

# The morphology of the mandibular coronoid process does not indicate that *Canis lupus chanco* is the progenitor to dogs

Luc Janssens<sup>1</sup>  · Rebecca Miller<sup>2</sup> · Stefan Van Dongen<sup>3</sup>

Received: 19 October 2015 / Revised: 12 December 2015 / Accepted: 30 December 2015  
© The Author(s) 2016. This article is published with open access at Springerlink.com

**Abstract** The domestication of wolves is currently under debate. Where, when and from which wolf sub-species dogs originated are being investigated both by osteoarchaeologists and geneticists. While DNA research is rapidly becoming more active and popular, morphological methods have been the gold standard in the past. But even today morphological details are routinely employed to discern archaeological wolves from dogs. One such morphological similarity between *Canis lupus chanco* and dogs was published in 1977 by Olsen and Olsen. This concerns the “turned back” anatomy of the dorsal part of the vertical ramus of the mandible that was claimed to be specific to domestic dogs and Chinese wolves *C. lupus chanco*, and “absent from other canids”. Based on this characteristic, *C. lupus chanco* was said to be the progenitor of Asian and American dogs, and this specific morphology has been continuously used as an argument to assign archaeological specimens, including non-Asian and non-American, to the dog clade. We challenged this statement by examining 384

dog skulls of 72 breeds and 60 skulls of four wolf sub-species. Only 20 % of dog mandibles and 80 % of *C. lupus chanco* showed the specific anatomy. In addition, 12 % of *Canis lupus pallipes* mandibles showed the “turned back” morphology. It can be concluded that the shape of the coronoid process of the mandible cannot be used as a morphological trait to determine whether a specimen belongs to a dog or as an argument in favour of *chanco* as the progenitor to dogs.

**Keywords** Dog · Wolf · Domestication · Morphology · *Canis lupus chanco* · Mandible · Coronoid process

## Introduction

The domestication of wolves into dogs is an active topic of research (Boudadi-Maligne and Escarguel 2014; Gernonpré et al. 2009; Larson et al. 2012; Morey and Jaeger 2015; Thalmann et al. 2013). Where, when and from which progenitor wolf sub-species dogs originated has been investigated both by osteoarchaeologists (Aaris-Sørensen 1977; Benecke 1987, 1994; Boudadi-Maligne and Escarguel 2014; Huxley 1880; Iljin 1941; Nehring 1888; Rüttimeyer 1861; Stockhaus 1965; Studer 1901; Sumiński 1975) and geneticists (Anderson et al. 2009; Ardalan et al. 2011; Axelsson et al. 2013; Brown et al. 2011; Freedman et al. 2014; Gundry et al. 2007; Ho et al. 2005; Irion et al. 2003; Karlsson et al. 2007; Khosravi et al. 2013; Kirkness et al. 2003; Klütsch and de Caprona 2010; Larson and Burger 2013; Leonard et al. 2002; Lindblad-Toh et al. 2005; Ostrander and Wayne 2005; Pang et al. 2009; Savolainen et al. 2002, 2004; Schmutz and Berryere 2007; Schoenebeck and Ostrander 2013; Thalmann et al. 2013; Tsuda et al. 1997; Vaysse et al. 2011; Verginelli et al.

---

Communicated by A. Schmidt-Rhaesa.

✉ Luc Janssens  
coatil@icloud.com

Rebecca Miller  
rmiller@ulg.ac.be

Stefan Van Dongen  
stefan.vandongen@uantwerpen.be

<sup>1</sup> Department of Archaeology, Leiden University, Einsteinweg 2, 2333 CC Leiden, The Netherlands

<sup>2</sup> Service of Prehistory, University of Liège, quai Roosevelt, 1, 4000 Liège, Belgium

<sup>3</sup> Department of Evolutionary Ecology, University of Antwerp, Groenenborgerlaan 171, 2020 Antwerp, Belgium

2005; Vila et al. 1999, 2005; Vilà et al. 1993, 1997; Vonholdt et al. 2010; Wayne 2012; Wayne and Ostrander 1999, 2007).

Briefly there are two current views. One group of researchers proposes an origin of dogs after the Last Glacial Maximum (LGM) in Europe and during the Magdalenian, about 18,000 years ago (Thalmann et al. 2013). This evidence is based on genetic research (Ho et al. 2005; Thalmann et al. 2013), and the morphology of canine archaeological remains that is distinctively smaller than those of wolves (Altuna et al. 1984; Boudadi-Maligne and Escarguel 2014; Boudadi-Maligne et al. 2012; Célérier 1994; Célérier et al. 1999; Chaix 2000; Larson and Burger 2013; Leesch et al. 2012; Morel and Müller 1997; Napierala and Uerpman 2012; Pionnier-Capitan 2010; Pionnier-Capitan et al. 2011; Street 2002).

The other group claims that dogs originated before the LGM, as early as in the Aurignacian and Gravettian and thus 35,000 years ago (Bocherens et al. 2014; Germonpré et al. 2009, 2012; Ovodov et al. 2011; Sablin and Khlo-pachev 2002). Although genetic analysis has not found any relationship between these old archaeological canine specimens (Thalmann et al. 2013) purported to be domesticated wolves and modern dogs, these researchers suggest that these animals were, however, domesticated, but did not produce surviving offspring (aborted domestication waves) (Germonpré et al. 2012; Skoglund et al. 2011). The arguments to place these pre-LGM specimens in the dog clade are based on morphology alone and mainly on wider and shorter snouts. Drake et al. (2015) have, however, demonstrated that this criterion (shorter and wider snouts) is not useful in distinguishing dogs from wolves and also identified some of the so-called pre-LGM dog fossils as wolves.

Many morphological differences have been described between wolves and dogs in the literature since the eighteenth century (Clutton-Brock 1962; Degerbøl 1961; Nehring 1888; Stockhaus 1965; Studer 1901; Wolfgram 1894). Three morphological methods were used to examine morphological differences:

- The “obvious” visual difference in appearance (morphology, *sensu stricto*) (Olsen and Olsen 1977).
- The difference in size (morphometry) (Benecke 1987, 1994; Boudadi-Maligne and Escarguel 2014; Napierala and Uerpman 2012).
- The difference in appearance (form) that cannot be recognized visually with certainty (geometric morphometrics) (e.g., Drake and Klingenberg 2010; Mile-nkovic et al. 2010; Pionnier-Capitan 2010; Schmitt and Wallace 2012).

The most frequently reported morphological and morphometric differences used to distinguish dogs from wolves are smaller stature and thus smaller anatomical parts (e.g., skull, teeth such as carnassials, etc.), shorter and wider snouts, tooth crowding, larger orbital angles and a “turned back” morphology of the dorsal side (apex) of the vertical ramus of the mandible (coronoid process) (Olsen and Olsen 1977, Fig. 1 and 2, p. 534–535). The latter morphological difference is based purely on difference in shape. This distinctive morphological characteristic was described in 1977 by Olsen and Olsen (Olsen and Olsen 1977). The authors state that the origin of Asian and American (New World) dogs must have originated in the Far East and proposed the Tibetan wolf (Chinese wolf, Asian wolf, *Canis lupus chanco*) as the dog’s ancestor (Olsen and Olsen 1977, 534). This opinion was based on the specific “turned back” morphology of the coronoid process of the mandible, claimed to be “specific to domestic dogs” and Chinese wolves, and to be “absent from other canids” (Olsen and Olsen 1977, 534). Based on this assumption, *C. lupus chanco* was said to be “the progenitor of dogs”, and this specific morphological trait is still used in recent publications to assign archaeological specimens to the dog clade (e.g., Ovodov et al. 2011).

We tested the statement of Olsen and Olsen (1977) by examining 384 dog mandibles of many breeds, of which six breeds are Asian or American, and 60 wolf mandibles of four sub-species. Our aim is to examine whether this “turned back” morphology is indeed present in “all” dogs and only in *C. lupus chanco* as hypothesized.

## Materials and methods

All examined mandibles are from reputable museum collections. These had been collected in historical and recent periods and were professionally prepared. All are intact and from adult animals. In total 444 dog and wolf skulls were examined (888 mandibles) including 384 dog skulls and 60 wolf skulls. For the wolves (Table 1), 37 are from the collection of The George S. Wise Faculty of Life Sciences, Department of Zoology at Tel-Aviv University, Israel (ZMTAU). Thirty-two of these were *Canis lupus pallipes* and five *Canis lupus arabs*. Seven skulls were examined from the collection of the Natural History Museum in London, Great Britain (BMNH): six *C. lupus arabs*, and one *C. lupus pallipes*. Eleven skulls are from the collection of the Natural History Museum Bern, Switzerland (NMBE), all from Eurasian wolves (*Canis lupus lupus*) from Central Europe or Russia. Five specimens of *C. lupus chanco* from the collection of the Department of Vertebrate Zoology, Smithsonian Institution at the National Museum

**Table 1** List of wolf skulls used in this study

Museum ID	Genus	Species	Sub-species	Region
BMNH ZD.1891.2.5.1	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Bouraida
BMNH ZD.1895.10.8.1	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Aden
BMNH ZD.1899.11.6.36	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Muscat
BMNH ZD.1924.8.13.1	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Jeddah
BMNH ZD.1940.193	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	?
BMNH ZD.1948.368	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	?
BMNH ZD.1897.1.14.4	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Jaquakar
NMBE1028185	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Russia
NMBE1028188	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Russia
NMBE1028189	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Russia
NMBE1028192	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028193	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Russia
NMBE1028204	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028205	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028206	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028207	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028209	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Poland
NMBE1028211	<i>Canis</i>	<i>lupus</i>	<i>lupus</i>	Russia
USNM00607	<i>Canis</i>	<i>lupus</i>	<i>chanco</i>	China
USNM00610	<i>Canis</i>	<i>lupus</i>	<i>chanco</i>	China
USNM00613	<i>Canis</i>	<i>lupus</i>	<i>chanco</i>	China
USNM00616	<i>Canis</i>	<i>lupus</i>	<i>chanco</i>	China
USNM00619	<i>Canis</i>	<i>lupus</i>	<i>chanco</i>	China
ZMTAU 09439	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 09460	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Sandiyia
ZMTAU 10334	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 10338	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 10355	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10402	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10608	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 10609	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10610	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10615	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10619	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10621	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10682	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10685	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10686	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10688	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 10692	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11041	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11109	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11110	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11118	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11119	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11121	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11250	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei

**Table 1** continued

Museum ID	Genus	Species	Sub-species	Region
ZMTAU 11275	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11417	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11418	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11475	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Negev
ZMTAU 11476	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11479	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 11516	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 11685	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Golan
ZMTAU 12130	<i>Canis</i>	<i>lupus</i>	<i>pallipes</i>	Galilei
ZMTAU 12130-2	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Negev
ZMTAU 12251	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Negev
ZMTAU 12254	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Muscat
ZMTAU 12279	<i>Canis</i>	<i>lupus</i>	<i>arabs</i>	Negev

Sub-species, institute and accession numbers (ID) are reported. BMNH: British Museum of Natural History. NMBE: Natural History Museum Bern, Switzerland, USNM: Department of Vertebrate Zoology, Smithsonian Institution at the National Museum of Natural History, Washington DC, USA, ZMTAU: Department of Zoology at Tel-Aviv University, Israel

of Natural History, Washington DC, USA (USNM), were also examined.

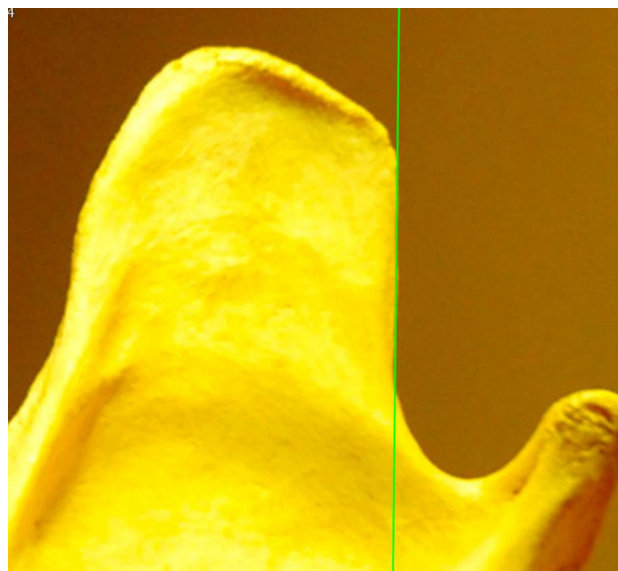
We also examined 123 dog skulls from the collection of the anatomy department of the school for Veterinary Medicine, Ghent University, Belgium, and 261 skulls from the collection of The Museum of Natural History, Bern, Switzerland (total 384) (Table 2). The skulls belong to 72 different breeds, of which six breeds and 33 skulls are Asian or American. These are Alaskan malamute (5), Canadian Eskimo dog (4), Chow–Chow (16), Shar Pei (1), Tibetan Mastiff (6) and Tibetan Terrier (1).

Each mandible was digitally photographed from a distance of 40–50 cm with a digital Nikon D 700 camera with a 50 mm lens. The photographs were imported in the OsiriX Imaging Software program. A straight vertical line was then drawn confluent with the straight part of the ventral caudal border of the mandible. The mandibles were divided in two categories based on the morphology of the coronoid process and by drawing a straight line (green on the figures) coinciding with the caudal border. For Category 1, the mandible has a perfect vertical straight caudal border (Fig. 1) or the uppermost part of the apex points minimally in the caudal direction, while the caudal border is straight (Fig. 2). In this category, the straight green line follows the caudal bony border of the vertical ramus and the dorsal aspect of the mandible does not cross the green line or transects only a very small part at the tip. For Category 2, the caudal border is concave over its entire length and has the form of a dolphin fin (Fig. 3). Here, the

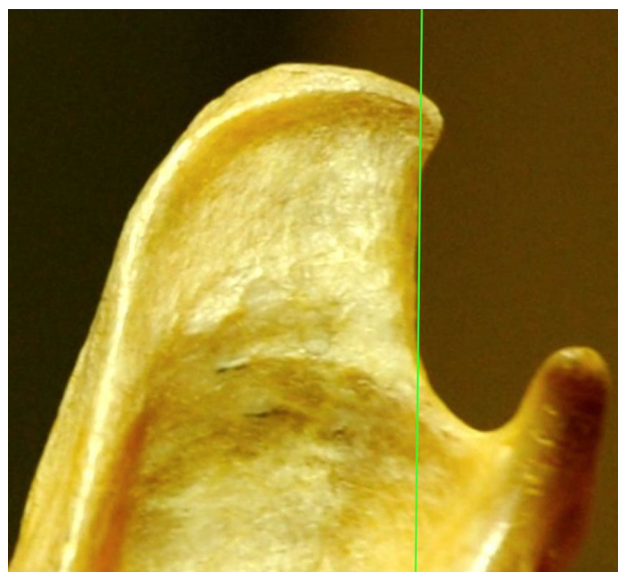
**Table 2** Dog skulls used in this study grouped alphabetically by breed

Breed	Nr	TB	Breed	Nr	TB
Afghan hound	13	2	Greyhound	10	1
Airedale terrier	4	1	Groenendael Belgian shepherd	18	1
<b>Akita Inu</b>	8	1	Hahoawu	1	
<b>Alaskan Malamute</b>	5	2	Irish setter	2	
Barzoi	11	2	Irish wolfhound	8	2
Basenji	1		Jagdterrier	2	
Batak hound	11	3	Karelian Bear dog	18	3
Beagle	9	2	Kuvasc	1	
Bearded collie	1		Labrador retriever	13	2
Berger de Brie	1		Leonberger	1	
Berner Sennenhund	32	4	Lundehund	2	
Bloodhound	7	1	Malinois Belgian shepherd	2	1
Border collie	5	3	Mastino Napolitano	1	
Bouvier des Flandres	4	2	Mayar Agar	2	1
Boxer	2		Pariah hound	10	2
Bull terrier	1		Pembroke Welsh Corgi	1	
Canaan dog	1		Pharaoh hound	4	
<b>Canadian Eskimo dog</b>	4		Pointer	1	1
<b>Chow Chow</b>	16	3	Poodle	6	2
Cocker spaniel	4		Rhodesian Ridgeback	2	2
Crossbred	5	3	Rottweiler	3	
Dalmatian	1		Saint Bernhard	2	
Dingo	3	2	Saluki	2	
Doberman pinscher	15	5	Samojeed	8	2
Entelbacher	1		Scottish collie	1	
Finnish spitz	3	1	Scottish terrier	16	
Flatcoat retriever	1		<b>Shar Pei</b>	1	
Fox terrier	1		Siberian Husky	14	3
Gaint schnauzer	1		Sloughi	1	
Galgo Espanjol	2		Swiss shepherd	1	
German braque	3	1	Tervueren Belgian shepherd	5	
German shepherd	10	3	<b>Tibetan Mastiff</b>	6	1
Golden retriever	6	1	<b>Tibetan spaniel</b>	1	
Great Dane	2		Weimaraner	1	
Great spitz	7	2	Whippet	4	2
Greenland dog	10	1	Wolfspitz	2	1
Total breeds	72		Total skulls	384	

In bold are New World and Asian breeds. Nr refers to the number of skulls examined. TB refers to “Turned Back” morphology



**Fig. 1** Category 1: Straight caudal border of the vertical ramus. The *vertical line* that coincides with the ventral part of the caudal border of the vertical ramus of the mandible does not cut through the dorsal caudal ramus

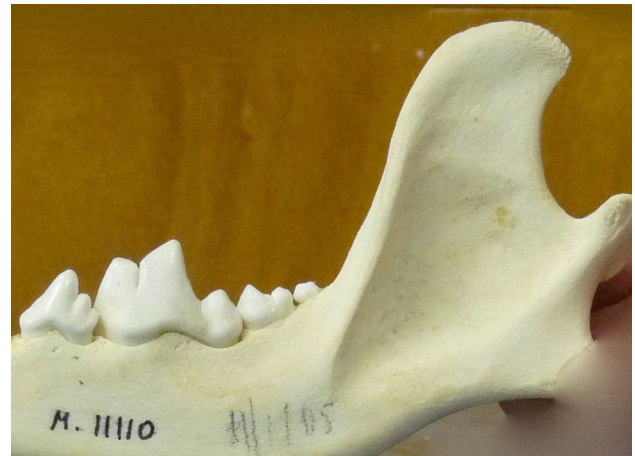


**Fig. 2** Category 2: Straight caudal border with minimal tip curvature. The *vertical line* that coincides with the ventral part of the caudal border of the vertical ramus of the mandible coincides with the caudal border and does only cut through the tip of dorsal caudal ramus

vertical line transects most of the caudal vertical ramus and the line cannot coincide with the caudal border which is concave.



**Fig. 3** Turned back morphology. The vertical line at the caudal border of the vertical ramus of the mandible does not coincide with the border and cuts through a large part of the dorsal ramus



**Fig. 4** A *Canis lupus pallipes* mandibular specimen with “turned back” morphology. Accession number ZMTAU1110 (George Wise faculty of Life Sciences, Israel)



**Fig. 5** The *Canis lupus chanco* mandibular specimen without the “turned back” morphology. Accession number 18B458- NHB 2015- USNM00610 (Smithsonian Institution, USA). Photo: D. E. Hurlbert

**Results**

All left and right mandibles from the same skull show identical anatomy; therefore, frequencies are per skull, not mandible. Fifty-two wolf skulls had a straight caudal border (87 %), while eight (13 %) had a “turned back” morphology (Table 3). Eurasian wolves and *C. lupus arabs* all had straight mandibles. *C. lupus pallipes* had four specimens with mandibles with the “turned back” morphology (12 %) (Fig. 4) and *C. lupus chanco* four out of five mandibles with “turned back” morphology (80 %) but one with straight morphology (20 %) (Fig. 5).

Of the 384 dog skulls, 312 had a straight caudal border (81 %) and 72 mandibles had “turned back” morphology

(19 %). There was no relation between the “turned back” anatomy and breed; this was spread across 37 breeds (Table 3).

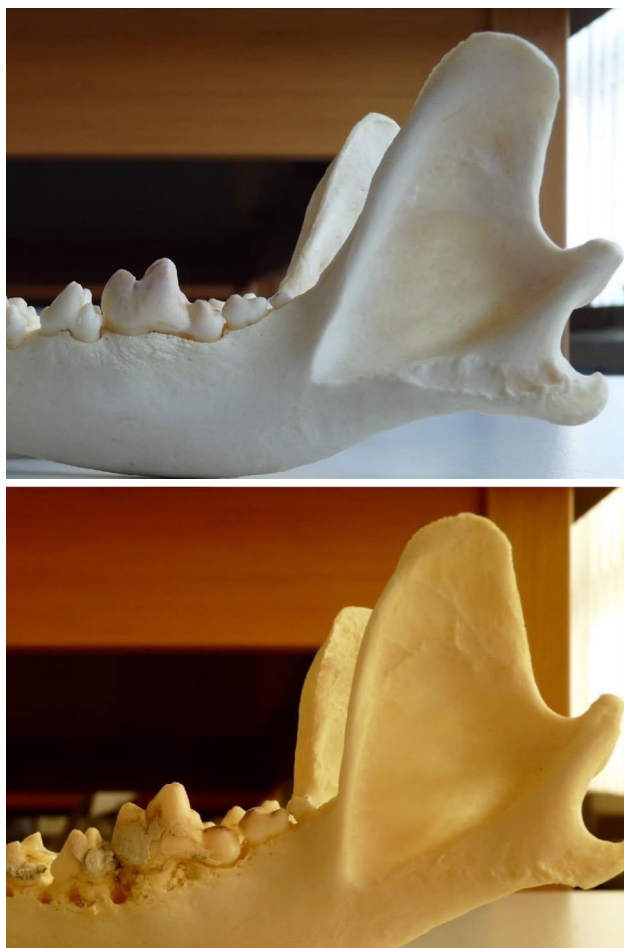
Three of seven Asian and American breeds (41 mandibles) had seven “tuned back” mandibles (17 %) so most mandibles in these breeds were straight (Fig. 6).

**Discussion**

Three main claims are made in Olsen and Olsen’s article (1977). The first is that the Chinese wolf is progenitor to Asian and New World dogs. When Olsen and Olsen’s

**Table 3** Morphological categories of the coronoid process of the mandible

	Dogs	<i>Canis lupus pallipes</i>	<i>Canis lupus arabs</i>	<i>Canis lupus chanco</i>	<i>Canis lupus Eurasian</i>	Wolves Total
Total number	384	37	7	5	11	60
Category 1: straight morphology	81 % (312)	88 % (33)	100 % (7)	20 % (1)	100 % (11)	52
Category 2: “Turned back” morphology	19 % (72)	12 % (4)		80 % (4)		8



**Fig. 6** A mandibular specimen of an Asian/American dog without the “turned back” morphology. *Top* Alaskan Malamute specimen. Accession number 1051378-313/78 (Museum of Natural History, Bern, Switzerland). *Bottom* Akita Inu specimen. Accession number 1051382-523/82 (Museum of Natural History, Bern, Switzerland)

article (1977) was published, it was still uncertain if only the wolf was a progenitor to dogs. In addition to the wolf, *Canis aureus* was said to be a possible forefather of small breed dogs (Darwin 1868; Lorenz 2002). It was also uncertain if there had been only one domestication wave, or if regional and different domestication phenomena had occurred and so for example local Asian wolves could then have been directly ancestral to Asian and New World dogs and Eurasian wolves to European dogs. The article should thus be viewed in this historical perspective. The fact that *C. lupus chanco* is called “the Chinese wolf” in the article, not Tibetan wolf (Pocock 1946), should also be placed in the same historical perspective as the 1970s were a period of a Sino-American rapprochement (Oksenberg 1982). Recent genetic analysis has confirmed that only wolves are progenitors to dogs, contradicting older theories about different geographic domestication waves (Duleba et al. 2015; Horard-Herbin et al. 2014; Larson et al. 2012;

Thalmann et al. 2013) and has revealed that New World dogs did not originate locally but invaded the continent together with early migration waves of *Homo sapiens* (Leonard et al. 2002; Savolainen et al. 2002).

The original article shows drawings of 13 mandibles of which only ten have sufficient intact anatomy to make interpretation possible (according to personal re-examination of the published drawings by LJ). Of these, six belong to dogs, one to *C. lupus chanco* and three to species other than *Canis lupus*. All dogs and all *C. lupus chanco* specimens show the “turned back” anatomy. It is not reported if more than these seven mandibles were examined. If not, it is difficult to understand why such a general statement was published. *C. lupus chanco* skulls are very difficult to find in zoological and natural history collections. This may explain why only one was reported in the article. We found only eleven skulls in many worldwide collections. Of these only five had intact mandibular anatomy, of which one (20 %) had a straight caudal mandibular ramus, contradicting Olsen and Olsen’s (1977) original statement.

The second assertion is that the “turned back” morphology is absent from other canids. This statement is unsupported as we have demonstrated the presence of the “turned back” morphology in *C. lupus pallipes* mandibles. Studer (1901) early on reported that from all examined wolf skulls *pallipes* and *chanco* were the most anatomically similar. This may explain why these two wolf sub-species share this “turned back” morphology, unseen in the two other wolf sub-species we examined.

The third statement is that “dogs have the turned back morphology”. At one point in the article this statement is made in general: “all dogs” have the turned back morphology (Olsen and Olsen 1977, 534, last paragraph), while in another location it refers to “New World and Asian dogs” (Olsen and Olsen 1977, 533, fifth paragraph), while the title of the article refers only to New World dogs. The “turned back” morphology is present in the six dog mandible drawings in the article, but the same pattern was not observed in the large group of dog mandibles we examined, not in general and not in Asian or New World dogs. Indeed, only a minority of dogs (20 %) have “turned back” morphology. In addition there are no differences in occurrence between Asian and/or New World dogs nor in the total group of dogs (18 % in these breeds vs. 20 % in total).

## Conclusion

The statement that all dogs have a specific “turned back” morphology of the mandibular coronoid process, and that they share this specific morphology with only one wolf sub-species (*C. lupus chanco*), is untenable. This morphological trait cannot therefore be used as an argument to

claim that archaeological remains belong to dogs, nor to argue that *C. lupus chanco* is the progenitor of dogs.

**Acknowledgments** We would like to thank Shai Meiri and Daniel Berkowic from Israel, Roberto Portela Miguez from the Natural History Museum in London, Paul Schmid and Marc Nussbaumer from Switzerland and Paul Simoens from Belgium for allowing us to use their collections for research. We thank Kristen Quarles from the Smithsonian institution for assistance with their collection and thank Thijs Van Kolfshoten for critical comments. David Jaggar is thanked for linguistic help. We are grateful to the anonymous reviewers of the article for improvements. Finally Christien De Paepe is thanked for assistance with the graphics.

**Open Access** This article is distributed under the terms of the Creative Commons Attribution 4.0 International License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made.

## References

- Aaris-Sørensen K (1977) The subfossil wolf, *Canis lupus* L. in Denmark. Vidensk Meddr dansk naturhistorisk Foren 29:129–146
- Altuna J, Baldeon A, Mariezkurrena K (1984) Dépôts rituels magdaléniens de la grotte d'Erralla (Pays Basque). Munibe 36:3–10
- Anderson T, Candille S, Musiani M, Greco C, Stahler D, Smith D, Padhukasahasram B, Randi E, Leonard J, Bustamante C (2009) Molecular and evolutionary history of melanism in North American gray wolves. Science 323:1339–1343
- Ardalan A, Kluetsch C, Zhang A, Erdogan M, Uhlén M, Houshmand M, Tepeli C, Ashtiani S, Savolainen P (2011) Comprehensive study of mtDNA among Southwest Asian dogs contradicts independent domestication of wolf, but implies dog–wolf hybridization. Ecol Evol 1:373–385
- Axelsson E, Ratnakumar A, Arendt M, Maqbool K, Webster M, Perloski M, Liberg O, Arnemo J, Hedhammar Å, Lindblad-Toh K (2013) The genomic signature of dog domestication reveals adaptation to a starch-rich diet. Nature 495:360–364
- Benecke N (1987) Studies on early dog remains from Northern Europe. J Archaeol Sci 14:31–49
- Benecke N (1994) Archäozoologische Studien zur Entwicklung der Haustierhaltung vol 64. Akademie Verlag Schriften zur Ur- und Frühgeschichte, Berlin
- Bocherens H, Drucker D, Germonpré M, Lázničková-Galetová M, Nait Y, Wissin C, Brůžek J, Oliva M (2014) Reconstruction of the Gravettian food-web at Předmostí I using multi-isotopic tracking of bone collagen. Quat Int 249:1–18
- Boudadi-Maligne M, Escarguel G (2014) A biometric re-evaluation of recent claims for early upper palaeolithic wolf domestication in Eurasia. J Archaeol Sci 45:80–89
- Boudadi-Maligne M, Mallye J-B, Langlais M, Barshay-Szmidt C (2012) 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
- Brown SK, Pedersen P, Niels C, Jafarishorije S, Bannasch D, Ahrens K, Wu J, Okon M, Sacks B (2011) Phylogenetic distinctiveness of middle eastern and southeast Asian village dog Y chromosomes illuminates dog origins. PLoS One 6:e28496
- Célérier G (1994) L'abri sous roche de Pont d'Ambon à Bourdeilles (Dordogne). Gallia préhistoire 36:65
- Célérier G, Tisnerat N, Valladas H (1999) Données nouvelles sur l'âge des vestiges de chien à Pont d'Ambon, Bourdeilles (Dordogne). Paleobiology 11:163–165
- Chaix L (2000) A preboreal dog from the northern Alps (Savoie, France). BAR Int Ser 889:49–60
- Clutton-Brock J (1962) Near eastern canids and the affinities of the Natufian dogs. Zeitschrift für Tierzüchtung und Züchtungsbiologie 76:326–333
- Darwin C (1868) The variation of animals and plants under domestication, vol 2. John Murray, London
- Degerbøl M (1961) On a find of a preboreal domestic dog *Canis familiaris* L. from Star Carr, Yorkshire, with remarks on other Mesolithic dogs. Proc Prehist Soc (New Ser) 27:35–55
- Drake AG, Klingenberg CP (2010) Large-scale diversification of skull shape in domestic dogs: disparity and modularity. Am Nat 175:289–301. doi:10.1086/650372
- Drake AG, Coquerelle M, Colombeau G (2015) 3D morphometric analysis of fossil canid skulls contradicts the suggested domestication of dogs during the late palaeolithic. Sci Rep. doi:10.1038/srep08299
- Duleba A, Skonieczna K, Bogdanowicz W, Malyarchuk B, Grzybowski T (2015) Complete mitochondrial genome database and standardized classification system for *Canis lupus familiaris*. Forensic Sci Int: Genet 19:123–129
- Freedman AH, Gronau I, Schweizer R, Ortega-Del Vecchyo D, Han E, Sil P, Galaverni M, Ma P, Lorente-Galdos B (2014) Genome sequencing highlights the dynamic early history of dogs. PLoS Genet 10:e1004016
- Germonpré M, Sablin MV, Stevens RE, Hedges RE, Hofreiter M, Stiller M, Després VR (2009) Fossil dogs and wolves from palaeolithic sites in Belgium, the Ukraine and Russia: osteometry, ancient DNA and stable isotopes. J Archaeol Sci 36:473–490
- Germonpré M, Lázničková-Galetová M, Sablin MV (2012) Palaeolithic dog skulls at the Gravettian Předmostí site, the Czech Republic. J Archaeol Sci 39:184–202
- Gundry RL, Allard MW, Moretti TR, Honeycutt RL, Wilson MR, Monson KL, Foran DR (2007) Mitochondrial DNA analysis of the domestic dog: control region variation within and among breeds. J Forensic Sci 52:562–572
- Ho SY, Phillips MJ, Cooper A, Drummond AJ (2005) Time dependency of molecular rate estimates and systematic overestimation of recent divergence times. Mol Biol Evol 22:1561–1568
- 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. Anim Front 4:23–31
- Huxley TH (1880) On the cranial and dental characters of the Canidæ. In: Proceedings of the zoological society of London. Wiley Online Library, 238–288
- Iljin NA (1941) Wolf–dog genetics. J Genet 42:359–414
- 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. J Hered 94:81–87
- Karlsson EK et al (2007) Efficient mapping of mendelian traits in dogs through genome-wide association. Nat Genet 39:1321–1328
- Khosravi R, Rezaei HR, Kaboli M (2013) Detecting hybridization between Iranian wild wolf (*Canis lupus pallipes*) and free-ranging domestic dog (*Canis familiaris*) by analysis of microsatellite markers. Zoolog Sci 30:27–34
- Kirkness EF, Baranowska I, Wade C, Hillbertz N, Zody M, Anderson N, Biagi T, Patterson N, Pielberg G, Kulbokas E (2003) The dog genome: survey sequencing and comparative analysis. Science 301:1898–1903
- Klütsch CF, de Caprona MDC (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 Biol* 8:119
- Larson G, Burger J (2013) A population genetics view of animal domestication. *Trends Genet* 29:197–205
- Larson G et al (2012) Rethinking dog domestication by integrating genetics, archeology, and biogeography. *PNAS* 109:8878–8883
- Leesch D, Müller W, Nielsen E, Bullinger J (2012) The Magdalenian in Switzerland: re-colonization of a newly accessible landscape. *Quat Int* 272:191–208
- Leonard JA, Wayne RK, Wheeler J, Valadez R, Guillén S, Vila C (2002) Ancient DNA evidence for old world origin of new world dogs. *Science* 298:1613–1616
- Lindblad-Toh K et al (2005) Genome sequence, comparative analysis and haplotype structure of the domestic dog. *Nature* 438:803–819
- Lorenz K (2002) *Man meets dog*. Psychology Press, Taylor and Francis group, Routledge, London, New York
- Milenkovic M, Šipetic VJ, Blagojevic J, Tatovic S, Vujošević M (2010) Skull variation in Dinaric–Balkan and Carpathian gray wolf populations revealed by geometric morphometric approaches. *J Mammal* 91:376–386
- Morel P, Müller W (1997) *Hauterives-Champgréveyres*, 11. Un campement magdalénien au bord du lac de Neuchâtel: étude archéozoologique (secteur 1). *Archéologie neuchâteloise*, 23. Neuchâtel
- Morey D, Jaeger R (2015) Paleolithic dogs: why sustained domestication then? *J Archaeol Sci: Rep* 3:420–428
- Napierala H, Uerpmann HP (2012) A ‘new’ palaeolithic dog from central Europe. *Int J Osteoarchaeol* 22:127–137
- Nehring A (1888) Zur Abstammung der Hunde-Rassen. *Zoologische Jahrbücher Abtheilung Systematik, Geographie und Biologie* 3:51–58
- Oksenberg M (1982) Reconsiderations: a decade of Sino-American relations. *Foreign Aff* 61:190
- Olsen SJ, Olsen JW (1977) The Chinese wolf, ancestor of new world dogs. *Science* 197:533–535
- Ostrander EA, Wayne RK (2005) The canine genome. *Genome Res* 15:1706–1716
- Ovodov ND, Crockford SJ, Kuzmin YV, Higham TF, Hodgins GW, 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
- Pang JF, Kluttsch C, Zo X, Zhang A, Lue L, Angleby H, Ardalan A, Ekström C, Sköllerm A, Lundeberg J (2009) mtDNA data indicate a single origin for dogs south of Yangtze river, less than 16,300 years ago, from numerous wolves. *Mol Biol Evol* 26:2849–2864
- Pionnier-Capitan M (2010) *La domestication du chien en Eurasie: étude de la diversité passée, approches ostéoarchéologiques, morphométriques et paléogénétiques*. PhD thesis, l’Université de Lyon
- Pionnier-Capitan M, Bemilli C, Bodu P, Célérier G, Ferrié J, Fosse P, García M, Vigne JD (2011) New evidence for upper palaeolithic small domestic dogs in South-Western Europe. *J Archaeol Sci* 38:2123–2140
- Pocock R (1946) External and cranial characters of some rare Asiatic mammals recently exhibited by the society. *Proc. Zool. Soc. Lond* 3:310–318
- Rütimeyer L (1861) *Die Fauna der Pfahlbauten der Schweiz. Geschichte der Wilden und der Haus-Saugetiere*. Neue Denkschrift der Allgemeinen Schweizerische Gesellschaft der ges. Naturwissenschaft, 19, Basel, Switzerland
- Sablin M, Khlopachev G (2002) The earliest ice age dogs: evidence from Eliseevichi 11. *Curr Anthropol* 43:795–799
- Savolainen P, Y-p Zhang, Luo J, Lundeberg J, Leitner T (2002) Genetic evidence for an East Asian origin of domestic dogs. *Science* 298:1610–1613
- Savolainen P, Leitner T, Wilton AN, Matisoo-Smith E, Lundeberg J (2004) A detailed picture of the origin of the Australian dingo, obtained from the study of mitochondrial DNA. *PNAS* 101:12387–12390
- 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. *J Osteoarchaeol* 24:42–50
- Schmutz S, Berryere T (2007) Genes affecting coat colour and pattern in domestic dogs: a review. *Anim Genet* 38:539–549
- Schoenebeck JJ, Ostrander EA (2013) The genetics of canine skull shape variation. *Genetics* 193:317–325
- Skoglund P, Götherström A, Jakobsson M (2011) Estimation of population divergence times from non-overlapping genomic sequences: examples from dogs and wolves. *Mol Biol Evol* 28:1505–1517
- Stockhaus K (1965) *Metrische Untersuchungen an Schädeln von Wölfen und Hunden*. *J Zoolog Syst Evol Res* 3:157–258
- Street M (2002) Ein wiedersehen mit dem Hund von Bonn-Oberkassel. *Bonner Zoologische Beiträge* 50:269–290
- Studer T (1901) *Die prähistorischen Hunde in ihrer Beziehung zu den gegenwärtig lebenden Rassen*. Zurcher und Furrer, Zurich
- Sumiński P (1975) Morphologische Unterscheidungsmerkmale zwischen Wolfs- (*Canis lupus* L.) und Hundeschädel (*Canis familiaris* L.). *Zeitschrift für Jagdwissenschaft* 21:227–232
- Thalmann O, Shapiro B, Cui P, Schuenemann VJ, Sawyer SK, Greenfield DL, Germonpré MB, Sablin MV, López-Girálde F, Domingo-Roura X (2013) Complete mitochondrial genomes of ancient canids suggest a European origin of domestic dogs. *Science* 342:871–874
- 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 Genet Syst* 72:229–238
- Vaysse A, Ratnakumar A, Derrien T, Axelsson E, Pielberg G, Sigurdsson S, Fall T, Seppälä E, Hansen M, Lawley C (2011) Identification of genomic regions associated with phenotypic variation between dog breeds using selection mapping. *PLoS Genet* 7:e1002316
- Verginelli F, Capelli C, Coia V, Musiani M, Falchetti M, Ottini L, Palmirota R, Tagliacozzo A, Mazzorin I, Mariani-Costantini R (2005) Mitochondrial DNA from prehistoric canids highlights relationships between dogs and South-East European wolves. *Mol Biol Evol* 22:2541–2551
- Vila C, Maldonado JE, Wayne RK (1999) Phylogenetic relationships, evolution, and genetic diversity of the domestic dog. *J Hered* 90:71–77
- Vila C, Seddon J, Ellegren H (2005) Genes of domestic mammals augmented by backcrossing with wild ancestors. *Trends Genet* 21:214–218
- Vilà C, Urios V, Castroviejo J (1993) Tooth losses and anomalies in the wolf (*Canis lupus*). *Can J Zool* 71:968–971
- Vilà C, Savolainen P, Maldonado J, Amorim I, Rice J, Honeycutt R, Crandall K, Lundeberg J, Wayne R (1997) Multiple and ancient origins of the domestic dog. *Science* 276:1687–1689
- Vonholdt B, Pollinger J, Lohmueller K, Han E, Parker H, Quignon P, Degenhardt J, Boyko A, Earl D, Auton A, Reynolds A (2010) Genome-wide SNP and haplotype analyses reveal a rich history underlying dog domestication. *Nature* 464:898–902
- Wayne RK (2012) Evolutionary genomics of dog domestication. *Mamm Genome* 23:3–18



Wayne RK, Ostrander EA (1999) Origin, genetic diversity, and genome structure of the domestic dog. *BioEssays* 21:247–257

Wayne RK, Ostrander EA (2007) Lessons learned from the dog genome. *Trends Genet* 23:557–567

Wolfgram A (1894) Die Einwirkung der Gefangenschaft auf die Gestaltung des Wolfshädels. *Zoologisches Jahrbuch (Abteilung für Systematik)* 7:773–822