mixture of Late Pleistocene and Postglacial species such as reindeer and horse on the one hand and pig, sheep/goat and roe deer on the other hand. Human manipulated bones consist among others of remains from large canids, fox, hare, horse, red deer and reindeer. AMS dates range from 24,250 BP to 4,430 BP. The latter date is on a cut human tibia. Several AMS dates pertain to the Magdalenian ranging in age from 12,800 to 12,220 BP^{79,82}.

2468-4 (radius). The sampled radius 2468-4 has a distal breadth (Bd) of 33.0 mm and an estimated body mass of approximately 39 kg. The Bd measurement falls within the observed range for both Pleistocene and Postglacial wolves, and outside the ranges for prehistoric and recent northern dogs⁸⁰, suggesting a wolf-like size. The AMS date of this specimen

(5,398 ± 30 BP, ETH-61243) shows that it is not part of the Pleistocene faunal assemblage but dates to the Postglacial.

Trou Magrite. The cave of Trou Magrite overlooks the River Lesse, less than 2 km upstream from its confluence with the River Meuse, near Dinant. Situated in a Carboniferous limestone cliff about 25 m above the present course of the Lesse, the cave consists of a large main chamber, a smaller vestibule, and a rear chamber. Its wide porch faces south-west^{69,88,89}. Trou Magrite was first discovered by the geologist Édouard Dupont during his systematic exploration of the Meuse valley in 1864. Excavations began the following year, and in total, Dupont recovered more than 11,000 lithic artefacts and over 50,000 faunal remains, which are stored since at the Royal Belgian Institute of Natural Sciences^{90,91}.

In his reports, Dupont distinguished three main sedimentary units: (1) an upper layer of clay with blocks, about 1 m thick; (2) stratified sandy-clay deposits, 2.5 m thick; and (3) a basal layer of rolled gravels, about 1 m thick⁶⁹. Within the stratified sandy-clay unit, he identified four archaeological horizons, or “bone-bearing levels.” Two of these were designated the “lower bone-bearing levels” and two the “upper bone-bearing levels.” During his work, Dupont also recovered two pieces of portable art: an anthropomorphic figurine and an engraved reindeer antler⁹². In the early 1990s, Marcel Otte and Lawrence G. Straus conducted new excavations to clarify the stratigraphy. Since the cave interior had been emptied and later refilled with back dirt, they focused on the margins of the terrace, where two test trenches were opened⁸⁸.

Subsequent analyses have shown that the archaeological sequence at Trou Magrite is exceptionally diverse. It contains several Mousterian facies⁹³, different Aurignacian sub-complexes^{72,94}, Gravettian levels^{72,95}, Magdalenian occupations^{72,96}, and traces of Mesolithic and Neolithic activity⁹⁶. The faunal assemblage from the Dupont excavation is dominated by remains from reindeer, woolly rhino and canids⁹⁷; the Otte-Straus faunal assemblage is dominated by remains from horse, reindeer and ibex⁸⁹. Anthropogenic modification occur among others on bone and tooth elements from reindeer, horse, ibex, and foxes^{86,98}. Recent AMS dates on the bone material excavated by Dupont range from 39,690 to 25,080 BP^{91,99}. Recent AMS dates on material from the Otte-Straus excavation range from 41,300 to 39,850 BP¹⁰⁰.

2425-53 (*tibia*). The sampled tibia 2425-53 has a distal breadth (Bd) of 25.7 mm and an estimated body mass of ~25 kg. The Bd measurement falls just outside the observed range of Postglacial wolves⁸⁰. It has an AMS date of 28,678 ± 30 BP (ETH-61248)¹⁰¹.

Trou de Praules. The cave of Trou de Praules (or Trou de Praule) is located about 500 m upstream from Furfooz, on the left bank of the river Lesse, at an elevation of ~30 m above the river. The entrance is easily accessible, measuring about 6 m in width and 3.5 m in length at the center. On either side of the main chamber, two narrow galleries extend to depths of 4 m and 8 m, respectively. This cave was explored by Édouard Dupont in 1866¹⁰². The Quaternary sediments inside were relatively thin. At the base, directly above the limestone bedrock, was a thin deposit of stratified sandy clays containing rolled pebbles and gravel in discontinuous lenses. This basal layer yielded a humerus and a canine of a large bear¹⁰². Overlying these basal deposits were yellow blocky clays, less than 1 m thick. These upper sediments contained, particularly at their base, faunal remains and a small number of

worked flints. The identified faunal species include bear, wolf, foxes, badger, horse, reindeer, red deer and goat¹⁰². The presence of goat indicates that the faunal assemblage is mixed and contains Pleistocene and Postglacial elements.

2506-1 (*mandible*). A fragment of a mandible from a large canid was sampled for analysis. The crown length of the lower carnassial (CLm1) measures 28.3 mm. This measurement falls within the observed ranges for both Pleistocene and recent Northern wolves, as well as Palaeolithic dogs⁸⁰. A discriminant function analysis based on the limited number of measurements available from this fragment assigns it to the group of recent Northern wolves (Germonpré, unpublished data). The AMS date of this specimen ($6,471 \pm 32$ BP, ETH-61242) indicates that it does not belong to the Pleistocene faunal assemblage but instead dates to the Postglacial¹⁰¹.

Trou de l'Ours. The cave of Trou de l'Ours is located near Walzin about 35 m above the Lesse River on its left bank. Before its excavation, it was used by badgers as a den. Excavations were carried out by E. Dupont during the summer of 1866. Once the work had advanced sufficiently to clear the entrance, access into the cave was possible by crawling on one's stomach for about fifteen meters. This required the removal of decayed leaves and grasses brought in by badgers for nesting. Near the entrance, the deposit of "argile à blocs" (clay with limestone blocks) was well developed, but this quickly diminished only two meters inside the cave. Further in, the sediment consisted of stratified sandy clays, with a thickness of 2.5 to 3 m⁹².

The faunal remains recovered from Trou de l'Ours were few in number and derived mainly from near the entrance. These included a large vertebra and a canine of cave bear, as well as a few other bone fragments⁹². In addition to bear and badger, other species identified at the site are beaver, fox, wolf, horse, reindeer, elk, red deer, and bison. According to Dupont, there was little evidence to indicate prolonged human occupation. Nevertheless, one horse bone from a juvenile individual bears clear cut-marks, which suggests some human activity in the cave. Overall, the evidence suggests that Trou de l'Ours was primarily a carnivore den, with only limited traces of human presence.

2508-32 (*upper carnassial*). The root of an isolated upper carnassial from Trou de l'Ours was sampled for DNA analysis. Its crown length (P4cl: 23.2 mm) falls within the observed range for Palaeolithic dogs and for recent Northern wolves, but outside the range for Pleistocene wolves and recent Northern dogs, as defined in⁸⁰. Its AMS date ($10,963 \pm 41$, ETH-61245) places it at the end of the Pleistocene¹⁰¹.

Caverne Marie-Jeanne. Caverne Marie-Jeanne is a cave site in the Belgian Ardennes, located 25 m above the right bank of the Féron River, a small tributary of the Meuse River, in a Carboniferous limestone. In the summer of 1943, a team from the Royal Belgian Institute of Natural Sciences, led by Maxime Glibert, began excavating the cave deposits¹⁰³. A detailed monograph of the findings and analyses on the material was later published by¹⁰⁴.

Six strata containing faunal remains were identified by Gilbert¹⁰⁵. Layers 6 to 2 are mainly composed of aeolian deposits (silty sands) and yielded the majority of the faunal material, including both large mammals and microfauna such as lemmings, voles, frogs, and vipers, along with a very small number of possible artefacts^{103,104,106–108}. The anthropogenic origin of

these artefacts remains highly debatable due to the absence of distinctive tool types, their high degree of edge damage and abrasion, the overall scarcity of lithic material, and the complete lack of anthropogenic marks on the faunal assemblage. Taken together, these factors suggest that the cave was not a significant site of prehistoric human occupation^{103,104}.

Recent AMS dates of the stratigraphic sequence indicate that layers 5 to 4 were deposited between ca. 47,600 and 40,500 BP, while the overlying layer 2 produced somewhat divergent dates ranging between 20,930 and 12,275 BP¹⁰⁶. The faunal assemblage is dominated by carnivores, especially cave hyena and foxes, although skeletal elements of large canids are also present. Among ungulates, woolly rhinoceros and horse are well represented. Evidence suggests that the cave functioned primarily as a hyena birth den for a period at least from around 47,600 to 43,000 BP¹⁰³.

Cvmj1 (mandible). A complete mandible (Cvmj1) from a large canid was sampled for analysis. The total length of the jaw (TL) is 180 mm, and the crown length of the lower carnassial (CLm1) is 30 mm. Both measurements fall within the observed ranges for these measurements for both Pleistocene and recent Northern wolves. In addition, a discriminant function analysis on several measurements on this jaw indicate that this specimen was wolf-like in size¹⁰⁹.

La Fru, France

Sites: La Fru

La Fru. The La Fru rock shelter (45°27' N, 05°47'E) is situated in the Northern Alps, eastern France, near the town of Chambéry. The site is located at 530 meters above sea level on a promontory overlooking an alluvial basin and at the foot of a 30-metre-high Urgonian limestone cliff. Excavations by G. Pion (1981–1993) revealed evidence of Magdalenian, Azilian and Mesolithic occupations across a strip approximately 100 m long and 3 to 4 m wide, divided into three Areas—I, II, and III—separated by huge boulders originating from the collapse of the ledge before the site was occupied¹¹⁰. The sedimentary deposits are 2.5 m thick in Area I, and seven lithostratigraphic horizons were identified, including including levels c2 and c3, which are Late and Early Azilian respectively, as well as levels c4A and c4B, which are Upper Magdalenian¹¹¹. Due to localised low sedimentation, Layer 2 transitions directly to Layer 3, and Layer 3 directly to Layer 4A across part of the excavated surface, with no intermediate level. Additionally, a small volume of the Azilian layers was disturbed by former clandestine excavations. Nevertheless, given the importance of the sequence, a series of analyses were carried out over time, including archaeo-stratigraphy, lithic technology, zooarchaeology, AMS radiocarbon dating, and stable isotope analysis of targeted species.

Radiocarbon dates on horse and bovine bones place layer 4A Magdalenian occupation between 15,240 and 14,980 cal BP (average date). The faunal spectrum of the Early Azilian Layer 3 reveals a high taxonomic richness, with 13 mammalian taxa, including five species of ungulate. The first species to be hunted were roe deer and red deer. Several bones of these two species have been radiocarbon dated to between 14,870 and 14,000 cal BP¹¹². A variety of wild carnivore species of all sizes have been identified, including canid remains attributed to the wolf (*Canis lupus*). These include various skeletal elements distributed throughout Layer 3 and at its interface with Layer 4A. A cervical vertebra (reference LF F14

#644, Z=72), which was zooarcheologically identified as belonging to a wolf and collected in square F14 at the 3/4A boundary in Area I, was radiocarbon dated to 12,460±60 BP (14,980-14,300 cal BP, 2 sigma) (not previously published). The wolf samples included in this study consist of two undated dental remains: one is an upper left half P4 from square E17 in Area I (reference LF E17 #580), and the other is a lower right I3 from the sieving of square E14 (reference E14 bucket 29, 3/4A). Given that these three skeletal elements were found in almost identical square metres, it is possible that they come from the same adult individual.

Boncuklu Höyük, Türkiye

Sites: Boncuklu Höyük

Boncuklu Höyük. Excavated between 2007 and 2023, Boncuklu Höyük is a c. 1 ha. settlement mound located on the Anatolian plateau, in the western Konya basin, next to Hayıroğlu village, Konya, Türkiye¹¹³. It is located at c. 1000m above sea level on a marl prominence in what in the early Holocene was a wetland/steppe mosaic. The occupation was established c. 9300 cal BC. The major excavated phases consist of a small sedentary settlement of mudbrick buildings dated c. 8350-7600 cal BC¹¹³. The settlement is a predecessor of nearby Çatalhöyük (7,100-6,000 cal BC), with which it demonstrates several cultural and architectural continuities¹¹⁴, and has the region's earliest pottery¹¹⁵. Boncuklu was part of a network of small PPN sites on the Konya Plain¹¹⁶ and was linked to regional exchange and cultural networks (imported obsidian and shells), though the population was reproductively distinct and did not see large scale immigration and mobility^{117,118}. The community derived much subsistence from foraging, with evidence for intensive use of the surrounding wetlands, aquatic, steppe and piedmont environments, small scale cultivation and animal herding is in evidence¹¹³. Aurochs and boar were a particular target of hunting, some caprines appear to be managed. Dogs could, therefore, have been used in either or both hunting or herding capacities or indeed as guard dogs given the ubiquity and potential threat from boar to people and crops.

The dog specimen was recovered from the bottom of a small pit in an open area between buildings (in Area R) and seems to derive from an early phase of occupation at the site according to the AMS date on this dog bone (Supplementary Data 2). It could have been deliberately placed in the pit, or discarded with other material when the pit was no longer serving its primary purpose. Boncuklu's sequence has been subject to extensive AMS radiocarbon dating program, with Bayesian modelling applied to refine the calibrated sequence¹¹³.

Aghitu-3, Armenia

Sites: Aghitu-3

Aghitu-3 is a basalt cave located in the village of Aghitu in the Syunik province of southern Armenia at an elevation of 1601 m. Excavations conducted by the Heidelberg Academy of Sciences and Humanities and the National Academy of Sciences of the Republic of Armenia between 2009 and 2025 unearthed several episodes of Upper Paleolithic occupation. These date between 40,000 and 24,000 cal BP based on 37 radiocarbon analyses of animal bones

and charcoal. The three well-preserved canid specimens involved in this study stem from the upper part of Archaeological Horizon (AH) VI and its interface with an overlying volcanic tephra layer named AH Ve (Kandel et al. 2017):

1. AGH3-I12-234.0 ($z = -2.76$ m) is a complete **skull** with both mandibles and preserves cut marks indicating human interaction as well as five puncture marks likely related to predation by another canid. The skull dated to 29,745-30,176 cal BP (MAMS-23306; $25,760 \pm 90$ uncal BP) and corresponds to genetic sample JK-1559 (previously analysed for mitochondrial DNA¹⁰¹).
2. AGH3-G11-98.0 ($z = -2.77$ m) is more than half of a proximal left **radius** dated to 31,003-31,227 cal BP (KIA-39642; $27,120 \pm 170$ uncal BP) and corresponds to genetic sample JK-1556 (previously analysed for mitochondrial DNA¹⁰¹).
3. AGH3-J12-355.0 ($z = -3.10$ m) is less than half of a distal left **humerus** dated to 31,296-31,516 cal BP (MAMS-23057; $27,680 \pm 110$ uncal BP) and corresponds to genetic sample JK-1557.

Based on spatial information, the bones were found within 2.7 m of one another, with the humerus lying 0.34 m deeper than the other finds. While the dating results suggest that the canid remains belong to different individuals, the representation of body parts does not rule out the possibility that these remains belong to one individual. Previous analyses of mitochondrial DNA from two of these specimens showed they carried lineages from a divergent and now extinct branch of western Eurasian wolf mitochondrial diversity¹⁰¹.

Frankfurt, Germany

Sites: NER 13/Grab 21, Frankfurt am Main-Nieder-Erlenbach

NER 13/Grab 21. Frankfurt am Main-Nieder-Erlenbach. The dog skeletons 1986,03.001.001 and 1986,03.001.002 (NER 13/Grab 21) come from dog burials of the Merovingian period from Frankfurt am Main-Nieder-Erlenbach¹¹⁹. A total of seven dog burials have been found in the cemetery¹²⁰. Based on the finds and features, NER 13/Grab 21 is dated to JM II + JM III (Jüngere Merowingerzeit = Late Merovingian), corresponding to 640 - 720 AD. The right M3 of both dogs was sampled. Merovingian dog burials in general are documented for the stages JM I/II and JM III, i.e. the Late Merovingian period (I=600-630/40 AD, II = 640-670 AD, III = 670/80-720 AD), according to Böhner¹²¹ and Ament¹²² (JM I/II = Böhner IV; JM III = Böhner V).

Frankfurt am Main-Heddernheim. Inventory number α19496 records a dog skull from the Roman town of Nida, today's Frankfurt am Main-Heddernheim. The upper left M3 was sampled. The dog skull was located in the fill of a cistern of area 39 at a depth of 155-355 cm, which is dated to the II B-III period¹²³ and the 2nd third of the 3rd century AD.

Předmostí I, Czechia

Sites: Předmostí I

Předmostí I is part of a series of large Gravettian open-air sites in Central Europe, characterized by distinctive lithic tools, such as backed bladelets, geometric microliths and

denticulated bladelets¹²⁴, as well as by the presence of human burials, mammoth remains, ivory and bone implements, ornaments, portable art, and human female representations^{125–130}. The mammal assemblage is dominated by mammoth^{131,132}. Large canids represent the second most abundant group, based on Minimum Number of Individuals calculations^{133,134}. Within this canid group, two morphotypes have been described^{98,109,135}: the Pleistocene wolf morphotype, comparable in size and shape to recent wild wolves from northern Eurasia; and the ‘Palaeolithic dog’ morphotype that has a unique morphology falling outside the size and shape variability of Pleistocene and recent Northern wolves. This dog-like morphotype is characterized by a smaller skull, a shortened snout with a proportionally wide palate, and a shorter, higher mandible compared to the wild type^{80,98,109,135–138}.

A right lower jaw (JK1560; 97-583-C-1891), with the molars in situ, was included in this study. The small size of the mandible and the short length of the lower carnassial (crown length m1: 21.5 mm) indicates that it falls outside the variability of the Palaeolithic dog morphotype and inside that of modern dogs. Based on its morphometric characteristics and its AMS date (2759 ± 37 BP, ETH-52774), this jaw does not originate from the Gravettian assemblage at Předmostí I¹⁰⁹. The genetic data obtained here confirms that it is a dog, displaying an ancestry expected of European dogs that lived in the last few thousand years.

This jaw was sampled in the context of the grant from the Czech Science Foundation, GAČR GA14-05961S: “The relationships between humans and large canids – the dogs and wolves of the Gravettian Předmostí site (Moravia)” and was financially supported by the Ministry of Culture of the Czech Republic by institutional financing of the long-term conceptual development of the research institution (the Moravian Museum, MK000094862).

Pontal da Barra, Brazil

Sites: Pontal da Barra

The site of PSG-07 is an earthen mound at Pontal da Barra, outside the city of Pelotas in Rio Grande do Sul, southern Brazil. These mounds are common across the Pampa biome of the lowlands of the La Plata Basin, and formed as deposits across successive occupations by hunter-gatherer societies living in the region over the past ~5,000 years. Molars and a maxilla, identified morphologically as domestic dog, were recovered from level 2 of the PSG-07 mound. Direct radiocarbon dating of the maxilla gave a date of 1.6 ka, making this the earliest observation of a domestic dog in Brazil¹³⁹.

With the focus of this study being the genetic history of dogs in Europe, we did not analyse the data from the Pontal da Barra dog in much detail. But we observe that it displays an ancestry profile very similar to that of previously published pre-Columbian dogs from North America, suggesting a shared origin with those dogs (Fig. 3a).

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