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

Chapter 6: Discussion and Conclusions

6.1. General conclusions

This thesis references papers that critically evaluate important historically-accepted classical morphometric and morphological osteological features that have been used to separate ancient dogs and ancient wolves. Our focus is those features that have not been re-evaluated the last two years. As reported in detail in the Introduction, an important driving factor for this work is that many historic morphological studies that focused on wolf-dog differences have needed thorough re-evaluation. Among those studies, a number of conclusions had been made based on small numbers of specimens; use of only modern specimens; exclusion of relevant data from older studies; and lack of critical evaluation of “axiomatic precepts”. In result, many earlier species assignments of specimens should be questioned. Fourteen generally-accepted traits have been re-evaluated, and conclusions are discussed. Criteria annotated with an asterix *, based on our research, no longer can be used to distinguish wolves and dogs.

1*. It has been accepted historically that the process of domestication introduced a number of **oral pathologies** in dogs (Andersone and Ozolins, 2007; Benecke, 1994; Stockhaus, 1965; Vila et al., 1993; Wobeser, 1992; Wolfgramm, 1894). However, our study shows that, among 60 wild wolves of two subspecies (1680 teeth), oral pathologies of wolves are neither fewer nor different than dogs (Chapter 2). Thus, oral pathologies cannot be used to distinguish modern dogs from modern wolves.

2*. The **dorsal coronoid process** of the vertical ramus of the mandible has been considered “typical” for dogs and ***C. lupus chanco.*** On that basis, the Tibetan wolf was proposed as the ancestor of dogs (Olsen and Olsen, 1977)**.** Our study of the skulls of 384 dogs and 60 wolves of 4 subspecies shows that this morphology cannot be used to distinguish modern dogs and modern wolves, since 20% of dogs and 80% of C. *l. chanco* specimens have the turned-back morphology.

Additionally, specimens of *C. l. pallipes* have the same morphological trait (Chapter 3). Genomic research also revealed that C. *l. chanco* is well-separated from the wolf group that lies along the pathway to the origin of dogs (Sharma et al., 2004). These studies support that the original idea of Olsen and Olsen is not correct (1977).

3. Orbital angle (OA) can be used to distinguish dogs and wolves, but only to a limited degree (Chapter 4). Angles above 60° clearly are recent dogs; angles under 35° are wolves. Mean orbital angles differ between wolves and dogs, with mean angle 42° in wolves and 55° in dogs. Neolithic dogs have mean angle 47° (range 35°-50°), in the 28^{o}-52^{o} range of modern wolves. Only a few OA have been reported from ancient wolves, and those are larger on average (44^{o}) than modern wolves (42^{o}) (Aaris-Sørensen, 1977). Thus, our results show that OA enlarged from 42° to 44° in wolves, to 47° in Neolithic dogs, and up to 55° in modern dogs.
Enlarged OA resulted from an enlarged orbital region, with lateralization of the frontal process of the zygomatic arch in dogs (Schmitt and Wallace 2012). Accompanying are: maxillary skull widening at M1 level and at the rostral region of the orbita; rostral and upward movement of frontals (stop formation); and widening of the orbital region (Drake et al. 2015). Interestingly, OA shows more fluctuating asymmetry (difference between left and right side) in Neolithic dogs than in modern dogs, with wolves being the most symmetrical. This agrees well with the evolutionary development of the three groups, with the oldest stable species being most symmetrical, and newly developing species having more asymmetry (Neolithic dogs).

4. Carnassial size reduction was advocated as a wolf-dog distinguishing trait, but comparative sample sizes were small. Based on our extensive literature search, we conclude that maxillary **P4** mesio-distal diameters above 22.5 mm indicate Pleistocene wolves, while ancient dogs have diameters under 21.8 mm. This landmark thus clearly differentiates ancient dogs and ancient wolves. Mandibular mesio-distal **M1** diameters under 22.5 mm clearly are Pleistocene dogs, and those above 26.9 mm are Pleistocene wolves. This metric thus allows for partial separation of ancient dogs and ancient wolves (Chapter 5, Tables 8 and 9).

5*. Micro-anatomy of the protocone in P4 cannot be used to assign specimens as wolf or dog (ancient or modern). This was our conclusion from a study that we conducted with modern Eurasian wolves, and from a literature search on Pleistocene wolves (Chapter 5).

6*. C**ontact points of the skull** on a horizontal plane, studied in more than 200 specimens, cannot be used to distinguish modern dogs and modern wolves. We observed considerable species overlap, with about 50% of all skulls resting on either canine teeth or M1 (Chapter 5).

7*. We studied the **caudal border of the hard palate** in nearly 250 dog specimens, and concluded that there is no general caudal shifting. Modern dogs and modern wolves, and Neolithic dogs, overlap greatly, but there was no significant difference between Neolithic dogs and modern wolves. Modern dogs did differ significantly from modern wolves and Neolithic dogs, having more rostrally positioned caudal palatine border in 80% of specimens. Among modern dogs, the palatine trait depends heavily on breed. German shepherd dogs express the trait at only 8% prevalence (Chapter 5). These results document differences between ancient and modern dogs. This should be taken into account when studying ancient dogs and wolves.

8*. Based on the literature, our own measurements, and conversion formulas, we could measure **snout indices** in more than 500 ancient and modern wolves and dogs. Our conclusions are that modern mesaticephalic dogs do not have significantly **shorter snout** index than modern wolves. Pleistocene wolves and ancient dogs did differ statistically (Chapter 5). This conclusion is of utmost importance. We are not the first to report this lack of snout shortening. Two earlier studies also made this observation (Morey, 1992, Wayne, 1986), although their results seemingly are ignored (Sablin and Khlopachev, 2002, Germonpré et al., 2009).

9. The **Snout width** index does differ in ancient wolf and ancient dog specimens, with dogs having a relatively wider snout. Modern wolves and modern dogs have narrower snouts than their ancient counterparts, suggesting a trend toward refinement (Cieri et al., 2014)(Chapter 5). In general, there is a trend among modern specimens to have narrower and shorter snouts, both in wolves and dogs.

10*. Mean **Snout height,** measured in more than 100 specimens**,** did not differ between ancient wolves and ancient dogs, but did differ between modern wolves and modern dogs. Still, very small snout height ratio (< 0.16) can be assigned as ancient dogs in only a few instances, thus limiting the utility of the trait (Chapter 5).

11. Mean **Skull height,** measured in more than 100 specimens**,** differs in ancient wolf and ancient dog specimens (Chapter 5). Modern dogs and modern wolves differ in both snout and skull height indices, indicating again that modern species are separated from one another to a greater degree than ancient members of each species. Skull height difference, larger OA, and wider snout, define dog skulls and align with conclusions from GM studies (Drake et al., 2015, Schmitt and Wallace 2012).

12. S**maller size** and isometrically related **reduced skull length** historically has been accepted as a very important trait to distinguish fossil wolves and dogs (Benecke, 1994, Boudadi-Maligne, et al., 2012, Clutton-Brock, 1962, Clutton-Brock, 2012, Dayan, 1994, Degerbøl, 1961b, Mertens, 1936, Napierala and Uerpmann, 2012, Pluskowski, 2006, Rütimeyer, 1861, Wolfgram, 1894, Zeuner, 1963). The theory of size reduction was not followed in studies of Upper Pleistocene canids, in which very large specimens were defined as dogs (Camaros et al., 2016, Germonpré et al., 2009, Germonpré et al., 2012, Germonpré et al., 2015, Germonpré et al., 2017, Pidoplichko et al., 2001, Sablin & Khlopachev, 2002). We studied weight and skull length in 359 modern wolf specimens of one sub-species (*C.l. pallipes*), and results confirm the rapid reduction of weight and skull length in an anthropogenic environment (Zuckerman and Kuhlman, 2000). We hypothesize that size reduction in ancient dogs is based on the concept of anthropomorphic island dwarfism, founder effects, and selection, and we consider this reduction to be paramount for documenting ancient dogs (Chapter 5).

13*. M**andibular mesio-distal diameters (horizontal ramus) and tooth row lengths** have been shown to differ among groups of Pleistocene canids. Based on these differences, specimens were assigned as dogs or wolves (Germonpré et al., 2015). We demonstrated the same subdivision in a group of 75 modern German shepherd dog skulls from a small geographic area. Thus, it is improbable that these metrics can be used to distinguish prehistoric wolves and dogs (Chapter 5).

14*. **The enigma of proposed large Paleolithic dogs**

Relatively recently, dog domestication has been proposed to have occurred about 20,000 years prior to earlier assumptions (cfr. Goyet in Belgium (34 kya)(Germonpré, et al., 2009). Previous reports also had proposed that earlier Paleolithic canid specimens were dogs, including the specimen from Mezhirich (Mezhyrich) (c. 14.5 kya) (Pidoplichko et al., 2001, Pidoplichko, 1998) and two from Eliseevichi (c. 17 kya) (Sablin and Khlopachev, 2002). More recently, additional insipient or proto-dogs were reported (adding to a total of 11) (Table 2 of chapter 1, introduction, including references). These assignments as putative or proto-dogs were based mainly on: a caudally-oriented coronoid process, size of the OA, shorter and wider snout, P4 medio-distal diameter less than M1+M2, and shorter skull length (not size reduction).

Concerns about the methodology and conclusions of these studies have been expressed (Boudadi-Maligne and Escarguel, 2014, Crockford and Kuzmin, 2012, Morey, 2014, Perri, 2013) and corroborated by genetic research as there is not relation between aDNA of these canids and modern dogs. Three specimens were evaluated for mtDNA (Thalmann et al., 2013). The Goyet and Razboinichya specimens were genetically far from modern, Neolithic, or Magdalenian dogs (Frantz, et al., 2016, Pionnier-Capitan, 2010, Thalmann, et al., 2013). The

Razboinichya specimen (Ovodov et al., 2011), originally classified as a dog (Dhruzkova et al. 2013), was re-assigned later as a wolf (Thalmann et al., 2013). Additional concerns regarding this research are included in Chapter 5, and are focused on methodology, that depended heavily on building a comparative dog group to which new specimens could be compared. This particular 'Adam and Eve' group consists of two Eliseevichi specimens, for which no solid evidence supports distinguishing from wolves. Newly added specimens to the group are thus also wolves with comparative physiognomy. Another concern is explaining the enormous difference in percentage of proto-dogs assigned based on skull measurements (only 13 reported from very many comparative Pleistocene wolf skull samples), compared to assignments from mandible measurements (>30%) from the same sites (Germonpré et al., 2015). At present, we see no evidence that would distinguish proto-dogs from Pleistocene wolves (Chapter 5).

15. The wider dog snout is the consequence of a shape change of the mid-face, maximized at the transversal plane of M1-P4. Enlargement can be noted in rostral and dorso-lateral directions of the orbital, frontal, and rostral zygomatic region (Studer, 1901; Drake, 2011; Rizk, 2012; Schmitt and Wallace, 2012). These changes create a wider OA (Drake, et al., 2015, Janssens, et al., 2016) based on dorso-lateralization of the frontal and orbital regions (Wolfgram, 1894, Drake, 2011, Rizk, 2012, Schmitt and Wallace, 2012; Janssens et al., 2016c), thus forming a stop, that is typical for dogs (Drake, 2011) (degree of angle change between nasal and frontal bone seen from a lateral view). The changes reported here are driven, at least in part, by the allelic composition and expression of the Runx2 gene. A hyperactive variant enhances dorsal and lateral maxillary bone growth, imposing adaptations on surrounding skull bones (Fondon and Garner, 2006).

6.2. Missing data

Although our research resolved several questions, it is clear that some information remains incomplete, especially regarding ancient specimens.

1. Oral pathologies could be studied further in ancient Eurasian wolves and ancient dogs. Due to the paucity of available dog skulls and teeth from the Pleistocene and early Holocene, other comparisons must be relied upon, including Mesolithic and Neolithic dog skulls from Danube, Scandinavia, and Alpine lakes (Becker and Johansson, 1981, Bökönyi, 1975, Dimitrijević, 2006, Dimitrijević and Vuković, 2012, Janssens et al, 2016a, Rütimeyer, 1875). Although interesting, these latter dogs are about 5000 (Mesolithic) or 8000 (Neolithic) years younger than the oldest known dogs, and probably they differ substantially. The recent publication on crowding in prehistoric wolves (Ameen et al., 2017) is interesting but it relates to American wolves. Previous, be it less complete and refined analysis, did report on higher crowing in European wolves (Benecke, 1984), thus exemplifying that phenomena, such as crowding, might be regional and defined by genetics, diet and geographical region.

2. The **dorsal coronoid process** of the vertical ramus of the mandible could be studied further in ancient specimens. However, odds do not favour finding valued new data because modern *C.l. chanco* is quite separate from dogs, based on available evidence (Sharma et al., 2004).

3. Further study of the **orbital angle** in ancient Eurasian wolves is desirable. Only one study reports angles in modern and ancient Scandinavian wolves (Aaris-Sørensen, 1977). They differ statistically, with ancient wolves having larger angles than modern specimens (resp. 44° versus 41°). However, a small number of specimens were examined, and new investigation should include many more ancient specimens from different (preferentially Eurasian) geographical regions.

4. Present conclusions about **carnassial size** reduction in dogs could change, if more Pleistocene dog samples were examined. One possibility would be finding a wider normal distribution, with more overlap between ancient dogs and ancient wolves.

5. There is a definite need for further study of the **micro-anatomy of P4** in a large group of Pleistocene wolves and ancient dogs. Such a study should have broad scope and should include detailed GM studies, also of other teeth (e.g. P3, P4, M1).

6.. Based on our study of **contact points** of the skull on a horizontal plane, we conclude that there is little value in studying this trait further in Pleistocene wolves and ancient dogs.

7. There might be a difference between Pleistocene wolves and ancient dogs, regarding the conformation of the **caudal border of the hard palate**. However, there is little possibility to pursue new research because very few intact Pleistocene dog skulls are known at present.

8-11. We studied a large number of ancient and modern specimens, in order to calculate **snout width** and **length,** as well as **skull a**nd **snout height indices.** Additional studies of even larger and more diverse fossil groups would be worthwhile.

12. Skull length and **stature-size reduction** are specific changes among early dogs. Since we rejected the assignment of large Pleistocene proto-dogs as actual dogs, we see no reason to reject the theory of size reduction as a paramount characteristic of early dogs. The very early generations of domesticated wolves must have been difficult to distinguish from wild wolves, as their smaller size likely remained within the normal size distribution (Gauss curve) of contemporaneous wolves. Nonetheless, there are indications that size reduction under anthropogenic selective pressure can occur very rapidly, leading to extreme size reduction in very few generations (Gutiérrez-Gil, et al., 2016). Such a rapid change in body size also can occur when gene flow is reduced or blocked (Berry, 1969), a phenomenon that must have occurred when wolves were bred in the human niche.

6.3. Conclusions on modern versus old

Several statistical differences between modern wolves and modern dogs differ when ancient specimens are studied.

The **orbital angle** of Neolithic dogs does not differ from modern wolves, while there is a difference (in extremes) between modern dogs and modern wolves (Chapter 3).

There is a need to compare fossil dogs with fossil wolves.

Tooth crowding is encountered much more among ancient wolves, compared to modern wolves (resp. 36 and 18%)(Ameen et al., 2017).

There is a need to compare crowding in fossil Eurasain wolves with fossil dogs.

The **caudal border of the hard palate** differs between Neolithic and modern dogs, but not between modern dogs and modern wolves (Chapter 5).

It should not be taken for granted that the physiognomy of modern wolves mimics that of Pleistocene specimens.

Mandible form differs between modern dogs and modern wolves, but not between ancient wolves and ancient dogs (Drake et al., 2017).

This might be explained by the ongoing process of diversification of the two sub-species.

Snout width. Modern wolves have significantly more narrow snouts than early Holocene specimens (Chapter 5).

Both dogs and wolves seem to go through a refinement process (from Plestocene to recent).

Skull and snout height (Chapter 5). While modern dogs and modern wolves can be distinguished using snout height and skull height index, snout height index cannot distinguish ancient dogs and ancient wolves (Chapter 5).

These differences suggest additional comparative research involving ancient specimens. The observations imply a large number of Pleistocene wolves from the origin regions of dogs (thus not American specimens). However, collections are: a) not always easily accessible or well-known (China); b) not always available for research (Denmark); c) sometimes small in number; d) sometimes consisting mainly of American specimens; and e) sometimes consisting mainly of heavily fragmented specimens.

Few Pleisocene dogs are available at present (n=18)(1 2), which limits comparative studies. Considering the 100+ years over which existing specimens were collected, the odds presently are low that large numbers of new Pleistocene dogs will be discovered in the near future. Pleistocene dogs are extremely rare and most are fragmented and incomplete. Mesolithic specimens from the Danube Gorges are quite restricted by sample size, Europe and Asia. Larger collections (hundreds of specimens) are Neolithic (Alpine lakes, Scandinavia, Danube, Greece).

6.4. New characteristics for morphological analyses

We propose that additional new anatomical structures need to be evaluated to investigate the speciation process. One prominent example is the inner ear that is located in the extremely hard *os petrosum*, suggesting lower probability of taphonomic damage. The petrous bone contains cavities in which basal sense organs are located, including the coiled cochlea for hearing, the three semicircular canals or labyrinths (anterior, lateral, osterior), and a vestibule for balance. The morphology of these structures tends to be consistently species-specific, with minor intraspecific variation among closely related taxa (Spoor 1993, Spoor and Thewissen 2008, Gunz et al. 2012, Grohé et al. 2016, Mennecart and Costeur 2016), and with unimportant changes related to size (Grohé et al. 2016). Inner ear morphology has been used to define phylogenetic patterns (Grohé et al. 2016, Mennecart and Costeur 2016) and distinguish even sub-species (chimpanzees) (Gunz et al. 2012). We have completed a micro-CT scan study of the inner ear of modern wolves and modern dogs, and have shown with GM methods that the species differ statistically (in press). The next step is to repeat this study with Pleistocene canids.

6.5. An overview of the major conclusions

In this thesis, we questioned the validity of all important traditional

morphometrics and morphologic criteria (Table 1 of chapter 1, introduction) that have been used to classify ancient canid specimens. Historically, conclusions from these methods were made based on small numbers of specimens, untested basic specimens used as reference material, and untested diagnostic methods and variables. We used much larger reference groups to explore whether some observed variations (identified historically as signs of domestication) possibly reflect natural variation of wolf physiognomy. It is our view that there is only limited use for classical morphometrics and morphology to distinguish for distinguishing ancient dogs and ancient wolves. From the traits that we have evaluated, most earlier methods must be rejected. Some need further study on additional Pleistocene specimens.
At present, the only acceptable wolf-dog distinguishing traits are:

1. Very small and/or very large OA
2. P4 mesio-distal diameter
3. Very small or large mesio-distal diameter of M1
4. Snout width index
5. Skull height index
6. Reduced size-stature, with isometrically-related morphology such as skull length.

The above criteria thus are powerful tools to use for further multivariate studies. The increasingly interdisciplinary combination of archaeozoology, classic and GM morphology and morphometrics, and archaeo-genetics, will be needed to determine conclusively the taxonomic identity of proposed early dogs.

7. References

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

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.

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

Becker, C., & Johansson, F. (1981). Die neolithischen Ufersiedlungen von Twann. *Tierknochenfunde (zweiter Bericht). Staatlicher Lehrmittelverlag, Bern*.

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

Berry, R. (1969). The genetical implications of domestication in animals. In *The domestication and exploitation of plants and animals* pp. 207-217.

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

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. (2012). 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.

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. (2012). *Animals as domesticates: a world view through history*. East Lansing: Michigan University Press.

Costeur, L., Mennecart, B., Müller, B., & Schulz, G. J. J. o. a. (2017). Prenatal growth stages show the development of the ruminant bony labyrinth and petrosal bone. *230*(2), 347-353.

Crockford, S.J., Kuzmin, Y.V., 2012. Comments on Germonpré et al., Journal of Archaeological Science 36, 2009 "Fossil dogs and wolves from Palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes", and Germonpré, Lázkičková-Galetová, and Sablin, Journal of Archaeological Science 39, 2012 "Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic", Journal of Archaeological Science 39, 2797-2801.

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

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

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., Coquerelle, M., Kosintsev, P. A., Bachura, O. P., Sablin, M., Gusev, A. V., . . . Losey, R. J. J. S. r. (2017). Three-dimensional geometric morphometric analysis of fossil canid mandibles and skulls. *7*(1), 9508.

Druzhkova, A. S., Thalmann, O., Trifonov, V. A., Leonard, J. A., Vorobieva, N. V., Wayne, R. K. (2013). Ancient DNA analysis affirms the canid from Altai as a primitive dog. *PLoS One, 8*(3), e57754.

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.

Gemonpré, 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.

Grohé, C., Tseng, Z. J., Lebrun, R., Boistel, R., & Flynn, J. J. J. J. o. A. (2016). Bony labyrinth shape variation in extant Carnivora: a case study of Musteloidea. *228*(3), 366-383.

Gunz, P., & Mitteroecker, P. J. H., the Italian Journal of Mammalogy. (2013). Semilandmarks: a method for quantifying curves and surfaces. *24*(1), 103-109.

Gutiérrez-Gil, B., Arranz, J.J., Wiener, P., 2016. An interpretive review of selective sweep studies in Bos taurus cattle populations: identification of unique and shared selection signals across breeds, Advances in Farm Animal Genomic Resources, 231-238.

Janssens, L., Spanoghe, I., Miller, R., Van Dongen, S., 2016a. Can orbital angle morphology distinguish dogs from wolves? Zoomorphology 135, 149-158.

Janssens, L., Verhaert, L., Berkowic, D., Adriaens, D., 2016b A standardized framework for examination of oral lesions in wolf skulls (Carnivora: Canidae: *Canis lupus*), Journal of Mammalogy, gyw058.

Janssens, L., Miller, R., Dongen, S., 2016c. The morphology of the mandibular coronoid process does not indicate that Canis lupus chanco is the progenitor to dogs, Zoomorphology 135, 269-277.

Jeffery, N., & Spoor, F. J. J. o. A. (2004). Prenatal growth and development of the modern human labyrinth. *204*(2), 71-92.

Jeffery, N., & Spoor, F. J. J. o. h. e. (2006). The primate subarcuate fossa and its relationship to the semicircular canals part I: prenatal growth. *51*(5), 537-549.

Mennecart, B., Rössner, G. E., Métais, G., DeMiguel, D., Schulz, G., Müller, B., & Costeur, L. J. J. o. m. (2016). The petrosal bone and bony labyrinth of early to middle Miocene European deer (Mammalia, Cervidae) reveal their phylogeny. *277*(10), 1329-1338.

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

Morey, D. (1992). Size, shape and development in the evolution of the domestic dog. *Journal of Archaeological Science, 19*(2), 181-204.

Morey, D.F., 2014. In Search of Paleolithic Dogs: A Quest with Mixed Results, Journal of Archaeological Science.

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

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

Ovodov, N.D., Crockford, S.J., Kuzmin, Y.V., Higham, T.F., Hodgins, G.W., van der Plicht, J., 2011. A 33,000-year-old incipient dog from the Altai Mountains of Siberia: Evidence of the earliest domestication disrupted by the Last Glacial Maximum, PLoS One 6, e22821.

Perri, A., 2013. Global Hunting Adaptations to Early Holocene Temperate Forests: Intentional Dog Burials as Evidence of Hunting Strategies, PhD Thesis, Durham University.

Pidoplichko, I., Allsworth-Jones, P., & Djindjian, F. (2001). Upper Paleolithic Dwellings of Mammoth Bones in the Ukraine. British Archeological Reports (BAR), International Series 712. In: JSTOR.

Pidoplichko, I. H. (1998). *Upper Palaeolithic Dwellings of Mammoth Bones in the Ukraine: Kiev-Kirillovskii, Gontsy, Dobranichevka, Mezin and Mezhirich* (Vol. 712): British Archaeological Reports Limited.

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),

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.

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.

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*.

Sharma, D. K., Maldonado, J. E., Jhala, Y. V., & Fleischer, R. C. (2004). Ancient wolf lineages in India. *Proceedings of the Royal Society of London B: Biological Sciences, 271*(Suppl 3), S1-S4.

Spoor, F., Garland, T., Krovitz, G., Ryan, T. M., Silcox, M. T., & Walker, A. J. P. o. t. N. A. o. S. (2007). The primate semicircular canal system and locomotion. *104*(26), 10808-10812.

Spoor, F., & Thewissen, J. (2008). Comparative and functional anatomy of balance in aquatic mammals.

Spoor, F., & Zonneveld, F. J. A. J. o. P. A. T. O. P. o. t. A. A. o. P. A. (1998). Comparative review of the human bony labyrinth. *107*(S27), 211-251.

Spoor, F., & Zonneveld, F. J. J. o. A. (1995). Morphometry of the primate bony labyrinth: a new method based on high-resolution computed tomography. *186*(Pt 2), 271.

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.

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.

Vila, C., Urios, V., Castroviejo, V., 1993. Tooth losses and anomalies in the wolf (Canis lupus), Canadian Journal of Zoology 71, 968-971.Vilà, C., Savolainen, P.,

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.

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

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).

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

Zuckerman, M., Kuhlman, D.M., 2000. Personality and risk - taking: common bisocial factors, Journal of personality 68, 999-1029.