# From wolf to dog

Janssens, L.A.A.

## Citation

Janssens, L. A. A. (2019, June 27). *From wolf to dog*. Retrieved from https://hdl.handle.net/1887/74477

**Author**: Janssens, L.A.A.
**Title**: From wolf to dog
**Issue Date**: 2019-06-27

# Introduction

## 1. Is the grey wolf the progenitor of the dog?

For over a century, scientists have been examining the origin of dogs (Galton, 1865; Gaudry & Boule, 1892; Rütimeyer, 1861; Studer, 1901; Wolfgram, 1894), asking where, when, and from which ancestor(s) dogs originated. The earliest writings consistently named two immediate ancestors: the grey wolf (*Canis lupus*) as the ancestor of large breed dogs, and the jackal (*Canis aureus)* as that of small breed dogs (Darwin, 1868; Lorenz, 2002). More recent authors, following mainly genetic evidence, rejected the latter species and pointed to the Eurasian grey wolf as the sole ancestor of dogs (Anderson et al., 2009; Ardalan et al., 2011; Axelsson et al., 2013; Brown et al., 2017; Freedman et al., 2014; Freedman et al., 2013; Gray, Sutter, Ostrander, & Wayne, 2010; Gundry et al., 2007; Hoopes, Rimbault, Liebers, Ostrander, & Sutter, 2012; Irion et al., 2003; Khosravi, Kaboli, Rezaei, & Montazemi, 2012; Klütsch & de Caprona, 2010; Klütsch & Savolainen, 2011; Larson & Burger, 2013; Larson et al., 2012; Leonard et al., 2002; Lindblad-Toh et al., 2005; Ostrander & Wayne, 2005; Pang et al., 2009; Randi & Lucchini, 2002; Randi, Lucchini, & Francisci, 1993; Savolainen, Zhang, Luo, Lundeberg, & Leitner, 2002; Schmutz & Berryere, 2007; Schmutz, Berryere, Barta, Reddick, & Schmutz, 2007; Schmutz, Berryere, & Dreger, 2009; Schoenebeck et al., 2012; Schoenebeck & Ostrander, 2013; Thalmann et al., 2013; Tsuda, Kikkawa, Yonekawa, & Tanabe, 1997; Vaysse et al., 2011; vonHoldt et al., 2010; vonHoldt et al., 2018; Wayne & Jenks, 1991; Wayne & Ostrander, 1999, 2007).

## 2. What are wolves, what are dogs?

Three main differences between (fossil and modern) wolves and dogs have been reported: non-osteological, genetic, and osteological.

### 2.2. Non-osteological differences

Non-osteological differences cannot be used in archaeological research, as they leave no visible traces. Recent genetic research has detected some typical dog genes, such as coat color genes, in archaeological remains. A few examples of genetic differences between wolves and dogs include:

**Coat structure** in dogs can be quite different (very long hair, curly hair, very short hair) compared to wolves (Drögemüller et al., 2008; Newsome & Corbett, 1985). These variants are defined by mainly three genes and their interactions: *FGF5, KRT71,* and *RSPO2* (Cadieu et al., 2009).

**Coat colour** differs among most dogs compared to wolves, with white spots, tricolour, merle, and other variants that are absent in wolves. For these dog colour variants, specific alleles have been defined (Kerns et al., 2007; Kim et al., 2005; Little, 1958; Schmutz & Berryere, 2007; Schmutz et al., 2007; Wayne & Jenks, 1991).

**External ear carriage** always is upright in wolves, while some dogs have floppy ears, or floppy ear tips, that are defined genetically by regions *CFA10* and *MSRB3* (Boyko et al., 2010).

## 2.2. Genetic differences

Genetics have become important in defining the origin of dogs, and trying to answer questions such as where and when wolves were domesticated or which wolf subtype was the immediate ancestor (for details, see **Table 1**).

Genetics studies can be done only if DNA can be extracted, if it is of reliable quality and quantity, and if the examined genes differ between wolves and dogs. Up to now, mainly mtDNA has been evaluated (**Table 1**). However, Y chromosome and partial and whole genome sequencing (nDNA) studies are becoming increasingly important (Frantz et al., 2016).

Mitochondrial DNA research has indicated the occurrence of 6 dog clades, of which 4 are major: I, II, III, IV or A, B, C, D (Vilà et al., 1997). Clade A is the largest group, including about 2/3 of the modern dog population and related to Chinese wolves (Savolainen et al., 2002). Chinese ancient specimens contain the highest number of haplotypes, unique haplotypes, and express more distant haplotypes (a higher number of mutations) than European specimens (Ardalen et al., 2011; Pang et al., 2009; Wang et al., 2016). These observations led to the conclusion that the origin of dogs must have been in South-East Asia, later diverged to the Middle East, and then Europe, a theory comparable to that of Frantz et al. (2016).

The latter authors propose two domestication centres: one in West Asia, giving rise to dogs carrying A and B haplotypes, and one in Europe, giving rise to C and D haplotypes (found most in the oldest dog remains in Europe)(**Table 2**). They further suggest that dogs from the Asian region migrated into Europe (possibly accompanying the Neolithic wave) because dog remains in Europe, from that time forward, are mostly haplotypes A and B (Deguilloux, Moquel, Pemonge, & Colombeau, 2009; Pionnier-Capitan, 2010). However, not all authors agree, and conflicting theories persist, suggesting Europe (Thalmann et al., 2013); South-West Asia; the Middle East (vonHoldt et al., 2010); Central Asia (Shannon et al., 2015); East Asia (Wang et al., 2013); and South-West China (Pang et al., 2009) as the region of dogs' origin.  Additionally, the dating of the wolf-dog divergence, based on genetic data, is controversial, with estimated divergence dates from 14.000 to 90.000 years ago (**Table 1, 2**)(e.g. Skoglund, Götherström, & Jakobsson, 2011).

### 2.3. Osteological differences

#### 2.3.1. Methods that have been used to define morphological-morphometric differences between wolves and dogs

Differentiating two closely related sub-species using morphological criteria can be quite difficult, especially if the divergence was recent. Three methods are used, two with a long history (classical morphology and morphometry) and one that is quite recent (morphometrics).  Differences between bones and teeth of wolves and dogs have been evaluated with: a) **classical morphology** (Galton, 1865; Gaudry & Boule, 1892; Nehring, 1888; Olsen & Olsen, 1977; Rütimeyer, 1861, 1875; Studer, 1901; Wolfgram, 1894); b) **classical morphometry** (Germonpré et al., 2017; Germonpré, Lázničková-Galetová, Losey, Räikkönen, & Sablin, 2015; Germonpré, Lázničková-Galetová, & Sablin, 2012; Germonpré et al., 2009); and c) **geometric morphometrics (GM)**(Drake, 2011; Drake, Coquerelle, & Colombeau, 2015; Drake & Klingenberg, 2008, 2010; Rizk, 2012, Schmitt & Wallace, 2012). **Classical morphology** looks at form. For example, is the ventral border of the horizontal mandibular ramus in dogs straight, as in wolves, or convex? If such obvious visual signals are absent, **classical morphometry** can be used. The latter is a more elaborate method in which height, width, diameter, circumference, and length are measured on individual bones or teeth, or on combined structures, such as an entire tooth row length. A concern with both morphology and morphometry is that individual differences do not always define species differences unequivocally. Individuals within species may differ considerably due to genetic variability, food choice and supply, climate, gender, and general health (Jolicoeur, 1959), thus yielding impressive ranges of normal variation within one population (Terrenato & Ulizzi, 1983). A partial solution to this dilemma is to employ **ratios (indices),** such as skull length/skull width ratio. This ratio confirms species identity because it is identical in Alaskan (80kg) and Arabian wolves (14kg) (because length and width in this case behave isometrically and a proportional relationship is preserved). However, ratios do not always behave isometrically in shape analysis, mainly because surface and volume of shapes (as bones) behave differently, based on much higher forces acting on bones (and cross-sectional diameter) when body size (volume) increases (Atchley et al., 1976; Atchley and Anderson, 1978). This phenomenon of allometry thus modulates relational interpretations.

**Geometric morphometrics (GM)** is a recently-developed comparative method that is used when differences are not clearly visible to the eye, such as form of a specific tooth (Pionnier-Capitan, 2011). GM focuses on form only by excluding size and orientation and using Procrustes superimposition and transposition around a centroid (Adams, Rohlf, & Slice, 2004; Bookstein, 1997; Thompson, 1977). Two different GM methods are predominant: 1) The outline method (Lawing & Polly, 2010), with landmarks and semi-landmarks, and 2) Fourier analyses (Stein & Weiss, 2016).

### 2.3.2. Morphological-morphometric differences reported between wolf and dog (Table 3)

Traits reported to differ between wolves and dogs, mentioned in the literature, have partially been rejected in the past or recently (see below, points 2, 3, 4, 5, 6, 8).

Those that are still accepted (nine traits) are questioned in this thesis (points 1, 6, 7, 9, 10, 11, 12, 13, 14, 15, 17).

1. Backward turning of the dorsal part of the **vertical mandibular ramus** originally was reported as typical in dogs and absent in wolves, apart from *C. lupus chanco* that “must have been” the ancestor of dogs (Olsen & Olsen, 1977).

2. A **reduced sagittal crest originally** was defined as present in dogs (sagittal crest is a bony protuberance along the midline sagittal suture, dorsally, at the level of the parietal bones) (Studer, 1901). However, the sagittal crest in some dogs is proportionately larger than in wolves (Lawrence & Bossert, 1967; Rizk, 2012), and thus it cannot be used as a distinguishing trait.

3. The size of the **tympanic** bulla originally was reported to be larger in wolves than in dogs (Studer, 1901; Wolfgram, 1894). However, its size is related isometrically to stature, with large dogs having larger bullae than wolves (Drake, 2011; Drake & Klingenberg, 2010; Stockhaus, 1965), and thus it cannot be used as a discerning trait.

4. Tooth crowding, among other **dental anomalies,** such as rotation of teeth, tooth agenesis, or supernumerary teeth, and occlusion pathologies were reported originally to be more prevalent in dogs than wolves (Andersone & Ozolins, 2000; Benecke, 1987, 1994; Stockhaus, 1965; Wobeser, 1992; Wolfgram, 1894). This was explained by mandibular shortening in the domesticated wolf-dog relative to the sum of mesio-distal diameters, being thus a spatial mismatch (Benecke, 1994; Wolfgram, 1894). Older studies found more tooth crowding in zoo wolves (defined as a modern sort of fast domestication event) and ancient dogs than in wild wolves ( Benecke, 1987;Clutton-Brock, 1962; Studer, 1901; Wolfgram, 1894; Zeuner, 1963). A recent GM study on a very large number of specimens contradicted the domestication-driven crowding hypothesis (Ameen et al., 2017) and proved that wolves can have more tooth crowding than dogs.

5. Dogs were reported to be **paedomorphic** wolves (having a juvenile–puppy

like appearance) (Morey, 1994; Waller et al., 2013). Recent GM research proved this hypothesis to be incorrect (Drake and Klingenberg, 2011).

6. Dogs were reported to have **smaller teeth** and **shorter tooth row lengths**, in **more massive mandibles**. Some specific ratios were proposed to differ from wolves, such as the mesio-distal diameter of mandibular P4, compared to the sum of the mesio-distal diameter of maxillary M1 and M2, with **M1+M2 < P4** in dogs, compared to wolves (Clutton-Brock, 1963). Other studies have contradicted the results of the Clutton-Brock (1963) study (which also was a low sample study) and have shown that all possible variations of dental length of M1+M2 versus P4 exist in dogs and in wolves (Gaudry and Boule, 1892; Wolfgram, 1894).

Several studies have reported reduction (in dogs) of total **tooth row length** (distance between the most rostral margin of the first premolar and the most caudal margin of the last molar) or partial tooth row length (Benecke, 1987, 1994; Bökönyi, 1975; Boudadi-Maligne, 2010; Clutton-Brock, 1995a; Dayan, 1994a; Dimitrijević & Vuković, 2012; Morey, 2010; Napierala & Uerpmann, 2012; Wolfgram, 1894; Zeuner, 1963). Reduced tooth row length has been attributed to stature reduction in dogs, with isometric reduction of maxillary and mandibular dental arch dimensions (Stockhaus, 1965). Recently, such reductions were used to discern between two morphotypes of large Pleistocene canids, as an argument to discern between wolves and proto-dogs (Germonpré et al., 2015).

Differences in **mandible mass** have been reported, with dogs said to have more massive mandibles (Clutton-Brock, 1962). Mass can be related to a combination of width, length, and height. Wider mandibles were reported in Jarmo dog specimens (Lawrence and Reed, 1983: 490-494), and Pleistocene canids (Germonpré et al., 2015: 12). Shorter mandibles were reported in Pleistocene canids (Germonpré et al., 2015). Taller mandibles were reported in Natufian (Tchernov and Valla, 1997) and Mesolithic/Neolithic dogs (Dimitrijević, 2006; Dimitrijević & Vuković, 2012). These studies all suffer from a paucity of specimens, or from conflicting results. Mandible mass, heigth, and length were studied recently in a large group of canine specimens (Drake et al., 2017) and not found to differentiate ancient wolves and dogs.

7. Dogs originally were reported to have large **orbital angles (OA)**, and wolves small OA (49°-55 in dogs 39°-46° in wolves)(Studer, 1901). These angles later were re-studied in additional specimens, and a little overlap was reported (Aaris-Sørensen 1977; Bockelmann, 1920; Iljin, 1941).

8. Dogs were reported to have a **convex ventral horizontal ramus of the mandible,** versus a straight mandible in wolves (Germonpré et al., 2015; Lawrence and Reed, 1983). The mandible form recently was examined in a large group of canids with the landmark method (Drake et al., 2017). There was no statistically diagnostic value for historical and ancient mandibles, due to the great variation in form (Drake et al., 2017).

9. Dogs were reported to have a difference in **contact points of the skull on a horizontal plane.** Wolf skulls would be resting on canines, dogs on P4, a feature that is thought to be caused by larger canines and a large tympanic bulla in wolves (Benecke, 1987; Zeuner, 1963).

10. Dogs were reported to have a different position of the **caudal border of the hard palate,** positioned caudally from a line in contact with and connecting both caudal borders of M2 (Benecke, 1987; Iljin, 1941).

11. Certain specific differences in **dental micro-anatomy,** related to the protocone of P4 (maxillary) were reported, with dogs having a protocone that is absent in wolves. This difference was used as argument to assign ancient specimens to the dog group (Camarós, Münzel, Cueto, Rivals, & Conard, 2016; Napierala & Uerpmann, 2012).

12. It is accepted generally that the relative **snout length** in dogs is shorter than in wolves (Clutton-Brock, 1995a; Crockford, 2005; Degerbøl, 1961a; Degerbøl, 1961b; Drake, 2011; Germonpré et al., 2009; Horard-Herbin et al., 2014; Huxley,

1880; Iljin, 1941; Koler-Matznick, 2002, 2016; Lawrence & Bossert, 1967; Lawrence & Reed, 1983; Mertens, 1936; Nehring, 1888; Olsen & Olsen, 1977; Sablin & Khlopachev, 2002; Stockhaus, 1965) although two important studies reject this hypothesis (Morey, 1992; Wayne, 1986).

13. It is accepted generally that the relative **snout width** is wider in dogs than in wolves (Clutton-Brock, 1995b; Crockford, 2005; Degerbøl, 1961b; Drake, 2011; Germonpré et al., 2009; Horard-Herbin et al., 2014; Huxley, 1880; Iljin, 1941; Koler-Matznick, 2002; Lawrence & Bossert, 1967; Mertens, 1936; Morey, 1992; Napierala & Uerpmann, 2012; Nehring, 1888; Olsen, 1985; Olsen & Olsen, 1977; Sablin & Khlopachev, 2002; Stockhaus, 1965; Studer, 1901; Wayne, 1986).

14. Dogs were reported recently to have a relatively higher **snout height** ratio compared to wolves (Pitulko & Kasparov, 2017).

15. Dogs were reported recently to have a relatively higher **skull height** ratio, compared to wolves (Pitulko & Kasparov, 2017).

16. Relative smaller **brain volume** was reported in dogs (Arbuckle, 2002; Belyaev, Plyusnina, & Trut, 1985; Stockhaus, 1965; Zeder, 2012), amounting to 25-30% size reduction, compared to wolves of the same size (Stockhaus, 1965; Zeder, 2012). This phenomenon generally is accepted and prevalent in all domesticated animals, from the very beginning (Kruska, 1986, 1988a, 1988b).

17. It is accepted generally that dogs have smaller **stature and overall size,** and isometrically related individual structures, when compared to wolves (Benecke, 1994; Boudadi-Maligne, 2010; Boudadi-Maligne & Escarguel, 2014; Boudadi-Maligne, Mallye, Langlais, & Barshay-Szmidt, 2012a, 2012b; Clutton-Brock, 1992; Dayan, 1994a, 1994b; Degerbøl, 1961a; Mertens, 1936; Napierala & Uerpmann, 2012; Pluskowski, 2006; Rütimeyer, 1861, 1875).

### 2.3.3. Which specimens were defined as Pleistocene prehistoric dogs?

Little is known about Pleistocene and early Holocene dogs (**Table 2**). Only 15 Pleistocene dog specimens have been reported. Most of them were found in Europe and date from ca. 14500 years ago, coinciding with the post-LGM Magdalenian spread over Europe (Miller, 2012). Only seven specimens have been recorded from the Pleistocene-Holocene transition. Early dogs are thus extremely rare, and remains are partial, incomplete, and fragmented, making it difficult-to-impossible to regard them as a population with mean values and standard deviations of their typology.

### 2.3.4. GM differences between dogs and wolves

#### 2.3.4.1. Molar 1 differences

The form of **Molar 1** (mandibular and maxillary) was studied in modern and ancient wolves and dogs (*n*-575), applying elliptical Fourier analyses. The results revealed a statistical difference between two groups, one from the Middle East and one from Europe (Pionnier-Capitan, 2010). This subdivision was confirmed recently by genetic studies (Frantz et al., 2016). Another GM study of the M1 of Pleistocene and modern wolves, applying the landmark method, indicated that form can vary considerably over time, and thus great care should be taken when comparing ancient dogs and wolves because the conclusion might differ depending which reference is chosen (Boudadi-Maligne, 2010).

#### 2.3.4.2. Tooth crowding differences

Tooth crowding was reported originally to occur more in dogs and zoo wolves compared to European wolves (Benecke, 1994; Wobeser, 1992; Wolfgramm, 1894). It was proven to be more prevalent in wild (Alaskan) Pleistocene wolves (Ameen et al., 2017) and it might be that the degree of crowding in wolves is different among different geographical populations, or differs over time (Pleistocene versus modern).

#### 2.3.4.3. Skull differences

When **dog skulls** of 25 breeds and all skull types (mesati-, brachy-, dolichocephalic) were examined using the landmark method (Fondon & Garner, 2007), nine parameters and five basic mathematical functions could explain all form variations (apart from extreme brachycephaly). These differences in skull form are mainly under the influence of two genes (*Runx-2* and *Twist*-1) (Fondon & Garner, 2007). Another study of **skulls** of 106 dog breeds and 397 modern wolf skulls (C. *lupus, C. latrans, C. aureus*), using the landmark method (Drake and Klingenberg, 2010), indicated that form variability among dog skulls is greater than in all wild canid populations. The wolf was the only canid with form variations comparable (but less extreme) to dogs. Most mesaticephalic dog skulls have, compared to wolves, forward-facing orbits and a pronounced angle between forehead and muzzle (stop), together with an elevated muzzle (Airorrhynchia) and shortened nasals (Drake and Klingenberg, 2010; Drake, 2011; Drake et al., 2015). When **skull shape** was measured in 40 wild canids (*C. lupus, rufus, aureus*) and 35 modern dogs, using the landmark method (Schmitt & Wallace, 2012), results revealed that dogs have a compressed and cranially flexed rostrum (Airorrhynchia), a larger orbital region, and an upward shift of the braincase, confirming the results presented by Drake and Klingenberg (2010). An additional study of **skull shape** involved 69 dog breeds and 120 modern wolves, using the landmark method (Rizk, 2012). The data revealed differences between wolves and brachycephalic and dolichocephalic skulls. Brachycephalic and dolichocephalic skulls clearly are not relevant to the study of domestication because all early dogs were mesaticephalic, as all wolves are. Differences observed between wolves and mesaticephalic dogs in this study were concentrated around M1, with widening and shortening leading to a larger orbital area, confirming earlier results (Drake & Klingenberg, 2010; Schmitt & Wallace, 2012). A study using the landmark method evaluated **skulls** defined as large Pleistocene proto-dogs (Goyet and Eliseevichi). These skulls were compared to a large group of modern and prehistoric wolves and dogs (Drake et al., 2015). The results indicate that the so-called proto-dogs actually are wolves, in that they lack the typical doglike skull flexion and the concavity nearby the orbits.

#### 2.3.4.4. Mandible differences

**Mandible convexity** was reported to be typical for dogs, while wolves were reported to have straight horizontal mandibular rami. This was confirmed in modern wolf and dog specimens in a GM study (Drake et al., 2017), but not in fossil wolf and ancient dog specimens.

# 3. Research questions and aims of this thesis

## 3.1. Introduction

The data presented on the preceding pages reveal a need for a thorough evaluation and re-evaluation of several generally accepted morphological and morphometric criteria that commonly are used to distinguish archaeological dogs from fossil wolves. Many past conclusions were drawn based on low numbers, lacking morphological variation. The latter is rather typical for the distribution of a trait with normal variation. Other reports describe different measuring methods, preventing direct comparisons. Still others have drawn conclusions based on generally accepted criteria, while sound studies critically evaluating those criteria and have shown them to be invalid (e.g. shorter snout)(Wayne, 1986). Many reports refer to earlier studies, but without being complete in the assessments. Others build on previous studies and accept those conclusions as axiomatic, despite the fact that critical evaluations have rejected them (Germonpré et al., 2009; Sablin and Khlopachev, 2002). It is clear that much of the past research should be re-evaluated critically, and possibly repeated. A number of the morphological parameters that were used historically to distinguish dogs and wolves have been refuted recently with GM studies (e.g. dental crowding, mandible form). Traits that were not re-studied recently should be reconsidered, with additional specimens included. Additionally, there is a need to publish a large overview of available morphological and morphometric data that include historical and non-English publications. The goal of this thesis is to fulfil part of these needs.

### 3.2. Questions asked in this thesis are:

1. Is there a higher degree of **oral pathology** in domesticated dogs versus wild wolves? (Chapter 2).

2. Is it correct that a **caudally-oriented dorsal coronoid process** of the vertical ramus of the mandible is typical for dogs (and *C. lupus chanco)*, and can one conclude that the latter must be the ancestor of today's dogs? (Chapter 3).

3. Can the **orbital angle** be used to distinguish dogs and wolves? (Chapter 4).

4. Can **carnassial** (maxillary P4 and mandibular M1) **size reduction** be used to distinguish dogs and wolves? (Chapter 5).

5. Can **micro-anatomical change in teeth (protocone)** be used with confidence to identify dogs? (Chapter 5).

6. Is there is a dog-wolf difference in **contact points of the skull**, when it is placed on a horizontal plane? (Chapter 5).

7. Is there a caudal shifting of the **caudal border of the hard palate** in dogs, so that the border exceeds a line connecting the caudal side of left and right M2? (Chapter 5).

8. Is it correct to state that dogs have relatively **wider snouts** than wolves? (Chapter 5).

9. Is it correct to state that dogs have relatively **shorter snouts** than wolves? (Chapter 5).

10. Is the **snout** (ratio) higher in dogs than wolves? (Chapter 5).

11. Is **skull height** (ratio) higher in dogs than wolves? (Chapter 5).

12. Is **smaller stature** present in the earliest archaeological dogs? Do we see stature reduction in modern wolves kept in an anthropomorphic environment? (Chapter 5).

13. Are **mandibular mesio-distal diameter, and tooth row lengths,** shorter in Paleolithic large proto-dog compared to contemporary isopatric wolves? (Chapter 5).

14. Do **proto-dogs** differ from Pleistocene wolves? (Chapter 5).

### 3.3. Answering these questions

To answer all of the questions stated above, each trait was re-examined by first applying the older methodologies and evaluating large groups of modern and fossil (when available) dogs and wolves (for numerical data on sample size see each individual article and chapters). A large literature was reviewed in great detail, including the very oldest reports, searching for measurements and data published in different languages. Although many measures have been reported, some ratios had not been calculated. In the latter instances, calculations were done by the author. Another problem was that some lengths and ratios could not be compared, based on difference in methodology (e.g. skull length measurement could be reported as TL, CbL and BL). For these measures, we developed reliable conversion formulae that allowed us to construct a large comparable database. Based on these methods, we undertook to answer the questions listed above (see Chapters 2-5).

## 4. Projects in the frame of this thesis

### 4.1. Project 1 (Chapter 2)

Oral pathology in dogs is reported widely in veterinary medicine. Similar data from wolves are scarce, and data on several pathologies are lacking. To test whether wolves have or had different oral pathology than dogs, our goal was to examine wild wolf skulls of different sub-types and from different locations. By comparing the wolf data with those from dogs, we could draw conclusions about differences in types of pathologies and/or their prevalence. The null hypothesis was that considerable difference could be anticipated due to the domestication process.

Chapter 2 is published in the Journal of Mammalogy as: A standardized framework for examination of oral lesions in wolf skulls (Carnivora: Canidae: *Canis lupus*) (2016; 97: 1111–1124) by: L. Janssens, L. Verhaert, D. Berkowic, D. Adriaens. DOI 10.1093:jmammal/gyw058

### 4.2. Project 2 (Chapter 3)

The “turned back” anatomy of the dorsal part of the vertical ramus of the mandible was reported in Science (1977) as specific for domestic dogs and Chinese wolves (*Canis lupus chanco)* (previously called Tibetan wolves). The claim was made by Olsen and Olsen (1977), two important zooarchaeologists in the USA during the 20th century. Critical reading of the original article revealed some weaknesses. Our project was to retest the original arguments based on a larger database of dogs and wolves of different sub-types.

Chapter 3 is published in Zoomorphology as: The morphology of the mandibular coronoid process does not indicate that *Canis lupus chanco* is the progenitor to dogs (2016; 135: 269–277) by: L. Janssens, R. Miller, S. Van Dongen. DOI 10.1007:s00435-015-0298-z

### 4.3. Project 3 (Chapter 4)

The data presented in the literature on the usefulness of the orbital angle were puzzling, and authors did not discuss the problematic experimental design as published in the original article from Studer (1901). There was a need for re-testing the method in a larger group of skulls, including a more varied wolf group, and also including archaeological dogs. Project 3 did so, and further tried to integrate the new results into practical diagnostic applications.

Chapter 4 is published in Zoomorphology as: Can orbital angle morphology distinguish dogs from wolves? (2016; 135: 149–158) by: L. Janssens, I. Spanoghe, R. Miller, S. Van Dongen. DOI 10.1007/s00435-015-0294-3

### 4.4. Project 4 (Chapter 5)

Based on results of earlier projects, a critical evaluation was made of many claims regarding morphological differences between wolves and dogs. Some of these claims were very old and had persisted for decennia (the short snout), some were novel (skull height was presented for the first time in 2016). While our earlier studies (Chapter 2-4) were focused more narrowly, Chapter 5 discusses a large number (11) of morphological and morphometric arguments that had been used to assign specific specimens to one specific group.
Projects 1-4 cover the widest possible critical evaluation of generally accepted differences between dogs and wolves. Chapter 5 also includes an evaluation and discussion of the large Pleistocene canids, recently (since 2009) defined as tamed wolves, proto-dogs, putative dogs, or insipient dogs.

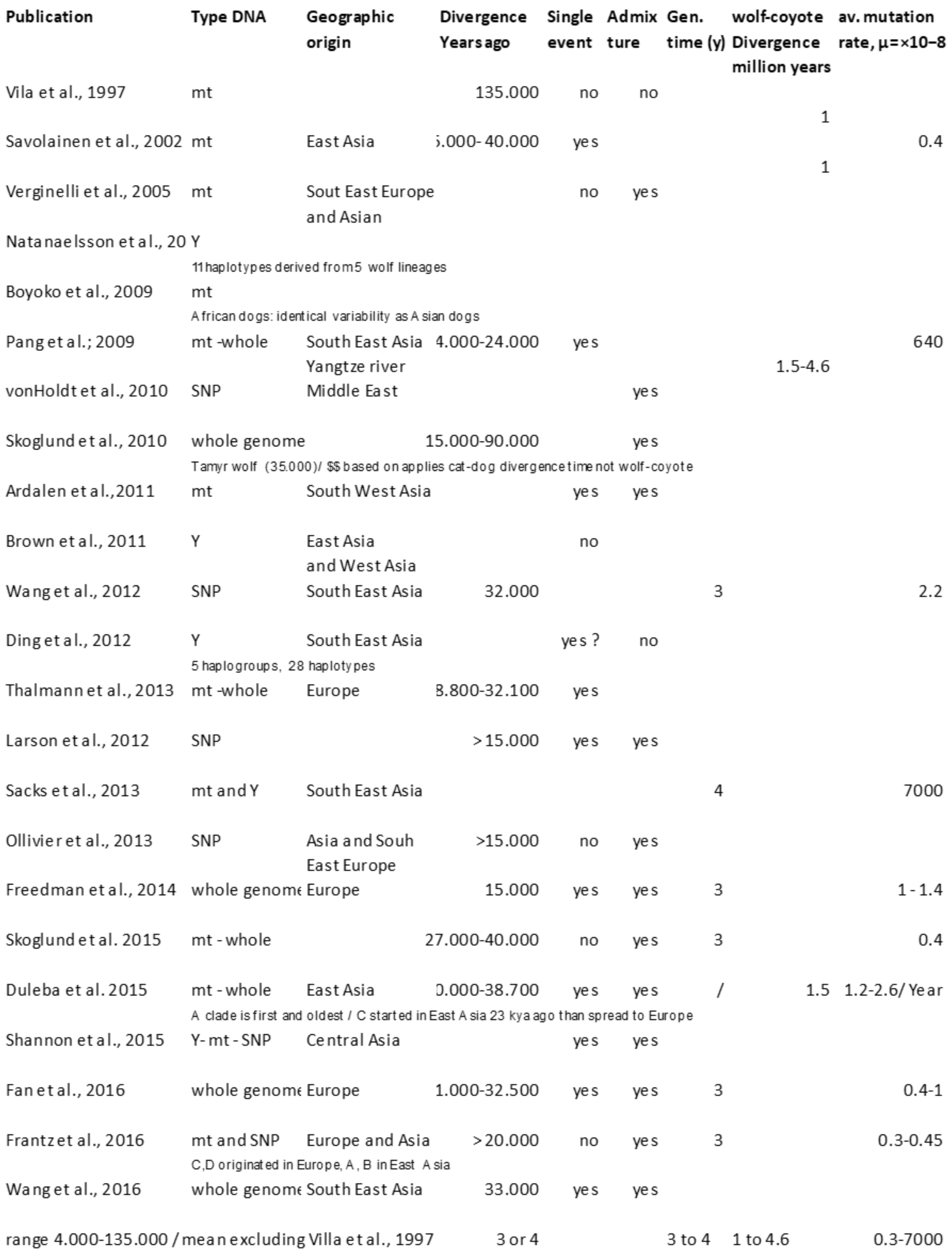
Chapter 5 is published in Journal of Archaeological Science: Reports as: An evaluation of classical morphological and morphometric parameters reported to distinguish wolves and dogs. by: L. Janssens, A. Perri, P. Crombé, S. Van Dongen, D. Lawler DOI 10.1016/j.asrep.2018.10.012

### 4.5. Project 5 (Chapter 6)

The thesis concludes with an overview of historically used morphometric and morphological differences reported between dogs and wolves, and which of these still stand based on and critical evaluation and results of former chapters (2-5). Next it suggests which research is still missing, and could be done it the future. A specific weak point of all published research, including the work in this thesis, is emphasised, being the paucity of studied Upper Palaeolithic material. The large stature Pleistocene canids, presented as proto- or insipient- dogs (Germonpré et al., 2009, 2011, 2015), cannot be differentiated from wolves according to our studies, and should be classified accordingly. We propose that new anatomical structures need to be added to the rather small fan of traits distinguishing wolves and dogs, one such structure could be the inner ear, housed in the petrous bone that could be studied with geometric morphometrics, a technique so much more powerful compared to classical morphology.

## 5. Tables

**Table 1. DNA research on wolf-dog divergence**



| Publication | Type DNA | Geographic origin | Divergence Years ago | Single event | Admix ture | Gen. time (y) | wolf-coyote Divergence million years | av. mutation rate, μ=×10−8 |
|---|---|---|---|---|---|---|---|---|
| Vila et al., 1997 | mt | | 135.000 | no | no | | | |
| | | | | | | | 1 | |
| Savolainen et al., 2002 | mt | East Asia | 5.000- 40.000 | yes | | | | 0.4 |
| | | | | | | | 1 | |
| Verginelli et al., 2005 | mt | Sout East Europe<br>and Asian | | no | yes | | | |
| Natanaelsson et al., 20 | Y | | | | | | | |
| | 11 haplotypes derived from 5 wolf lineages | | | | | | | |
| Boyoko et al., 2009 | mt | | | | | | | |
| | African dogs: identical variability as Asian dogs | | | | | | | |
| Pang et al.; 2009 | mt -whole | South East Asia | 4.000-24.000 | yes | | | | 640 |
| | | Yangtze river | | | | | 1.5-4.6 | |
| vonHoldt et al., 2010 | SNP | Middle East | | | yes | | | |
| Skoglund et al., 2010 | whole genome | | 15.000-90.000 | | yes | | | |
| | Tamyr wolf (35.000)/ $$ based on applies cat-dog divergence time not wolf-coyote | | | | | | | |
| Ardalen et al.,2011 | mt | South West Asia | | yes | yes | | | |
| Brown et al., 2011 | Y | East Asia<br>and West Asia | | no | | | | |
| Wang et al., 2012 | SNP | South East Asia | 32.000 | | | 3 | | 2.2 |
| Ding et al., 2012 | Y | South East Asia | | yes ? | no | | | |
| | 5 haplogroups, 28 haplotypes | | | | | | | |
| Thalmann et al., 2013 | mt -whole | Europe | 8.800-32.100 | yes | | | | |
| Larson et al., 2012 | SNP | | >15.000 | yes | yes | | | |
| Sacks et al., 2013 | mt and Y | South East Asia | | | | 4 | | 7000 |
| Ollivier et al., 2013 | SNP | Asia and Souh<br>East Europe | >15.000 | no | yes | | | |
| Freedman et al., 2014 | whole genome | Europe | 15.000 | yes | yes | 3 | | 1 - 1.4 |
| Skoglund et al. 2015 | mt - whole | | 27.000-40.000 | no | yes | 3 | | 0.4 |
| Duleba et al. 2015 | mt - whole | East Asia | 0.000-38.700 | yes | yes | / | 1.5 | 1.2-2.6/ Year |
| | A clade is first and oldest / C started in East Asia 23 kya ago than spread to Europe | | | | | | | |
| Shannon et al., 2015 | Y- mt - SNP | Central Asia | | yes | yes | | | |
| Fan et al., 2016 | whole genome | Europe | 1.000-32.500 | yes | yes | 3 | | 0.4-1 |
| Frantz et al., 2016 | mt and SNP | Europe and Asia | >20.000 | no | yes | 3 | | 0.3-0.45 |
| | C,D originated in Europe, A, B in East Asia | | | | | | | |
| Wang et al., 2016 | whole genome | South East Asia | 33.000 | yes | yes | | | |
| range 4.000-135.000 / mean excluding | | Villa et al., 1997 | 3 or 4 | | | 3 to 4 | 1 to 4.6 | 0.3-7000 |

**Table 2. Pleistocene canids; with details on Pleistocene small stature dogs**

| **Specimen** | **Dating** | **aDNA** | **Country** | **MNI** | **Publication** | **Osteological rests** |
|---|---|---|---|---|---|---|
| **A. Small stature do** | indirect | clade | | | | |
| **A1. Pleistocene n=1** | is bold | mt DNA | | | | |
| | kya | | | | | |
| Eralla | 12 or 19 | | Spain | lost | Altuna et al., 1984, Vigne, 2005 | humerus part R |
| Bonn-Oberkassel | 14.3 | C | Germany | 2 | Street, 2002; Janssens et al., 20 | C1, T3, L3, P2, mandible L |
| | | | | | | humerus part L maxilla rostral part R<br>metacarpus 4 L, I2, I3, P1, P3, M1 maxilla R<br>radius part L P1, P3 maxilla L<br>ulna part L/R, I2, I3, C, P4, M1, M2 mandible R |
| Kartstein | 12.5 | C | Germany | | Baales, 1992 | 6 phalanges |
| Monruz | 16 | | Switzerland | 2 | Leesch et al., 2012 | Pd4,Pd3 (n=3), Cd |
| Kesslerloch | 14.3 | C | Switzerland | | Napierala and Uerpmann, 2010 | P4, M1 mandibular, maxilla part M1,M2, M3 |
| Hauterive-Champréveyre | **15.5** | | Switzerland | | Mörel and Muller, 1997 | C partial maxilla Left |
| Montespan | **14.5** | | France | | Pionnier-Capitan et al., 2011 | femur R, C1 |
| Le Closeau | **14.4** | | France | | Pionnier-Capitan et al., 2011 | mandible, skull, cervical vertebrae, humerusL |
| Duruthy | Azilian13.5 | | France | | Boudadi-Maligne et al,. 2018 | |
| Troubat | Azilian13.5 | | France | | Boudadi-Maligne et al,. 2018 | |
| Mège | Magdalian14.5 | | France | | Boudadi-Maligne et al., 2018 | |
| Le Morin | 14.5 | | France | 2 | Boudadi-Maligne et al., 2012 | femur, tibia, humerus, radius, teeth |
| Ain Mallaha | **11.5** | | Israel | 2 | Tchernov and Valla 1997 | mandible |
| | **14.5** | | | | Grosman, et al., 2013 | complete skeleton (pup) |
| Pelegawra | 12500 | | Iraq | lost? | Turnbull and Reed, 1974 | mandible |
| **A2. Pleistocene-Holocene transition n=13** | | | | | | |
| Pont d'Ambon | 11.5 | C | France | 3 | Pionnier-Capitan, et al., 2011 | many fragments |
| Saint-Thibaud-de-Couz | 11.6 | | France | | Chaix , 2000 | skull cervical vertebrae, mandible, teeth, femur |
| Bedburg | **11.6** | | Germany | 3? | Street, et al., 2016 | skull and long bones |
| Senckenberg-Moor | **11.0** | | Germany | | Mertens, 1936 | skull complete |
| Shillourokambos | **11.4** | | Cyprus | | Vigne, et al., 2011 | falanx |
| Hayonim | 12 | | Israel | 2 | Tchernov and Valla 1997 | many fragments |
| Star Carr | 11700 | | Great Britain | | Degerbøl, 1961 | skull, femur, tibia |
| Seamer Carr | 11200 | | Great Britain | | Day, 1996 | 6 cervical vertebrae |
| Tell Mureybet | 11500 | | Syria | | Gourichon and Helmer, 2008 | mandibles and skull |
| **B. Large stature presumed Paleolithic dogs n=11** | | | | | | |
| Goyet 2860 | 34 | | Belgium | | Germonpré et al., 2009 | |
| Mezin 5490 | 14 | | The Ukraine | | Pidoplichko et al., 2001 | |
| Mezirhich 4493/24° | 14 | | The Ukraine | | Germonpré et al., 2009 | |
| Eliseevichi 447/5298 | 16 | | Russia | | Sablin and Khoplachev, 2002 | |
| Eliseevichi 23781/24 | 15 | | Russia | | Sablin and Khoplachev, 2002 | |
| Předmostí OK1060 | 26.5 | | Czech republic | | Germonpré et al., 2012 | |
| Předmostí OK1069/3 | 26.5 | | Czech republic | | Germonpré et al., 2012 | |
| Předmostí - | 26.5 | | Czech republic | | Germonpré et al., 2012 | |
| Ulakhan Sular 1346 | 17 | | Russia | | Germonpré et al., 2017 | |
| Razboyincha | 33 | | Russia | | Ovodov et al., 2011 | |
| Hohle Fels | 40 | | Germany | | Camaros et al., 2016 | |

**Table 3. Morphometric and morphological differences mentioned as distuinguishing criteria between wolves and dogs, as reported in the literature**

| Reported as specific for dogs | Reference | Partially or totally Contested by |
|---|---|---|
| Backward turning of the dorsal part of the vertical mandibular ram | Olsen and Olsen, 1977 | Janssens et al., 2017? |
| Oral abnormalities including tooth agenesis and crowding | Andersone and Ozolins, 2007, Benecke, 1994, Germonpré, et al., 2015, Stockhaus, 1965, Wobeser, 1992 | Janssens et al., 2017 b? |
| Paedomorphosis | Morey, 1994, Waller et al., 2013 | Drake, 2011 |
| Reduced length of P4 compared to M1+2 | Clutton-Brock, 1962 | Gaudry and Boule, 1892, Wolfgram, 1884 |
| Smaller saggital crest | Studer, 1901 | Lawrence and Bossert, 1967, Rizk, 2012 |
| Larger orbital angle | Aaris-Sørensen 1977, Bockelmann, 1920, Iljin, 1941, Sablin and Khlopachev, 2002, Studer, 1901 | Janssens et al., 2017C |
| Convex and "sturdy-massive" mandible | Bökönyi, 1975, Clutton-Brock, 1962, Germonpré, et al., 2015, Lawrence and Reed, 1983, Tchernov and Valla, 1997 | Drake et al., 2017 |
| Smaller tympanic bulla | Benecke, 1987, Bökönyi, 1975, Zeuner, 1963 | Stockhaus, 1965 |
| Difference in contact points of the skull on a horizontal plane | Zeuner, 1963 | Janssens et al., this thesis |
| Caudal shifting of the caudal hard palate border | Benecke, 1987, Iljin, 1941 | Janssens et al., this thesis |
| Smaller stature with isometric smaller skull | Benecke, 1987, Degerbøl, 1961, Stockhaus, 1965, Studer, 1901, Vigne and Marinval-Vigne, 1988, Wolfgram, 1894 | |
| Shorter snouts | Benecke, 1987, Bökönyi, 1975, Clutton-Brock, 1995, Iljin, 1941,, Nehring, 1888, Olsen, 1985, Ovodov et al., 201, Pidoplichk | Janssens et al., this thesis, Morey, Wayne, 19 |
| Tooth crowding | Benecke, 1994, Wolfgram, 1894 | Ameen et al., 2017 |
| Wider snout | Morey, 1994, Rizk, 2012, Schmitt and Wallace, 2012, Stockhaus, 1965, Studer, 190, Tchernov and Valla 1997, Wayne 1986 | |
| Protcone difference | Camaros et al., 2016 | Janssens et al., this thesis |
| Higher skull index | Pitulko and Kasparov, 2017 | |
| Higher snout index | Pitulko and Kasparov, 2017 | Janssens et al., this thesis |
| Carnassial size reduction | Clutton-Brock, 1962, Lawrence and Reed, 1983, Morey, 1992, Morey, 201, Tchernov and Horwitz, 1991, Tchernov and Valla, 1997 | |

## 6. References

Aaris-Sørensen , K. (1977). The subfossil wolf, *Canis lupus* L. in Demark. *Vidensk. Meddr dabsk naturhistorisch Forensen*(140), 129-146.

Adams, D. C., Rohlf, F. J., & Slice, D. E. (2004). Geometric morphometrics: ten years of progress following the 'revolution'. *Italian Journal of Zoology, 71*(1), 5-16.

Ameen, C., Hulme-Beaman, A., Evin, A., Germonpré, M., Britton, K., Cucchi, T., . . . Dobney, K. (2017). A landmark-based approach for assessing the reliability of mandibular tooth crowding as a marker of dog domestication. *Journal of Archaeological Science, 85*, 41-50.

Anderson, T. M., Candille, S. I., Musiani, M., Greco, C., Stahler, D. R., Smith, D. W., . . . Bustamante, C. D. (2009). Molecular and evolutionary history of melanism in North American gray wolves. *Science, 323*(5919), 1339-1343.

Andersone, Z., & Ozolins, J. (2000). Craniometrical characteristics and dental anomalies in wolves Canis lupus from Latvia. *Acta Theriologica, 45*(4), 549-558.

Arbuckle, B. S. (2002). *Experimental animal domestication and its application to the study of animal exploitation in prehistory.* Paper presented at the International Conference of Archaeozoology Durham.

Ardalan, A., Kluetsch, C. F., Zhang, A. b., Erdogan, M., Uhlén, M., Houshmand, M., . . . Savolainen, P. (2011). Comprehensive study of mtDNA among Southwest Asian dogs contradicts independent domestication of wolf, but implies dog–wolf hybridization. *Ecology and evolution, 1*(3), 373-385.

Axelsson, E., Ratnakumar, A., Arendt, M.-L., Maqbool, K., Webster, M. T., Perloski, M., . . . Lindblad-Toh, K. (2013). The genomic signature of dog domestication reveals adaptation to a starch-rich diet. *Nature, 495*(7441), 360-364.

Belyaev, D., Plyusnina, I., & Trut, L. (1985). Domestication in the silver fox (Vulpes Fulvus Desm): Changes in physiological boundaries of the sensitive period of primary socialization. *Applied Animal Behaviour Science, 13*(4), 359-370.

Benecke, N. (1987). Studies on early dog remains from Northern Europe. *Journal of Archaeological Science, 14*(1), 31-49.

Benecke, N. (1994). *Archäozoologische Studien zur Entwicklung der Haustierhaltung* (Vol. 64). Berlin: Akademie Verlag Schriften zur Ur- und Frühgeschichte

Bockelmann, H. (1920). *Untersuchungen an Wolfsbastarden nach Ziichtungsversuchen im Haustiergarten zu Halle a. S.* Dissertation, Universit Halle,

Bökönyi, S. (1975). *Vlasac: an early site of dog domestication*. Amsterdam: North Holland Publishing Company

Bookstein, F. L. (1997). *Morphometric tools for landmark data: geometry and biology*: Cambridge University Press.

Boudadi-Maligne, M. (2010). *Les Canis pleistocenes du sud de la France: approche biosystematique, evolutive et biochronologique.* (PhD), Université Bordeaux 1, Bordeaux.

Boudadi-Maligne, M., & Escarguel, G. (2014). A biometric re-evaluation of recent claims for Early Upper Palaeolithic wolf domestication in Eurasia. *Journal of Archaeological Science, 45*, 80-89.

Boudadi-Maligne, M., Mallye, J.-B., Langlais, M., & Barshay-Szmidt, C. (2012a). Des restes de chiens magdaléniens à l'abri du Morin (Gironde, France). Implications socio-économiques d'une innovation zootechnique. *PALEO. Revue d'archéologie préhistorique*(23), 39-54.

Boudadi-Maligne, M., Mallye, J.-B., Langlais, M., & Barshay-Szmidt, C. (2012b). Magdalenian dog remains from Le Morin rock-shelter (Gironde, France). Socio-economic implications of a zootechnical innovation. *PALEO. Revue d'archéologie préhistorique*(23), 39-54.

Boyko, A. R., Quignon, P., Li, L., Schoenebeck, J. J., Degenhardt, J. D., Lohmueller, K. E., . . . Cargill, M. (2010). A simple genetic architecture underlies morphological variation in dogs. *PLoS biology, 8*(8), e1000451.

Brown, E. A., Dickinson, P. J., Mansour, T., Sturges, B. K., Aguilar, M., Young, A. E., . . . Varon, S. (2017). FGF4 retrogene on CFA12 is responsible for chondrodystrophy and intervertebral disc disease in dogs. *Proceedings of the National Academy of Sciences*, 201709082.

Cadieu, E., Neff, M. W., Quignon, P., Walsh, K., Chase, K., Parker, H. G., . . . Byers, A. (2009). Coat variation in the domestic dog is governed by variants in three genes. *Science, 326*(5949), 150-153.

Camarós, E., Münzel, S. C., Cueto, M., Rivals, F., & Conard, N. J. (2016). The evolution of Paleolithic hominin–carnivore interaction written in teeth: Stories from the Swabian Jura (Germany). *Journal of Archaeological Science: Reports, 6*, 798-809.

Clutton-Brock, J. (1962). Near Eastern canids and the affinities of the Natufian dogs. *Zeitschrift für Tierzüchtung und Züchtungsbiologie, 76*, 326-333.

Clutton-Brock, J. (1963). The origins of the dog. *Science in archaeology*, 269-274.

Clutton-Brock, J. (1995a). Origins of the dog: domestication and early history. *The domestic dog: Its evolution, behaviour and interactions with people*, 7-20.

Clutton-Brock, J. (1995b). Origins of the dog: domestication and early history. In J. Serpell (Ed.), *The domestic dog: Its evolution, behaviour and interactions with people* (pp. 7-20). Cambridge: Cambridge University Press.

Clutton-Brock, J. (2012). *Animals as domesticates: a world view through history*. East Lansing: Michigan University Press.

Clutton-Brock, J. (1992). The process of domestication. *Mammal Review, 22*(2), 79-85.

Crockford, S. J. (2005). *Native dog types in north America before arrival of European dogs.* Paper presented at the Oral presentation at World Small Animal Veterinary Association Congress, Mexico City.

Darwin, C. R. (1868). Variation of plants and animals under domestication.

Dayan, T. (1994a). Carnivore diversity in the Late Quaternary of Israel. *Quaternary Research, 41*(3), 343-349.

Dayan, T. (1994b). Early domesticated dogs of the Near East. *Journal of Archaeological Science, 21*(5), 633-640.

Degerbøl, M. (1961a). On a find of a Preboreal domestic dog *Canis familiaris* L. from Star Carr, Yorkshire, with remarks on other Mesolithic dogs. *Proceedings of the Prehistoric Society (New Series), 27*, 35-55.

Degerbøl, M. (1961b). Der Hund, das älteste Haustier Dänemarks. *Zeitschrift für Tierzüchtung und Züchtungsbiologie, 76*(1 - 4), 334-341.

Deguilloux, M., Moquel, J., Pemonge, M., & Colombeau, G. (2009). Ancient DNA supports lineage replacement in European dog gene pool: insight into Neolithic southeast France. *Journal of Archaeological Science, 36*(2), 513-519.

Dimitrijević, V. (2006). Vertebrate fauna of Vinča-Belo Brdo: Excavation campaigns 1998-2003. *Starinar*(56), 245-269.

Dimitrijević, V., & Vuković, S. (2012). Was the dog locally domesticated in the Danube Gorges? Morphometric study of dog cranial remains from four Mesolithic–Early Neolithic archaeological sites by comparison with contemporary wolves. *International Journal of Osteoarchaeology, 22*(1), 12-34.

Drake, A. G. (2011). Dispelling dog dogma: an investigation of heterochrony in dogs using 3D geometric morphometric analysis of skull shape. *Evolution & development, 13*(2), 204-213.

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*.

Drake, A. G., & Klingenberg, C. P. (2008). The pace of morphological change: historical transformation of skull shape in St Bernard dogs. *Proceedings of the Royal Society B: Biological Sciences, 275*(1630), 71-76.

Drake, A. G., & Klingenberg, C. P. (2010). Large-scale diversification of skull shape in domestic dogs: disparity and modularity. *The american naturalist, 175*(3), 289-301.

Drögemüller, C., Karlsson, E. K., Hytönen, M. K., Perloski, M., Dolf, G., Sainio, K., . . . Leeb, T. (2008). A mutation in hairless dogs implicates FOXI3 in ectodermal development. *Science, 321*(5895), 1462-1462.

Fondon, J. W., & Garner, H. R. (2007). Detection of length-dependent effects of tandem repeat alleles by 3-D geometric decomposition of craniofacial variation. *Development genes and evolution, 217*(1), 79-85.

Frantz, L. A., Mullin, V. E., Pionnier-Capitan, M., Lebrasseur, O., Ollivier, M., Perri, A., . . . Dimopoulos, E. A. (2016). Genomic and archaeological evidence suggest a dual origin of domestic dogs. *Science, 352*(6290), 1228-1231.

Freedman, A. H., Gronau, I., Schweizer, R. M., Ortega-Del Vecchyo, D., Han, E., Silva, P. M., . . . Lorente-Galdos, B. (2014). Genome sequencing highlights the dynamic early history of dogs. *PLoS genetics, 10*(1), e1004016.

Freedman, A. H., Schweizer, R. M., Gronau, I., Han, E., Vecchyo, D. O.-D., Silva, P. M., . . . Lorente-Galdos, B. (2013). Genome Sequencing Highlights Genes Under Selection and the Dynamic Early History of Dogs. *arXiv preprint arXiv:1305.7390*.

Galton, F. (1865). The first steps towards the domestication of animals. *Transactions of the Ethnological Society of London, 3*, 122-138.

Gaudry, A., & Boule, M. (1892). Les oubliettes de Gargas. *Matériaux pour l'Histoire des Temps Quaternaires, 4*, 130.

Germonpré, M., Fedorov, S., Danilov, P., Galeta, P., Jimenez, E.-L., Sablin, M., & Losey, R. J. (2017). Palaeolithic and prehistoric dogs and Pleistocene wolves from Yakutia: Identification of isolated skulls. *Journal of Archaeological Science, 78*, 1-19.

Germonpré, M., Lázničková-Galetová, M., Losey, R. J., Räikkönen, J., & Sablin, M. V. (2015). Large canids at the Gravettian Předmostí site, the Czech Republic: the mandible. *Quaternary International, 359*, 261-279.

Germonpré, M., Lázničková-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., Stevens, R. E., Hedges, R. E., Hofreiter, M., Stiller, M., & Després, 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.

Gray, M. M., Sutter, N. B., Ostrander, E. A., & Wayne, R. K. (2010). The IGF1 small dog haplotype is derived from Middle Eastern grey wolves. *BMC biology, 8*(1), 16.

Gundry, R. L., Allard, M. W., Moretti, T. R., Honeycutt, R. L., Wilson, M. R., Monson, K. L., & Foran, D. R. (2007). Mitochondrial DNA analysis of the domestic dog: control region variation within and among breeds. *Journal of forensic sciences, 52*(3), 562-572.

Hoopes, B. C., Rimbault, M., Liebers, D., Ostrander, E. A., & Sutter, N. B. (2012). The insulin-like growth factor 1 receptor (IGF1R) contributes to reduced size in dogs. *Mammalian Genome, 23*(11-12), 780-790.

Horard-Herbin, M.-P., Tresset, A., & Vigne, J.-D. (2014). Domestication and uses of the dog in western Europe from the Paleolithic to the Iron Age. *Animal Frontiers, 4*(3), 23-31.

Huxley, T. H. (1880). *On the Cranial and Dental Characters of the Canidæ.* Paper presented at the Proceedings of the Zoological Society of London.

Iljin, N. A. (1941). Wolf-dog genetics. *Journal of Genetics, 42*(3), 359-414.

Irion, D., Schaffer, A., Famula, T., Eggleston, M., Hughes, S., & Pedersen, N. (2003). Analysis of genetic variation in 28 dog breed populations with 100 microsatellite markers. *Journal of Heredity, 94*(1), 81-87.

Jolicoeur, P. (1959). Multivariate geographical variation in the wolf Canis lupus L. *Evolution*, 283-299.

Kerns, J., Cargill, E., Clark, L. A., Candille, S., Berryere, T., Olivier, M., . . . Barsh, G. (2007). Linkage and segregation analysis of black and brindle coat color in domestic dogs. *Genetics*.

Khosravi, R., Kaboli, M., Rezaei, H., & Montazemi, S. (2012). Evaluation of genetic variability in Iranian wolf *(Canis lupus pallipes*) and free-ranging dog (*C. familliaris*) populations using microsatellite markers. In: J Novin Genetics.

Kim, J. H., Kang, K. I., Sohn, H. J., Woo, G. H., Jean, Y. H., & Hwang, E. K. (2005). Color-dilution alopecia in dogs. *Journal of veterinary science, 6*(3), 259-261.

Klütsch, C. F., & de Caprona, M. D. C. (2010). The IGF1 small dog haplotype is derived from Middle Eastern grey wolves: a closer look at statistics, sampling, and the alleged Middle Eastern origin of small dogs. *BMC biology, 8*(1), 119.

Klütsch, C. F., & Savolainen, P. (2011). Geographical origin of the domestic dog. *eLS*.

Koler-Matznick, J. (2002). The origin of the dog revisited. *Anthrozoos: A Multidisciplinary Journal of The Interactions of People & Animals, 15*(2), 98-118.

Koler-Matznick, J. (2016). *Dawn of the dog, The Genesis of a Natural Species*. Oregon, USA: Cynology Press.

Kruska, D. (1986). How fast can total brain size change in mammals? *Journal fur Hirnforschung, 28*(1), 59-70.

Kruska, D. (1988a). Effects of domestication on brain structure and behavior in mammals. *Human Evolution, 3*(6), 473-485.

Kruska, D. (1988b). Mammalian domestication and its effect on brain structure and behavior. In *Intelligence and evolutionary biology* (pp. 211-250): Springer.

Larson, G., & Burger, J. (2013). A population genetics view of animal domestication. *Trends in Genetics, 29*(4), 197-205.

Larson, G., Karlsson, E. K., Perri, A., Webster, M. T., Ho, S. Y., Peters, J., . . . Fredholm, M. (2012). Rethinking dog domestication by integrating genetics, archeology, and biogeography. *Proceedings of the National Academy of Sciences, 109*(23), 8878-8883.

Lawing, A. M., & Polly, P. D. (2010). Geometric morphometrics: recent applications to the study of evolution and development. *Journal of Zoology, 280*(1), 1-7.

Lawrence, B., & Bossert, W. H. (1967). Multiple character analysis of Canis lupus, latrans, and familiaris, with a discussion of the relationships of Canis niger. *American Zoologist, 7*(2), 223-232.

Lawrence, B., & Reed, C. A. (1983). The dogs of Jarmo. *Prehistoric Archeology Along the Zagros Flanks. Chicago: University of Chicago Oriental Institute*, 485-489.

Leonard, J. A., Wayne, R. K., Wheeler, J., Valadez, R., Guillén, S., & Vila, C. (2002). Ancient DNA evidence for Old World origin of New World dogs. *Science, 298*(5598), 1613-1616.

Lindblad-Toh, K., Wade, C. M., Mikkelsen, T. S., Karlsson, E. K., Jaffe, D. B., Kamal, M., . . . Zody, M. C. (2005). Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature, 438*(7069), 803.

Little, C. (1958). Coat color genes in rodents and carnivores. *The Quarterly Review of Biology, 33*(2), 103-137.

Lorenz, K. (2002). *Man meets dog*. New York: Psychology Press, Taylor and Francis group.

Mertens, R. (1936). Der Hund aus dem Senckenberg-Moor, Ein Begleiter des Urs. *Natur und Volk, 66*, 506-510.

Miller, R. (2012). Mapping the expansion of the Northwest Magdalenian. *Quaternary International, 272*, 209-230.

Morey, D. F. (1992). Size, shape and development in the evolution of the domestic dog. *Journal of Archaeological Science, 19*, 181-204.

Morey, D.F., (1994). The early evolution of the domestic dog. Am. Sci. *82*, 336–347.

Morey, D. (2010). *Dogs: domestication and the development of a social bond*. Cambridge: Cambridge University Press.

Napierala, H., & Uerpmann, H. P. (2012). A 'new'Palaeolithic dog from Central Europe. *International Journal of Osteoarchaeology, 22*(2), 127-137.

Nehring, A. (1888). Zur Abstammung der Hunde-Rassen.

Newsome, A., & Corbett, L. (1985). The identity of the dingo III.* The incidence of dingoes, dogs and hybrids and their coat colours in remote and settled regions of Australia. *Australian Journal of Zoology, 33*(3), 363-375.

Olsen, S. J. (1985). *Origins of the domestic dog: the fossil record*: University of Arizona Press Tucson.

Olsen, S. J., & Olsen, J. W. (1977). The Chinese wolf, ancestor of New World dogs. *Science, 197*(4303), 533-535.

Ostrander, E. A., & Wayne, R. K. (2005). The canine genome. *Genome research, 15*(12), 1706-1716.

Pang, J.-F., Kluetsch, C., Zou, X.-J., Zhang, A.-b., Luo, L.-Y., Angleby, H., . . . Lundeberg, J. (2009). mtDNA data indicate a single origin for dogs south of Yangtze River, less than 16,300 years ago, from numerous wolves. *Molecular biology and evolution, 26*(12), 2849-2864.

Pionnier-Capitan, M. (2010). *La domestication du chien en Eurasie: étude de la diversité passée, approches ostéoarchéologiques, morphométriques et paléogénétiques.* Lyon, École normale supérieure (Sciences),

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.

Pluskowski, A. (2006). Where are the wolves? Investigating the scarcity of European grey wolf (*Canis lupus lupus*) remains in medieval archaeological contexts and its implications. *International Journal of Osteoarchaeology, 16*(4), 279-295.

Randi, E., & Lucchini, V. (2002). Detecting rare introgression of domestic dog genes into wild wolf (*Canis lupus*) populations by Bayesian admixture analyses of microsatellite variation. *Conservation Genetics, 3*(1), 29-43.

Randi, E., Lucchini, V., & Francisci, F. (1993). Allozyme variability in the Italian wolf (Canis lupus) population. *HEREDITY-LONDON-, 71*, 516-516.

Rizk, O. T. (2012). Insight into the Genetic Basis of Craniofacial Morphological Variation in the Domestic Dog, Canis familiaris.

Rütimeyer, L. (1861). *Die Fauna der Pfahlbauten der Schweiz. Geschichte der Wilden und der Haus-Saugetiere*. Basel: Neue Denkschrift der Algemeinne Schweizerische Geselschaft der ges.Naturwissenschaft, 19.

Rütimeyer, L. (1875). *Die Knochenhöhle von Thayingen bei Schaffhausen*: F. Vieweg & Sohn.

Sablin, M., & Khlopachev, G. (2002). The earliest ice age dogs: evidence from Eliseevichi 11. *Current Anthropology, 43*(5), 795-799.

Savolainen, P., Zhang, Y.-p., Luo, J., Lundeberg, J., & Leitner, T. (2002). Genetic evidence for an East Asian origin of domestic dogs. *Science, 298*(5598), 1610-1613.

Schmitt, E., & Wallace, S. (2012). Shape change and variation in the cranial morphology of wild canids (Canis lupus, Canis latrans, Canis rufus) compared to domestic dogs (Canis familiaris) using geometric morphometrics. *International Journal of Osteoarchaeology*.

Schmutz, S., & Berryere, T. (2007). Genes affecting coat colour and pattern in domestic dogs: a review. *Animal genetics, 38*(6), 539-549.

Schmutz, S. M., Berryere, T. G., Barta, J. L., Reddick, K. D., & Schmutz, J. K. (2007). Agouti sequence polymorphisms in coyotes, wolves and dogs suggest hybridization. *Journal of Heredity, 98*(4), 351-355.

Schmutz, S. M., Berryere, T. G., & Dreger, D. L. (2009). MITF and white spotting in dogs: a population study. *Journal of Heredity, 100*(suppl_1), S66-S74.

Schoenebeck, J. J., Hutchinson, S. A., Byers, A., Beale, H. C., Carrington, B., Faden, D. L., . . . Ostrander, E. A. (2012). Variation of BMP3 Contributes to Dog Breed Skull Diversity. *PLoS genetics, 8*(8). doi:10.1371/journal.pgen.1002849

Schoenebeck, J. J., & Ostrander, E. A. (2013). The genetics of canine skull shape variation. *Genetics, 193*(2), 317-325.

Shannon, L. M., Boyko, R. H., Castelhano, M., Corey, E., Hayward, J. J., McLean, C., . . . Bondjengo, N. I. (2015). Genetic structure in village dogs reveals a Central Asian domestication origin. *Proceedings of the National Academy of Sciences, 112*(44), 13639-13644.

Skoglund, P., Götherström, A., & Jakobsson, M. (2011). Estimation of population divergence times from non-overlapping genomic sequences: examples from dogs and wolves. *Molecular biology and evolution, 28*(4), 1505-1517.

Stein, E. M., & Weiss, G. (2016). *Introduction to Fourier analysis on Euclidean spaces (PMS-32)* (Vol. 32): Princeton university press.

Stockhaus, K. (1965). Metrische Untersuchungen an Schädeln von Wölfen und Hunden. *Journal of Zoological Systematics and Evolutionary Research, 3*(1 ‐ 2), 157-258.

Studer, T. (1901). Die prähistorischen Hunde in ihrer Beziehung zu den gegenwärtig lebenden Rassen.

Terrenato, L., & Ulizzi, L. (1983). Genotype-environment relationships: an analysis of stature distribution curves during the last century in Italy. *Annals of Human Biology, 10*(4), 335-346.

Thalmann, O., Shapiro, B., Cui, P., Schuenemann, V., Sawyer, S., Greenfield, D., . . . Domingo-Roura, X. (2013). Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science, 342*(6160), 871-874.

Thompson, D. (1977). 'AW 1942. On growth and form. In (pp. 1-346): Cambridge University Press, Cambridge.

Tsuda, K., Kikkawa, Y., Yonekawa, H., & Tanabe, Y. (1997). Extensive interbreeding occurred among multiple matriarchal ancestors during the domestication of dogs: evidence from inter-and intra-species polymorphisms in the D-loop region of mitochondrial DNA between dogs and wolves. *Genes & genetic systems, 72*(4), 229-238.

Vaysse, A., Ratnakumar, A., Derrien, T., Axelsson, E., Pielberg, G. R., Sigurdsson, S., . . . Lawley, C. T. (2011). Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLoS genetics, 7*(10), e1002316.

Vilà, C., Savolainen, P., Maldonado, J. E., Amorim, I. R., Rice, J. E., Honeycutt, R. L., . . . Wayne, R. K. (1997). Multiple and ancient origins of the domestic dog. *Science, 276*(5319), 1687-1689.

Vonholdt, B., Pollinger, J. P., Lohmueller, K. E., Han, E., Parker, H. G., Quignon, P., . . . Reynolds, A. (2010). Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature, 464*(7290), 898-902.

vonHoldt, B. M., Ji, S. S., Aardema, M. L., Stahler, D. R., Udell, M. A., & Sinsheimer, J. S. (2018). Activity of Genes with Functions in Human Williams–Beuren Syndrome Is Impacted by Mobile Element Insertions in the Gray Wolf Genome. *Genome biology and evolution, 10*(6), 1546-1553.

Waller, B. M., Peirce, K., Caeiro, C. C., Scheider, L., Burrows, A. M., McCune, S., & Kaminski, J. (2013). Paedomorphic facial expressions give dogs a selective advantage. *PLoS One, 8*(12), e82686.

Wang, G.-d., Zhai, W., Yang, H.-c., Fan, R.-x., Cao, X., Zhong, L., . . . Cheng, L.-g. (2013). The genomics of selection in dogs and the parallel evolution between dogs and humans. *Nature communications, 4*, 1860.

Wayne, R. K. (1986). Cranial morphology of domestic and wild canids: the influence of development on morphological change. *Evolution, 40*, 243-261.

Wayne, R. K., & Jenks, S. M. (1991). Mitochondrial DNA analysis implying extensive hybridization of the endangered red wolf Canis rufus. *Nature, 351*(6327), 565.

Wayne, R. K., & Ostrander, E. A. (1999). Origin, genetic diversity, and genome structure of the domestic dog. *BioEssays, 21*(3), 247-257.

Wayne, R. K., & Ostrander, E. A. (2007). Lessons learned from the dog genome. *Trends in Genetics, 23*(11), 557-567.

Wobeser, G. (1992). Traumatic, degenerative, and developmental lesions in wolves and coyotes from Saskatchewan. *Journal of wildlife diseases, 28*(2), 268-275.

Wolfgram, A. (1894). Die Einwerkung der Gefangenschaft auf die Gestaltung des Wolfschädels. *Zoologisches jahrbuch (Abteilung Systematik), 7*(773-822).

Zeder, M. A. (2012). The domestication of animals. *Journal of Anthropological Research, 68*, 1-161.

Zeuner, F. (1963). *The dog*. New York: Harper and Row.