The history of domesticated dogs in the Americas

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Abstract

Records of domestic dogs in the Americas include specimens from North American sites dating as far back as 10,000 to 8,400 ybp and from the Andes of South America from 5,600-5,000 ybp. Dogs accompanied humans in several migrations from Asia to America BCE, as revealed by different haplotypes reported from ancient DNA studies. Dog acquisition by Amazonian cultures began towards the end of the nineteenth century. Pre-Columbian size and shape diversity in North America is first recorded around 4,000 ybp, with varieties such as the hairless, short nosed and loberro dogs. The humped kind may represent a phenotype associated with mutations in the myostatin gene. Pre-Columbian forms from the Andes included a shepherd-like, hairless, dachshund-like, bulldog, shortened snout and long snout kinds. More than 41 domestic dog breeds that originated in the Americas are currently recognized by kennel clubs. Some records previously attributed to domestic dogs are from other canids, such as *Dusicyon avus*. Hybridization with wolves and coyotes may have been an old practice contributing genetic diversity to pre and post-Columbian American dogs. Archaeological, historical, and ethnographic records reveal dogs being used for hunting, transport, food, rituals, company, and defense. The Coast Salish First Nations exploited so-called woolly dogs for manufacturing blankets, with practices associated with their care and marine food diet, as documented by isotopic studies and accounts from the beginning of the nineteenth century.

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Keywords

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

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Running Head: Dogs in the Americas

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L'histoire des chiens domestiqués dans les Amériques

Résumé

Les enregistrements de chiens domestiques dans les Amériques comprennent des spécimens de sites nord-américains datant d'il y a 10000 à 8400 années et des Andes d'Amérique du Sud d'il y a 5600 à 5000 années. Les chiens ont accompagné les humains dans plusieurs migrations de l'Asie vers l'Amérique avant notre ère, comme le révèlent différents haplotypes provenant d'études anciennes sur l'ADN. L'acquisition de chiens par les cultures amazoniennes a commencé vers la fin du XIXe siècle. La diversité précolombienne des tailles et des formes en Amérique du Nord est d'abord enregistrée il y a environ 4 000 ans, avec des variétés comme les chiens sans poils, les chiens au nez court et les chiens loberro. Le type bossu pourrait représenter un phénotype associé à des mutations dans le gène de myostatine. Les formes précolombiennes des Andes comprenaient un type de berger, sans poils, ressemblant à un teckel, un bouledogue, des types à museau raccourci et à long museau. Plus de 41 races de chiens domestiques originaires des Amériques sont actuellement reconnues par les fédérations cynologiques. Certains enregistrements précédemment attribués aux chiens domestiques proviennent d'autres canidés, tels que le Dusicyon avus. L'hybridation avec les loups et les coyotes pourrait avoir été une pratique ancienne contribuant à la diversité génétique des chiens américains pré et post-colombiens. Les archives archéologiques, historiques et ethnographiques révèlent que les chiens étaient utilisés pour la chasse, le transport, la nourriture, les rituels, la compagnie et la défense. Les Premières nations salishes de la côte exploitaient les chiens dits laineux pour la fabrication de couvertures, avec des pratiques associées à leurs soins et à leur

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alimentation marine, comme le montrent des études isotopiques et des récits du début du XIXe siècle.

Mots clés

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

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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*), alpaca (*Vicugna pacos*), and the guinea pig or cui (*Cavia porcellus*), all in the Andean region; among birds, the Muscovy duck (*Cairina moschata*) in the Amazon region, and the turkey (*Meleagris gallopavo*) 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*). It predates the multiple exchanges and introductions 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. This review brings together contributions from different disciplines, including zooarchaeology, ethnology, molecular biology and evolutionary morphology. We will help identify open questions and gaps of knowledge, and make explicit how new methodological tools (Evin 2016, Sykes *et al*. 2019, Evin 2020) 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 both systematic search using online available information, as well as annotations from sources found after consultation with experts and in our own work. The information compiled ranged from 1651 (Hernández) to 2020 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.

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 analysis of a small bone fragment at Hinds Cave (Texas 2011, Tito *et al*. 2011) 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, 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 2016). 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.

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), which 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 around 15,000 to 20,000 ybp. 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 recorded (Larson *et al*. 2012). 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.

In South America, the archaeological record of dogs is relatively rich in the Andean region of Peru, Chile and Ecuador, with records as old as from 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 recently recovered fossils in Patagonia and a reanalysis of evidence suggest that these records may belong to *Dusicyon avus* or other canids (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). Because the ancestor, the wolf, is not a tropical animal, its descendants would not have adapted to tropical parasites (Mitchell 2017). On the other hand, Uhl *et al*. (2019) indicated that the flux of diseases is generally the opposite, from domestic dogs to wild canids. Perhaps DNA studies can provide in the future assessments of these ideas, as when tracing the origin of a contagious cancer transferring during mating that manifests as genital tumors. This cancer was originated by cells of a founder 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 variety in shape and size (Allen 1920, Schwartz 1998, Ensminger 2017). The two oldest domestic dog specimens found in America (i.e. Koster & Stiwell II sites) exhibit different skull shape and size (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 variations in size and shape were

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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). 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.

Manin and Lefèvre (2016) suggested that not all contemporary societies of central Mexico in Classic and the Conquest periods, 200-1521CE, were specialized in the breeding and production of domestic dogs. 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). 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 (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

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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 depicted in (Figs 2-4). Dog populations in South America were diverse in 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

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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 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 historical relationships of breeds in a network were generated based on genomic data (Parker *et al*. 2017), with some breeds considered as basal (e.g. Alaskan Malamute, American Eskimo). However, 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 also a partial replacement by modern

European dogs, but maintaining a common origin of African, Euro-Asian, Oceanic dogs, and American dogs (e.g. van Asch *et al*. 2013, Brown *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). This still unrecognized breed seems to have high morphostructural uniformity, sexual dimorphism, and a combination of its own phenotypic features (Barrios *et al*. 2016).

Hybridization of domestic dogs with other canids

Several studies on genetic introgression, have argued for the existence of evidence for crossbreeding between domestic dogs and North American wolves or coyotes (e.g. Adams *et al*. 2003, Lehman *et al*. 1991, Roy *et al.* 1996, Walker & Frison 1982, Valadez *et al*. 2006, Valadez *et al*. 2001, 2002a, b), 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) 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).

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 customs of collecting *Lycalopex gymnocercus* 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* 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) 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 (*C. rufus*) 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 suggest an important integration of wild canids in human society and their domestic dogs.

In South America, large species such as *Lycalopex culpaeus* or the Maned Wolf (*Chrysocyon brachyurus*), the first more common in archaeological sites, could be confounded if the remains are scarce or fragmentary, but differences in skull

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morphology between those species and *Canis* exist (Loponte & Acosta 2016, Prevosti 2010, Prevosti *et al*. 2015). Beyond these observations, taphonomic processes can also lead to problematic recognition of a dog fossil record, particularly in humid areas.

Non-traditional uses of dogs in the Americas - Dogs as a source of food

Indigenous domesticated dogs, 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 tribes implemented a range of diverse strategies for domestication, culling populations, and caring for maternal health (e.g., Bozell 1988). The usage of dogs by Native Americans is geographically and temporally variable, with dogs being used for hunting, transport, food, rituals, company, and defense (e.g., Allen 1920, Allison *et al*. 1982, Barsh *et al*. 2002, Bozell 1988, Teit 1909, Winship 1904).

Even today, dogs are used as food in some regions of Asia, although in the Americas this is not practiced. 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., Allen 1920, Bozell 1988, Catlin 1841). It is also possible to reconstruct this behaviour 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

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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 (1000 BC-500 BCE) than in the Classical period (500 BCE-1200 CE) (Pohl 1990, Olsen 1972), maybe 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). 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 amount of food caused by 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 some 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

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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 tribes 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 across many different tribes in the Americas, with variation in how the dogs were kept, used, and trained (Morey 2010). For example, the Klamath tribe 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 tribes commonly noted to have bred and trained domestic dogs for hunting include the Salish tribes of the Pacific Northwest, the Inuit tribes of the north, and the Hidatsa, among others (Allen 1920, Barsh *et al*. 2002, Teit 1909, Wilson 1924).

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

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early as the 1500's in Mexico (Allen 1920, Winship 1904). The Pawnee tribes 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 cultures during the twentieth century, many sled dogs were killed by the US government, leading to a heightened sense of responsibility and connection between these tribes and their dogs (Laugrand & Oosten 2002). In addition, sleds dogs were also used in the Arctic of western Alaska by tribes 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 Native tribes used dogs to herd animals such as llamas (Chiribaya culture, Peruvian coast), although the use of dogs for this purpose is questionable (Wylde 2017, Schwartz 1998). 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 people 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, Barsh *et al*. 2002, Crockford 1994, 1997, Crockford & Pye 1997, Gleeson 1970, Gunther 1972, Crockford 2005). 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). The Coast Salish First Nations exploited their thick fur 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 remains 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 people, 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 (Barsh *et al*. 2002, Croes 2015, Suttles 1983, Wells 1969). 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).

There are scattered reports of dogs for weaving and shearing recorded by Europeans among other cultures, including tribes in New Mexico (1500s; Winship 1904) as well as tribes 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 people, 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

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practiced by different cultures, although never with the sophistication employed by the Salish people (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. The relationships between breeds of American lineage, as well as the genetic contribution of wolves or other American canids are still much discussed, and the genetic and morphological relationships of new specimens 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, mainly from the genus *Canis*. Revisionary work based on ancient DNA and radiocarbon dating (Popovic *et al*. 2020), and morphology (Manin & Evin in review), is likely to contradict many previous attributions of materials to domestic dogs or claims of hybridizations with local canids.

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*. 2019). 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

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was never quantitatively examined in the context of the diversity of wolves and other American canids. 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 domesticate 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 of it are needed. For example, isotopic work 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 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 in Europe and Asia (Larson *et al*. 2012, Leathlobhair *et al*. 2018).

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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/n4/mode/2up

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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/1681616637/1/ Drawings are not to scale.

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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.

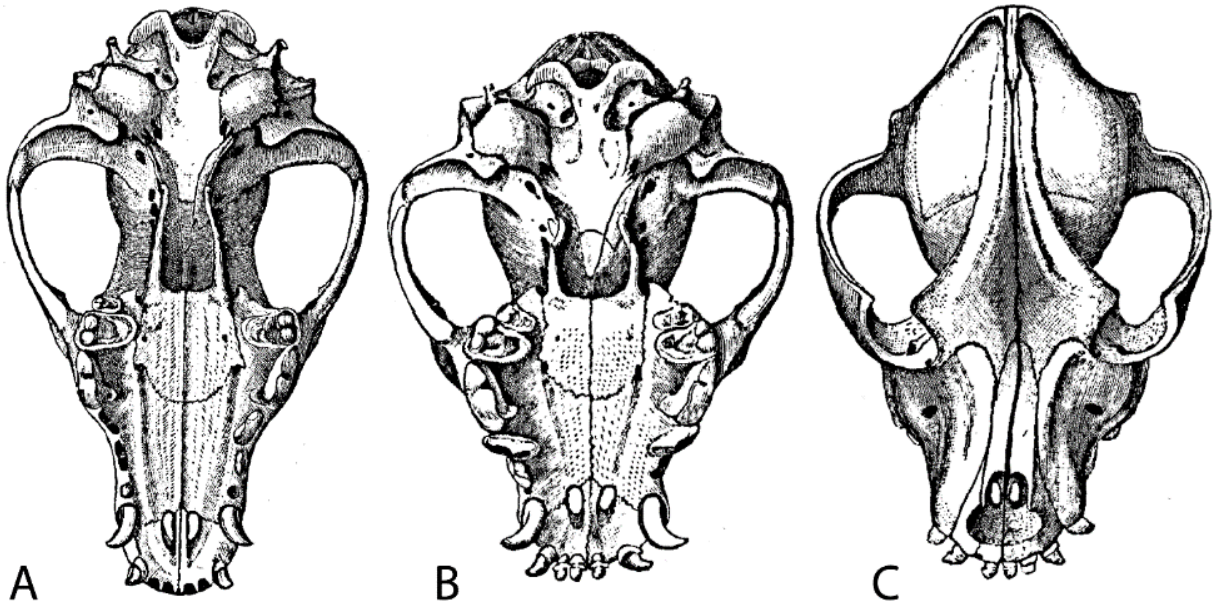

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Fig. 4. - Skulls of pre-Columbian domestic dogs at the Museum für Naturkunde Berlin, Germany. A, “Inca dog” from Ancon, Peru (Nehring 1884).

B, Precolumbian dog 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 1 cm. Further information of sources and references are in Appendix 2.

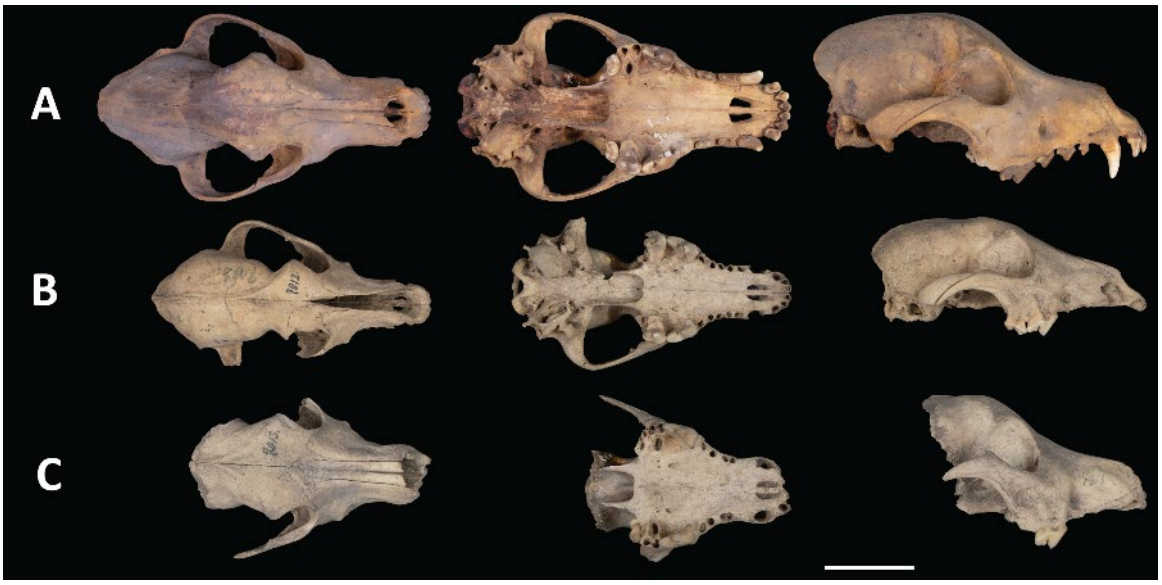

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Fig. 5. - Photos of selected dog breeds originating in the Americas. Top and middle panel show dogs from North America; bottom panel shows dogs from South and Central America and Cuba. Photo credits (Shutterstock) are listed in Appendix 3. Top panel from left to right: Alaskan Malamute, Longhaired whippet; American bulldog puppy; American cocker spaniel; three American hairless terriers. Middle panel: Chesapeake Bay retriever; American Akita; Silken Windhound; Siberian Husky; Miniature American shepherd. Bottom panel: young chihuahuas; Xoloitzcuintli, Mexican hairless dog; Peruvian hairless dog; young Bichon Havanese dog; Brazilian Fox-terrier; Argentinian Dogo.

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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 New World 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).

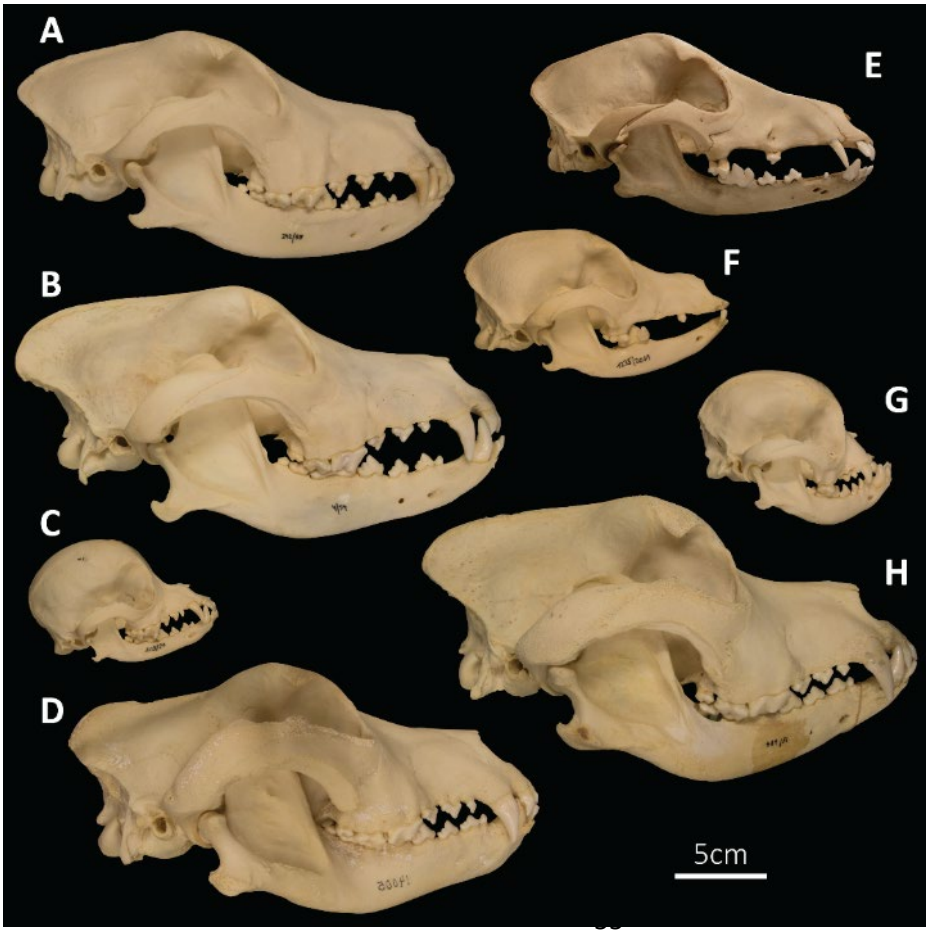

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Fig. 7. - Cranium of a Salish woolly dog (Specimen #1) excavated in 1977 from the Semiahmoo Spit, WA (45WH17), dated to 420-900 years before present (Montgomery 1979). A, Lateral view; B, Dorsal view; C, Occlusal view (Scale bar: 1 cm).