

Eurasian Grey and White wolf ancestors—800,000 years evolution, adaptation, pathologies and European dog origins

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Abstract

The oldest known wolf appears 800,000 years ago (Marine Isotope Stage 21) in Eurasia with the unspecialized short-legged old Mammoth steppe wolf *Canis lupus bohemica* nov. spec. From this species, about 600,000–420,000 years ago (MIS 15–11), the interglacial *Canis lupus mosbachensis* (Soergel, 1925) short-legged Mosbach grey wolf subspecies roamed Eurasia. In the late Middle Pleistocene, there are two lineages, the southern interglacial grey and northern glacial White wolves in Eurasia. Since 320,000 (MIS 8), the short-legged White wolf *Canis lupus spelaeus* (Goldfuss, 1823) was the glacial Mammoth steppe-adapted wolf. Parallel to the “cave wolf” (found in the German Zoolithen Cave), the warm climate grey wolf *Canis lupus brevis* Kuzmina and Sabinin, 1994 existed. *C. l. spelaeus* relates to the Holocene (MIS 1) extant Holarctic Greenland *Canis lupus arctos* and Siberian *Canis lupus albus* (Kerr, 1792). The Late Palaeolithic (MIS 2) “Gravettian Goyet dogs” fall into the DNA pool of *C. l. spelaeus* and are identified herein as pathological bite trauma individuals, which braincase shortened during the healing process. European prehistoric Neolithic dogs seem to have been imported from Central Asia with the Bandkeramik people (approx. 7000 BP) first, which have the stepped frontals originating from grey wolves.

KEY WORDS

C. l. brevis (MIS 8–5d), *C. l. mosbachensis* (MIS 15–9), *C. l. spelaeus* (MIS 8–2), *Canis lupus bohemica* nov. spec., cave bear feeder, dog revision and origin, Mid-Late Pleistocene phylogeny of Grey and White wolves, oldest known wolf ancestor (MIS 20, 800,000 BP)

1 | INTRODUCTION

The debate about wolf evolution and origin of dogs is recently based on either landmark cranial analyses osteometric or DNA studies, which did not solve the European wolf evolution or dog origin yet but separated several wolf subspecies all over the globe and suggested different breeding regions for dogs (https://en.wikipedia.org/wiki/Subspecies_of_Canis_lupus; Fan et al., 2016; Germonpré et al., 2009; Mech, 1981; Mech & Boitani, 2007; Nowak, 1995; Thalmann et al., 2013; Wozencraft, 2005).

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The most currently accepted wolf taxonomy recognizes the largest canid carnivore, the grey or white wolf *Canis lupus* Linnaeus 1758 of Eurasia and North America, as a single wide-spread species with 38 extant subspecies (https://en.wikipedia.org/wiki/Subspecies_of_Canis_lupus; Fan et al., 2016; Germonpré et al., 2009; Mech, 1981; Mech & Boitani, 2007; Nowak, 1995; Thalmann et al., 2013; Wozencraft, 2005). To the cold

climate northern hemisphere, the American White wolf subspecies belong the largest of all, the arctic wolf *C. l. arctoides*. For Eurasia, ten white and grey wolf subspecies are distinguished based on their cranial morphology: *C. l. lupus*, *C. l. albus*, *C. l. pallipes*, *C. l. cubanensis*, *C. l. communis*, *C. l. arabs*, *C. l. hattai*, *C. l. hodophilax* and *C. l. lupaster* and *C. l. filchneri* (https://en.wikipedia.org/wiki/Subspecies_of_Canis_lupus; Fan et al., 2016; Germonpré et al., 2009; Mech, 1981; Mech & Boitani, 2007; Nowak, 1995; Thalmann et al., 2013; Wozencraft, 2005).

The rare Middle Pleistocene wolf bone records were not yet possible to include in DNA studies. Furthermore, there was a lack of fossil records from this time, except those which were compiled as "*C. l. mosbachensis*." None of the aforementioned studies included the forgotten fossil late Middle to Late Pleistocene "cave wolf" *C. l. spelaeus* (Goldfuss, 1823) from the Central European southern German Zoolithen Cave (Diedrich, 2014; Goldfuss, 1823). Its material is partly analysed herein based on the largest amount of material ever found of Pleistocene wolves in Europe including skeletal remains, several crania (incl. holotype and paratype, Figure 2) and more than 1224 bones of at minimum 12 individuals. The crania and mandibles are compared to other cranial material from several German caves and some open-air warm and cold climate Middle to Late Pleistocene-aged sites (Figures 1 and 2). A revision is possible here now due to important new finds from the Middle Pleistocene of Europe.

Herein, the oldest fossil wolf is presented with a cranium (Figure 2.2) and postcranial material originating from the Interglacial of the earliest Middle Pleistocene (MIS 20, 800,000 years ago) of the Czech Republic, that lived within the *M. trogontheri* savannah fauna. It comes from a hyaena and wolf den cave, the Bat Cave. Another new middle Middle Pleistocene (MIS 11-9) cranium (Figure 2.4) from a gravel pit open-air site Grossrohrheim in the Upper Rhine Graben of Germany extends the Mosbach wolf diagnosis that was based only on a mandible (Figure 2.3). This first complete cranium allows the identification of the English wolf crania described by Reynolds in 1902 (Reynolds, 1902; Figure 2.5) of similar ages from two hyaena and wolf den caves. Including the latest Middle Pleistocene to Late Pleistocene (MIS 8-3) aged Zoolithen Cave and open-air site Gröbern (Figure 2.7; Eemian Interglacial) and Rixdorf (Figure 2.8; Weichselian Glacial) wolves; all those new and former finds allow a new view into the Eurasian wolf evolution of two lineages, the grey and the white wolves (Figure 3). Their warm and cold climate such as geographic North–South separated related appearance and disappearance within the past 320,000 years in Eurasia is the key to understand the controversially discussed origin of the earliest dogs of Europe. All Goyet, or in general Late Palaeolithic dog crania, are

revised in pathological context to represent not the earliest dogs (Figure 4).

2 | MATERIALS AND METHODS

The material includes important new crania discoveries and gives a first overview of sites with many isolated remains from different periods or glacial and interglacial climates and locality types. Most material is from Germany, few are added from the Czech Republic.

Cranium of *C. etruscus* No. IQW 1982/18052 (coll. Quartärforschungsstelle Weimar, mei 17,572)—Early Pleistocene of Untermaßfeld, Thuringia, Germany (from Sotnikova, 2001).

Cranium (Holotype) of *C. l. bohemica* no. PAL SlujCal (coll. PaleoLogic)—Early Middle Pleistocene (MIS 20, early Cromerian, Rhumian Interglacial, *Microtus savini* micromammal zone), Sluji IV Cave of the Bat Cave System, Central Bohemia, Czech Republic. Besides the cranium other cranial and some postcranial remains are present including one radius.

Cranium (Paratype) of *C. l. mosbachensis* no. ME-Can1 (coll. F. Menger) is the first known of this species from the gravel pit Grossrohrheim, Upper Rhine Graben, Germany. The late Cromerian Mosbachian-Hoxnian (MIS 11) or Holsteinian (MIS 9) of the German record. It is the first Mosbach wolf cranium that was found few kilometres from the Mosbach wolf holotype (mandible, Figure 1) site which holotype mandible (cf. Soergel, 1925) is refigured herein after the original study in the Naturhistorische Museum Mainz. The perfect preserved. Non-water transported new cranium and its bone preservation with stronger pyrite impregnation, such as manganese coloured dentition fit similar preservation of the MIS 11 Interglacial megafauna of the Rhine River terrace gravel pit site at Grossrohrheim, that also includes besides a typical warm period forest elephant megafauna the older type of *Hippopotamus amphibius major* Cuvier 1824, that is also known from the English Hoxnian Interglacial. The Grossrohrheim megafauna are similar to the Mosbach megafauna and therefore the wolf cranium must come from the Mosbachian Interglacial, MIS 11.

Cranium fragment and mandible with postcranial remains of one individual from the MIS 5e Eemian Interglacial of Gröbern Lake, Germany (Figure 2.7), and one mandible from the Rixdorf-Horizon (also MIS 5e; Figure 2.8; coll. Natural History Museum Berlin).

Several Crania of *C. l. spelaeus* Goldfuss, 1823 (incl. Paratype) from the Zoolithen Cave (coll. Natural History Museum Berlin, and PaleoLogic). Several other cranial fragments, mandibles and abundant postcranial remains are included in this study, in total 1224 bones of about 12



FIGURE 1 Early (1 Mio. Years) to Late Pleistocene (12,000 BP) *Canis etruscus* such as white and grey wolf *Canis lupus* subsp. sites (skeletons, crania and footprints) with wolf den centres in karstic cave-rich regions of Central Europe. [Colour figure can be viewed at wileyonlinelibrary.com]

individual skeletons. Wolf remains are dated by stratigraphy including absolute data of speleothems and newest unpublished results of the megafauna, especially by the three cave bear subspecies evolutionary stages (*Ursus spelaeus eremus*, *U. s. spelaeus*, *U. s. ingens*), between the MIS 8-2 (cf. Diedrich, 2014).

Cranium of *C. l. spelaeus* Goldfuss, 1823 (coll. Reiss-Engelhorn Museum, without no.) from Arnheim gravel pit,

Upper Rhine Graben, Germany. It has typical bone preservation and tooth impregnation colour that is found in the upper Rhine River terrace, which is dated in MIS 3 of age including the glacial mammoth steppe megafauna (*Mammuthus primigenius*, *Coelodonta antiquitatis* or *Bison priscus*).

Crania photographs of modern extant wolves come from different collections (*C. l. canadensis*, University of Alberta) or websites.

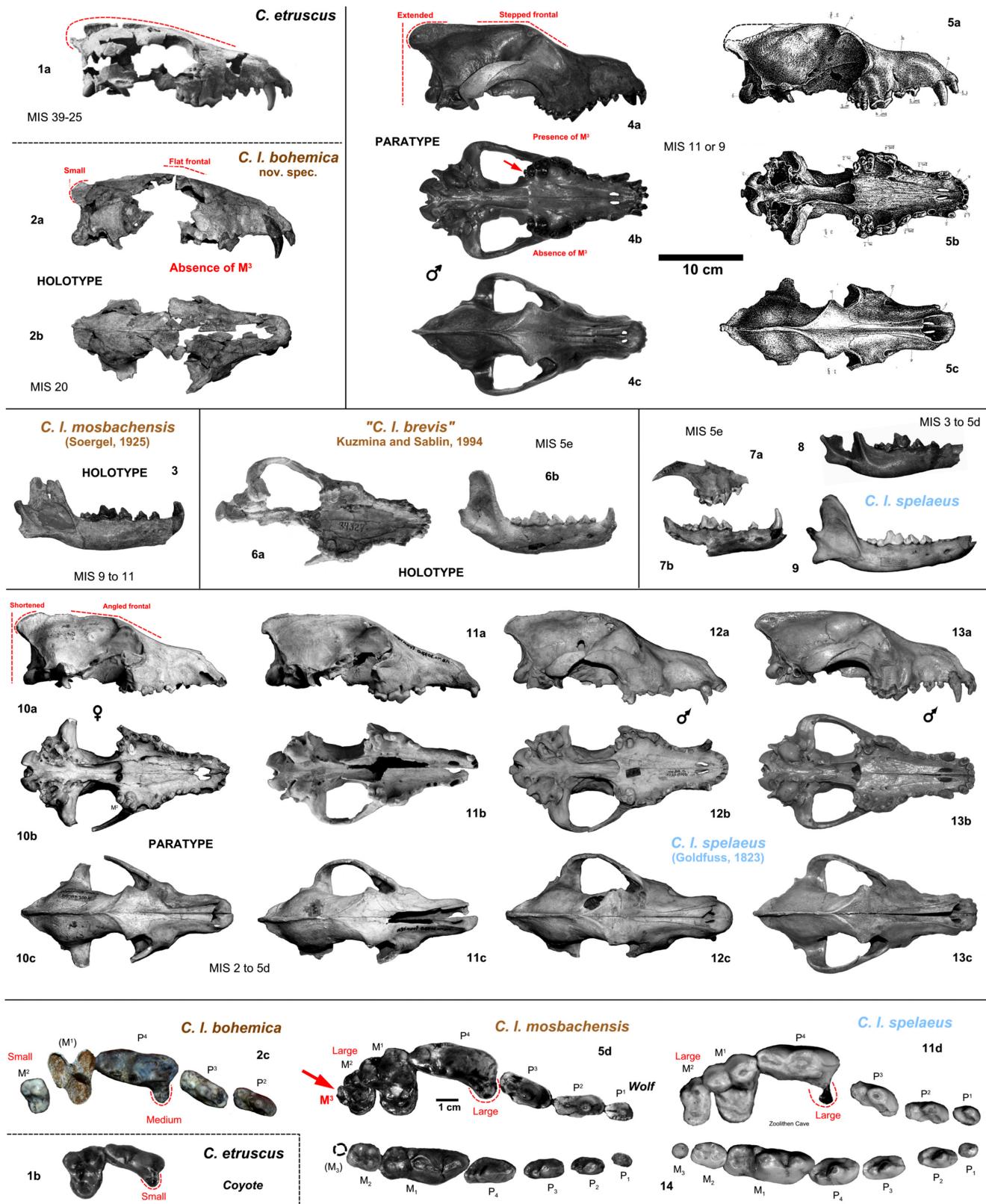


FIGURE 2 Comparison of three distinct extinct Ice Age warm and cold climate grey and white wolves of Europe. 1. Coyote *Canis etruscus* cranium from the late Early Pleistocene MIS 39–25 of Schalksberg, Germany (from Sotnikova, 2001). 2. *C. l. bohemica* nov. subspec. Holotype cranium from the early Middle Pleistocene early Cromerian, MIS 20, of the Bat Cave, Srbsko, Czech Republic. 3. *C. l. mosbachensis* (Soergel, 1925) holotype mandible from Mosbach, Germany, late Cromerian to Holsteinian (MIS 15–11). 4. *C. l. mosbachensis* (Soergel, 1925) paratype cranium from the Middle Pleistocene Mosbachian or Holsteinian MIS 11 or 9 of Grossrohrheim, Rhine River terraces of the Upper Rhine Graben, Germany. 5. *C. l. mosbachensis* (Soergel, 1925) cranium from Kents Cavern, England (from Reynolds, 1902). 6. *C. l. brevis* Kuzmina & Sablin, 1994, holotype cranium and mandible from the Eemian Interglacial (MIS 5e) of Siberia, Russia (from Kuzmina & Sablin, 1994). 7. *C. lupus* subsp., cranium fragment and mandible from the Eemian Interglacial (MIS 5e) of the Gröberner Lake, Germany. 8. *C. l. spelaeus* (Goldfuss, 1823) mandible from the Late Pleistocene Glacial (MIS 5a–d) of Rixdorf, Germany. 9. *C. l. spelaeus* (Goldfuss, 1823) mandible from the latest Middle to Late Pleistocene MIS 8–3 of the Zoolithen Cave, Germany. 10. *C. l. spelaeus* (Goldfuss, 1823) paratype cranium from the latest Middle to Late Pleistocene MIS 8–3 of the Zoolithen Cave, Germany. 11. *C. l. spelaeus* (Goldfuss, 1823) cranium from the latest Middle to Late Pleistocene MIS 8–3 of the Zoolithen Cave, Germany. 12. *C. l. spelaeus* (Goldfuss, 1823) cranium from the latest Middle to Late Pleistocene MIS 8–3 of the Zoolithen Cave, Germany. 13. *C. l. spelaeus* (Goldfuss, 1823) cranium from the latest Middle to Late Pleistocene MIS 8–3 of the Upper Rhine Valley gravel pit site x, Germany. 14. *C. l. spelaeus* (Goldfuss, 1823) mandible dentition from the latest Middle to Late Pleistocene MIS 8–3 of the Zoolithen Cave, Germany. [Colour figure can be viewed at wileyonlinelibrary.com]

3 | RESULTS

3.1 | Early Pleistocene canid

1.3 million years old Late Villafranchian (MIS 39–25) canids are described for the Eurasian record with its oldest believed wolf ancestor as *Canis etruscus* Forsyth-Major, 1877 (Bartolini Lucenti et al., 2017; Cherin et al., 2014; Forsyth-Major, 1877; Schütt, 1974; Sotnikova, 2001), which is placed herein different into the coyote phylogeny lineage. A typical wolf-like canid is not yet recorded before 800,000 years ago in Europe. The coyote most distinct character to those Mid-Pleistocene grey and White wolves is a non-stepped flat frontal and convex developed sagittal crest of the short braincase, whereas the ratio 44% brain case-anterior part 56% of the cranium (Figure 2) is plesiomorph reflecting with its dentition an unspecialized canid ecomorph. Furthermore, the M¹ is in typical coyote and jackal shape which paraconid is small in contrast to the large and strong angled ones of wolves (Figure 2). *C. etruscus* lived in Eurasia parallel with a smaller jackal (*C. aranensis*; Lytras, 2009; Sotnikova, 2001). German localities with *C. etruscus* crania and other skeletal parts of this coyote-sized canid are the hyaena den bone accumulation open-air site of Würzburg-Schalksberg (Schütt, 1974) and early human-influenced hyaena bone accumulation open-air site Untermassfeld (Sotnikova, 2001; Figure 1). From Untermassfeld, the nearly complete cranium is refigured (Figure 2) which was identified as “*C. mosbachensis*” (Sotnikova, 2001).

3.2 | Early middle Pleistocene—the grey and white wolf ancestor

The new cranium from the Srbsko Sluj IV Cave (Bat Cave system), Czech Republic (Figure 2.2) is important

to understand the evolution of our New World wolves. This skull has already the probably full absence of the M³, whereas a single cranium is not representative for the palaeopopulation, where the M³ might have been partly present. The M¹ is different from *C. etruscus* in its larger size and largely developed paracone (cf. Figure 2.2), which latter is characteristic for all Mid-Late Pleistocene wolves (cf. Figures 2 and 3). The cranium has in lateral view already a wolf-shape without convex sagittal crest (such as in *C. etruscus*), but without stepped frontal, that links more to extant White wolves (Figures 2 and 3). Another character is found in the braincase/anterior part ratio of the skull with 47/53%. In all grown-up wolves, the braincase has 47%–50% of the total cranial length, which is higher as in coyotes (44% and *C. etruscus*, Figure 3). Differences in the dentition are found between *C. l. bohemica* and the younger *C. l. mosbachensis*. a smaller M¹ and much smaller M². The M¹ paracone in *C. l. mosbachensis* is also larger. The *C. l. bohemica* dentition is plesiomorph with the M² in fewer amounts of conids and less specialized compared with the younger Mid-Late Pleistocene wolves.

The further fossil record of the early Cromerian MIS 19–16 stays unknown. At that time, the cranium shape must have changed as a result of adaptation to more specialized guilt feeding in the new mammoth steppe environments of Europe and its fauna changes.

3.3 | Middle mid-Pleistocene—large Mosbach interglacial grey wolf

The biostratigraphical range of the real grey wolf *C. l. mosbachensis* (cf. Adam, 1959; Bonifay, 1971; Garcia & Arsuaga, 1998; Musil, 1972; Reichenau von, 1906; Reynolds, 1902; Soergel, 1925; Weitzel, 1936) can be limited now into the Mid-Pleistocene Cromerian-Elsterian-Holsteinian (MIS 15–9). The Late Cromerian (MIS

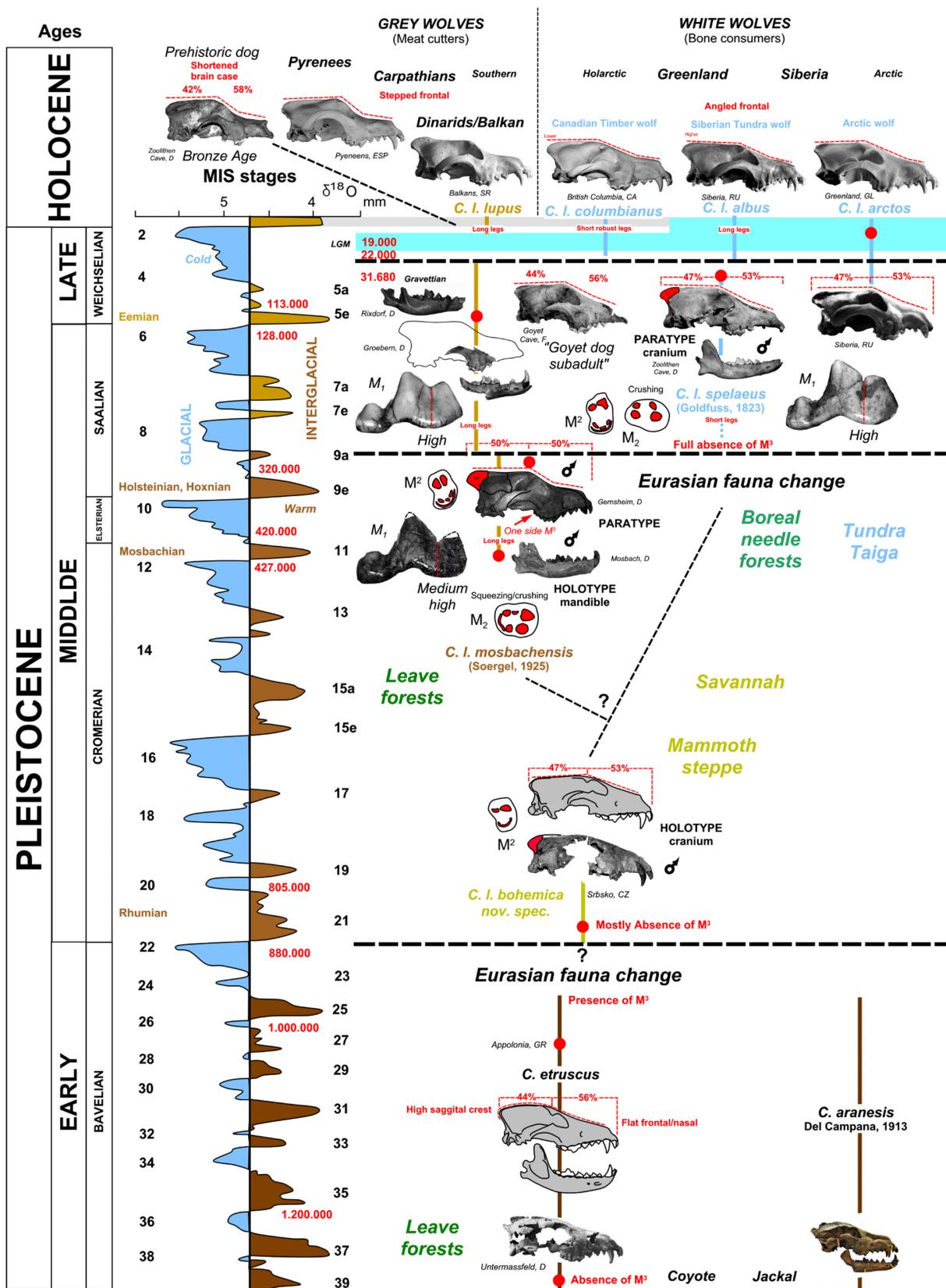


FIGURE 3 Phylostratigraphy and main cranial characters of extinct Ice Age and modern extant grey and white wolves of Europe. (material: Neolithic-Bronze Age dog cranium, Zoolithen Cave, modern Spanish grey wolf cranium; middle Middle Pleistocene cranium, Grossrohrheim, Early Middle Pleistocene cranium, Bat Cave, Srbsko, Czech Republic). [Colour figure can be viewed at wileyonlinelibrary.com]

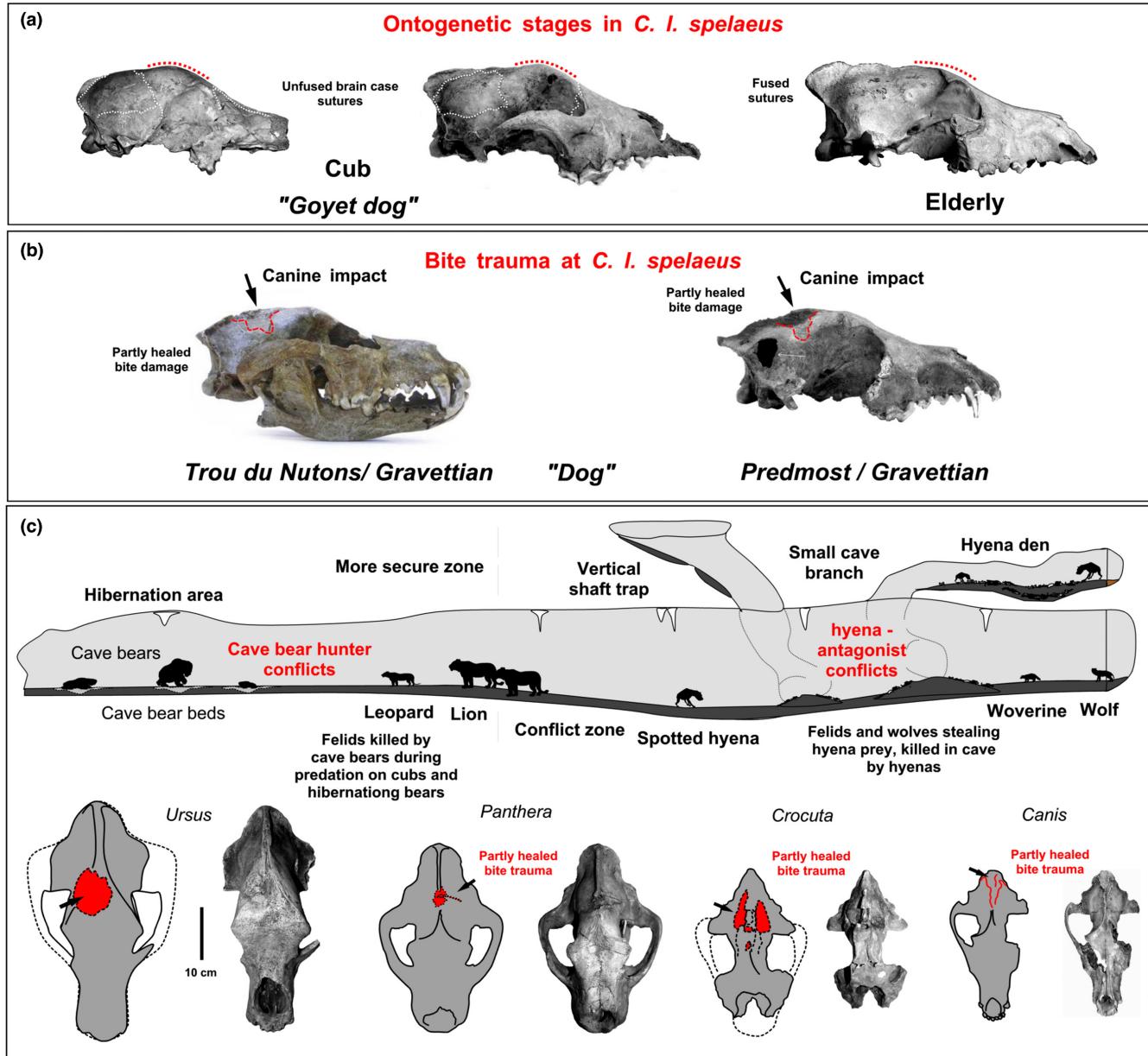


FIGURE 4 (a) Ontogenetic stages in the extinct tundra wolf *C. c. Spelaea* crania compared between a cub and elderly cranium of the German Zoolithen Cave. The “Goyet dog” in-between represents a subadult *C. c. Spelaea* individual. (b) Pathologic bite trauma deformed wolf crania which are misinterpreted as Palaeolithic dogs. (c) Such similar braincase deformation is found at all cave bear den using or dwelling predators such as cave bears, steppe lions, ice age spotted hyaenas or wolves. Such cranial bite traumas are typical for intraspecies fights. [Colour figure can be viewed at wileyonlinelibrary.com]

15–9) wolves were described as the “large Mosbach wolf *C. mosbachensis* Soergel, 1925” (Reichenau von, 1906; Soergel, 1925; Weitzel, 1936) based only on two mandibles from the German site Mosbach in the Rhine Graben Valley nearby Wiesbaden, which are partly refigured (Figure 2.3). Those date into the MIS 15 or the Mosbachian interglacial (MIS 11). It seems to reach into the few younger Holsteinian (or English Hoxnian, MIS 9) interglacial (Reynolds, 1902). Records of such Mosbach wolves were thought to be known for long only by few mandibles or teeth or postcranial elements from other

Middle Pleistocene cave sites of Europe (Adam, 1959; Bonifay, 1971; Garcia & Arsuaga, 1998; Musil, 1972). Others described from the Ural (Baryshnikov, 2015) or China (Wagner et al., 2018), are indeed coyote or jackal teeth according to the direct comparisons to, for example *C. etruscus* (cf. Figure 2).

A complete cranium from the open-air river terrace site Gernsheim in the German Upper Rhine River Valley is added to represent the *C. l. mosbachensis* paratype cranium (Figure 2) which is of either late Cromerian (MIS 11) or Holsteinian Interglacial (MIS 9) in age according

to its deep stratigraphic position within the gravel pit and typical Mid-Pleistocene bone preservation (heavy and pyrite mineralized) such as accompanied fauna (e.g. *M. trogontheri*, *C. cuvieri*, *B. murrensis*, *H. a. major*). It has only on one side an M³. Similar in the Zoolithen Cave, a maxillary with a morphologically identical M³ is present, which shows the mix of wolves in this cave of different cold and warm period times within the late Middle Pleistocene (MIS 11–9). The partly presence of the M³ is an important plesiomorph character, which wolves do not show any more at all after the MIS 8. Compared to new dated faunas of the English Kents Cavern, the Reynolds 1902 MIS 9 aged figured crania (Reynolds, 1902; Figure 2), represent obviously the same interglacial frontal-stepped subspecies of the Mosbach wolf (there M³ absent), that was spread all over Europe (Adam, 1959; Garcia & Arsuaga, 1998; Lyras, 2009; Reichenau von, 1906; Reynolds, 1902; Soergel, 1925; Weitzel, 1936). The Mosbach wolf material also contains few undescribed postcranial bones that indicate a short-legged subspecies. The grey wolf-sized *C. l. mosbachensis* (Soergel, 1925) was always seen in direct lineage to the European wolves (Koufos, 2018; Salari et al., 2017). This oldest true wolf is presented to have already a developed cranial shape very close to modern European grey wolves at the end of the Cromerian MIS 11. It cannot be placed as ancestral subspecies of all today known ecomorph types (White wolves). The Mosbach wolf is now important for indirect dating (biostratigraphy) and the European wolf evolution, climate adaptation, guild specialization and their palaeobiogeography shifts.

3.4 | Latest middle to late Pleistocene

The wolf records from the (MIS 8–2) are the most common in Europe, especially from caves (e.g. as the Zoolithen Cave). Fewer remains come from open air sites which are mostly in hyaena den bone assemblage context (Baryshnikov, 2015; Bonifay, 1971; Diedrich, 2011, 2012, 2013a,b, 2014; Goldfuss, 1823; Koufos, 2018; Musil, 1972; Salari et al., 2017; Stiner, 2004; Wagner et al., 2018; Figure 1). There is still much confusion about the subspecies identification of the described MIS 8–3 specimens of “*C. lupus*” (Kuzmina & Sablin, 1994; Leonard et al., 2007). Although many crania and some postcranial remains were recently compiled from Italian sites (Fabbri et al., 2014; Mecozzi & Lucenti, 2018; Salari et al., 2017; Stiner, 2004), the Eemian Interglacial Equi Cave site (Bonifay, 1971), and DNA studies distinguished a Late Pleistocene “specialized ecomorph” (Leonard et al., 2007). A clarification about Late Pleistocene subspecies within glacials and interglacials lack, also in the more confusing DNA based or cranial morphometric analysis debate about the

origin of dogs (Benecke, 1994; Botigué et al., 2017; Drake et al., 2015; Geiger et al., 2017; Germonpré et al., 2012; Mikkel-Holger et al., 2020; Pitulko & Kasparov, 2017; Thalmann et al., 2011). The Central European Late Pleistocene wolves of the maximum glaciation were published already 195 years ago as “*C. spelaeus* Goldfuss, 1823” (Cuvier, 1812; Esper, 1774; Goldfuss, 1810; Rosenmüller, 1794), based on a cranium of the Zoolithen Cave, which was completely forgotten in the European wolf evolution debate by both, DNA and morphometric studies. The Zoolithen Cave is indeed the richest site of Central Europe in fossil MIS 9–2 aged wolf remains that counts 1224 bones including several crania and several part-skeletons of larger males and smaller females. This and described “*C. l. maximus*” (Boudadi-Maligne, 2012) seem to represent a single extant species, or ancestral form of a Holarctic cold climate subspecies, such as *C. l. albus* or *C. l. arctos*. *C. l. brevis* Kuzmina & Sablin, 1994 from the Late Pleistocene of Siberia was separated from the modern *C. l. albus* Kerr, 1792 by its shorter leg bone proportions. Taking this character into account, it has affinities to the shorter-legged Late Pleistocene *C. c. spelaeus*, which was not compared in the studies of Kuzmina & Sablin, 1994. Their report is so far important, as it demonstrated probably in cases of synonymy of *C. l. spelaeus* Siberian extension (Gennady et al., 2009; Heptner & Naumov, 1998) or migration at the end of the Late Pleistocene following the retreat of the glacial mammoth steppe megafauna.

The northern Eurasian tundra or Turukhan wolf *C. l. albus* Kerr, 1792 (Mech, 1988; Mech & Packard, 1990) is native to Eurasia's tundra and forest-tundra zones from Finland to the Kamchatka Peninsula (Bibikow, 2003). This cold-adapted large subspecies, with adult males measuring 118–137 cm and females 112–136 cm in body length is larger than the European grey wolf *C. l. lupus*, but the unrecognized sexual dimorphism often misleads to the separation of “small and large species” of the same taxon.

3.5 | Wolf cub crania—ontogeny

The “Goyet dog” from the Belgian cave (cf. Germonpré et al., 2009) can be placed within the three main ontogenetic stages of the Late Pleistocene *C. l. spelaeus* (Figure 4a). From the Zoolithen Cave, a *C. l. spelaeus* cub cranium in partly milk dentition has the dog-like stepped frontal, which is less developed after full tooth change. The “Goyet dog” with its partly unfused sutures and full changed dentition is identified herein as a subadult wolf (Figure 4a). Its braincase is therefore similar to dogs still short and is therefore easily misidentified as the dog (cf. Germonpré et al., 2009). The adult cranium of the White wolf *C. l. spelaeus* from the Zoolithen Cave has finally the

flattened frontal (Figure 4a). Patterns of juvenile-to-adult morphological change are first nearly similar in wolves and domestic dogs. Dog skulls have already shorter brain cases and keep the unique stepped frontal features, whereas in wolves either the braincase elongate also with a large interparietal (in grey wolves) or the frontal flattens (in White wolves). Both later cranial characters are absent in adult early Neolithic and younger prehistoric dogs (cf. Iron Age dog cranium, Figure 3). The only argument for the Goyet wolf to be a “dog” fails to prove oldest dogs which 3D-morphometric analysis of fossil canid skulls also contradicts the suggested domestication of dogs during the late Palaeolithic (cf. Drake et al., 2015).

3.6 | Pathologic wolf crania—misidentification of early dogs

The Late Palaeolithic Gravettian wolf crania from Trou du Nutons or Predmost (cf. Germonpré et al., 2009, 2012) expose cranial trauma deformation in the healing stage (Figure 4c). Those individuals did not survive the attack of another predator onto its head. In such healing, the braincases can be strongly deformed, which is known for all other top predators that lived in the times of *C. l. spelaeus* to which those species belong to. Similar braincase deformation is described and figured for Ice Age spotted hyenas and lions, or even on their guilts, cave bears (Figure 4c, cf. Diedrich, 2013b, 2014, 2011). Those cranial damages and sagittal crest deformations result from interspecies fights, especially at cave sites (cf. Diedrich, 2013b, 2014). *C. l. spelaeus* was indeed not yet restudied osteometrically on the holotype and large amount of 1224 remains of the Zoolithen Cave, nor was material included in any DNA analysis about wolf and dog origin debates (cf. Diedrich, 2013b, 2014; Fabbri et al., 2014; Leonard et al., 2007; Thalmann et al., 2011). The Gravettian “Palaeolithic dog” was anyway described by DNA tests to fall into the range of wolf subspecies (cf. Fabbri et al., 2014; Leonard et al., 2007; Thalmann et al., 2011). It is highly doubted, that Aurignacians to Gravettians or any Late Palaeolithic kept any dogs. Descriptions from other sites do not report crania, which would be the only diagnostic (frontal shape and braincase length) to separate a possible Late Palaeolithic dog from the White wolf *C. l. spelaeus* palaeopopulation of Europe. In the Holocene, prehistoric dogs were bred, but in Europe, the cranial record can suggest now originating not from the Holarctic subspecies. Instead, those come from warm period or southern European/Asian grey wolves, which have similar strong stepped frontals. Most probably, not before the Neolithic Bandkeramik migration, the first dogs, 7223–7040 cal. BP (Botigué et al., 2017) came to Central Europe from the

Central Asian region (cf. Botigué et al., 2017), where their DNA even exclude the link to the northern hemisphere extant and extinct Pleistocene White wolves (cf. Botigué et al., 2017) and therefore to those of *C. l. spelaeus*. White wolves cannot yet be proven to have accompanied any Late Palaeolithic humans, which remains at many Palaeolithic sites (Kuzmina & Sablin, 1994) seem to represent simply killed wolves.

Ancient mtDNA analyses of Palaeolithic dogs suggest these were not related to present-day dogs and may instead represent a population that underwent an independent domestication trajectory and did not contribute to modern domestic dogs (Ramos-Madrigal et al., 2021). A previous study based on mtDNA data from Pleistocene canids spanning the Northern Hemisphere found that most of the oldest specimens from Northeast Siberia, including the >50-ka-old Tirekhtyakh and 48-ka-old Bunge-Toll-1885 canids, fall at the base of present-day wolf and dog diversity (Ramos-Madrigal et al., 2021). In contrast, younger specimens from the same region, including the 16.8-ka-old Siberian Ulakhan Sularand Tumat 2 were placed within the mtDNA diversity of modern wolves and dogs (Ramos-Madrigal et al., 2021). Though four specimens represent extinct wolf lineages, they do not form a monophyletic group. Instead, each Pleistocene Siberian canid branched off the lineage that gave rise to present-day wolves and dogs (Ramos-Madrigal et al., 2021).

4 | CONCLUSIONS

The ancestral forms of European wolves are not reaching back 2 million years ago in the Early Pleistocene Villafranchian *C. etruscus* (Forsyth-Major, 1877), which canid was more likely ancestral to the Eurasian-African coyote or jackal. The first real *C. lupus* is presented with new cranial and postcranial discoveries from the time of climate and European landscape change about 800,000 years ago (Middle Pleistocene, early Cromerian MIS 21). This *C. l. bohemica* nov. spec. record from the Czech Republic Bat Cave is a missing link to both, the modern European warm/interglacial grey and Holarctic/glacial Tundra-Arctic wolves. The wolve diversified into different climatic and environmental and guilt specialized wolf lineages goes back about 600,000 years ago (middle Cromerian, MIS 15–16). The warm period lineage continued in *C. l. mosbachensis* (Soergel, 1925), also known as the large Mosbach wolf, of which for the first time a complete cranium (paratype) from Germany can be presented. 420,000 years ago, in the interglacial late Cromerian Hoxnian-Mosbachian to Holsteinian Interglacials, MIS 11 and 9, this subspecies once roamed Europe up to southern England to which now several historically described

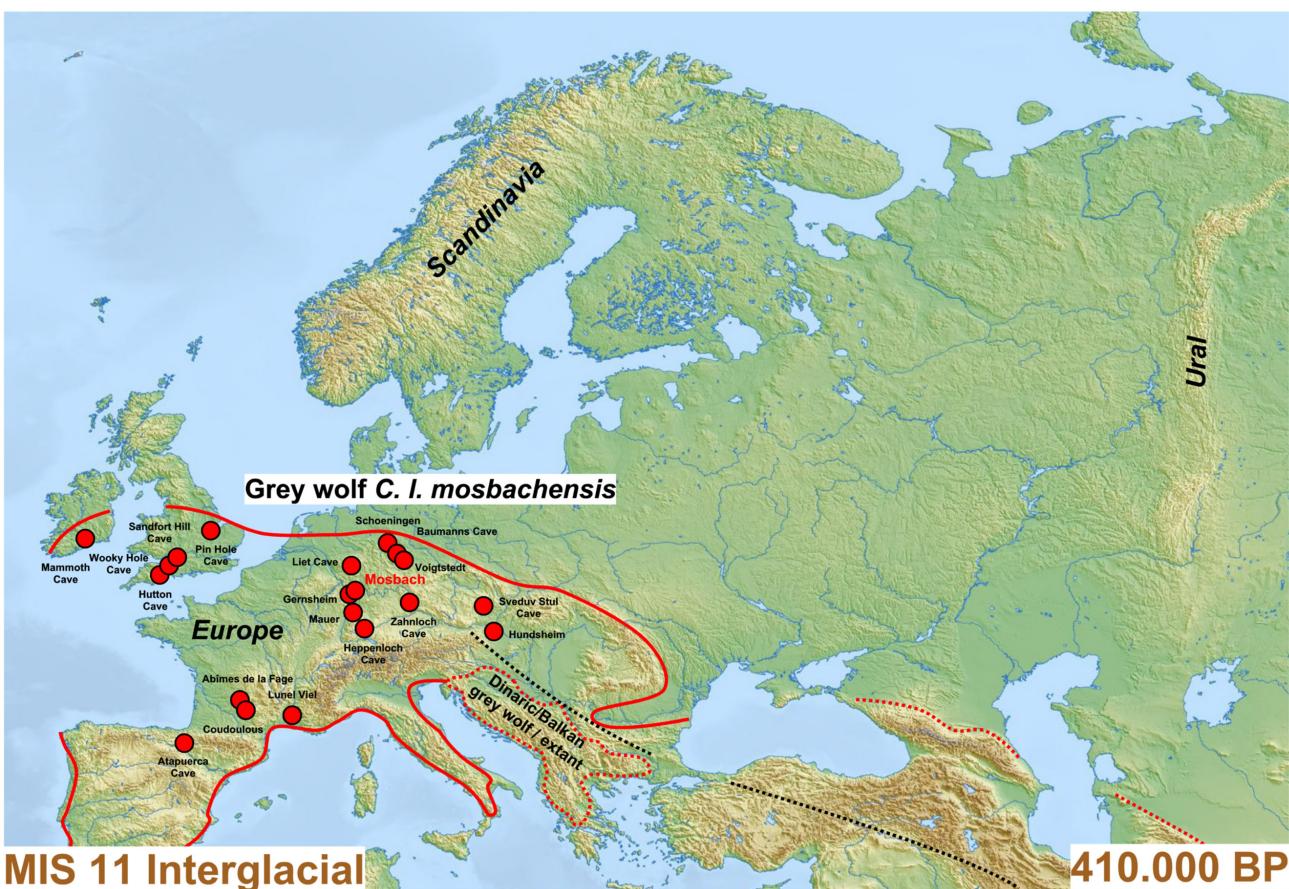


FIGURE 5 Palaeobiogeography examples of European extant grey and extinct Holarctic white wolf relationship for the MIS 11 (Mosbachian), 9 interglacial (Holsteinian), and MIS 2 (last glacial maximum or LGM). *C. l. arctos* photograph from: <https://howlingforjustice.files.wordpress.com/2012/03/arctic-wolf-desktop-nexus.jpg>, *C. l. albus* photograph from <https://www.flickr.com/photos/wildspiritwolves/3249459172/> [Colour figure can be viewed at wileyonlinelibrary.com]

crania from England can be attributed. It was spread probably over the Ural Mountains up to China, Eurasia. A posterior extended and high sagittal crest such as strong crushing breaking-scissor dentition including a third molar M³ was developed, which made those canids highly competitive to three different sympatric hyaena species. This was a shorter-legged wolf subspecies adapted as a specialized carcass feeder of the older *M. trogontheri* mammoth steppe megafauna. Its cranial shape is nearly identical to the extant *C. l. lupus* Dinarid-Balkan wolf haplotype (Milenković et al., 2010), which might represent a relict population of the formerly European roaming Middle Pleistocene subspecies that evolved further with reduction in the M³. Somewhat in the Saalian (MIS 8-6), or even before in a glacial period, a first Holarctic wolf subspecies evolved or appeared in Europe with *C. l. spelaeus* (Goldfuss, 1823), in which large amounts of remains come from the holotype wolf den site of the Zoolithen Cave. Many European cave sites, which overlap with cave bear and Ice Age spotted hyaena dens, contain those wolf subspecies remains. This forgotten historic excavated material gives a new view into the evolution and complex changing palaeobiogeography to the ancestors of extant Holarctic wolf species. Compared osteometric with the Holarctic Greenland *C. l. arctos* and Siberian *C. l. albus* (Kerr, 1792), indeed the valid Pleistocene subspecies *C. l. spelaeus* was shorter-legged, exactly in between a grey wolf and a tundra wolf, whereas its overlap in leg sizes correlates best with arctic wolves. It might be seen to be its ancestral form, which disappeared with the mammoth steppe and cave bear fauna at the end of the Late Pleistocene, somehow between 24,000 and 12,000 BP. All three extinct and extant Holarctic White wolves have very different cranial shapes with typically flattened frontals, which are in morphology distinct to the strong stepped frontals of grey wolves, which character is found also today in dogs, which originate in European Holocene times from southern grey wolves. The *C. l. spelaeus* habitat comprised in the MIS 8-3 glacial two different palaeoenvironments, the mammoth steppe and boreal needle forests. In the middle-high elevated mountain regions all over Europe, those wolves were spread as a result of the extended Scandinavian and alpine such as other smaller mountain glaciers down to the Mediterranean and specialized in feeding on cave bear carcasses in caves. Those wolves damaged by more bone cave bear consuming more often their teeth as any other wolf subspecies, which is

known best from the Zoolithen Cave *C. l. spelaeus* cranial record. The confusing inclusion into osteometric landmark statistics that did not take the important cranial frontal shape character into high account including carnivore bite damage trauma deformed pathologic and even subadults with different cranial shape separated the earliest dogs—“Palaeolithic Gravettian Goyet dogs,” which even fall into the DNA pool of *C. l. spelaeus*. It doubted based on the new important crania, detail analyses of *C. l. spelaeus* and review of DNA or landmark statistics that all die not to include the holotype or largest European Holarctic extinct wolf palaeopopulation of *C. l. spelaeus* that Late Palaeolithic modern human Aurignacians to Gravettians and even younger Palaeolithic kept any dogs. If so, in northern Europe its ancestral form must have been the Holarctic wolf *C. l. spelaeus* (Figure 5) to which the Goyet dog cranium belongs, also according to its DNA tests. As also suggested by several newer DNA studies, breeding in the Holocene dogs instead originates from the warm period or southern European grey wolves with their stepped frontal. Those have been imported into Central Europe by Early Neolithic, Bandkeramik settlers, about 7000 BP. The breeding later happened in different regions, which cranial main character of the stepped sagittal crest plus typical braincase shortening as the main character for the dogs.

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REFERENCES

- Adam, K. D. (1959). Mittelpaläozäne Caniden aus dem Heppenloch bei Gutenberg (Württemberg). *Stuttgarter Beiträge zur Naturkunde*, 27, 1–46.

- Bartolini Lucenti, S., Alba, D. M., Rook, L., Moyà-Solà, S., & Madurell-Malapeira, J. (2017). Latest early Pleistocene wolf-like canids from the Iberian Peninsula. *Quaternary Science Reviews*, 162, 12–25.
- Baryshnikov, G. F. (2015). Late Pleistocene Canidae remains from geographical society cave in the Russian Far East. *Russian Journal of Theriology*, 14(1), 65–83.
- Benecke, N. (1994). Der Mensch und seine Haustiere: Die Geschichte einer jahrtausendealten Beziehung. Theiss, Stuttgart, 470 pp.
- Bibikow, D. I. (2003). Der Wolf – *Canis lupus*. Neue Brehm-Bücherei, Wittenberg; p. 198.
- Bonifay, M. F. (1971). Carnivores quaternaires du sud-est de la France. *Mémoires du Muséum National d'Histoire Naturelle Paris C*, 21(2), 43–377.
- Botigué, L. R., Shiya Song, S., Scheu, A., Gopalan, S., Pendleton, A. L., Oetjens, M., Taravella, A. M., Seregely, T., Zeeb-Lanz, A., Arbogast, R.-M., Bobo, D., Daly, K., Unterländer, M., Burger, J., Kidd, J. M., & Veeramah, K. R. (2017). Ancient European dog genomes reveal continuity since the early Neolithic. *Nature Communications*, 8, 16082.
- Boudadi-Maligne, M. (2012). Une nouvelle sous-espèce de loup (*Canis lupus maximus* nov. subsp.) dans le Pléistocène supérieur d'Europe occidentale. *Comptes Rendus Palevol*, 11(7), 475–484.
- Cherin, M., Bertè, D. F., Rook, L., & Sardella, R. (2014). Re-defining *Canis etruscus* (Canidae, Mammalia): A new look into the evolutionary history of early Pleistocene dogs resulting from the outstanding fossil record from Pantalla (Italy). *Journal of Mammalian Evolution*, 21(1), 95–110.
- Cuvier, G. (1812). Recherches sur les ossements fossiles du quadrupedes IV. Mémoire sur les espèces des animaux carnassiers dont on trouve les os mêlés à ceux d'ours dans les cavernes d'Allemagne et de Hongrie. *Annales du Muséum d'histoire Naturelle*, 4(3), 1–12.
- Diedrich, C. (2011). The *Crocuta crocuta spelaea* (Goldfuss, 1823) population and its prey from the late Pleistocene Teufelskammer cave hyena den besides the famous Palaeolithic Neanderthal cave (NRW, NW Germany). *Historical Biology*, 23(2/3), 237–270.
- Diedrich, C. (2012). Late Pleistocene *Crocuta crocuta spelaea* (Goldfuss, 1823) clans as prezwalski horse hunters and woolly rhinoceros scavengers at the open-air commuting den and contemporary Neanderthal campsite Westeregeln (Central Germany). *Journal of Archaeological Science*, 39(6), 1749–1767.
- Diedrich, C. (2013a). Impact of the German Harz Mountain Weichselian ice-shield and valley glacier development onto Paleolithic and megafauna disappearance. *Quaternary Science Reviews*, 82, 67–198.
- Diedrich, C. (2013b). Late Ice Age wolves as cave bear scavengers in the Sophie's Cave of Germany – Extinctions of cave bears as a result of climate/habitat change and large carnivore predation stress in Europe. *ISRN Zoology*, 2013, 1–25.
- Diedrich, C. (2014). Holotype skulls, stratigraphy, bone taphonomy and excavation history in the Zoolithen cave and new theory about Esper's "great deluge". *Eiszeitalter und Gegenwart E&G Quaternary Science Journal*, 63(1), 78–98.
- Drake, A. G., Coquerelle, M., & Colombeau, G. (2015). 3D morphometric analysis of fossil canid skulls contradicts the suggested domestication of dogs during the late Paleolithic. *Scientific Reports*, 5, 8299.
- Esper, J. F. (1774). Ausführliche Nachricht von neuentdeckten Zoolithen unbekannter vierfüssiger Thiere und denen sie enthaltenden, so wie verschiedenen anderen, denkwürdigen Gräften der Oberbürgischen Lande des Margrathums Bayreuth. Nürnberg; p. 148.
- Fabbri, E., Caniglia, R., Kusak, J., Galov, A., Gomercic, T., Arbanasic, H., Huber, D., & Randi, E. (2014). Genetic structure of expanding wolf (*Canis lupus*) populations in Italy and Croatia, and the early steps of the recolonization of the eastern Alps. *Mammalian Biology*, 79(2), 138–148.
- Fan, Z., Silva, P., Gronau, I., Wang, S., Armero, A. S., Schweizer, R. M., Ramirez, O., Pollinger, J., Galaverni, M., Ortega Del-Vecchyo, D., Du, L., Zhang, W., Zhang, Z., Xing, J., Vilà, C., Marques-Bonet, T., Godinho, R., Yue, B., & Wayne, R. K. (2016). Worldwide patterns of genomic variation and admixture in gray wolves. *Genome Research*, 26(2), 163–173.
- Forsyth-Major, C. I. (1877). Considerazioni sulla fauna dei Mammiferi pliocenici e postpiocenici della Toscana. III. Cani fossili del Val d'Arno superiore e della Valle dell'Era. *Memorie della Società Toscana di Scienze Naturali*, 3, 207–227.
- Garcia, N., & Arsuaga, J.-L. (1998). The carnivore remains from the hominid-bearing Trinchera-Galeria, sierra de Atapuerca, middle Pleistocene site (Spain). *Geobios*, 31, 659–674.
- Geiger, M. A. E., Sánchez-Villagra, M. R., Gascho, D., Mainini, C., & Zollkofer, C. P. E. (2017). Neomorphosis and heterochrony of skull shape in dog domestication. *Scientific Reports*, 7, 13443.
- Gennady, B. F., Mol, D., & Tikhonov, A. N. (2009). Finding of the late Pleistocene carnivores in Taimyr peninsula (Russia, Siberia) with paleoecological context. *Russian Journal of Theriology*, 8(2), 107–113.
- Germonpré, M., Lázníčková-Galetová, M., & Sablin, M. V. (2012). Palaeolithic dog skulls at the Gravettian Předmostí site, The Czech Republic. *Journal of Archaeological Science*, 39(1), 184–202.
- Germonpré, M., Sablin, M. V., Mikhail, M., Rhiannon, V., Robert, E. S., Stevens, E., Hedges, E. M., Hofreiter, M., Stiller, M., & Desprése, V. R. (2009). Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: Osteometry, ancient DNA and stable isotopes. *Journal of Archaeological Science*, 36(2), 473–490.
- Goldfuss, G. A. (1810). Die Umgebungen von Muggendorf. Ein Taschenbuch für Freunde der Natur und Altertumskunde. Erlangen, p. 351.
- Goldfuss, G. A. (1823). Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt. V. Ueber den Hoehlenwolf (*Canis spelaeus*). *Nova Acta Physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosum*, 3(2), 451–455.
- Heptner, V. G., & Naumov, N. P. (1998). *Mammals of the Soviet Union Vol. II part 1a – Sirenia and carnivora (sea cows; wolves and bears)* (pp. 182–184). Science Publishers Inc.
- Kerr, R. (1792). *The animal kingdom, or zoological system, of the celebrated Sir Charles Linnaeus: containing a complete systematic description, arrangement, and nomenclature, of all the known species and varieties of the Mammalia, or animals which give suck to their young*. A. Strahan, and T. Cadell, and W. Creech. p. 137.
- Koufos, G. D. (2018). New material and revision of the carnivora, Mammalia from the lower Pleistocene locality Apollonia 1, Greece. *Quaternary*, 1(6), 2–38.

- Kuzmina, I. E., & Sablin, M. V. (1994). Wolf *Canis lupus* L. from the late Paleolithic sites Kostenki on the Don River. *Trudy Zoologicheskogo Instituta*, 256, 44–58.
- Leonard, J. A., Vilà, C., Dobbs, K. F., Koch, P. L., Wayne, R. K., & Van Valkenburgh, B. (2007). Megafaunal extinctions and the disappearance of a specialized wolf Ecomorph. *Current Biology*, 17(13), 1146–1150.
- Lytras, G. A. (2009). The evolution of the brain in Canidae (Mammalia: Carnivora). *Scripta Geologica*, 139, 1–93.
- Mech, L. D. (1981). *The wolf: The ecology and behavior of an endangered species*. University of Minnesota Press. p. 353.
- Mech, L. D. (1988). *The Arctic wolf: Living with the pack*. Voyageur Press, Inc. 128 pp.
- Mech, L. D., & Boitani, L. (2007). *Wolves behavior, ecology, and conservation*. University of Chicago Press. p. 472.
- Mech, L. D., & Packard, J. M. (1990). Possible use of (*Canis lupus*) den over several centuries. *Canadian Field-Naturalist*, 104, 484–485.
- Mecozzi, B., & Lucenti, S. B. (2018). The late Pleistocene *Canis lupus* (Canidae, Mammalia) from Avetrana (Apulia, Italy): Reappraisal and new insights on the European glacial wolves Italian. *Journal of Geosciences*, 137(1), 138–150.
- Mikkel-Holger, S., et al. (2020). Arctic-adapted dogs emerged at the Pleistocene-Holocene transition. *Science*, 368(6498), 1495–1499.
- Milenković, M., Jojic, V., Blagojević, J. V., & Vujošević, M. (2010). Skull variation in Dinaric-Balkan and Carpathian gray wolf populations revealed by geometric morphometric approaches. *Journal of Mammalogy*, 91(2), 376–386.
- Musil, R. (1972). Die Caniden der Stránská skála. *Anthropos*, 20, 107–112.
- Nowak, R. M. (1995). Another look at wolf taxonomy. In Carbyn, L. N., Fritts, S. H., & Seip, D. R. (Eds.), *Ecology and conservation of wolves in a changing world: proceedings of the second North American symposium on wolves*, Edmonton, Canada (pp. 375–397).
- Pitulko, V. V., & Kasparov, A. K. (2017). Archaeological dogs from the early Holocene Zhokhov site in the eastern Siberian Arctic. *Journal of Archaeological Science: Reports*, 13, 491–515.
- Ramos-Madrigal, J., Sinding, M.-H. S., Carøe, C., Mak, S. S. T., Niemann, J., Castruita, J. A. S., Fedorov, S., Kandyba, A., Germonpré, M., Bocherens, H., Feuerborn, T. R., Pitulko, V. V., Pavlova, E. Y., Nikolskiy, P. A., Kasparov, A. K., Ivanova, V. V., Larson, G., & Frantz, L. A. F. (2021). Genomes of Pleistocene Siberian wolves uncover multiple extinct wolf lineages. *Current Biology*, 31(1), 198–206.
- Reichenau von, W. (1906). Beiträge zur näheren Kenntnis der Carnivoren aus den Sanden von Mauer und Mosbach. *Abhandlungen der Hessischen Geologischen Landesanstalt zu Darmstadt*, 4(2), 189–313.
- Reynolds, S. H. (1902). Monograph of the British Pleistocene Mammalia II (III), the Canidae. *Monograph of the Palaeontographical Society London*, 1902, 1–28.
- Rosenmüller J. C. (1794). Quedam de ossibus fossilibus animalis cuiusdam, historiam eius et cognitionem accuratiorem illustrantia, dissertatio, quam d. 22. Octob. 1794 ad disputandum proposuit Ioannes Christ. Rosenmüller Heßberga-Francus, LL.AA.M. Theatro anatom Lip Pros assumto socio Io Chr Aug Heinroth Lips Med Stud Cum tabula aenea Leipzig (pp. 1–34).
- Salari, L., Achino, K. F., Gatta, M., Petronio, C., Rolfo, M. F., Silvestri, L., & Pandolfi, L. (2017). The wolf from Grotta Mora Cavorso (Simbruini mountains, Latium) within the evolution of *Canis lupus* L., 1758 in the quaternary of Italy. *Palaeogeography Palaeoclimatology Palaeoecology*, 476, 90–105.
- Schütt, G. (1974). Die Carnivoren von Würzburg-Schalksberg: mit einem Beitrag zur biostratigraphischen und zoogeographischen Stellung der altpleistozänen Wirbeltierfaunen von Mittelmain (Unterfranken). *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 147, 61–90.
- Soergel, W. (1925). Die Säugetierfauna des altdiluvialen Tonlagers von Jockgrim in der Pfalz. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 77, 405–438.
- Sotnikova, M. (2001). Remains of Canidae from the lower Pleistocene site of Untermaßfeld. In R. D. Kahlke (Ed.), *Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 2* (pp. 607–632). Habelt Verlag.
- Stiner, M. C. (2004). Comparative ecology and taphonomy of spotted hyenas, humans, and wolves in Pleistocene Italy. *Revue de Paléobiologie*, 23(2), 771–785.
- Thalmann, O., Greenfield, D., Meyer, M., Sawyer, S., Cui, P., Germonpré, M., Sablin, M. V., Lopez-Giraldez, F., LePont, D., Worthington, B., Blick, J. P., Leonard, J. A., Green, R. E., & Wayne, R. K. (2011). Inferences on dog domestication – Genetic analysis of the most ancient dogs utilizing DNA capture arrays. <https://retrieverman.net/tag/ancient-dogs/>
- Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V. J., Sawyer, S. K., Greenfield, D. L., Germonpré, M. B., Sablin, M. V., López-Giráldez, F., Domingo-Roura, X., Napierala, H., Uerpmann, H. P., Loponte, D. M., Acosta, A. A., Giemsch, L., Schmitz, R. W., Worthington, B., Buikstra, J. E., Druzhkova, A., ... Wayne, R. K. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science*, 342, 871–874.
- Wagner, J., Wong, W., & Chen, J. (2018). Taxonomical revision of fossil *Canis* in middle Pleistocene sites of Zhoukoudian, Beijing, China and a review of fossil records of *Canis mosbachensis variabilis* in China. *Quaternary International*, 482(24), 93–108.
- Weitzel, K. (1936). Überreste von Mosbacher Wölfen. *Notizbl Ver Erdkunde Hess Geol Landesanst*, 5(17), 79–82.
- Wozencraft, W. C. (2005). *Order Carnivora. Mammal species of the world: A taxonomic and geographic reference* (3rd ed., pp. 532–628). Johns Hopkins University Press.

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