# From wolf to dog

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# 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

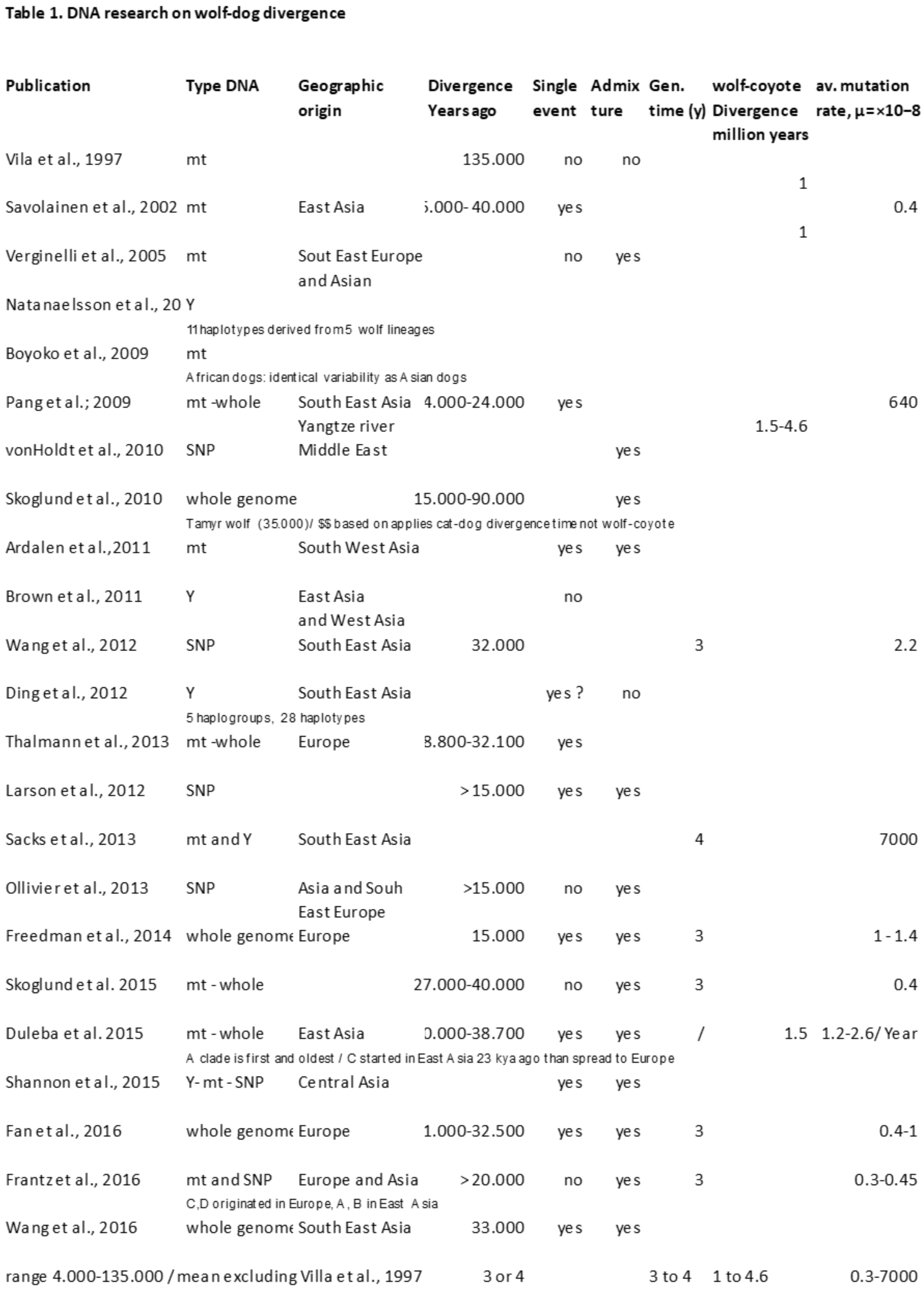

**Table 1. DNA research on wolf-dog divergence**

| Publication | Type DNA | Geographic origin | Divergence Years ago | Single event | Admixture | Gen. time (y) | wolf-coyote Divergence million years | av. mutation rate, $\mu = \times 10^{-8}$ |
|---|---|---|---|---|---|---|---|---|
| Vila et al., 1997 | mt | | 135.000 | no | no | | | |
| | | | | | | | 1 | |
| Savolainen et al., 2002 | mt | East Asia | .000- 40.000 | yes | | | | 0.4 |
| | | | | | | | 1 | |
| Verginelli et al., 2005 | mt | Sout East Europe 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<br>Yangtze river | 4.000-24.000 | yes | | | 1.5-4.6 | 640 |
| 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 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 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 | |

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