

Distinguishing between the Archaeological Remains (Teeth and Bones) of Dogs and Wolves

ABSTRACT

Scientists have long theorized about the origin of dogs. Once it was clear that they originated from wolves, the challenge was to discern between wolf and dog bones in archaeological settings. In recent years, interest in wolf domestication soared because it is by far the earliest domesticated animal and the only one domesticated already in the Pleistocene. Based on this interest, genetics were used to resolve the wolf domestication puzzle. At the same time, a renewed interest in morphological research blossomed and most historically reported differences were re-examined. This led to the rejection of many of them as discerning landmarks. Some survived, however, of which the most important ones are size reduction, relative brain size reduction, difference in maxillary premolar 4 mesio-distal diameter, orbital angle, and snout width and height.

KEYWORDS

Domestication / wolf / dog / morphometrics / morphology

Wolves, Dogs and Human Beings

Most of us will know Charles Perrault's (and Jacob and Wilhelm Grimm's later version of it) 17th-century fairy tale »Little Red Riding Hood«, an Anglo-Saxon title adaptation of the original »Little Red-Cap«, which is a more accurate translation of the oldest »Le Petit Chaperon Rouge« version¹. Apart from being a sensually loaded story, it covers many opposites: youth versus old age, caring versus being cared for, danger (wolf) versus safety (hunter), and nature versus culture. It also exemplifies a worldwide-accepted opinion: wolves (*Canis lupus lupus*) must be distrusted and feared.

Although wolves may genetically be very closely related to dogs, both groups have a very different interaction pattern with humans. In general, there seems to be a ubiquitous fear of wolves and a close and friendly interaction with their domesticated descendants: dogs. Since dogs were domesticated from wolves at some time during the late Pleistocene, and since osteological canid remains are excavated frequently in archaeological contexts from that period, it is important to distinguish between both groups, first to document the process, location and timing of the domestication of wolves, but also to understand

¹ <https://beq.ebooksgratuits.com/vents/Perrault-contes.pdf> (accessed 6.8.2025).

human interactions with wolves and dogs before the existence of writing. The excavated remains of wolves might indicate that they were trapped, hunted, caught, and slaughtered for fur, sinew, tooth ornaments and more, while the excavated dog re-

mains might indicate that they were domestic and were used as barking guardians or for defence, for hunting, for help with finding one's way back in the dark, and for much more, not least for emotional reasons.

The Search for the Origin of Dogs

Scientists have examined the origin of dogs for over a century (Rüttimeyer 1861; Galton 1865; Gaudry/Boule 1892; Wolfgram 1894; Studer 1901), questioning where, when, and from which ancestor dogs originated. Not so long ago, it was suggested that two immediate ancestors existed: the grey wolf, being the ancestor of large dogs, and the jackal (*Canis aureus*) as the ancestor of small dogs (Darwin 1868; Lorenz 1954).

Is the Wolf the Sole Ancestor of the Dog?

More recent authors (as well as Nobel Prize winner Lorenz himself in later publications), mainly following recent genetic evidence, rejected the jackal and pointed, without doubt, to the wolf as the sole ancestor of the dog (Lindblad-Toh et al. 2005; Anderson et al. 2009; VonHoldt et al. 2010; 2018; Klütsch/Savolainen 2011; Larson et al. 2012; Larson/Burger 2013; Thalmann et al. 2013; Freedman et al. 2014).

From Which Wolf Clade, and thus Where, Did the Dog Originate?

Hypotheses about the number of times that wolves were domesticated include that it was a single event (as for almost all other domesticated species; see Savolainen et al. 2002; Freedman et al. 2014), and that there were dual (Frantz et al. 2016) or even multiple origins (Vilà et al. 1997; Skoglund et al. 2011).

It was first suggested, based on mitochondrial DNA (mtDNA), that the Eurasian (not American) wolf must have been the dog's ancestor (Thalmann et al. 2013), a suggestion that has been confirmed several times by additional, more recent, nuclear DNA (nDNA) studies.

As for the more specific origin region and related wolf clade, studies pointed respectively to Asia (Botigué et al. 2017), the Far East (Pang et al. 2009), Central Asia (Shannon et al. 2015), the Middle East (Gray et al. 2010) and Southeast Asia, the latter based on the high allelic variability in the local dogs there (Wang et al. 2013). A more recent large-scale study proposed a possible dual ancestry of dogs (two different wolf clades and regions contributing; Bergström et al. 2020; 2022), while another recent study proved the Japanese wolf (*Canis lupus hodophilax*) to be the most closely related to dogs (of all the wolf clades ever examined; Gojobori et al. 2021). Interestingly, and considering that dogs originated around the Last Glacial Maximum (LGM; see also below), Eastern Asia then had sea levels 125 m lower than today, with Japan being connected to mainland China by a massive land bridge.

If the Southeast Asian origin is correct (and there are several strong genetic arguments in that direction), dogs must have spread from there to the west, accompanying humans. On that route, and in the Middle East, a genetic input from local wolves (probably *Canis lupus pallipes*) must have taken place, explaining – at least partially – the small stature of archaeological dogs. Size reduction in dogs occurred in part by the introduction of the IGF1 allele, present in *Canis lupus pallipes* (Gray et al. 2010; Klütsch/de Caprona 2010). However, even without the Middle Eastern genetic input, we know that the oldest dogs were considerably smaller than wolves but clearly larger than *Cuon alpinus* (dhole) or the jackal, two contemporary and isopatric species in Europe and Asia. Neolithic dogs from the Alpine and Scandinavian regions areas are, for example, comparable in size to modern toy-poodles. Large dogs are only found in excavations from the Bronze Age on.

When Did Dogs Originate?

The next question to resolve is how long have dogs existed? Because, simply said, if they originated e.g. 400,000 years ago, archaeologists must carefully

consider carnivore bones, discovered in excavated *Homo heidelbergensis* or *neanderthalensis* deposits, to possibly be those of dogs. Luckily, life is simpler

and, although the modern wolf originated about 400,000 years ago (Sotnikova/Rook 2010), dogs have only been present for a few tens of thousands of years, first appearing in late Palaeolithic *Homo sapiens* contexts. The dating of the first emergence of the dog can be investigated by the dating of excavated dog bones and by genetics.

Archaeological Dating

Only a few Palaeolithic and very early Holocene dogs are reported in the literature around the world (c. 30 specimens; **tab. 1**). Often the excavated bone remains are fragmented, partial, and incomplete, making determination less straightforward.

The »oldest« dog has long been the German Bonn-Oberkassel specimen (**fig. 1**), which was discovered more than 100 years ago and has recently been redated to 14,300 cal BP (Janssens et al. 2018). The dog remains were accidentally discovered by quarrymen and found along with those of a man and woman, all carefully buried together with grave goods under a thick stone slab. Of a similar age are several dog remains – also from burials – from the

excavations at the Natufian settlements of Hayonim and Lake Gallilei-Eynan in Israel (Clutton-Brock 1962; 1963; Dayan 1994a; 1994b). Recently, even older specimens have been reported: some in Italian caves and in French excavations, of which the pinnacle specimen is the Spanish Erralla dog, dating to 17,300 cal BP (Hervella et al. 2022).

The information we have on early dog remains is heavily influenced by culture. Western Europe has a long tradition of extensive archaeological research, not only in its home countries but also in colonies, protectorates and countries that were under strong political and economic Western influence (such as the Middle East by Great Britain). Based thereon, the oldest dogs have all been excavated in these regions. There is a phenomenal vacuum regarding excavations that report on Pleistocene wolf and dog remains in countries such as China, Korea and Japan: countries that might well be the cradle of dogs.

Considering that there must have been a time lapse between the dog's origin in Southeast Asia and the presence of the Erralla dog in Spain, we may assume that the origin of the dog dates to at least 18,000 years ago.



Fig. 1 The remains of the Bonn-Oberkassel dog (14,300 cal BP), long considered to be the earliest dog in the world. – (Photo J. Vogel, LVR-LandesMuseum Bonn).

Specimens	Dating of dog remains (Lab. code and uncalibrated result BP [if not stated otherwise])	cal BP (kya)	mtDNA clade	Country	MNI	References
Pleistocene						
Eralla	Ua-56946: 14,221 ± 48	17.3	C	Spain	1	Altuna et al. 1984; Hervella et al. 2022
Monruz		16.0		Switzerland	2	Leesch/Müller 2012
Hauterive-Champréveyres		15.5		Switzerland	1	Morel et al. 1997
Montespan		14.5		France	1	Pionnier-Capitan et al. 2011
Le Morin	OxA-23627: 12,540 ± 55; OxA-23628: 12,450 ± 55	14.5		France	2	Boudadi-Maligne et al. 2012
Montespan	GifA-99102: 10,730 ± 100 (12,952-12,451)	14.5		France	1	Pionnier-Capitan et al. 2011
Mège		14.5		France	?	Boudadi-Maligne et al. 2018
Le Morin		14.5		France	1	Boudadi-Maligne et al. 2012
Hayonim and Lake Gallilei-Eynan		14.5		Israel	2	Tchernov/Valla 1997; Grosman et al. 2013
Le Closeau-Rueil Malmaison		14.4		France	1	Pionnier-Capitan et al. 2011
Bonn-Oberkassel	KIA-41161/41162/41163: 12,279; OxA: 14793 ± 100*	14.2	C	Germany	2	Street 2002; Street/Jöris 2015; Janssens et al. 2018
Kesslerloch	KIA-33350: 12,225 ± 45	14.1	C	Switzerland	1	Napierala/Uerpmann 2012
Anton Koba		14.0		Spain	1	Hervella et al. 2022
Grotta Paglicci	OxA-26316: 12175 ± 55	13.8	B	Italy	1	Boschin et al. 2020
Duruthy		13.5		France	1	Boudadi-Maligne et al. 2018
Pont d'Ambon	GifA-99102: 10,730 ± 100; 12,952-12,541 cal BP	12.7	C	France	3	Pionnier-Capitan et al. 2011; Boudadi-Maligne et al. 2018
Pelegawra		12.5		Iraq	1	Turnbull/Reed 1974
Troubat	OxA-36550: 10,600 ± 45	12.4		France	?	Boudadi-Maligne et al. 2018

Specimens	Dating of dog remains (Lab. code and uncalibrated result BP [if not stated otherwise])	cal BP (kya)	mtDNA clade	Country	MNI	References
Pleistocene-Holocene (start 11.6 kya) transition						
Saint-Thibaud-de-Couz	LY23/OxA-4404; 10.050 ± 100; 12,027-11,311 cal BP*	11.6		France	1	Chaix 2000
Bedburg		11.6		Germany	1	Street 1991
Shubayqa 6	RTD-9338/Poz-76085/RTD-9341/RTD-9342/ RTD-9343; 10,521-11,933 cal BP	11.5		Jordan	1	Yeomans et al. 2019
Tell Mureybet	LY11.624/11.788/11.787; 9,945-9,905 ± 155 BP*	11.5		Syria	1	Gourichon/Helmer 2008
Ain Mallaha		11.5		Israel	2	Tchernov/Valla 1997; Grosman et al. 2013
Kartstein		11.4	C	Germany	1	Baales 1992
Shillourkambos		11.4		Cyprus	1	Vigne et al. 2011
Grotta Romanelli		11.2	C	Italy	1	Boschin et al. 2020; Calcagnile et al. 2019
Senckenberg-Moor		11.0		Germany	1	Mertens 1936; Degerbøl 1961a

Tab. 1 The oldest known dog specimens worldwide. Dating is non-calibrated as in the original publications (if not stated otherwise). - * indicates different fragments examined or repeat examinations by different laboratories. - MNI: minimum number of individuals; cal BP: dating result, calibrated Before Present (1950); mtDNA: mitochondrial DNA. - (Table M. Boudadi-Maligne / L. Janssens).

Genetic Dating

Genetic dating has travelled a bumpy road, with early studies placing the dog's origin in awkwardly unrealistic time periods, such as six thousand years ago (Savolainen et al. 2002), which is far more recent than archaeological finds and thus impossible, or 135,000 years ago, which would mean that Neanderthals or Denisovans could have domesticated wolves.

Recent genetic studies are, however, quite consistent and more realistic and report a time frame between 35,000 and 25,000 years ago for the ancestor of today's dogs (Thalmann et al. 2013; Skoglund et al. 2015; Botigué et al. 2017).

Genetic dating is based on DNA differences between the dog and the wolf (the greater the difference, the longer ago they must have split), and it is based on two presumptions:

- 1) the mutation rate of canine DNA; in other words, the frequency at which mutations occur per nucleotide base pair. The mutation rate of *Canis lupus* is estimated to be $\sim 1 \times 10^{-8}$ per nucleotide, per generation, and

How to Define a Wolf and a Dog?

There are three main differences between dogs and wolves, of which the latter two are of value to archaeologists:

- 1) non-osteological differences, such as e. g. starch digestion, ear- and tail-carriage, coat colour, eye colour, behaviour, etc. (Cadieu et al. 2009; Axelson et al. 2013),
- 2) genetic differences, and
- 3) osteological (bones and teeth) differences.

Genetic Differences

Genetic studies are possible if DNA can be extracted that is of reliable quality and enough quantity. The results of mtDNA studies (Thalmann et al. 2013; Thalmann/Perri 2018) have established that there are four major dog mtDNA clades: A, B, C and D (Thalmann et al. 2013). In modern dogs, clade A makes up the largest group (two-thirds of all current dogs), but almost all the oldest archaeological known late Palaeolithic dogs carry the C clade (Hervella et al. 2022). Currently, Y-chromosome and partial and whole genome sequencing studies are becoming increasingly important (Frantz et al. 2016; Bergström et al. 2020; 2022), and progressively more

- 2) the generation time – this defines how long it takes to pass on a surviving mutation to the next generation. Generation time is defined by the first breeding age of an animal, then all the next breeding ages are added, and finally the sum is divided by the number of breeding events. If thus a dog breeds for the first time when one year old (Spotte 2012), then once every year, up to a mean of six years old, the generation time is 3.5 years $(1 + 2 + 3 + 4 + 5 + 6 = 21 / 6)$. The generation time given for dogs was three years in almost all publications (Mech et al. 2017). For wolves, this three-year generation time was also generally used but has been contested (Mech et al. 2017), as wolves on average breed for the first time when four and a half years old. If they then breed yearly for three consecutive years, their generation time would be six years $(4.5 + 5.5 + 6.5 + 7.5 = 24 / 4)$. A more realistic generation time for wolves and dogs taken together would thus better be five years, not three. This difference (five versus three years) will have an influence on the calculations regarding the timing of the dog-wolf split and will place the genetically defined origin of dogs further back in time.

archaeological dog remains will be sequenced, generating a better understanding about the location of origin, dog migration routes and times (Neolithic spread, Bronze Age migrations, etc.).

Osteologic, Morphologic and Morphometric Differences

Methods

In the past, differences between the bones and teeth of wolves and dogs have been evaluated by the following methods: classical morphology (Rütimeyer 1861; 1875; Galton 1865; Nehring 1888; Gaudry/Boule 1892; Wolfgram 1894; Studer 1901), classical morphometry (Germonpré et al. 2009; 2012; 2015; 2017), and Geometric Morphometrics (Drake/Klingenberg 2008; 2010; Drake 2011; Rizk 2012; Schmitt/Wallace 2012; Drake et al. 2015).

Classical morphology looks at form in the following ways: Is the ventral border of the horizontal mandibular ramus straight or convex? In the past it was thought that this border was convex in dogs and straight in wolves. Is the dorsal vertical ramus of the mandible in dogs turned backwards, as it was

claimed to be in *Canis lupus chanco* (Tibetan wolf), or not? Based on the idea that it was curved backwards in dogs, it has been suggested that *chanco* might be the dog's ancestor. Recent genetic research, however, has shown that *chanco* DNA differs significantly from dog DNA.

Classical morphology is only of value if differences are consistent and easily discernible. Such clear differences are not often to be expected between archaeological dogs and wolves, considering they split off genetically only a few thousand years ago.

If obvious morphological differences are dubious or absent in remains, classical morphometry can be used. This is a more elaborate method, in which height, width, diameter, circumference, angle, and length are measured. This can be done on individual structures (e. g. the length of the skull, or the mesiodistal diameter of the mandibular premolar 4 [P4]²), or on combined structures, such as a partial or entire tooth row length (e. g. rostral maxillary premolar 1 to caudal molar 2 [p1-m2]).

A concern with both morphology and morphometry is that observed differences do not always define a (sub-)species unequivocally. Individuals within a (sub-)species may differ considerably in form or size due to genetic variability, food choice, food supply, climate, geography, gender, social status, and health status (Jolicoeur 1959; Pilot et al. 2012; 2014), yielding an impressive range of morphometric variation, and thus creating a possible morphometric overlap with a related (sub-)species (Terrenato/Ulizzi 1983).

This variability of form and size in *Canis lupus* is enormous as shown by a Geometric Morphometrics (GM) study of the skulls of all 122 canid species (Drake/Klingenberg 2010). The study demonstrates that dogs show the highest variability (not unexpected, considering how very different in form recent breeds can be). But the variability seen in wolf skulls is quite close to that seen in dogs, exemplifying how much variety is present in *Canis lupus*, too. All other canid species show considerably less plasticity.

A (partial) solution to the above problem is to employ ratios (indices), such as e. g. the »skull length versus skull width« ratio, which focuses not on size but on form (as a small ratio will be seen in a short, wide skull, and a high ratio in a long, slender skull). A ratio can confirm species identity even if the size differs greatly (Alaskan wolves can weigh 84 kg, Arabian wolves only 12 kg, but they have the same skull length versus skull width ratio). This is because a ra-

tio does not break the isometry law; skull length and width (both unidimensional) behave isometrically in a species. As a result, their ratio is preserved.

Unfortunately, not all ratios behave isometrically, some behave allometrically (Atchley et al. 1911). Allometry thus modulates and complicates relational-ratio interpretations. To illustrate this with a simple example: a cube with a 1-m-width has a surface of 6 m² and its volume is 1 m³. If its width is 10 m, so ten times as large, its surface is 600 m², thus 100 times larger, and its volume 1000 m³, thus 1000 times as large. Therefore, for instance, if a mid humeral diameter is twice as long in individual B compared to A, its surface will be four times larger in B, not just twice as large.

GM is a computerized, refined method that is used to differentiate when differences are not clearly visible with the naked eye as, for example, the form of a specific tooth. It focuses on »form only« and excludes size and orientation. It uses Procrustes superimposition to arrange comparative specimens to identical size and uses transposition around a centroid (Thompson 1917; Bookstein 1997; Adams et al. 2004).

Two GM methods are predominantly used: 1) the outline method (Lawing/Polly 2010), with landmarks and semi-landmarks, and 2) Fourier analysis (Stein/Weiss 2016).

The method was used with great success for the mandibular molar 1 (M1) in archaeological dogs and wolves and revealed a clear statistical difference between Middle Eastern and European specimens (Pionnier-Capitan 2010). Another GM study of the M1 in Pleistocene and modern wolves indicated that form varies considerably over time. Thus, great care should be taken when comparing modern *Canis lupus* specimens to archaeological ones because conclusions may differ depending on which comparative group is chosen (Boudadi-Maligne 2010). Yet another study (Janssens et al. 2019b) showed that modern mesaticcephalic dogs, with skull lengths identical to those of modern wolves, differed significantly in inner ear anatomy (in dogs: smaller centroid size, larger size of lateral semi-circular canal, cochlea streamline length decreased one third of a turn, etc.; see Janssens et al. 2019b). This is certainly a study that should best be repeated with archaeological specimens with an intact *Os petrosum*, to investigate if the same differences were already present in the earliest dogs.

² Upper case letters are used here for mandibular teeth, lower case letters for maxillary teeth. P/p = premolar; M/m = molar.

Morphological Wolf-Dog Differences Reported in Earlier Literature

- 1) The backward turning of the dorsal part of the vertical mandibular ramus was reported as typical in dogs and absent in wolves, apart from *Canis lupus chanco*, the Tibetan wolf, concluding that »this subspecies must have been the ancestor of dogs« (Olsen/Olsen 1977; see **fig. 2**).
- 2) A reduced sagittal crest (the dorsal bony protuberance along the midline skull suture at the level of the parietal bones) was defined in dogs versus wolves (Studer 1901).
- 3) The size of the tympanic bulla was reported to be larger in wolves than in dogs (Wolfgram 1894; Studer 1901).
- 4) Tooth crowding, among other dental anomalies, such as tooth rotation, tooth agenesis, or supernumerary teeth, and occlusion pathologies, were reported to be more prevalent in ancient and modern dogs and in zoo wolves (these wolves have been defined as undergoing a nowadays fast domestication phenomenon) compared to ancient and modern wolves (Wolfgram 1894; Studer 1901; Clutton-Brock 1962; Zeuner 1963; Stockhaus 1965; Benecke 1987; 1994; Wobeser 1992). This was explained by mandibular shortening (in the dog), while teeth were assumed to react »conservatively« to the size decrease caused by domestication and thus be »too large for the available space«. This creates, according to that theory, a spatial mismatch between tooth row length and mandibular length (Wolfgram 1894; Benecke 1994). Based thereon, the tooth row length (distance between the most rostral margin of the first premolar and the most caudal margin of the last molar) was thought to be shorter in dogs compared to wolves (Wolfgram 1894; Zeuner 1963; Benecke 1987; 1994; Dayan 1994a; 1994b; Clutton-Brock 1995; Morey 2010; Dimitrijević/Vuković 2012; Napierala/Uerpmann 2012). Recently, this criterion was used to discern between two morphotypes of large Pleistocene canids, arguing that those with a shorter tooth row length ratio were »proto dogs« (Germonpré et al. 2015). Dogs were also reported to have smaller teeth, specifically the carnassials (defined as the mandibular M1 and the maxillary p4; Clutton-Brock 1962). Next, a specific difference in the dental micro-anatomy of the protocone (one of the several cups of a molar) of the maxillary p4 was reported, with dogs having a protocone, which would be absent in wolves (Napierala/Uerpmann 2012; Camarós et al. 2016).
- 5) Dogs were reported to be paedomorphic wolves (having a juvenile puppy-like appearance) (Morey 1994; Waller et al. 2013), which was assumed to be a factor that aided in the domestication process, as paedomorphic appearance is emotionally attractive to humans.
- 6) Originally, dogs were reported to have larger orbital angles (OA) than wolves (49°–55° in dogs, 39°–46° in wolves; Studer 1901). More recent studies have shown, however, that there is some overlap between both groups (Bockelmann 1920; Iljin 1941; Aaris-Sørensen 1977; see **fig. 3**).
- 7) Dogs were reported to have a convex ventral horizontal ramus of the mandible, versus a straight mandible in wolves (Lawrence/Reed 1983; Germonpré et al. 2015; see **fig. 4**). In relation to this, a more »massive« mandible was reported in dogs compared to wolves (Clutton-Brock 1962).
- 8) Dog skulls were reported to have different contact points when positioned on a horizontal plane. Wolf skulls would rest on the canines, dogs on the fourth maxillary premolars, a feature thought to be caused by larger canines and a larger tympanic bulla in wolves (Zeuner 1963; Benecke 1987; see **fig. 5**).
- 9) Dogs were reported to have a more caudal position of the caudal border of the hard palate, being positioned caudally from a line, in contact with, and connecting both caudal borders of m2. In wolves, the caudal hard palate border would be positioned rostrally from that line (**fig. 6**; see Iljin 1941; Benecke 1987).
- 10) It was generally accepted that the snout length ratio/index (in some of the literature the word »index« is used for »ratio«) in dogs is smaller than in wolves (Huxley 1880; Nehring 1888; Mertens 1936; Iljin 1941; Degerbøl 1961a; 1961b; Stockhaus 1965; Lawrence/Bossert 1967; Lawrence/Reed 1983; Clutton-Brock 1995; Sablin/Khlopachev 2002; Germonpré et al. 2009; Drake 2011; Horard-Herbin et al. 2014). This ratio is measured differently depending on the study. Measures are generally according to those determined by Von den Driesch (1976). This index divides the length of the skull measured from the prosthion to:
 - the most caudal part of the skull (total length [TL] – measure 1),

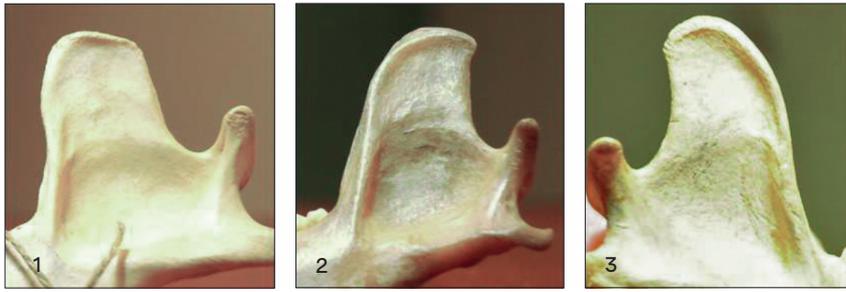


Fig. 2 The straight (1) versus backwards (3) turning of the dorsal process of the vertical ramus of the mandible of dogs, with (2) exemplifying that there are transitional forms which are difficult to classify. – (Photos L. Janssens).

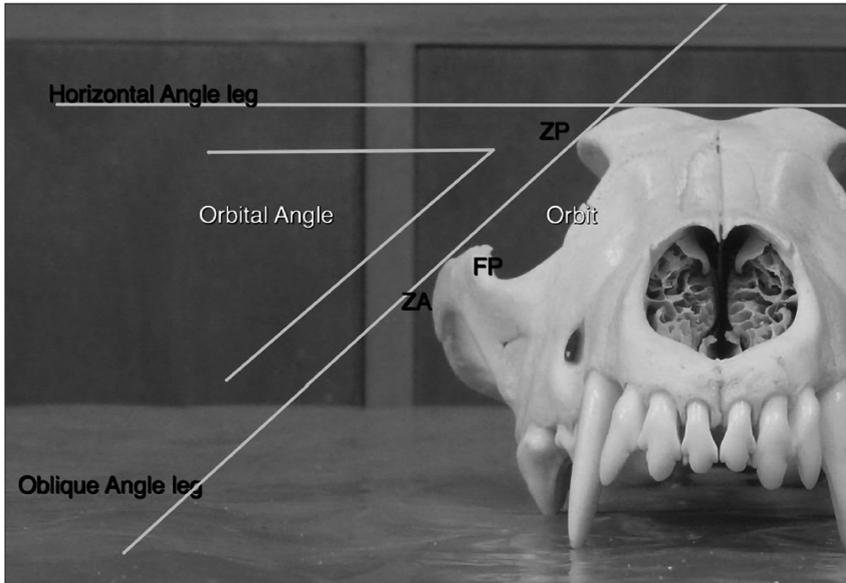


Fig. 3 The orbital angle (OA) is measured viewing the skull from the front. It is the angle between a horizontal line (here shown on top of the frontal skull bones) and an oblique line that touches the zygomatic process (ZP) of the frontal bone and the frontal process (FP) of the zygomatic arch (ZA). – (Photo and graphics L. Janssens).



Fig. 4 The ventral border of the mandible of a dog. This specimen (Bonn-Oberkassel) has a ventral convex border. – (Photo J. Vogel, LVR-LandesMuseum Bonn).

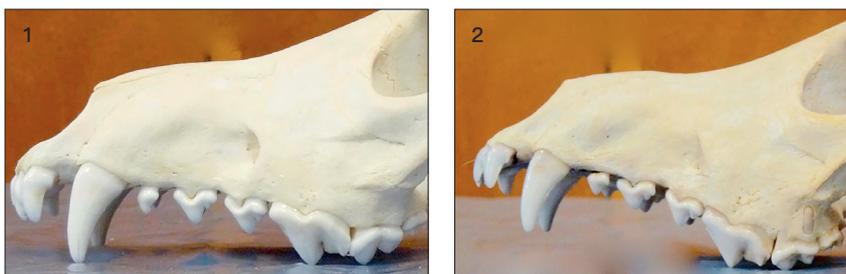


Fig. 5 Two dog specimens documenting the position of the skull on a horizontal plane. 1 stability is obtained by resting on the canines and the p4 or the *bulla tympanica*. – 2 the skull is stabilised by resting on the p4 and the *bulla tympanica*; the canines are not touching the plane. – (Photos L. Janssens).

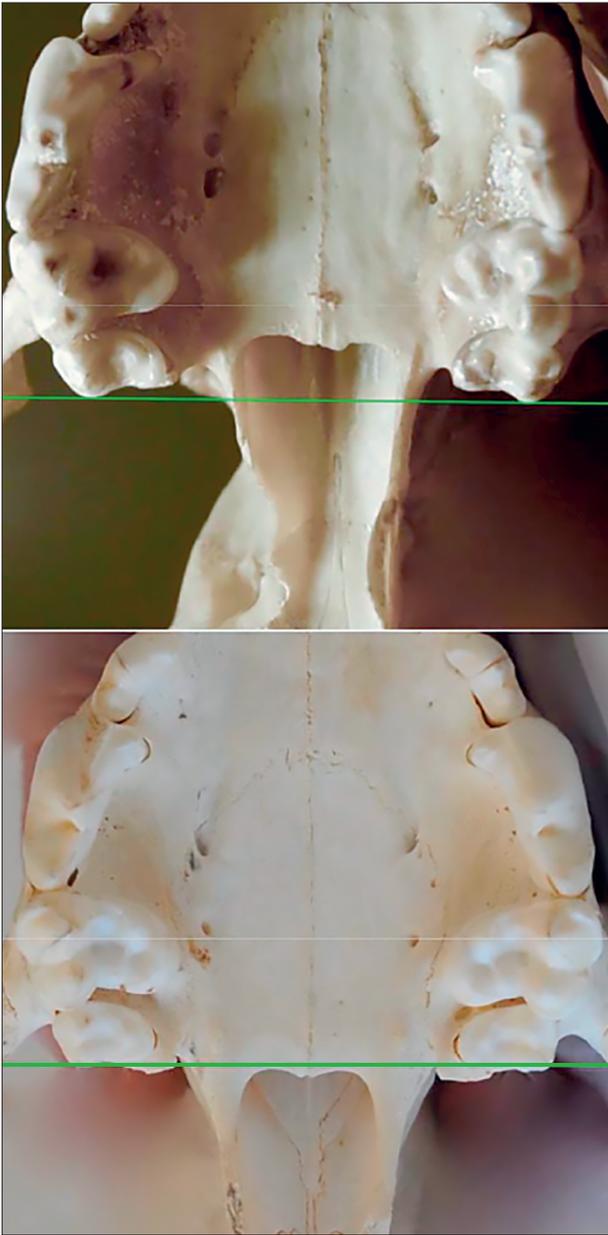


Fig. 6 Ventral view of the position of the caudal border of the hard palate in two dog specimens. The green line drawn between the caudal side of both maxillary molars 2 is the guideline. The hard palate border can be positioned caudally or rostrally from this line, as shown in the pictures. – (Photos and graphics L. Janssens).

- the ventral central point of the occipital foramen (basal length [BL] – measure 3),
 - the caudal part of the condyles (condylobasal length [CbL] – measure 2);
- by nasal length measured from the prosthion to:
- the nasion (viscerocranium – measure 8),
 - the frontal midpoint (facial length – measure 9),
 - the oral borders of the orbits («snout» length – measure 12),
 - the intra-oral staphylon (measure 13).

11) It was generally accepted that the snout width ratio is larger in dogs than in wolves (Huxley

1880; Nehring 1888; Studer 1901; Mertens 1936; Iljin 1941; Degerbøl 1961b; Stockhaus 1965; Lawrence/Bossert 1967; Olsen 1985; Wayne 1986; Morey 1992; Clutton-Brock 1995; Sablin/Khlopachev 2002; Germonpré et al. 2009; Drake 2011; Napierala/Uerpmann 2012; Horard-Herbin et al. 2014). This ratio is calculated by dividing skull length by skull width (measure 34 according to Von den Driesch 1976).

- 12) In one study, dogs were reported to have a relatively higher snout height and skull height ratio compared to wolves (Pitulko/Kasparov 2017).
- 13) A relatively smaller brain volume (ratio) was reported in dogs, which is comparable to several studies in other domesticated species (Kruska 1986; 1988a; 1988b). This ratio is calculated by measuring brain volume (measured by filling the brain case with small seeds, mostly millet, then measuring the weight of these and dividing this by the specific gravity of the grains), but more recently volume has been measured by 3D CT or MRI scan technology. Once defined, this volume is divided by a length measure, such as skull length.
- 14) All of the oldest reported archaeological dog specimens (up to the Bronze Age) have a smaller stature and smaller isometrically related structures (e.g. humerus length) compared to wolves (Rütimeyer 1861; 1875; Mertens 1936; Degerbøl 1961a; Clutton-Brock 1992; Benecke 1994; Dayan 1994a; 1994b; Pluskowski 2006; Boudadi-Maligne 2010; Boudadi-Maligne et al. 2012; Napierala/Uerpmann 2012; Boudadi-Maligne/Escarguel 2014). Almost all Pleistocene and early Holocene dogs have calculated weights of about 14 kg and are about 40–50 cm high at the shoulder (top of scapula). Pleistocene wolves were larger than Holocene specimens (Bergmann's rule; McNab 1971), which should be considered when comparing groups.
- 15) There are some authors who have published personal interpretations on differences that have never been re-tested nor published in the international peer reviewed literature, and which describe multiple minor differences that are mostly subjective interpretations of specific anatomical landmarks, e.g. the jugular foramen should be wedge-shaped in dogs and arrow-shaped in wolves (Stubbe 1981). These are not reported in this overview.

Signatures (not) Withstanding Critical Analysis

- 1) Backward turning of the dorsal part of the vertical mandibular ramus?
Our own study (Janssens et al. 2016a) shows that this landmark cannot be used to distinguish

modern dogs from modern wolves, as only 20 % of dogs have turned-back morphology, thus 80 % do not. Four arguments refute the statement of Olsen/Olsen (1977) that *Canis lupus chanco* is the dog's ancestor (based on this specific landmark): first, only 80 % of *chanco* specimens have the turned-back morphology; second, other wolf subspecies also show this morphology (e. g. 12 % of *Canis lupus pallipes*); third, genomic research found *Canis lupus chanco* to be quite distant from the »origin of dog« wolf clade (Sharma et al. 2004) and fourth, as stated before, far from all dogs carry this signature.

2) A reduced sagittal crest in dogs?

This argument can be rejected as two studies showed that the sagittal crest in some dogs can be larger than that in wolves (Lawrence/Bossert 1967; Rizk 2012).

3) A smaller tympanic bulla in dogs?

Several studies contradict this statement, as tympanic bulla size seems to be isometrically related to stature/size; thus, large dogs have even larger bullae than wolves (Stockhaus 1965; Drake/Klingenberg 2010; Drake 2011).

4) Dental differences?

Concerning dental pathology and tooth crowding, in our own study we could not find fewer, or different dental pathologies in wild wolves compared to dogs. Pathologies reported in the veterinary literature as being specifically related to domestication occurred as frequently in wild wolves, thus refuting this widely held prejudice (Janssens et al. 2016b).

A GM study on a very large number of specimens additionally contradicted the domestication-driven tooth crowding hypothesis and proved that it is Pleistocene wolves that have considerably more crowding than dogs; thus, dogs and wolves cannot be discerned based on this feature (Ameen et al. 2017).

Tooth row lengths are smaller in dogs because dogs are smaller than wolves, and teeth size and tooth row lengths behave isometrically (Stockhaus 1965). As thus, this signature does not define (sub-)species: it defines only size.

One study used this parameter as an argument for very early dog domestication (up to 34,000 years ago; Germonpré et al. 2015). This was challenged in our own study (Janssens et al. 2019a): we analyzed the same mandibular and dental lengths in one modern dog breed using the same methods as in Germonpré et al. (2015). The result was that this dog breed could also be split into two subgroups, based on the same criteria as were used in the original study (Germonpré et al. 2015). This

proved that one species – even one breed – can statistically be subdivided, due to anatomical variability, not because of a possible domestication event.

Dogs generally have smaller teeth than wolves, which is isometrically related to their stature (Stockhaus 1965). Based thereon, the mesio-distal diameter of the maxillary p4 can be used to divide wolves from dogs, as even the largest modern dogs have a smaller maxillary p4 than wolves. A maxillary mesio-distal p4 diameter longer than 22.5 mm can only be from a wolf, while dogs always have diameters smaller than 21.8 mm.

The mandibular M1 is less useful. A mesio-distal M1 diameter under 22.5 mm belongs to an archaeological dog; between 22.5 mm and 26.9 mm the specimen might be from a dog or a wolf, and above 26.9 mm the tooth belongs to a Pleistocene wolf (Janssens et al. 2019a).

The dental micro-anatomy of the protocone of the maxillary p4 cannot be used to assign specimens as a wolf or a dog (ancient or modern), as was shown by our own study (Janssens et al. 2019a) of 15 modern Eurasian wolves that all had a protocone. Also, our literature search on Pleistocene wolves (drawings or photos published) showed that most had a protocone. In conclusion, the protocone is not a »dog only« signature, and thus it cannot be used to separate dogs from wolves.

Considering the mesio-distal diameter of the maxillary p4 compared to the m1 + m2, some studies show that $m1 + m2 < p4$ is not only encountered in dogs, but that all possible variations of the formula $m1 + m2$ versus p4 exist in both dogs and wolves (Gaudry/Boule 1892; Wolfgram 1894).

5) Are dogs paedomorphic wolves?

A recent extensive and very detailed GM study proved this hypothesis to be incorrect; dogs have no paedomorphic traits compared to wolves (Drake/Klingenberg 2010).

6) Is the orbital angle larger in dogs?

We studied the OA in many different subspecies of modern wolves and in archaeological and modern dogs (Janssens et al. 2016a). In conclusion, the OA can be used to a limited degree to distinguish dogs from wolves. The smallest angle measured was 28° (wolf), the widest angle was 72° (Border Collie; fig. 7). Angles above 60° belong to modern dogs only, and angles under 35° can with certainty be attributed to wolves. Angles between 35° and 60° can belong to dogs or wolves. However, the mean OA of wolves is smaller than that of dogs (42° and 55°, respectively). Neolithic dogs have a mean angle of 47° (range 35°–50°) and are thus embedded in the modern wolf range (28°–52°).

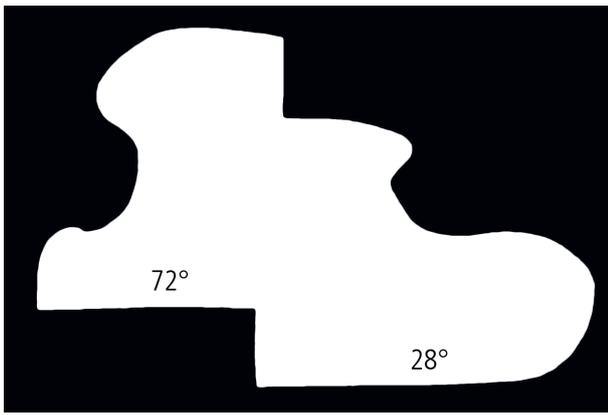


Fig. 7 Drawing of a transverse cut through the skull at the rostral orbit (see fig. 3), showing the widest OA measured, which is 72° in a dog, and the smallest OA measured, which is 28° in a wolf. The drawing also shows the expansion of the orbital area in a dorso-lateral direction (expanded in dogs compared to wolves). - (Drawing L. Janssens).

Only a few OA data are available from ancient wolves. These are larger on average (44°) than those of modern wolves (42°; see Aaris-Sørensen 1977).

In conclusion, our results show that the mean OA increased from 42° in ancient wolves to 44° in modern wolves, to 47° in Neolithic dogs, and to 55° in modern dogs.

A larger OA in dogs results from the bony expansion around the orbit, based on: 1) the lateralization of the frontal process of the zygomatic arch in dogs (Schmitt/Wallace 2012); 2) the maxillary skull widening at the level of the first molar; 3) the rostral and dorsal expansion of the frontal bones (leading to stop formation in dogs – the angle between nasal and frontal bones, seen from a lateral view); and 4) the widening of the orbital region (Drake et al. 2015).

Interestingly, the OA shows a more fluctuating asymmetry (the difference between the OA on the left and right side) in Neolithic dogs than in modern ones, with wolves' being the most symmetrical. This agrees well with the evolutionary development of the three groups, with the longest existing species being the most symmetrical (wolves are estimated to have originated 400,000 years ago) and newly developing species having more asymmetry. Thus, Neolithic dogs were the most asymmetrical, as they were an emerging newly developing species, and as asymmetry tends to stabilize over time, modern dogs are thus already a little more symmetrical (Janssens et al. 2016a).

- 7) Do dogs have more massive mandibles and a convex ventral border?

Most studies that report on massive mandibles in dogs suffer from a paucity of specimens, or from

conflicting results. Mandible form, mass, width, height, and length were studied recently with GM in a large group of canine specimens (Drake et al. 2015) and no difference was found between wolves and dogs. Thus, this trait cannot be used as a discerning parameter.

Mandible form, including the convexity of the ventral border, was also examined in a large group of canids with the GM landmark method (Drake et al. 2015), and although a statistical difference between dogs and wolves existed in modern skulls, no such difference could be found in archaeological specimens.

- 8) Are the contact points of the skull on a horizontal plane different in dogs?

In our own study (Janssens et al. 2019a) of more than 200 specimens of modern dogs and modern wolves, we observed considerable species overlap, with about 50 % of both wolf and dog skulls resting on the the first maxillary molars, the other 50 % on the canines. So, this test cannot discern dogs from wolves.

- 9) Do dogs have a more caudal position of the caudal hard palate border?

From our own study (Janssens et al. 2019a), we concluded that there is a trend, with wolves having a rostrally placed caudal border significantly more often ($p < 0.0001$).

In modern dogs, the »expected« caudal hard palate border is present in only 58 %. Thus, 42 % of dogs do not have the expected caudal border. In modern wolves, the »expected« rostrally placed border is present in only 69 %. Thus, 31 % of wolves do not have the expected morphology. Neolithic dogs have a rostral hard palate border in 81 % of cases (they are thus more wolf-like). In conclusion, this landmark cannot separate individual dog and wolf specimens.

- 10) Is the snout length ratio of dogs smaller than that of wolves?

Recently, the snout length ratio of more than 500 ancient and modern wolves and dogs was studied (Janssens et al. 2019a). The conclusion is that modern (mesaticephalic) dogs do not have a significantly smaller snout index than modern wolves. However, modern dogs and wolves have a statistically greater snout index than their archaeological/fossil counterparts.

We were not the first to report the lack of snout shortening in dogs. Two important earlier large-scale studies also reported this (Wayne 1986; Morrey 1992). Yet these results have seemingly been ignored, and the tendency to use this parameter as a distinctive landmark persists (see Sablin/Khlopachev 2002; Germonpré et al. 2009).

11) Is the snout width ratio of dogs larger than that of wolves?

In our study (Janssens et al. 2019a) we concluded that snout width ratio does differ significantly between ancient wolves and ancient dogs, with dogs having a relatively wider snout.

The wider dog snout is the consequence of a mid-face shape change, which is maximal at the transversal plane in the carnassial region. These changes are driven, at least in part, by the allelic composition and expression of the *Runx2* gene. A hyperactive allelic variant enhances dorsal and lateral maxillary bone growth, imposing adaptations on surrounding skull bones (Fondon/Garner 2006).

12) Is the snout and skull height ratio of dogs larger than that of wolves?

The snout and skull height ratio of more than 100 specimens were re-studied after Pitulko/Kasparov 2017 (Janssens et al. 2019a). In conclusion, there is considerable overlap in the snout height ratio between wolves (0.16–0.18) and dogs (0.13–0.25). A ratio below 0.16 or above 0.18 certainly belongs to a dog. Also, mean dog and wolf values differ significantly (both in modern and archaeological specimens).

The skull height ratio did not differ significantly between ancient wolves and ancient dogs. However, in modern specimens it did, indicating that modern wolves and dogs are separated from one another to a greater degree than their ancient counterparts.

13) Is relative brain volume reduced in the dog?

A 25–30 % smaller brain-size was repeatedly reported in dogs versus wolves in the literature

(Stockhaus 1965; Belyaev et al. 1985; Arbuckle 2005; Zeder 2012). This size reduction is mainly caused by the smaller size of specific brain stress centres (Nehring 1888; Stockhaus 1965; Olsen/Olsen 1977; Nobis 1981; Olsen 1985; Morey 1992; 2010; Hemmer 2005; Healy/Rowe 2006; Zeder 2012), such as the hypothalamus and the reticulo-activated system (RAS) in the metencephalon (Kruska 1988a; 1988b; O'Regan/Kitchener 2005; Zeder 2012). These centres reduce in size in all domesticates and document the considerably less stressful anthropogenic environment (Arbuckle 2005; Hemmer 2005).

14) Are dogs small wolves?

Based on very many studies, it is well accepted that dogs are generally smaller and have isometrically related smaller body parts (e.g. the femur) when compared to wolves (Rüttimeyer 1861; 1875; Mertens 1936; Degerbol 1961a; Clutton-Brock 1992; Dayan 1994a; 1994b; Pluskowski 2006; Boudadi-Maligne 2010; Boudadi-Maligne et al. 2012; Napierala/Uerpmann 2012; Boudadi-Maligne/Escarguel 2014). The earliest dogs probably weighed around 14 kg and had a shoulder height of 45 cm, which is roughly 40–60 % smaller than most wolves (*Canis lupus arabs* being the exception, but genetic research points out that this subspecies is not very close to the dog's origin clade). Neolithic dogs from the Alpine lakes and from Scandinavia are even smaller, being comparable to present-day toy-poodles. Larger dogs only started to emerge in the Bronze Age (Horard-Herbin et al. 2014). In conclusion: yes, dogs are anatomically small wolves (apart from some giant modern breeds).

Conclusions

To study and discern bone- and tooth-related differences between modern and archaeological wolves and dogs, three points are important from the start:

1) Brachycephalic and dolichocephalic dog skulls and achondroplastic dog skeletons are not relevant to the study of dog domestication because all early dogs were mesaticephalic, as are all wolves. Yet in some recent (mainly GM) studies, these cephalic variants were used, which cannot produce sound conclusions (Schweizer et al. 2017).

2) It is important to realise that Final Pleistocene wolves were anatomically different in size and morphology to modern wolves: they were larger and sturdier probably due to Bergmann's rule. But was that also the case for the original wolf clade from which dogs originated? We do not know, as very few Final

Pleistocene wolves from East Asia have been examined, which has created a considerable void.

3) The reported wolf-dog differences should not be seen as isolated phenomena: they are part of one global morphology-size change; dogs get smaller and, in that process, they experience progenesis (early production of sex hormones) with earlier and different closing times of growth plates. This then creates skull differences, mainly around the orbital area.

The criteria listed below are the ones that withstand critical analysis; some are related to size, others are not. Together, they can be of great diagnostic value if used in multivariate analyses.

Differences related to size reduction are important:

- Dogs and wolves can be separated at the extremes of the mandibular M1 mesio-distal diameter,

- dogs have an absolute shorter maxillary p4 mesiodistal diameter, there is no overlap in dogs and wolves, and
- the bones of the appendicular and axial skeleton, as well as the mandibles and the skull, are smaller in dogs than in wolves, and they can be used to calculate body mass and shoulder height (using specific formulas).

Differences related to facial morphology include:

- Dogs have a wider mean snout width index,

- dogs have a higher mean snout height index and this index can be diagnostic at its extremes, and
- dogs have a wider mean OA and this can be diagnostic at its extremes.

Differences related to the brain are also to be mentioned:

- Dogs have a smaller brain size ratio than wolves, and
- (modern) dogs have specific inner ear measurements that differ from those in wolves.

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