Biological and cultural history of domesticated dogs in the Americas

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Abstract

Domestication had a dramatic influence on the cultural evolution of human histories, and on the biological evolution of domesticated species. Domestic dogs occurred earlier in the Americas than other domesticated animals. Older records in the continent come from North America, dated 11,000-8,400 ybp, and in the Andes from 5,600-5,000 ybp. In order to present an overview of human-dog interaction in the Americas, and to identify gaps in knowledge of this subject, we reviewed 178 publications on zooarchaeological record of burials, genetics, morphology, and ethnological information of American dogs, revisiting the history and interactions across the continent. There is no evidence of an in-situ dog initial domestication. Pre-Columbian diversity in North America includes at least three varieties, whereas in South America six varieties were documented. Historical descriptions of phenotypes (e.g. humped dog) may represent an expression associated with mutations. We find that archaeological, historical, and ethnographic records reveal non-traditional uses and hybridizations with other canids. For example, the Coast Salish people exploited woolly dogs for manufacturing blankets. Dog acquisition by some Amazonian cultures began towards the end of the nineteenth century. Overall more than 41 dog breeds originated in the Americas and are currently recognized by kennel clubs. The main gap in knowledge points to the relationships between American breeds, local hybridizations, migratory routes of dogs following Indigenous peoples' social networks, historical-cultural contexts, and quantification of morphological diversity. North and Central American dogs have been more intensively studied than those from the Amazon regions or Patagonia. We find that the history of domestication in the Americas is far from simple and integrative studies are needed.

Keywords

Archaeology, Morphology, ancient DNA, feralisation, hybridization, breed,

Salish dogs*, Canis,* skulls

Running Head: Dogs in the Americas

Résumé

La domestication a eu une influence considérable sur l'évolution culturelle de l'histoire humaine et sur l'évolution biologique des espèces domestiquées. Les chiens domestiques sont apparus plus tôt en Amérique que les autres animaux domestiqués. Les premières occurrences de chiens domestiques dans les Amériques comprennent des spécimens de sites nord-américains datant d'il y a 11000 à 8400 années et des Andes d'il y a 5600 à 5000 années. Afin de présenter une vue d'ensemble des interactions entre l'homme et le chien sur le continent américain et d'identifier les lacunes dans la connaissance de ce sujet, nous avons passé en revue 178 publications sur l'enregistrement zooarchéologique des sépultures, la génétique, la morphologie et les informations ethnologiques des chiens américains, en revisitant l'histoire et les interactions à travers le continent. Nos recherches montrent qu'il n'existe aucune preuve de domestication initiale du chien *in situ*. La diversité des races canines précolombiennes comprend au moins trois variétés en Amérique du Nord, alors que six variétés ont été documentées en Amérique du Sud. Les descriptions historiques des phénotypes, comme le chien bossu par exemple, pourraient être associées à des mutations génétiques. Les archives archéologiques, historiques et ethnographiques révèlent que les chiens étaient utilisés de façon non traditionnelle et hybridés avec d'autres canidés. Par exemple, les Premières nations Salish de la côte exploitaient les chiens dits laineux pour la fabrication de couvertures. L'acquisition de chiens par certaines cultures amazoniennes a commencé vers la fin du XIXe siècle. Au total, plus de 41 races de chiens domestiques sont originaires des Amériques et sont actuellement reconnues par les fédérations cynologiques. Cependant, nous avons constaté un manque de connaissances concernant les relations entre les

races de chiens américaines, les hybridations locales, les routes migratoires des chiens suivant les réseaux sociaux des peuples indigènes, les contextes historico-culturels et la quantification de la diversité morphologique. Les chiens d'Amérique du Nord et centrale ont été plus étudiés que ceux des régions amazoniennes ou de Patagonie. Pour conclure, cette étude montre que l'histoire de la domestication dans les Amériques est loin d'être simple et que des approches intégratives permettaient de mieux comprendre ce sujet.

Mots clés

Archaeology, Morphology, ancient DNA, feralisation, hybridization, breed, Salish dogs*, Canis,* skulls

INTRODUCTION

Aside from the polar regions, the Americas were the last continents populated by humans, at least 15,000 years before present (ybp) (Moreno-Mayar *et al*. 2018). The human-animal interactions that occurred since then include domestication, an activity that has dramatically influenced human history and biological evolution. Only a few animals were and still are domesticated by Indigenous people in the Americas: among mammals, the llama (*Lama glama* Linneaus, 1758), alpaca (*Vicugna pacos* Molina, 1782), and the guinea pig or cui (*Cavia porcellus* Linneaus, 1758), all in the Andean region; among birds, the Muscovy duck (*Cairina moschata* Linneaus, 1758) in the Amazon region, and the turkey (*Meleagris gallopavo* Linneaus, 1758) in areas of what is today Mexico (Larson & Fuller 2014). One domesticated animal occurred much earlier in the Americas than the others: the dog (*Canis familiaris* Linneaus, 1758). It predates the multiple exchanges and introduction of other domesticates between the Americas and the rest of the world after the year 1492 (Leonard *et al*. 2002, Leathlobhair *et al*. 2018).

Here we review much of the literature that pertains to the tempo and mode of domestic dog evolution, and interactions with humans in the Americas, since their arrival in late Pleistocene or early Holocene times. We bring together contributions from different disciplines including zooarchaeology, ethnology, molecular biology and evolutionary morphology. We help identify open questions and knowledge gaps, and note how new methodological tools (Evin 2016, 2020, Sykes *et al*. 2019) and conceptual developments (Sykes 2014)

being applied in Europe, Asia and Africa could help elucidate the patterns of dog domestication in the Americas.

METHODS

Our work included literature searches using online available information, mainly based on databases such as Google Scholar, Scopus, Scielo, PubMed, Latindex, Redalyc, DOAJ, Biodiversity Heritage library, Library Genesis, and Internet Archive. Our search strategy was carried out using the following terms: *dog domestication, American dog, dog history*, followed by selection of all publications on the topic restricted to the Americas, taking into account all languages. We reviewed 178 articles (i.e. 118 papers in scientific journals, 31 books, 22 book chapters, and 7 dissertation theses) focusing on topics developed in this report (general knowledge, antiquity of dogs in the Americas, morphology of American dogs, hybridization, and non-traditional uses of American dogs). The information compiled ranged from the years 1651 (See Hernández 1992) to 2021 (e.g. Perri *et al*.) and included archaeological, ethnological, and zoological publications. The bibliography included references that cannot be found easily in conventional searches to material published in traditional journals, and spanned from detailed chronicles and anecdotal experiences to information written exclusively about this topic. Many references of works in Spanish were obtained through personal contact from reliable sources not commonly available, helping thus to circumvent the biases resulting from standard searches that are formally correct but de facto potentially ignore relevant works (Nuñez & Amano 2021).

RESULTS

Antiquity of dogs in the Americas

The antiquity of *Canis familiaris* in the Americas is controversial (Larson *et al*. 2012, Perri *et al*. 2019). The more ancient records come from North America, dated to approximately 10,000 ybp (Rick *et al*. 2008, Barnosky *et al*. 2014). The earliest record in North America was originally in Jaguar Cave site (Idaho) dated 10,400 ybp (Lawrence 1968), although subsequent revisions placed it at 3,500 and 1,000 ybp (Gowlett *et al*. 1987). Genomic analyses were performed on a small bone fragment at Hinds Cave (Texas, Tito *et al*. 2011) that has been dated to around 9,200 ybp. Additional records of ancient dogs in North America come from Stilwell II (10,190-9,630 ybp, Illinois; Perri *et al*. 2019), Koster (10,130-9,700 cal bp, Illinois; Perri *et al*. 2019), Rodgers Shelter (c. 8,800 ybp, Missouri; McMillan 1970), Modoc Rock Shelter (c. 8,400 ybp, Illinois; Ahler 1993), and Dust Cave (c. 8,400 ybp, Alabama; Walker *et al*. 2005).

Identifying dog remains at archaeological sites is complex, as is discriminating between dogs and wolves (*Canis lupus* Linneaus, 1758), as incipient domesticated dogs were likely wolf-like (Nowak 2005, Larson *et al*. 2012). This matter is further complicated by the morphological plasticity of *Canis* (Drake *et al*. 2015, Janssens *et al*. 2016, Drake *et al*. 2017, Morey & Jeger 2017). A recent and comprehensive review of morphological and morphometric parameters that have been used to distinguish dogs from wolves (Janssens *et al*. 2019) found that recent large Pleistocene canids reported as Paleolithic dogs fit within the morphometric distribution of Pleistocene wolves. However, a recent reanalysis (Galeta *et al*. 2020) reinforces the evidence of the morphological

differences of Paleolithic dogs (beyond the small sample size) with respect to Pleistocene or recent wolves and recent dogs, in agreement with previous hypotheses (e.g. Germonpré *et al*. 2018). Putative Paleolithic dogs show morphological uniformity based on a combination of a relatively shorter skull and a relatively wider palate and braincase, as a signal of incipient domestication. In fact, Bergström *et al*. (2020) demonstrated the presence of at least five ancestral lineages of dogs at 11,000 ybp, suggesting a deeper and older history of human-dog relationship than has been traditionally considered.

Often zooarchaeologists studying the Paleoindian Period in North America cannot determine the true status of canid remains based on the geographical or morphological records alone (Larson *et al*. 2012, Perri 2016, Perri *et al*. 2019). Some authors have argued for the possibility of an *in situ* domestication of wolves (e.g. Koop *et al*. 2000, Witt *et al*. 2015), but this is in disagreement with ancient DNA analyses (Vilà *et al*. 1997, Leonard *et al*. 2002, von Holdt *et al*. 2010, Freedman *et al*. 2014, Leathlobhair *et al*. 2018, Bergström *et al*. 2020, Sinding *et al.* 2020), which have suggested that dog domestication centers were restricted to Asia and Europe. Accordingly, domestic dogs are hypothesized to have colonized the Americas by accompanying humans that came over and rapidly dispersed into the continent from around 15,000 ybp onwards (Bergström *et al*. 2020, Perri *et al.* 2021). Although some archaeological dog specimens (from North America) show genetic markers of relatedness to North American wolves (Koop *et al*. 2000, Witt *et al*. 2015), Perri *et al*. (2019) considered this the result of post-domestication admixture of domestic dogs and wolves rather than North American wolf domestication.

Dogs appear south of the original wolf distribution in Eurasia and North America, recorded in most places where agriculture is documented (Larson *et al*. 2012, Bergström *et al.* 2020). This pattern was also consistent in the Neotropics, including Mexico (Coxcatlan Cave, 5,200 ybp; Flannery 1967) and southern South America (1,000 ybp; Prates *et al*. 2010), where dogs are contemporarily associated with a sedentary mode of life related to agriculture. However, recent evidence suggests that the depth of human-dog mutualism may decrease with the development of agriculture, because dogs tend to lose importance as hunting companions (Perri 2016, Morey & Jeger 2017, Chambers *et al*. 2020).

In South America, the archaeological record of dogs is relatively rich in the Andean region of Peru, Chile, and Ecuador, with records from as old as 5,600-5,000 ybp (Loma Alta, Ecuador; Rosamachay, Chile and Peru; Byrd 1976, Stahl 1984, Mac Neish & Vierra 1983). A 2,000 ybp record was reported for southern Brazil (Guedes Milheira *et al*. 2017). Farther south in South America records are scarce, but some are equally old to those mentioned above, although their pertinence to *Canis familiaris* is questioned. For instance, the sites of Arroyo Seco (Argentina, 12,300-8,400 ybp), Cueva Tixi (Argentina, 10,400-10,000 ybp), Fell's Cave (Chile, 10,340-10,020 ybp), and Los Toldos (Argentina, 9,200-8,200 ybp), are among the most important "oldest dog" sites (Caviglia 1986, Caviglia *et al*. 1986, Clutton-Brock 1988, Gutiérrez & Martinez 2008). These reports suggest a long history of dogs in southern South America, but recovered fossils in Patagonia and a reanalysis of evidence suggest that these records may belong to *Dusicyon avus* (Oliver 1926) or extant canids such as *Lycalopex culpaeus* Molina, 1782 or *L. griseus* Gray, 1837 (Langguth 1975, Caviglia *et al*.

1986, Fidalgo *et al*. 1986, Mazzanti & Quintana 1997, Amorosi & Prevosti 2008). The apparent discrepancy in the age of the records is another factor that limits temporal accuracy. Dog acquisition in the Amazonian cultures is notably recent (end of nineteenth century; Koster 2009, Stahl 2014). However, groups on the margin of the rainforest possessed dogs before the Europeans arrived (Pohl 1985, Guedes Milheira *et al*. 2017). Infectious diseases may have constrained the spread of dogs into some Neotropical environments (e.g. Amazonian region; Mitchell 2017, Chambers *et al*. 2020). Because the ancestor (the wolf) is not a tropical animal, its descendants would not have adapted to tropical parasites (Mitchell 2017). Recent studies considering cultural contexts in human-dog co-evolution (e.g. Chambers *et al*. 2020) also point to significant ecological constraints in the degree of mutualism, as warm climate and pathogenic stress can negatively affect the coexistence via less mutual utility. On the other hand, Uhl *et al*. (2019) indicated that the flux of diseases is generally in the opposite direction, from domestic dogs to wild canids. DNA studies may address these ideas, as when tracing the origin of a contagious canine cancer transferring during mating that manifests as genital tumors. This cancer was originated by cells of a founder domestic dog in America that lived 8,225 years ago and leaves a minimal genetic legacy in modern dog populations (Leathlobhair *et al*. 2018).

The morphological diversity of pre-Columbian American domestic dogs

In North America, records show variation in shape and size (Allen 1920, Schwartz 1998, Ensminger 2017). The two oldest domestic dog specimens found in North America (i.e. Koster & Stiwell II sites) exhibit different sizes (Perri

et al. 2019). In contrast, some studies have highlighted the small size variation in the oldest records from North America (Morey & Wiant 1992, Crockford 2005) and argued that significant variation in skull size and shape (e.g. brachycephalic dogs) was not apparent until after about 4,000 ybp (e.g. Haag 1948, Crockford 1997). Reportedly, there is little evidence to point to a deliberate selection of specific phenotypes, especially for small dogs (Crockford 2005). Manin and Lefèvre (2016) suggested that not all contemporary societies of central Mexico in Classic and the Conquest periods, 500-1800 ybp, were specialized in the breeding and production of domestic dogs. Skull shape and size diversity in pre-Columbian North American dogs includes Mexican varieties such as the *itzcuintle* (common dog), *xoloitzcuintle* (Mexican hairless dog), *techichi* or *tlalchichi* ("mat [floor] dog"), the short-nosed dog, and a hybrid between dog and wolf called "loberro" (Blanco Padilla *et al*. 1999, Valadez *et al*. 2000, 2001, Blick *et al*. 2016). The highly unusual Mexican "humped" dog (Hernández 1651, Fig. 1) has been dismissed as a caricature (Ueck 1961). However, there is the possibility that such form represents a phenotype associated with mutations in the myostatin gene, which leads to abnormally heavy muscling in homozygous whippet dogs (''bully'' whippets), mice, cattle, sheep, and humans. Such mutation was observed in selected racing breeds, being positively selected in some cases (Mosher *et al*. 2007).

In North America, four additional size and kind categories of domestic dogs have been recognized, including a large, wolf-like form found in North Dakota, a smaller, coyote-like form associated with some of the central Plains Indigenous groups, as well as both short-faced and long-faced 'Pueblo' dogs (Allen 1920, Olsen 1974). Variation in coat color was also present, as descriptions of both

white and black dogs have been recounted in the Pacific Northwest (Crockford 1997, Barsh *et al*. 2002), and the 'Basketmaker' mummified dogs, dated to approximately 2,000 ybp, have a piebald black and white coat and a tawny coat (Guernsey & Kidder 1921, Wormington 1947, Olsen 1974, Crockford 1997, Fugate 2008).

Examples of skulls of pre-Columbian domestic dogs from South America are shown in Figs 2-4. Dog populations in South America were diverse in skull shape and size before Europeans arrived (Gallardo 1965, Allen 1920, Fernandez de Oviedo y Valdés 1944, Valadez *et al*. 2000, Valadez & Mendoza 2005, Acosta *et al*. 2011, Blick *et al*. 2016). Spanish chroniclers described many varieties of canids that could, however, have been tamed wild forms confused with domestic dogs (Stahl 2013, Segura & Sánchez-Villagra in review).

Peruvian dogs were diverse, including a "shepherd-like" dog, a "hairless dog" (Tschudi 1844-46), a "dachshund-like" dog, a "bulldog" type dog (Nehring 1884, Reiss & Stübel 1880-1887, Gilmore 1950, Gallardo 1965), a dog with a somewhat shortened snout (Noak 1916), and a medium-sized dog with a long snout (Wing 1989). As in Mexico, Peru also developed its own hairless dog; both are currently recognized by the International Kennel Club (Vásquez *et al*. 2016, Appendix 1). Although the European origin of the modern Mexican *xoloitzcuintle* and the Peruvian hairless dog due to post-contact interbreeding was suggested (Leathlobhair *et al*. 2018), the archaeological record, based on artistic depictions and abnormal tooth morphology of skulls, showed that there were hairless dogs in Peru prior to the European invasion (Tschudi 1844, Leicht

1960). Shared genetic markers among modern and archaeological specimens assigned to hairless dogs also suggest common ancestry (Manin *et al*. 2018).

The Inca chronicler (and draftsman) Guamán Poma de Ayala described several types of dogs in Peru, including long-snouted, brachycephalic, and hairless dogs (Mendoza & Valadez 2003). In other regions of South America, the chronicles and archaeological record recorded “large and small dogs like ours, that they much esteem” (Fernandez de Oviedo y Valdés 1944, on lower Paraná River), a medium-sized dog from the Southern Cone (Acosta *et al*. 2011), and “small dogs, raised in houses, which are mute and do not bark” (Fernandez de Oviedo y Valdés 1944, on La Plata River Basin). Columbus reported two types of dogs in the Caribbean: larger mastiff-type dogs, and smaller, terrier-type dogs (Blick *et al*. 2016), which were recorded in archaeological sites (Grouard *et al*. 2013). Dogs reported from the extreme south (Patagonia and Tierra del Fuego) were also diverse in size, appearance and uses (Allen 1920, Cooper 1946, Schwartz 1998).

The morphological diversity of post-Columbian, American domestic dogs

In the Americas, Kennel clubs have been established since the late nineteenth century (e.g., 1884 in the case of the USA American Kennel club, 1888 the Canadian one) and today, more than 41 domestic dog breeds that originated in the Americas are recognized (Appendix 1). These American dog breeds exhibit remarkable variation in terms of body size, head shapes, dentition, and fur quality, which is comparable to – and even exceeding – the variation seen in dog breeds worldwide (Fig. 5).

The short and dorsally rotated rostrum, which is typical of brachycephalic breeds, characterizes breeds of different origins and size, including the Boston Terrier and American Bulldog (Fig. 6), among others such as the Alapaha Blue Blood Bulldog. There are also dolichocephalic breeds (e.g., American Foxhound, Silken Windhound), which tend to have narrow and elongated snouts and more lateral orbits. American dog breeds vary greatly in body size, ranging from the massive Newfoundland dog to the world's smallest breed, the Chihuahua (Figs 5-6). Moreover, there are several modern breeds of fully or partially hairless domestic dogs that originated in the Americas, which also exhibit reduced tooth number in dental formulae (e.g., Peruvian hairless dog and Mexican Xoloitzcuintle; Kupczik *et al*. 2017).

Hypotheses about the phylogenetic relationships between breeds have been generated from genomic data (Parker *et al*. 2017), with some modern American breeds considered as basal (e.g. Alaskan Malamute, American Eskimo). There is substantial zooarchaeological and molecular evidence suggesting that pre-Columbian dogs are mostly extinct (including hairless dogs), and that these were replaced by the various European dog lineages (Leonard *et al*. 2002, Castroviejo-Fisher *et al*. 2011, Larson *et al*. 2012, Thalmann *et al*. 2013, Leathlobhair *et al*. 2018, Manin *et al*. 2018). Other authors have found evidence for a pre-Columbian origin and no modern European influence on Arctic ancient breeds such as Inuit, Eskimo, and Greenland dogs (Ameen *et al*. 2019), as well as the Mexican Chihuahua, suggesting just a partial replacement by modern European dogs (e.g. Brown *et al*. 2013, van Asch *et al*. 2013).

Several endemic breeds from the Americas originate mainly from crossbreeding between breeds of mostly European lineages (e.g. Larson *et al*. 2012, Leathlobhair *et al*. 2018), not all of which are currently recognized by Kennel clubs. For instance, several old American breeds (e.g. Alaskan Malamute, Eskimo dog, Xoloitzcuintle, Peruvian hairless dog) are currently recognized by the International Canine Kennel Club, whereas the endemic and very old Carolina Dog (genetically distinctive, Oskarsson 2012, van Asch *et al*. 2013) is recognized only by the smaller United Kennel Club and partially by the American Kennel Club. Another example of post-Columbian dog phenotypes created in the Americas is the Ovejero Magallanico from southern Chile's Magallanes and Antarctica Region (Barrios *et al*. 2016), which originates from European breeds such as the extinct British breed Old Welsh Grey, and several varieties of Collies (Fuenzalida 2006). The Ovejero Magallanico or "Patagonian Sheepdog" is still an unrecognized breed, and seems to have high morphostructural uniformity, sexual dimorphism, and a combination of its own phenotypic features (Barrios *et al*. 2016, 2019).

Hybridization of domestic dogs with other canids

Recent reports (e.g. Frantz *et al*. 2020; Sinding *et al*. 2020) highlighted the importance of the genetic introgression of wild populations of *Canis* (*latrans* and *lupus*) that did not participate in the initial domestication process. Several evidences on genetic introgression have argued for the existence of crossbreeding between domestic dogs and North American wolves or coyotes (*Canis latrans* Say, 1823) (e.g. Walker & Frison 1982, Lehman *et al*. 1991, Roy *et al.* 1996, Valadez *et al*. 2001, 2002a, b, Adams *et al*. 2003, Valadez *et al*.

2006), what could have been an old practice contributing genetic diversity to the lineages of pre and post-Columbian American dogs. New and more powerful molecular techniques currently available (Sykes *et al*. 2019, Frantz *et al.* 2020) could be used to test these hypotheses. The analysis of ancient DNA of Koster's dog, one of the oldest records in North America, revealed a strong affinity with coyotes, with which it may have been mixed (Perri *et al*. 2019). A recent dietary study based on isotopes (Monagle *et al*. 2018) demonstrated that coyotes may have had a special role for Arroyo Hondoans people, and the Ute people kept and tamed coyotes in the Great Basin (Stewart 1942). However, a recent report (Sinding *et al.* 2020) found no significant gene flow between modern and ancient American sled dogs and modern American–Arctic wolf populations, in comparison with the Eurasian wolf. Such results suggest that modern American wolves have not contributed to the sled dog gene pool at least for the last 9,500 years, and support that the lack of gene flow from modern American-Arctic wolves into sled dogs potentially implies selection against hybrids.

The chronicles are clear in referring to the admixture of dogs with wolves or foxes, ancestrally practiced by many Native American cultures (e.g. Latcham 1823, Allen 1920, Valadez *et al*. 2001, Stahl 2013). For instance, the chronicles of Rengger of his trip to Paraguay in the nineteenth century describe the Indigenous peoples' customs of collecting *Lycalopex gymnocercus* Fisher, 1814 puppies, taming, keeping, and even interbreeding them with domestic dogs (Mivart 1890, Latcham 1823). The chronicles of Fernandez de Oviedo y Valdés (1944) also mentioned the taming and interbreeding of *Cerdocyon thous* Linneaus, 1766 with European domestic dogs, and perhaps with pre-Columbian

American dogs. According to the chronicles compiled by Roth (1924) and Cabrera and Yepes (1960), the Makusi of Guiana kept foxes (*C. thous*) adopted from pups, which they presumably crossed with their domestic dogs in order to obtain better specimens for hunting. The Selk Fuegians also likely tamed specimens of *L. culpaeus* (Petrigh & Fugassa 2013) which were crossed with dogs in pre-Columbian times.

The viability of generations of hybrids of dogs with South American endemic canids has been questioned based on empirical (Gilmore 1950) and chromosomal (Wayne *et al*. 1987, Sillero-Zubiri *et al*. 2004, Vilà & Leonard 2012) data. Furthermore, on the basis of dental morphology, a sole ancestry of pre-Columbian domestic dogs from the wolf, but not the coyote, has been suggested (Ueck 1961). However, the gene pool available from *Canis* species from North America and Mesoamerica has been well exploited by the native peoples of these regions, and possibly also by Europeans. Records of possible hybrid dog-wolves on the Plains were reported from old burials (Walker & Frison 1982). The chronicles of Richardson on the Plains described by Young and Goldman (1944) detailed the similarities between domestic dogs and wolves, and argue that hybrids demonstrate more strength than ordinary dogs for hunting. All these noteworthy claims require testing with comparative anatomical comparisons and modern DNA and morphometric tools.

Heppenheimer *et al*. (2018) reported a genetic signal of the extinct red wolves (*Canis rufus* Audubon & Bachman, 1851) in a living wild population of *Canis familiaris* in Galveston, Texas. Monagle *et al*. (2018) studied the diet of several archaeological specimens in Arroyo Hondo Pueblo (Mexico) through isotopes,

finding an overlap in the diet of domestic dogs and wild coyotes, what may have resulted from similarity in the contacts to human settlements. These facts could suggest integration of wild canids in human society and their domestic dogs and/or commensal behavior of wild coyotes.

In South America, large species such as the Culpeo (*Lycalopex culpaeus*) or the Maned Wolf (*Chrysocyon brachyurus* Illiger, 1815), the former more common in archaeological sites, could be confounded if the remains are scarce or fragmentary, but differences in skull morphology between those species and *Canis* exist (Prevosti 2010, Prevosti *et al*. 2015, Loponte & Acosta 2016). Beyond these observations, taphonomic processes can also lead to problematic recognition of a dog fossil record, particularly in humid areas.

Dogs as a source of food

Dogs domesticated by Indigenous people, much like the dogs of today, played a number of roles in pre-colonial American societies (e.g. Bozell 1988). As part of this practice, Indigenous people implemented a range of diverse strategies for domestication, culling populations, and caring for maternal health (e.g. Bozell 1988). The usage of dogs by Indigenous people is geographically and temporally variable, with dogs being used for hunting, transport, food, rituals, company, and defense (e.g. Winship 1904, Teit 1909, Allen 1920, Allison *et al*. 1982, Bozell 1988, Barsh *et al*. 2002, Cunningham-Smith & Emery 2020).

Even today, dogs are used as food in some regions of Asia, although this is not practiced in the Americas. In contrast, some past American cultures, such as

Maya and Aztec, are associated with the earliest Mesoamerican remains of domestic dogs used as food (Wing 1978, Fritz 1994). There are several reports from European colonizers that document this practice, primarily in times of famine or as part of socio-cultural rituals (e.g., Catlin 1841, Allen 1920, Bozell 1988). It is also possible to reconstruct this behavior through the zooarchaeological records of middens, dumps for domestic waste, which include bones with cut marks suggesting butchery. In many cases, there was a heterogeneous use of the resource over time. For instance, Mayans living at Pasion River site (Guatemala) showed a strong temporal variation in the consumption of animals such as dogs, deer, and turtles in their dumps, eating more dogs during the Formative period than in the Classical period (Olsen 1972, Pohl 1990), perhaps because the practice of intensive agriculture increased in the latter stage (Schwartz 1998). Aztecs from the Tehuacán Valley (Mexico) also showed a change in the consumption of dog over time as related to changes in climate and population sizes (Flannery 1967). In fact, archaeological evidence from North American and Japanese dog burials suggests that the development of agriculture reduced dogs' importance (Perri 2016, Morey & Jeger 2017, Chambers *et al*. 2020). For the Incans, eating a dog was considered unpleasant and a bad habit, moreover they prohibited the consumption by those living in the Empire (Weiss 1970). Consumption could have been triggered or practiced more frequently by the lack of sufficient food caused by an increase in local population sizes, or by environmental changes that forced the management of some species for their own benefit (Morey 1994).

In the case of Caribbean groups, and some cultures of southeastern USA (Florida), dog eating was a habit, although in some cases rarely practiced by all groups in stratified societies (Wing 1978, Clayton *et al*. 1993). In the west and northwest of North America, archaeological excavations have found cut marks suggestive of butchery on dog remains (e.g., in Alaska, McManus-Fry *et al*. 2018), and the consumption of dogs has been linked to religious rituals and festivities (Catlin 1841). Rituals of the Dog-Eaters, a 'secret society' of the Tsimshian of the Pacific Northwest, were associated with social distribution of wealth and selective breeding of village dogs (Boas & Tate 1916, Allison *et al*. 1982, Ruttle 2010, McAllister 2011). During the course of the ritual, dogs that had left the village and associated with wolves were killed, thereby selecting for more obedient village dogs (McAllister 2011). There are varying reports of dog flesh consumed during the ritual, but some accounts reported that as little flesh as possible was consumed, emphasizing that this was not a common food source (Frazer 1910).

In general, a pattern is observed where the habit of consuming dogs as a meat supplement was developed in agricultural cultures, and not so much in hunter-gatherer societies (Schwartz 1998). On the other hand, many hunter-gatherer peoples did strive to create breeds of certain domestic animals for defined purposes (e.g. for hunting or for use in making textiles, so not including the dog as a food source was a decision and not an accident) (Valadez & Mendoza 2005).

Dogs for hunting, transportation, and herding

According to ethnographic and historical records, hunting dogs were commonly utilized by many different peoples in the Americas, with variation in how the dogs were kept, used, and trained (Morey 2010). For example, the Klamath people of Oregon utilized dogs for hunting of small animals such as the beaver, whereas the Fuegian dogs of southern South America were commonly used by the Selk'nam people to hunt otter (Allen 1920). Other peoples commonly noted to have bred and trained domestic dogs for hunting include the Salish people of the Pacific Northwest, the Inuit people of the north, and the Hidatsa, among others (Teit 1909, Allen 1920, Wilson 1924, Barsh *et al*. 2002).

In addition to hunting, transportation was a task employed by dogs in the Americas. European colonizers wrote about the use of sled dogs, or *travois*, as early as the 1500's in Mexico (Winship 1904, Allen 1920). The Pawnee people of eastern North America commonly used dogs as 'beasts of burden', pulling sleds, or sledges (Bozell 1988), as did the Hidatsa (Allen 1920, Wilson 1924). The Inuit, most widely associated with sled-dogs, used them to transport goods and people across the tundra (e.g., Laugrand & Oosten 2002, Ameen *et al*. 2019). As part of the forced suppression of Indigenous people during the twentieth century, many sled dogs were killed by the US government, leading to a heightened sense of responsibility and connection between these peoples and their dogs (Laugrand & Oosten 2002). In addition, sleds dogs were also used in the Arctic of western Alaska by peoples like the Yup'ik to transport umiak, or large skin boats, to fishing sites (McManus-Fry *et al*. 2018).

Herding dogs were much less common in pre-Columbian Americas, although they are documented starting with European colonization, particularly as

herders of horses, for example among the Cherokee (Allen 1920). It has been widely reported that Indigenous people used dogs to herd animals such as llamas (Chiribaya culture, Peruvian coast), although the use of dogs for this purpose is questionable (Schwartz 1998, Wylde 2017). However, Inca Chronicler Guamán Poma de Ayala drew a young girl as herder with two llamas and a dog (Mendoza & Valadez 2003).

Dogs for wool

One use that was practiced by Indigenous peoples, which is absent from today's culture, was the use of dogs in the textile industry for weaving and shearing. An entire textile industry for dog wool was developed by the Salish peoples. According to historical accounts and oral histories, the Salish peoples kept two types of domestic dog – one referred to as the 'village dog' and one referred to as the 'woolly dog' (Fig. 7; Howay 1918, Gleeson 1970, Gunther 1972, Crockford 1994, 1997, 2005, Crockford & Pye 1997, Barsh *et al*. 2002). The woolly dog is described as medium bodied, with thick matted hair and a curly tail, and has been repeatedly compared to the Spitz (found across Europe and Asia), and Japanese Shiba and Akita (Howay 1918, Keddie 1993). As early as Howay (1918), and consistent with our understanding of the peopling of the Americas today, the Salish woolly dogs have been used as evidence for a genetic relationship between Asian and American dogs (e.g., Koop *et al*. 2000), and Asian and American peoples (e.g., Hlusko *et al*. 2018).

However, researchers have not yet been able to determine the existence of a single lineage that characterizes and differentiates woolly dogs from other Coast Salish dogs (see Anza-Burgess *et al.* 2020). The Coast Salish First

Nations exploited the thick fur of these dogs for manufacturing blankets (Howay 1918, Schulting 1994, Crockford & Pye 1997). Historical accounts report that the woolly dogs were kept separate from the village dogs and left to their own accord on small islands in the Salish sea with a large quantity of dried salmon to ensure that they would not starve, and then shorn short in the fall (Jenness 1934). Isotopic investigations of dog remain at archaeological sites in the Pacific Northwest demonstrate that, like many coastal Pacific Indigenous peoples, dogs in the archaeological record had a diet dominated by marine foods, particularly fish and shellfish (Cannon *et al*. 1999, Hofman & Rick 2014, Ames *et al*. 2015, West & France 2015, McManus-Fry *et al*. 2018).

The thick hair of the Salish woolly dogs was used extensively in the textile traditions of the Salish peoples, particularly in weaving (e.g., Schulting 1994, Tepper *et al*. 2017). Before the 1900s, blankets were an integral part of the currency of the Salish peoples, and Salish groups developed a unique weaving style and weaving technology that is prolific in the archaeological record (Wells 1969, Suttles 1983, Croes 2015, Barsh *et al*. 2002). Several Salish blankets have been identified in museum collections and sampled using proteomics with the results demonstrating that these blankets have significant amounts of dog hair in the weave (Solazzo *et al*. 2011). None of the blankets were made exclusively of dog hair – the textiles were made from interwoven dog hair and other fibers, particularly mountain goat hair which would have been a rare commodity in the coastal populations of the Salish Sea (e.g., Solazzo *et al*. 2011). With increasing numbers of colonial Europeans on the Pacific Coast, Salish blankets became devalued, and by all accounts, the woolly dog breed

was completely lost by the mid-1800s (Barsh *et al*. 2002, Croes 2015, Anza-Burgess *et al.* 2020).

There are scattered reports of dogs for weaving and shearing recorded by Europeans among other cultures, including Indigenous peoples in New Mexico (1500s; Winship 1904) as well as peoples of the MacKenzie River in Canada and among the Chono of Chile (Allen 1920, Cooper 1946). Several authors (Cooper 1917, Samitier 1967, Urbina-Burgos 2007) reported that the Chono peoples, inhabitants of the southern tip of Patagonia in Tierra del Fuego, bred small woolly dogs that helped with the hunting of otters, whose fur was also used for making blankets. Although the Chono did not develop a refined technique for textile production and breeding of these varieties of dogs, they also used dog hair for textile making. In North America, the Zuni people (New Mexico) also bred varieties of long-haired dogs they used to make clothes, according to the chronicles of the Spaniard Francisco Vázquez de Coronado y Luján (Winship 1896, Schwartz 1998). This custom, although rare, seems to have been practiced by different cultures, although never with the sophistication employed by the Salish peoples (Amoss 1993, Crockford 2005).

CONCLUSIONS

Recent advances in isotope analysis techniques, analytical morphology, analysis of ancient DNA and other techniques, as well as the discovery of new archaeological sites related to dogs in the Americas, provided a great boost to the knowledge of the history of dogs on these continents. However, there are still many gaps in our knowledge. The historical relationships between breeds of

American lineage (Parker *et al.* 2017), as well as the genetic contribution of wolves or other American wild canids to the domestic dogs are still much discussed, and the genetic relationships and morphological similarities of new specimens found in the archaeological record suggest alternative hypotheses of dispersion and crossing events with wolves. American dog populations today may or may not have a strong genetic component originating from pre-Hispanic dogs, as well as from wild canids from the genus *Canis*. Revisionary work based on ancient DNA, radiocarbon dating (Popovic *et al*. 2020, Frantz *et al*. 2020), and morphology (Manin & Evin 2020), is likely to contradict many previous attributions of materials to domestic dogs or claims of hybridizations with local canids. Even for well-known species such as the dog, many uncertainties remain regarding important topics, such as migratory routes of humans and dogs in the Americas, and dog dispersal following Indigenous peoples' social networks, historical cultural contexts, local hybridizations, quantification of dog morphological diversity (past and present), and phylogenetic relationships of current American breeds. Perhaps comparative ethnological work can provide insights into the cultural evolution of dog domestication in the Americas.

It is necessary to address knowledge gaps in anatomical characters that contribute to differences between domestic dogs and wolves, mainly those specimens from times of incipient domestication (Janssens *et al*. 2016, 2019, Galeta *et al*. 2020). The knowledge of the variation of cranial and dental characters in wolves (Perri 2016) and basal breeds of domestic dogs (Geiger *et al*. 2017) is an aspect still under study. The morphological diversity of pre-Hispanic American varieties was never quantitatively examined in the context of the diversity of wolves and other American canids. A comprehensive study of

variation of available skulls or their parts, and of dentitions, are needed, if possible using three-dimensional geometric morphometrics to best capture shape differences. This will identify the temporal and geographic patterns of change and make evident where the gaps of samples in the zooarchaeological record exist. An *in situ* domestication process in the Americas cannot be totally excluded, given the complex process of the dog's entry into the continent, but there is no evidence of this until now, nor of domestication of any other canid species (Segura & Sánchez-Villagra in review). Another challenging topic is to decipher the reasons why the Amazonian people did not possess dogs until (in the case of most groups) the 20th century, and to test if indeed that vast region never hosted domestic dogs before that time. The history of domestication in the Americas is far from simple, and integrative studies are needed. For example, isotopic work (carbon, nitrogen, and oxygen isotopes) has allowed researchers to trace trade routes, as with Mayan people bringing dogs to Ceibal from distant, highland regions (Sharpe *et al*. 2018). This study provided the earliest evidence for live-traded dogs and possible captive-reared specimens of wild taxa in the Americas, with possible ceremonial contexts suggesting that animal management and trade began in the Mayan area to promote special activities and played an important role in the symbolic development of political power. The topics addressed in this work were summarized for American dogs based on 178 scientific papers identified via literature search of databases and libraries. 41% of these focused exclusively on North American and Mesoamerican dogs, 26% on South American dogs, and the other 33% on general aspects of all American dogs, or dogs from the rest of the world. The existing bias in the studies carried out on dogs from North and Central America may reflect differences in research traditions and efforts in these regions and

the older age of interaction and coexistence with humans in North America as compared to the Amazonian forest or southern Patagonia.

The access to collections and the integration of samples in studies of morphometrics and ancient DNA will be important to reconstruct the tempo and mode of domestic dog evolution in the continent, as in current studies being carried out primarily in Europe and Asia (Larson *et al*. 2012, Leathlobhair *et al*. 2018, Bergström *et al*. 2020).

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Fig. 1. - "Canis mexicana", a domestic dog with peculiar humps and apparent muscle hypertrophy, as depicted in Hernández' (1651). Previously dismissed as a caricature (Ueck 1961), it may actually illustrate a phenotype associated with mutations in the myostatin gene. Picture retrieved from The Internet Archive, https://archive.org/details/rerummedicarumno00hern/page/466/mode/1up?q=hump

Fig. 2. - Remains of pre-Columbian domestic dogs as reported in the nineteenth century. Drawings of remains of domestic dogs excavated from the graves of Ancon in Peru, as depicted in Reiss & Stübel (1880-1887; Plates 117 and 118, picture modified to exclude the depiction of a fox-like animal). Left side, mummies, as well as skull with mandible of one mummy, of shepherd-like domestic dogs. Right side, skulls and mandibles of shepherd-like, dachshund-like, and bulldog-like domestic dogs as well as long bones of the forelimb of a dachshund-like domestic dog. Two of these skulls are also depicted in (Fig. 3). Available from the Ibero-Amerikanisches Institut (Preussischer Kulturbesitz), https://digital.iai.spk-berlin.de/viewer/image/1681616637/225/ and https://digital.iai.spk-berlin.de/viewer/image/1681616637/229/ Drawings are not to scale.

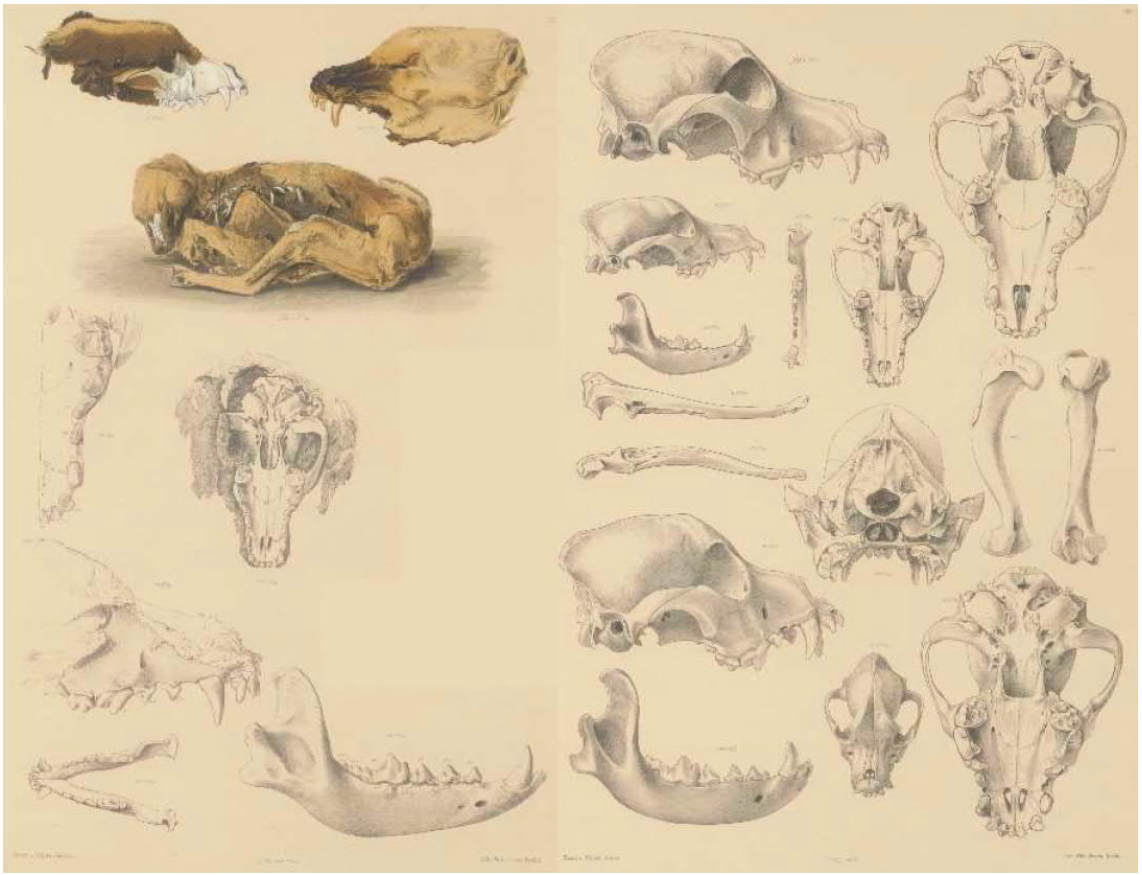


Fig. 3. - Drawings of skulls of pre-Columbian domestic dogs. These drawings were published as part of Alfred Nehring's work (1884) and show skulls of domestic dogs that have been excavated in the Inca burial ground of Ancon, Peru. The same skulls are also depicted in (Fig. 2). A, shepherd-like dog in ventral view; B, bulldog-like dog in ventral view; C, same dog as in B but from dorsal view. Drawings are not to scale.

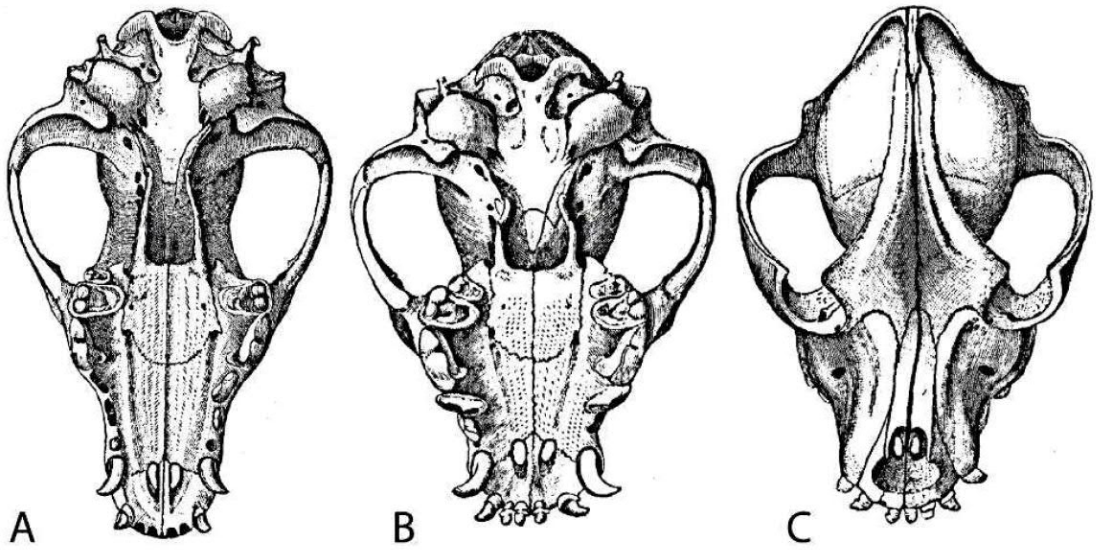


Fig. 4. - Skulls of putative pre-Columbian domestic dogs at the Museum für Naturkunde Berlin, Germany. Skulls are housed in the Nehring-Collection (Zoologische Sammlung der Königlichen Landwirtschaftlichen Hochschule zu Berlin). A, “Inca dog” from Ancon (Zm 355), Peru (Nehring 1884). B and C, Pre-Columbian dogs (7031 and 7013) from Puebla, Mexico, Nehring-Collection. Specimens are without present-day collection numbers. Every skull is depicted in dorsal, ventral, and lateral view (from left to right), where the lateral view of B is mirrored. Skulls are to scale and the scale bar equals 5 cm. A, «Zm 355» is annotated as “Inca dog from Ancon, 1889” (as noted in the collection catalogue (1886) and as written on the actual specimen). This specimen most likely does not belong to the collection described by Nehring (1884, see Fig. 3) and Reiss & Stübel (1880-1887, see Fig. 1), which also originated from the graves in Ancon, Peru, but which are assumed to have been destroyed in the World Wars (Ueck 1961). B, “7031” and C, “7013” although also housed in the Nehring-Collection, were found by Prof. Seler in Berlin (as described in the collection files). In contrast to A, these apparently unpublished remains are described as “from an old grave in the district Chalchicomula, close to Jalapazco, Puebla Mexico”. Further, both skulls are described as to be “surely from a time before the conquest of Mexico”

Fig. 5. - **Photos of selected dog breeds originating in the Americas**. Top and middle panel show dogs from North America; bottom panel shows dogs from South and Central America and Cuba. All photo images are from Shutterstock, photo credit is indicated in parenthesis. Top panel from left to right: Alaskan Malamute, 19 months old (Eric Isselee); Longhaired whippet (MirasWonderland); American bulldog puppy 5 months old (Erik Lam); American cocker spaniel standing with reflection on white background - 3 years old (WilleeCole Photography); three American hairless terriers (Dora Zett). Middle panel: Chesapeake Bay retriever (Erik Lam); American Akita (Jagodka); Silken Windhound (Erik Lam); Siberian Husky 4 years old (Eric Isselee); Miniature American shepherd (MirasWonderland). Bottom panel: young chihuahuas (cynoclub); Xoloitzcuintli, Mexican hairless dog (Masarik); Peruvian hairless dog 1 year old (Rosa Jay); young Bichon Havanese dog (Dorottya Mathe); Brazilian Fox-terrier (venturinirica); Argentinian Dogo (GeptaYs).

Fig. 6. - Selection of skulls of dog breeds originating in the Americas (selection not exhaustive). These dogs demonstrate the great variation in skull shape and body size of modern American breeds, from slender to short snouted and from giant to dwarf sized varieties, including hairless forms with oligodontia. A, Chesapeake Bay Retriever (NMBE 1051681); B, Alaskan Malamute (NMBE 1051387); C, Chihuahua (NMBE 1052001); D, Fila Brasileiro (I.f.H 14005, mirrored); E, Mexican hairless dog (ZMUZH 13754); F, Peruvian hairless dog (NMBE 1062857); G, Boston Terrier (NMBE 1051959); H, Newfoundland (NMBE 1050502). I.f.H, Zoologisches Institut/Populationsgenetik (former Institut für Haustierkunde), Christian-Albrechts-Universität zu Kiel, Germany; NMBE, collection of the Albert-Heim-Foundation at the Naturhistorisches Museum Bern, Switzerland; ZMUZH, Zoologisches Museum der Universität Zürich, Switzerland (Scale bar: 5 cm).

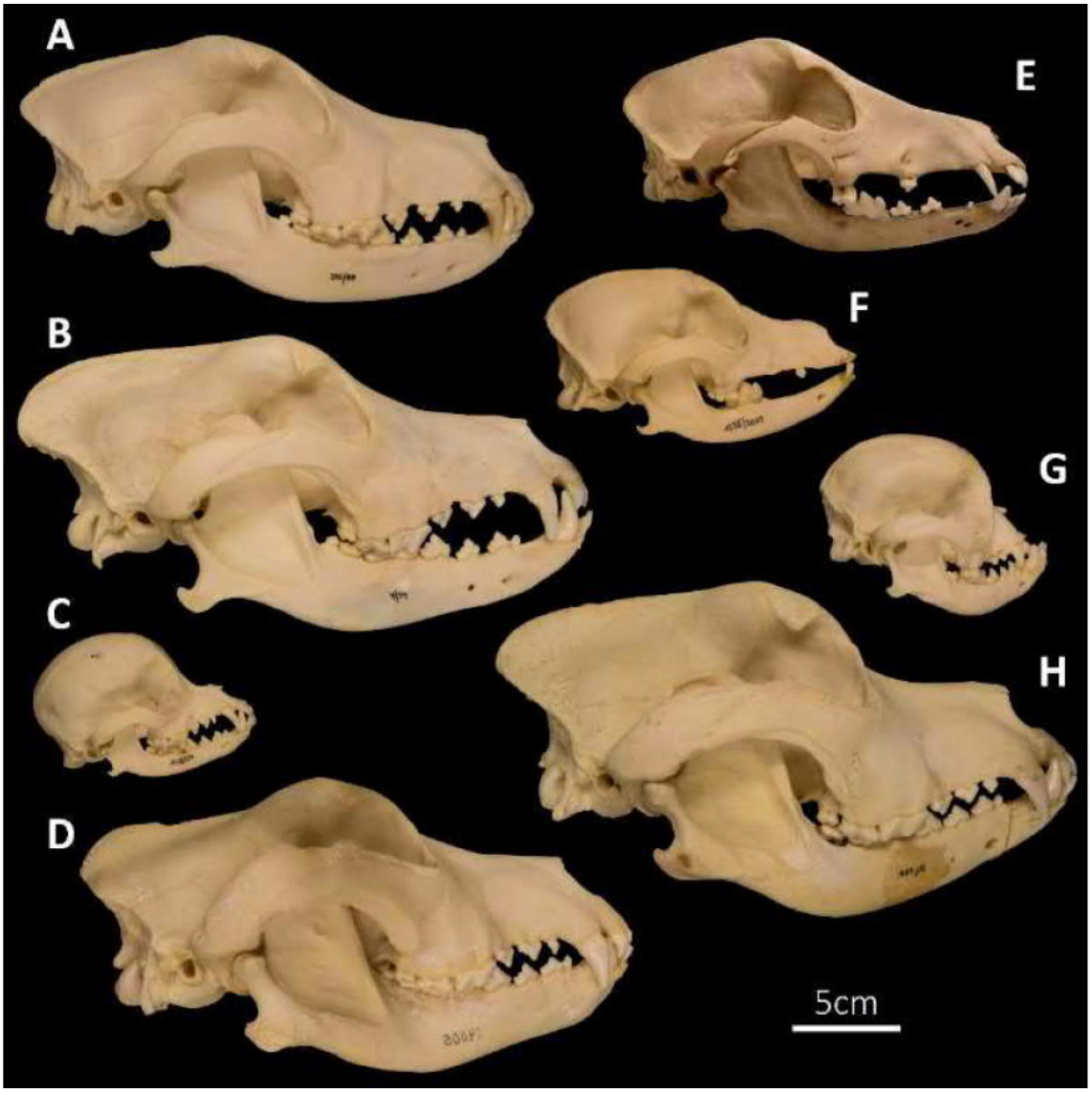
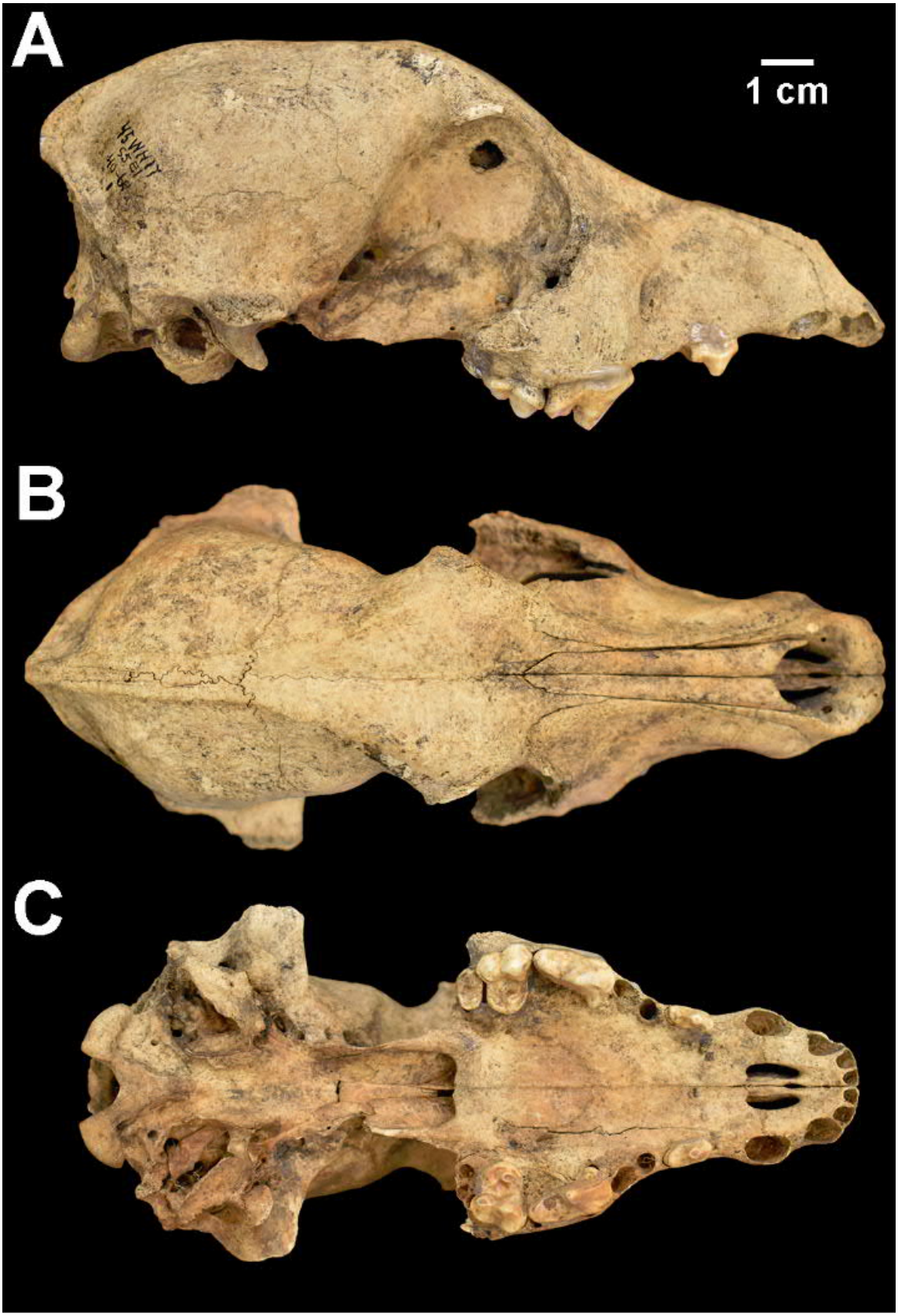


Fig. 7. - Cranium of a Salish woolly dog (Specimen #1) excavated in 1977 from the Semiahmoo Spit, WA (45WH17), dated to 420-900 years before present (Montgomery 1979). A, Lateral view; B, Dorsal view; C, Occlusal view (Scale bar: 1 cm).



Appendix 1. - American domestic dog breeds in their different group types, are recognized by the International Canine Kennel Club (www.internationalcaninekennelclub.com, accessed March 2020). By the nineteenth century, dog fanciers began breeding and trading dogs that were “specialized” for both physical and behavioral traits. With the advent of the Kennel Club in 1873, lineages became standardized by appellation, bloodline, appearance, and behavior. Breeds are the result of pre-zygotic selection – the deliberate mating of preferred animals to perpetuate a specific, observable phenotype. Not listed here are landraces, defined as those resulting from post-zygotic selection; that is, the culling or disposal of unwanted dogs with no direct control over the dog’s reproduction (Lord *et al*. 2016).

Breed	Country of origin	Group
Alapaha Blue Blood Bulldog	United States of America	Pinscher and Schnauzer - Molossoid and Swiss
Alaskan Klee Kai	United States of America	Spitz and primitive types
Alaskan Malamute	United States of America	Spitz and primitive types
American Akita	United States of America	Spitz and primitive types
American Bulldog	United States of America	Pinscher and Schnauzer - Molossoid and Swiss
American Cocker Spaniel	United States of America	Retrievers - Flushing Dogs - Water Dogs
American English Coonhound	United States of America	Scent hounds and related breeds
American Eskimo-standard &	United States of America	Spitz and primitive types
American Foxhound	United States of America	Scent hounds and related breeds
American Hairless Terrier	United States of America	Terriers
American Staffordshire Terrier	United States of America	Terriers
American Water Spaniel	United States of America	Retrievers - Flushing Dogs - Water Dogs
Australian Shepherd	United States of America	Sheepdogs and Cattledogs (except Swiss Cattledogs)
Black and Tan Coonhound	United States of America	Scent hounds and related breeds
Bluetick Coonhound	United States of America	Scent hounds and related breeds
Boston Terrier	United States of America	Companion and Toy Dogs
Boykin Spaniel	United States of America	Retrievers - Flushing Dogs - Water Dogs
Brazilian Terrier	Brazil	Terriers
Canadian Eskimo Dog	Canada	Spitz and primitive types
Chesapeake Bay Retriever	United States of America	Retrievers - Flushing Dogs - Water Dogs
Chihuahua	Mexico	Companion and Toy Dogs
Cimarrón Uruguayo	Uruguay	Pinscher and Schnauzer - Molossoid and Swiss
Dogo Argentino	Argentina	Pinscher and Schnauzer - Molossoid and Swiss
Fila Brasileiro	Brazil	Pinscher and Schnauzer - Molossoid and Swiss
Havanese	Cuba	Companion and Toy Dogs
Labrador Retriever	Canada	Retrievers - Flushing Dogs - Water Dogs
Longhaired Whippet	United States of America	Sighthounds
Lousiana Catahoula Leopard	United States of America	Sheepdogs and Cattledogs (except Swiss Cattledogs)

Miniature American Shepherd	United States of America	Sheepdogs and Cattledogs (except Swiss Cattledogs)
Newfoundland	Canada	Pinscher and Schnauzer - Molossoid and Swiss
Nova Scotia Duck Tolling	Canada	Retrievers - Flushing Dogs - Water Dogs
Olde Victorian Bulldogge	United States of America	Pinscher and Schnauzer - Molossoid and Swiss
Peruvian Hairless Dog	Peru	Spitz and primitive types
Redbone Coonhound	United States of America	Scent hounds and related breeds
Shiloh Shepherd	United States of America	Sheepdogs and Cattledogs (except Swiss Cattledogs)
Siberian Husky	United States of America	Spitz and primitive types
Silken Windhound	United States of America	Sighthounds
Treeing Tennessee Brindle	United States of America	Scent hounds and related breeds
Treeing Walker Coonhound	United States of America	Scent hounds and related breeds
Xoloitzcuintle	Mexico	Spitz and primitive types

Appendix 2. Information related to skulls of pre-Columbian domestic dogs at the Museum für Naturkunde Berlin, Germany.

The following designations refer to the Fig. 4 of the main text. A, «Zm 355» is housed in the Nehring-Collection (Zoologische Sammlung der Königlichen Landwirtschaftlichen Hochschule zu Berlin) and described as “Inca dog from Ancon, 1889” (as noted in the collection catalogue (1886) and as written on the actual specimen). This specimen most likely does not belong to the collection described by Nehring (1884, see Fig. 3) and Reiss & Stübel (1880-1887, see Fig. 1), which also originated from the graves in Ancon, Peru, but which are assumed to have been destroyed in the World Wars (Ueck 1961).

B, “7031” and C, “7013” are also housed in the Nehring-Collection, but have been found by Prof. Seler in Berlin (as described in the collection files). In contrast to A, these apparently unpublished remains are described as “from an old grave in the district Chalchicomula, close to Jalapazco, Puebla Mexico”. Further, both skulls are described as to be “surely from a time before the conquest of Mexico”