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The Southernmost Pre-Columbian Dogs in the Americas: Phenotype, Chronology, Diet and Genetics

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ABSTRACT

The archaeological record shows the presence of medium-sized dogs with mesocephalic skulls in Southeast South America, from at least the end of the third millennium BP to historical times, along 700 km from southern Brazil to the wetlands of the Paraná River in Argentina. These dogs, associated with complex hunter-gatherers, do not appear to have been the product of exchange with Andean societies as previous theories suggested, but rather of a local breeding process, probably reflecting the offspring of a founder population introduced in the area before at least the third millennium BP. Isotopic values show a C_3 omnivorous pattern, resulting from a broad and opportunistic niche, not overlapping with that of humans. The relationships between humans and their dogs were very complex; some of the dogs were buried in mortuary areas, in double human-dog burials, meanwhile others were used as a source of raw material. Shortly after the introduction of European dogs, they were quickly assimilated by these introduced dogs, which is supported by the pairwise distance analysis. Phylogenetic analysis illustrates the maternal lineage of these pre-Columbian and modern dogs, both belonging to the haplogroup A, supporting a common ancestry.

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Introduction

The dog is the oldest domestic animal which has accompanied man since the end of the Pleistocene, reaching every corner of the planet where man has colonised. Within this global scenario, South America is a particularly interesting case due to the fragmented distribution. Indeed, until very recent times, dogs had only been recognised in Andean societies, excluding in an intriguing way the rest of South America. Here, we present a different picture based on recent findings of pre-Columbian dogs in the Lowlands of southeastern South America, that change our perception about their distribution in the subcontinent. In this study we include chronological, morphometric, phenotypic, isotopic and genetic data, which also contribute to understanding the global expansion of this species. To contextualise the framework of this study, we will briefly review the current state of the discussion about the domestication of the dog and its presence in the New World.

The Origin of the Dog and Its Arrival in America

Molecular studies showed that the closest relative of modern dogs is the grey wolf (*Canis lupus*) (Vilà et al. 1997), a widely distributed species in Eurasia at the end of the Pleistocene (Boeskorov and Baryshnikov 2013). Recent palaeogenomic studies have argued that the wolf population which gave rise to modern dogs has become extinct. Therefore, current grey wolves would not be their direct ancestors, and it is likely that modern dogs which are most closely related to these wolves are the result of subsequent genetic mixtures (Thalmann et al. 2013; Freedman et al. 2014; Frantz et al. 2016). This process would have been part of the bottleneck experienced by ancient wolf populations during the Last Glacial Maximum, a situation that later led to the repopulation, expansion and replacement of ancestral populations by current ones (Loog et al. 2019; Schweizer and Wayne 2020).

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Most of the oldest fossil remains assigned to domestic dogs (*Canis lupus familiaris*) were recovered in Europe, ranging from 36,500 to 17,000 years BP (Thalmann and Perri 2018). Some of them could correspond to potential proto-dogs or wolf-dogs derived from failed domestication events, or genetically truncated lineages, such is the case, for example, of the specimens found in the Goyet cave in Belgium (Germonpré et al. 2009), and the Altai dog in Siberia (Ovodov et al. 2011). This would indicate that there may have been several attempts or events of domestication and at different times and places (Pierotti and Fogg 2017; Thalmann et al. 2013; Thalmann and Perri 2018). In this sense, the geographical and temporal origin of dogs has been the subject of intense debate. Based on genetic information of the last two decades, different origins have been proposed, such as Europe (Thalmann et al. 2013), East Asia (Perri et al. 2021; Savolainen et al. 2002; Pang et al. 2009; Wang et al. 2013), the Middle East (VonHoldt et al. 2010), and Central Asia (Shannon et al. 2015). Faced with the primary idea of the existence of a certain place of origin, Frantz et al. (2016) proposed a dual model stating that dogs would have been domesticated at least twice. Dual domestication would be the result of two independent events from potentially extinct wolf populations that occupied eastern Asia and western Eurasia during the Paleolithic. This phenomenon would also involve the dispersal of eastern dogs, which would have migrated together with humans and then would have partially replaced the indigenous western Eurasian dogs around 14,000–6,400 years BP. However, in a new study, Botigué et al. (2017) argued that, contrary to what Frantz et al. (2016) state, genetic evidence suggests that indigenous European dogs had some continuity over time, and would not have been replaced by populations of independently domesticated dogs in East Asia.

Dogs arrived in America probably with the first human groups (da Silva Coelho et al. 2021; Fiedel 2005), although at the moment the archaeology does not show exactly this match. The oldest records of dogs in North America correspond to the Lawyer's Cave site (Alaska), Koster, and Stilwell II (Illinois, USA) sites, with early Holocene taxon-dates of 9020 ± 85; 8,820 ± 30 and 8,840 ± 80 ^{14}C years BP respectively (da Silva Coelho et al. 2021; Perri et al. 2019), meanwhile humans had undoubtedly reached the southern extreme of South America 11,000 ^{14}C years BP (Prieto and Labarca 2011: Table 2).

Analysis of mitochondrial genomes demonstrated, based on samples from the north of the continent, that pre-Columbian dogs are within a monophyletic group (haplogroup A), which descend from a common ancestor of ~14,600 years ago, which in turn shared a common ancestor with the dogs of eastern Siberia ~16,700 years ago (da Silva Coelho et al. 2021; Ní Leathlobhair et al. 2018; see also Leonard et al. 2002; Thalmann et al. 2013; van Asch et al. 2013). Other researchers have raised the possibility that dogs had also been independently domesticated in America, around 10,000 years ago BP from populations of American wolves (Witt et al. 2015). This hypothesis, however, according to the results obtained in other genetic analyses, has not received further support (*e.g.* Leonard et al. 2002; VonHoldt et al. 2010; Freedman et al. 2014; Ní Leathlobhair et al. 2018). This does not imply that native dog populations have not been exposed to subsequent hybridisation processes with American wolves, even coyotes (Ní Leathlobhair et al. 2018; Perri et al. 2019). In South America, there are no records of coyotes or wolves, so any eventual hybridisation must have occurred in North America. DNA analyses of pre-Columbian South American dogs are substantially scarcer (Leonard et al. 2002; Thalmann et al. 2013), and therefore the addition of new samples from this region is key to contrast previous results here and in the north of the continent.

Area of Study

The Lowlands of southeastern South America region we analysed in this study comprises the Pampean plain from southern Brazil to northern Patagonia. In ecological terms, it is a temperate prairie under great oceanic influence. The Paraná and Uruguay rivers divide it into two large blocks, the northernmost includes the southern plains of Brazil and Uruguay (sector I, Figure 1) where an important record of pre-Columbian dogs was recovered, while in the southernmost Argentine pampean area (sector III, Figure 1), no pre-Columbian dogs have been identified. Between these two great plains flow the Paraná and Uruguay rivers, which converge in the central sector forming the lower Paraná wetland (Sector II, Figure 1). This integrates the lower valleys of both rivers and the entire wide territory between them, forming an area of approximately 17,000 km^2 with a significant record of pre-Columbian dogs. This wetland is a subtropical environment with azonal characteristics for the Pampas biome because both the Uruguay and Paraná Rivers reproduce here the ecological conditions of their headwaters. Indeed, the Paraná River originates from rainfall in the tropics that is mostly produced by the South American summer monsoon (SASM), which is associated with the intertropical convergence zone (Gan, Kousky, and Ropelewski 2004; Vuille et al. 2003; Zhou and Lau 1998). The Uruguay River originates from extratropical rainfalls from the cyclonic activity over the Atlantic Ocean at middle latitudes, but is also affected by monsoon rains (especially during the summer) (Cruz et al. 2009; Rao, Cavalcanti, and Hada 1996), and a

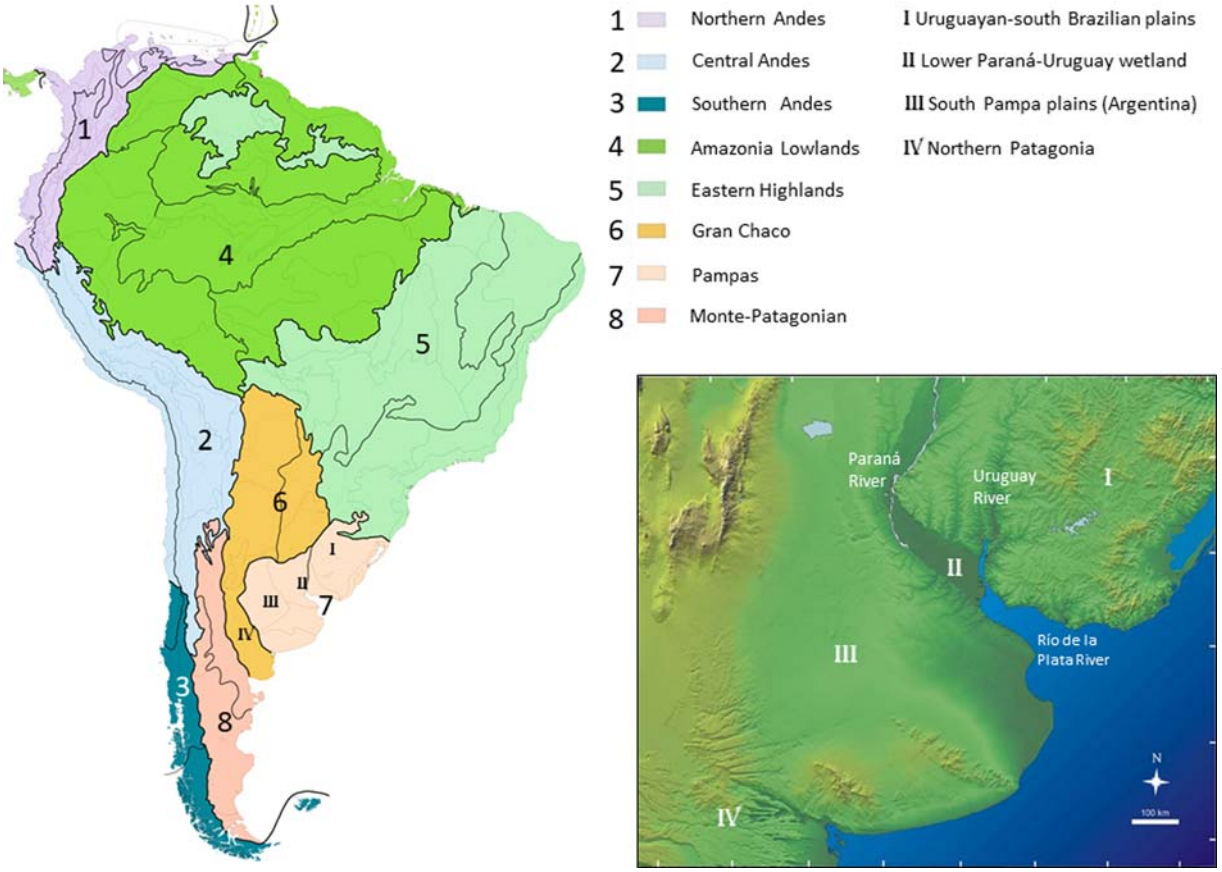

Figure 1. Location of the study area. The left base map is taken and modified from http://ecologicalregions.info.

significant section of its watercourse runs through the warm and humid subtropical forest. Finally, in the extreme southernmost area is sector IV of this study (Figure 1), which is a semi-desert environment, at the southern and western ends of the Pampean plains, with a limited record of dogs.

As sectors I and II of Figure 1 are those with the greatest concentration of record of pre-Columbian dogs, we will describe in some detail the associated archaeological contexts of both sectors.

Archaeological Background: The Wetland of the Lower Paraná-Uruguay River and Middle Paraná´s Valley (Sector II)

Complex hunter-gatherer societies developed in this region (Sector II, Figure 1) since at least the end of the third millennium BP, grouped into different archaeological units that nevertheless share numerous techno-stylistic similarities. The observed cultural variability suggests the existence of different groups but with a very dynamic interrelation between them, associated with a high demography, which led to the development of density-dependent behaviours. Subsistence was based mainly on freshwater fish of the interconnected Uruguay-Paraná´s fluvial system, complemented with the exploitation of local deer, small to medium rodents and freshwater clams. Agroforestry of local palms and the development of sporadic small gardens has also been postulated based on historical sources and some archaeological features (Acosta 2005; Acosta and Ríos Román 2013; Acosta, Leiva, and Malec 2013; Bonomo et al. 2011a, 2011b; Caggiano 1984; Ceruti and González 2007; Colobig and Ottalagano 2016; Cornero and Rangone 2015; Gascue et al. 2016, 2019a; Krapovickas 1996; Loponte 2008; Lothrop 1932; Ottalagano 2013; Rodríguez 2001; Sánchez et al. 2013; Zucol and Loponte 2008). Maize was consumed at levels not isotopically detected, and most of the diets show a remarkable intake of animal protein, suggesting that both cultivated and wild plant resources had a marginal role in subsistence, and demonstrating a trend towards intensification of fish resources rather than plant food production (Bracco et al. 2000; Gascue et al. 2016; Loponte, Acosta, and Corriale 2016c; Ottalagano and Loponte 2017; Loponte 2020). The settlement was based on central place foraging of medium to high stability. Most of the settlements are located on natural elevations (fluvial banks and coastal ridges; Figure 2), with elevation artificially increased by debris disposal (Bortolotto et al. 2021; Gascue et al. 2019b; Loponte and Acosta 2016b, 2017). Substantiated evidence of the construction of these mounds has only been identified in very few of them (Loponte, Acosta, and Tchilinguirián 2016d; see also some other settlements that

Figure 2. Túmulo de Campana site 1, located on a natural river bank (light green) raised mainly by natural sedimentation and secondarily by human disposal of debris (pottery, bones, etc.). Residential site occupied discontinuously between ~1300 and ~1800 years BP (Loponte and Acosta 2017).

have been postulated as being built in Castiñeira et al. 2013, and the references there). Large cemeteries have been discovered at many sites, some of them were used over generations. The mortuary behaviours were extremely complex, including primary, single and multiple secondary burials, possibly cremations, and unstructured human bone accumulations (Boretto et al. 1973; Gascue et al. 2016; Gaspary 1950; Guarido, Mazza, and Turk 2016, 2021; Loponte 2008; Lothrop 1932; Mazza and Loponte 2012; Mazza et al. 2018; Ottalagano 2016; Ottalagano et al. 2015; Scabuzzo and Ramos van Raap 2017; Torres 1911). This complex relationship with the dead includes the manufacture of instruments made from human bones (Mazza et al. 2018). Mortuary pottery specially manufactured for ceremonial purposes has been postulated for these groups, which would be placed on the surface of the tombs (Gaspary 1945, 1950; Loponte et al. 2020), as well as miniature pottery used, perhaps, for burial offerings (Ottalagano 2020b). Small to medium-sized pottery vessels were produced in large quantities to process food and to extract nutrients by boiling, resulting in a notable tendency in the intentional fragmentation of the bones of large and medium mammals (the average length of bone splinters is less than 5 cm) to increase the capacity of extraction of nutrients. Practically all the vessels show evidence of fatty acids and isotopic signals ($\delta^{13}C$ and $\delta^{15}N$) associated with vegetable and animal foods (Naranjo, Malec, and Pérez 2010; Ottalagano 2019; Pérez et al. 2013). Ornamental artefacts made of metal and green rocks (malachite, turquoise, chrysocolla, etc.), allochthonous to the region have been recovered; these would have arrived through a slow process of exchange from Andean areas of northwest Argentina. Pendants made from local carnivorous canine teeth and freshwater mollusc shells were also recovered. In one of the local archaeological units (Plain Pottery Cluster) T-shaped shellfish labrets ('tembetás') are recognised, probably with a strong ethnic significance (Acosta, Buc, and Davireux 2015; Buc et al. 2017; Gascue et al. 2019a; Loponte 2008, 2020) (Figure 3). While there is some weak evidence (from historical sources) suggesting the existence of chiefdoms during times of war, archaeological studies have not yet been able to identify the existence of institutionalised inequality. Although the identification of differential status has been elusive so far, an initial process of the differential accumulation of goods cannot be ruled out (Loponte 2008; Mazza and Loponte 2012).

The Uruguayan and South Brazil Plains (Sector I)

In the Uruguayan and south Brazil pampean plains (Sector I, Figure 1), thousands of mounds with estimated chronologies between 5000 years BP and historical times have been identified, which can be up to a maximum of 80 m diameter (average ~35 m), and heights that reach 7 m, although in general they are less than 2–3 m high (Bracco 2019; Milheira, Attorre, and Borges 2019; Schmitz, Girelli, and Rosa 1997) (Figure 4). The layers older than ~3500–3000 years BP appear to correspond to pre-pottery hunters, so a slow transition has been postulated, which seems to be consistent according to multiple records observed through numerous investigations (Rogge 2005; Schmitz, Girelli, and Rosa 1997).

In this way, these mounds began to form at the end of the Middle Holocene, which to a great extent explains the large number found in these plains, and intermittently occupied over millennia. In general terms, they are located at the edges of marshes and wetlands (Bracco and Duarte 2020; Schmitz, Girelli, and Rosa 1997), where resources are denser, predictable and concentrated (fish and plants with edible parts). In these mounds, even for late periods, there is no record of complexity equivalent to that observed in the lower Paraná-Uruguay wetland sites. The few quantified archaeofaunal assemblages published show a subsistence based on deer hunting, complemented by freshwater fish. Near the Atlantic coast, some of them include marine fish (Cabrera 2005; Capdepont and Pintos 2006; Moreno 2017; Pintos 2000; Schmitz, Girelli, and Rosa 1997). At the PSG-07 site (located in a coastal lagoon in South Brazil) the incidence of marine fish reaches 90% of the NISP of the faunal assemblage (Milheira, Attorre, and Borges 2019).

The pottery vessels are of little volume (< 5 litres), often smooth, or with simple decorations, without the stylistic complexity of those from the lower Paraná-Uruguay wetland (Bracco, del Puerto, and Inda 2008; Milheira, Attorre, and Borges 2019; Rogge 2005; Schmitz, Girelli, and Rosa 1997). There are no specific analyses of the weapon systems of these late contexts, but these look much simpler, consisting mainly of hollowed points and bola-sling stones (Pintos 2001; Schmitz, Girelli, and Rosa 1997). The lithic

Figure 3. Paraná´s wetland archaeological record of complex hunter-gatherers. (a) T-shaped lip labret ('tembetá'). (b) Ornamental artefact made of tooth of capybara. (c) Pendant made of fox tooth. (d) Pendants made of green rocks. (e) Shell beds. (f) Zoomorphic vessel appendage. (g) Harpoon tip made of antler. (h) Hollowed point made on metapodial of deer (hollowed out the proximal metaphysis of the metapodium). (i) Bone projectile point. (j) Lithic projectile point. (k) Hook of spear-thrower. (L) Bola stone. Bottom figures, incised/painted pottery. Scales are approximate.

artefacts were mostly made from local rocks, but silicified limestones and others are found 150–200 km from some mounds (López Mazz, Gascue, and Moreno 2009, 2010; López Mazz and Gascue 2007; Gascue et al. 2019a). Although ornamental artefacts are recovered, these are scarce and in general consist of earrings made of teeth of local species and shells from the nearby Atlantic coast (Gascue et al. 2019a; Milheira, Attorre, and Borges 2019).

The complexity of this record is essentially based on the construction of the mounds and the development of agriculture. The mounds of the plains of Uruguay and Brazil do not have a fluvial origin, and their formation processes are completely attributed to human activity; however, the process of accretion is debated (Bracco 2006). Detailed chronological analyses in some of them showed that they are the product of slow growth from successive reoccupations (Bracco and Duarte 2020; see also Schmitz, Girelli, and Rosa 1997). Within the architectural complexity assigned to these mounds by some authors, the existence of squares and public spaces have been postulated for areas adjacent to or between mounds (Iriarte et al. 2016), but this is not well supported by actual archaeological evidence (Bracco and Duarte 2020). Regarding agricultural practices, micro-remnants of *Zea mays, Phaseolus* sp. and *Curcurbita* sp. were recovered, suggesting an ancillary agriculture from 3000 years BP (Del Puerto 2015; Mut 2015). Isotopic studies in precolonial humans recovered in these mounds did not reveal identification of C_4 plants consumption (*i.e.* maize), probably due to its low incidence. However, the spacing values between both carbon sources show a significant intake of plants (Bracco et al. 2000; Mut 2015) that could be both cultivated and

Figure 4. Mound 'Cerro Pelado', at eastern Uruguayan plain.

wild. In this sense, charred remains of palm seeds, *Canna glauca, Typha dominguensis* and *Typha latifolia*, which are wild species with edible parts typical of the local wetlands, have been recovered. Concurrently, the Sr/Ca ratio in humans is similar to or even higher than that of local herbivores, indicating a high consumption of plants (Bracco et al. 2000; Bracco and Duarte 2020), while $\delta^{15}N$ values indicate omnivorous diets. It is expected that isotopic signals of marine resources will be identified for those humans who exploited the coastal lagoons, as we see in the dog recovered at the coastal mound PSG-07 (see below). There are no early ethnographic sources for this region, but for a later period, an equestrian complex is described, without any sign of architectural or cultural complexity as postulated for previous stages.

The South American Dogs

A General Overview

South American pre-Columbian dogs have been widely recognised in Andean societies from the beginnings of archaeological and zoological investigations (Ambrosetti 1906; Cabrera 1934; Eaton 1916; Ihering 1913; Nehring 1884, 1887; Tschudi 1844). On the contrary, no records have been found from the Amazon rainforest, Chaco, Patagonia and most of the Pampas plains (Koster 2009; Mitchell 2017). In fact, remains assigned to dogs in the last two regions by Saxon (1976), Clutton-Brock (1977, 1978) and Tonni and Politis (1981) were identified as native foxes in later reviews (Caviglia 1985–1986; Prevosti, Bonomo, and Tonni 2004; Amorosi and Prevosti 2008). The refutation of the Pampean – Patagonian findings circumscribed the presence of pre-Columbian dogs to complex and agricultural Andean societies, excluding nearly the rest of the subcontinent. This apparent fragmentary distribution has an intrinsic problem for American archeology, since in North America a wide distribution of pre-Columbian dogs has been reported (Ahler 1993; Hayden and Schulting 1997; Morey and Wiant 1992; Schwartz 1997; Tito et al. 2011; Walker, Morey, and Relethford 2005, among others), and also in Mesoamerica, where dogs were distributed even in modified forests during the Holocene (Valadez Azúa et al. 2013). Some authors have suggested adaptive problems related to different infectious diseases which restricted their distribution in extra-Andean South America (Mitchell 2017). These diseases would have infected the dogs in biogeographically diverse environments, such as the Amazon Forest, the temperate Chaco-Pampean plains, and the semi-arid and cold steppes of Patagonia, regions that are articulated by ecotones with the Andes. This restricted distribution has in some way been reinforced by historical sources, which mention different types of American dogs for the Andean area (*e.g.* Bertonio [1612] 1993; Fernández de Oviedo y Valdés [ca. 1536] 1944; Garcilazo de la Vega [1609] 1995), but for other South American regions, they often indicate the presence of small dogs that did not bark (Fernández de Oviedo y Valdés [ca. 1536] 1944). This particularity has led to them being considered as foxes (Stahl 2013). We discuss this issue briefly in the section related to historical sources.

The restricted distribution hypothesis based on infections has an inherent problem related to the rapid expansion of the dog introduced in the sixteenth century in the Chaco, Pampean and Patagonian plains (Cabrera 1932). The European pools not only began to be frequent among the indigenous people of these regions, but there was also a remarkable proliferation of wild feral dogs without any control or human care, and that became a nightmare for the early Spanish livestock breeding establishments due to the constant attack on cattle (Acosta and Loponte 2011a, 2011b). This dispersal process suggests that there were no environmental restrictions to the distribution of the dog in the South American temperate plains, or a different (and unproven) adaptive capacity from the European pools (see also Mitchell 2017).

The Pre-Columbian Andean Dogs

Dog records appear at different sites in the Andean area around 5000–4500 years BP, based on taxon-dates and according to the sampling available today (Mitchell 2017: Table 2). These dates suggest an earlier introduction into South America (sixth millennium before present a least). These middle Holocene contexts already belong to populations with some socioeconomic complexity (Byrd 1976; Stahl 1984). In the later Andean contexts (Tiahuanaco, Chancay, Chimú, Moche, Inca and others), dog records become very abundant, concomitantly with the large amount of archaeological research carried out on these societies. In this sense, we do not know if the absence of the dog for early Andean hunter-gatherers echoes a particular state of the currently available sampling, or if it's a real absence.

As a result of the large number of dogs recovered for the late Andean contexts, different morphotypes have been proposed (Allen 1920; Angulo 2014; Brothwell, Malaga, and Burleigh 1979; Cabrera 1934; Cornejo et al. 2012; Mendoza España and Valadez Azúa 2006; Venegas Gutiérrez 2019). The easiest to identify corresponds to the hairless dog, carrying an ectodermal dysplasia due to a mutation in the FOXI3 gene that produces the total or partial absence of hair, missing or abnormally shaped teeth (missing incisors and the premolar series), plus alterations in exocrine glands (Drögemüller et al. 2008). In this way, the

identification of the mandibles and the skull in the zooarchaeological collections is quite simple. The withers heights of this breed ranges between 39 and 60 cm. This size variation is due to the existence of different varieties (Valadez Azúa 2009: Table 3). Hairless dogs began to be identified in Mexico 2000 years ago BP, beginning with a slow diffusion towards the south of Mesoamerica (Valadez Azúa et al. 2013), and reaching the Andean region perhaps 1500 years BP. Older dates have been suggested based on representations in Andean pottery (Vásquez et al. 2016).

The most reliable Andean morphotypes of hairy dogs are based on mummies, which preserve most of the bones and their fur. In the case of the late Horizon Inca site of Pachacámac (Peru) (1470–1533 CE; sample size = 'more than twenty dogs') two morphotypes of mesocephalic dogs from yellow to brown hair were identified, one of medium size (wither heights 38–42 cm) with short and pricked ears (morphotype 1), and another one larger (wither heights 45–52 cm) (morphotype 2), in addition to a third brachycephalic skull morphotype, also of medium size (Cornejo et al. 2012; Pozzi-Escot et al. 2012). Later, Angulo (2014) and Segura (2016, in Venegas Gutiérrez 2019) analysed dogs buried in the site Huaca 33 of the Parque de las Leyendas (Lima, Peru) belonging to the Late Intermediate period (900–1476 CE). On the basis of the height, length of the body, shape of the skull and colour of the fur, they were classified into different morphotypes, which were later grouped into four by Venegas Gutiérrez (2019), based on a larger sample of 63 individuals from the same site, which they also seem to subsume morphotypes 2 and 3 identified by Cornejo et al. (2012). Since all these works are also based on complete (or almost complete specimens), the reconstructions were skeleton-based, so there is no specific detail of the sizes of the bones except for a few exceptions (see below).

In this more comprehensive classification by Venegas Gutiérrez (2019), types 1 and 2 correspond to brachycephalic dogs with some abnormal dentition. The first lower premolar, and sometimes the upper premolar teeth are missing. The wither height ranges between 30–39 and 41–43 cm, respectively, both with yellow and brown hair 2.5 cm long. Type 1 has a skull with a length between 13 and 16 cm, and short and crooked limbs (humerus length 10.1–12.1 cm; radius length 9–11.4 cm). Type 2 is similar to the little known 'Chiribaya shepherd' (Venegas Gutiérrez 2019, 108), identified previously in other sites in Peru (skull length 15–16 cm; humerus length 11.8–13.7 cm; radius length 11–13.2 cm). The type 2, according to the available descriptions, has dimensional ranges similar to the morphotype 3 of Cornejo et al. (2012), both with a brachycephalic skull.

Type 3 is extremely interesting for our study area, because its metric values are similar to those recovered in the Lowlands of south-eastern South America (see below). It includes a 17 cm long mesocephalic skull, with the absence of the pm1 (and eventually PM1 in some individuals). The wither height is greater than 44 cm (humerus length 14–14.8 cm; radius length 13.1–14.5 cm). The maximum measurements provided by this author for the length of the humerus (14.8 cm) and the radius (14.5 cm), applying the formulas of Harcourt (1974), yields a wither height of ~ 48 cm. The hair of the recovered mummies is yellow to brown, so it seems to be somewhat similar to the previous types. Described this way, it is comparable to morphotype 2 of Cornejo et al. (2012). It is also similar to the individuals 176386 and 176309 of the 'Inca dogs' of Allen (1920, 473), that present the same range dimensions of skull (17.2 cm), humerus (14.7 cm) and radius (14.0 cm); pm1 is frequently missing in this type. Skull length of this type is also within the range of the Group A from Brothwell, Malaga, and Burleigh (1979). The estimated live weight is 20 kg, by comparing the mummies with the wither height and length with live dogs (Angulo 2014; Venegas Gutiérrez 2019). Finally, type 4 corresponds to a small brachycephalic canid 28 cm high, but it is represented by a single specimen (Venegas Gutiérrez 2019).

Andean dogs were also recognised in many places in Bolivia, most of them are described in general terms. At the Chiripa site (post-classic Tiahuanaco period; 800–1200 CE) the most significant dog (because it certainty differs with from those described for Peru) is a large individual with a withers height of 61 cm, mesocephalic skull, and possibly pricked ears (Mendoza España and Valadez Azúa 2006). Although this study does not focus on Andean dogs, the important issue for our analysis is to highlight the morphological variability observed, which comprises at least seven different types (the hairless dog, the four of Venegas Gutiérrez, the Cornejo et al. (2012) morphotype 1, and the large specimen from Chiripá site in Bolivia). It cannot be ruled out that some of them are sample points of a continuous variability of urban dog populations (see also Brothwell, Malaga, and Burleigh 1979). Nevertheless, we will see that this variability is not at all observed in the lowlands of southeastern South America. There are also simple descriptions of dogs-types based mainly on skull metrics, and historical and pictorial information (Allison, Focacci, and Santoro 1982; Allen 1920; Brothwell, Malaga, and Burleigh 1979; Cabrera 1934; Mendoza España and Valadez Azúa 2006; Vásquez Sánchez, Rosales Tham, and Dorado Pérez 2009, among others), but it is difficult to articulate them with the previously described types because they use different descriptive criteria, however, most of them probably are subsumed in the Andean dogs previously described. We also incorporate some of these metric values in order to compare with our results.

The Pre-Columbian Dog Record in the Lowlands of Southeastern South America

The records of dogs that were identified with certainty from the South American Lowlands began with the findings in Uruguay of three individuals intentionally buried in artificial mounds. Two of them were recovered at CH2D01 site (Curbelo et al. 1990; Bracco 1995) and the third one at Potrerillo de Santa Teresa (PST), just 60 cm away from a human burial (González 1999; López Mazz et al. 2018) (see Table 1 of this study). These specimens remained relatively unknown to American archaeology. Although initially none of these three findings had direct dating of the canid specimens, the careful stratigraphic excavations and radiocarbon dating of the contexts indicated a reasonable pre-Columbian antiquity, an age recently corroborated for the last specimen, directly dated 1590 ± 110 ^{14}C year BP (López Mazz et al. 2018; see Table 1). However, it should be noted that the layer where this specimen was buried was dated 2320 ± 50 ^{14}C year BP, suggesting that it was buried in a pit, making the contextual dates of the layers in the Cerritos-type sites unreliable to date intentionally buried dogs (Bracco 2006; Bracco and Duarte 2020). Later, two other individuals were identified at Puntas del San Luis and Cráneo Marcado-B sites, associated with human burials, also in the Uruguayan plains (López Mazz et al. 2018). However, morphometric data of both specimens are still unknown, and their identification as dogs should be considered provisional.

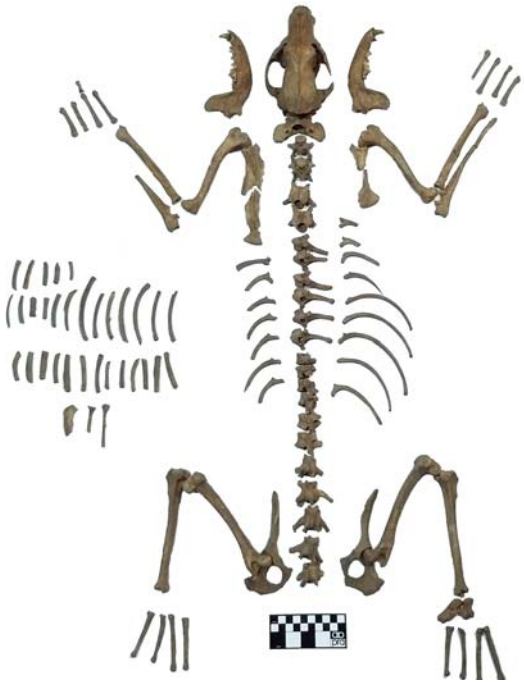

Figure 5. Dog remains recovered at Cerro Lutz site (individual code INAPL/CL1-UE3).

In the Lowlands of Argentina there was also a turning point with the discovery in 2005 of an almost complete dog skeleton (Figure 5, Table 1) at the Cerro Lutz site, located in the Lower Paraná-Uruguay wetland. Although the identification of this species had been mentioned in other sites in this region a few decades

Table 1. Distribution and chronology of pre-Columbian dogs in south-eastern South America lowlands.

Site	Sector	MNI*	Sample	Age ^{14}C BP	Code Lab.	Province/State	Country	Ref.
CH2D01-B	I	1	Context	1090 ± 70 (2)	URU 0024	Rocha Dpt.	Uruguay	(a)
CH2D01-II	I	1	Context	1610 ± 50 (2)	URU 030 / URU 027	Rocha Dpt.	Uruguay	(a)
Puntas del San Luis	I	1	Context	3430 ± 100 (2)	URU 099	Rocha Dpt.	Uruguay	(a)
Potrerillo Sta. Teresa (PST)	I	1	PST dog	**1590 ± 110** (1)	URU 0582	Rocha Dpt.	Uruguay	(a)
Cráneo Marcado – B	I	1	Context	2760 ± 60 (2)	GrA-15608	Rocha Dpt.	Uruguay	(a-g)
PSG-07	I	1	115-04 PSG-07	**1720 ± 30 (1)**	Beta-415598	Rio Grande do Sul	Brazil	(b)
Cerro Lutz	II	2	INAPL/CL1-UE3	**916 ± 42** (1)	AA77312	Entre Ríos	Argentina	(c-d)
Cerro Mayor	II	2	INAPL/CM-113	**1594 ± 59** (1)	AA103658	Entre Ríos	Argentina	(c)
La Argentina	II	1	Context	979 ± 44 (2)	Beta-147108	Entre Ríos	Argentina	(c)
Arroyo Las Mulas 1	II	1	Context	619 ± 24 (2) 950 ± 120 (2)	AA108376 INGEIS 2495	Entre Ríos	Argentina	(h)
La Palmera V	II	1	Context	640 ± 70 (2)	LP-905	Entre Ríos	Argentina	(i)
Sambaquí de Puerto Landa	II	2*	MAMA-SPL-A	**1119 ± 26 (1)**	AA106806	Entre Ríos	Argentina	(i)
Cerros de los Pampas	II	1	MAMA-CP-244	**1918 ± 29 (1)**	AA106805	Entre Ríos	Argentina	(i)
La Lechuza	II	1	MRA-LZA-D7-130	**2413 ± 28 (1)**	D-AMS-025193	Santa Fe	Argentina	(i)
Anahí	II	1	Context	1020 ± 70 (2)	Beta-147108	Buenos Aires	Argentina	(c)
La Bellaca site 2 (LBS2)	II	1	Context	680 ± 80 (2)	LP-1263	Buenos Aires	Argentina	(c)
El Cazador 3 (ECS3)	II	1	Context	921 ± 43 (2) 1091 ± 46 (2)	AA97470 AA103656	Buenos Aires	Argentina	(d)
Las Marías	II	1	Context	1590 ± 40 (2) 1820 ± 50 (2)	CURL-6072 CURL-6073	Buenos Aires	Argentina	(j)
La Yeguada	II	1	Context	510 ± 45 (2) 560 ± 70 (2)	URU 0178 URU 0176	Río Negro Dpt.	Uuruguay	(e)
Cañada Saldaña (CS)	II	3	CS 49136 CS 38341	**1714 ± 29** (1) **1746 ± 31** (1)	AA113921 AA113922	Soriano Dpt.	Uuruguay	(d)
Chenque 1	IV	1	ME E 41-2	**930 ± 30 (1)**	UGA 02006	La Pampa	Argentina	(f)
Angostura 1	IV	1	Context	938 ± 45 (2)	AA 2551	Río Negro	Argentina	(f)
Total		27						

*Minimal number of individuals. Age ^{14}C BP: (1) taxon-date (in bold); (2) contextual dates. References: (a) González (1999) and López Mazz et al. (2018). (b) Milheira et al. (2016). (c) Loponte and Acosta (2016a); (d) this study; (e) Loponte et al. (2016a); (f) Prates, Berón, and Prevosti (2010); (g) Capdepont et al. (2016); (h) Ottalagano (2020a). (i) Castro et al. (2020). (j) Day Pilaría (2018).

before (*i.e.* Serrano 1946), they were anecdotal identifications. The Cerro Lutźs dog was found in a test-pit separated from 10 m of an excavated human mortuary area. Due to the fact that it was recovered in an isolated 1 × 0.7 m quadrat, it is not yet known whether there was an association with a particular human burial or it was an exclusive grave for the dog. It was the first pre-Columbian dog from an extra-Andean region in South America to which genomic and radiocarbon analysis were carried out (Acosta and Loponte 2010; Thalmann et al. 2013). At the same time, another well-identified specimen was recovered at Chenque 1 (see Table 1 of this study), in a double human-dog burial (Prates, Berón, and Prevosti 2010; Prates, Prevosti, and Berón 2010), in the semiarid centre of Argentina (sector IV of Figure 1). This succession of complete dog skeleton findings facilitated the identification of isolated post-cranial remains which were previously and generically identified as Canidae indet., as well as new direct radiocarbon dates (Acosta, Loponte, and Buc 2021; Loponte and Acosta 2016a). Later, other studies with Uruguayan and Brazilian colleagues identified new specimens in sites located in these countries (Loponte et al. 2016a; Milheira et al. 2016, See Table 1 of this study), spatially extending the record of south-eastern South American pre-Columbian dogs, and generating a new panorama as seen in Table 1 and Figure 6.

Morphometrics

The pre-Columbian dogs in the core area (Figure 6) display little dimensional variability, suggesting the existence of a single dog morphotype. See metric data listed in Supplemental Table 1. Measures were taken with a digital calliper with an accuracy of 0.01 mm; most of the measurements were rounded to the first decimal place. In general, the anatomical nomenclature follows Sisson and Grossman (2000). As many were isolated specimens, this table contains bones/teeth with different codes for the same sites (especially for Cañada Saldaña site), noted by unique museum codes. For other methodological aspects, see Supplemental information text 1.

Skull

In the core area (Figure 6) only three complete skulls were recovered (INAPL/CL1-UE3, CH2D01-B and PST) (Supplemental Table 1 and Figure 7). The cephalic index of them are grouped in a narrow range between 56.2 and 62.4, close to the lower threshold (55) of mesocephalic dogs (Evans 1993; Sisson and

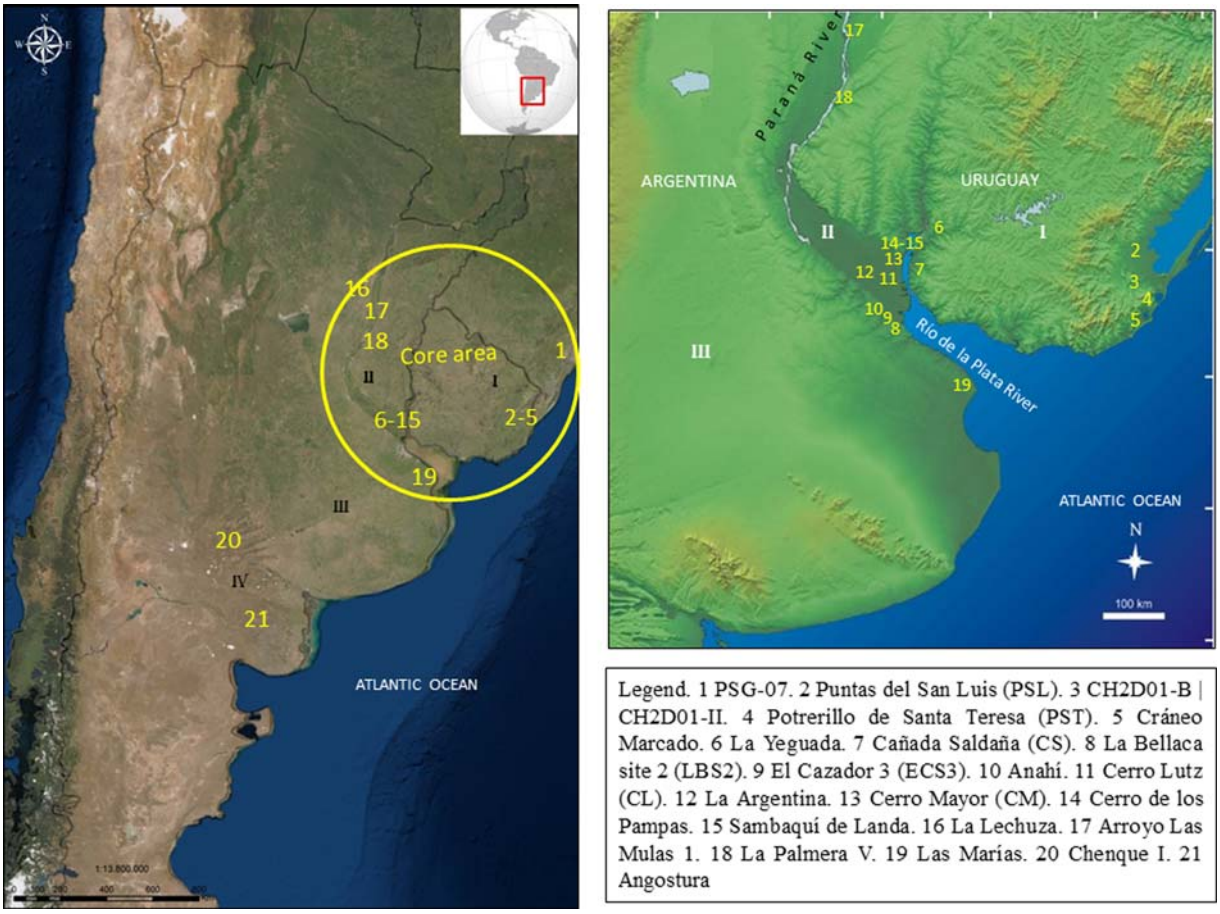

Figure 6. Geographical range of the southern pre-Columbian dogs in America. The encircled area shows the concentration of findings in the southeast ('core area of findings'), which is amplified on the right map.

Figure 7. A = Skull CH2D01-B; B = Skull INAPL/CL1-UE3. Mandibles, C = CS 38342; D = CH2D01-B; E = CH2D01-II; F = INAPL/CL1-UE3. Skulls and mandibles are on different scales, which are approximate.

Grossman 2000). These skulls range between ~17.5 and 15.7 cm, with a low coefficient of variation (5.7%). Since two of these individuals (CH2D01-B and PST) are subadults between 12 and 15 months, this range should be less variable in adults, which reached 17.5 cm in length (INAPL/CL1-UE3). This specimen and other two (CH2D01-B and MAMA-SPL-A) lack left pm1, and CH2D01-II lacks right pm1. The absence of the pm1 is a relatively common feature in pre-Columbian dogs (Allen 1920; Colton 1970). The length of the mandibles of specimens >12 months have a very narrow range between 129 and 131.5 mm (condyle process – infradentale) (see Supplemental Table 1 and Figure 7). The height of the mandible behind m1 is similar among the seven available measurements (Supplemental Table 1), showing a very low variability (x_7 = 23.0 ± 1.3 mm; CV = 5.9%). The only specimen that behaves somewhat differently in this and other measures is MAMA-CP-244 from the 'Cerro de los Pampas' site. Although it has a similar value to the adults (24.3 mm), according to Castro et al. (2020) it corresponds to a 6–8-month-old specimen (see discussion of this specimen below). Other craniometric variables in specimens > 12 months of the core area are also similar, including dental features (see Supplemental Table 1). For instance, m1 length (x_{14}; $\bar{x}$ = 20.0 ± 0.9 mm; CV = 4.7%), m1 width (x_{10}; $\bar{x}$ = 8.3 ± 0.6 mm; CV = 7.2%), C1 length (x_4; $\bar{x}$ = 8.5 ± 0.8 mm; CV = 9.1%); C1 width (x_5; $\bar{x}$ = 5.6 ± 0.5 mm; CV = 9.1%), c1 length (x_8; $\bar{x}$ = 9.2 ± 0.6 mm, CV = 6.2%), and c1 width (x_7; $\bar{x}$ = 6.3 ± 0.5 mm, CV = 7.7%). Again, the specimen MAMA-CP-244 is dissonant in this distribution, because although it has similar values than the rest of the dogs >12 months, the age category indicated for this specimen is 6–8 months, so it needs to be re-analysed with more detail. For the specimen from Brazil (just maxillary teeth) located in the extreme north of the core area (site PSG-07), the M1 size is equivalent to those specimens (>12 months) from Uruguay and the sites located in the Paraná wetland (Supplemental Table 1).

Comparing the craniometric data with those published for Andean dogs, the Cerro Lutz specimen is grouped with the largest Allen's 'Inca dogs', and with Brothwell's Group A, sharing other similarities. The Hualfin specimen (northwest Argentina) is also close to this cluster (Figure 8). The Type 3 of Venegas Gutiérrez (2019) (which has also a mesocephalic skull) do not have metric information on the skulls except for the total length (17 cm), similar to the only complete adult dog of the Lowlands recovered at Cerro Lutz. In Northwest Argentina, other dog-types were

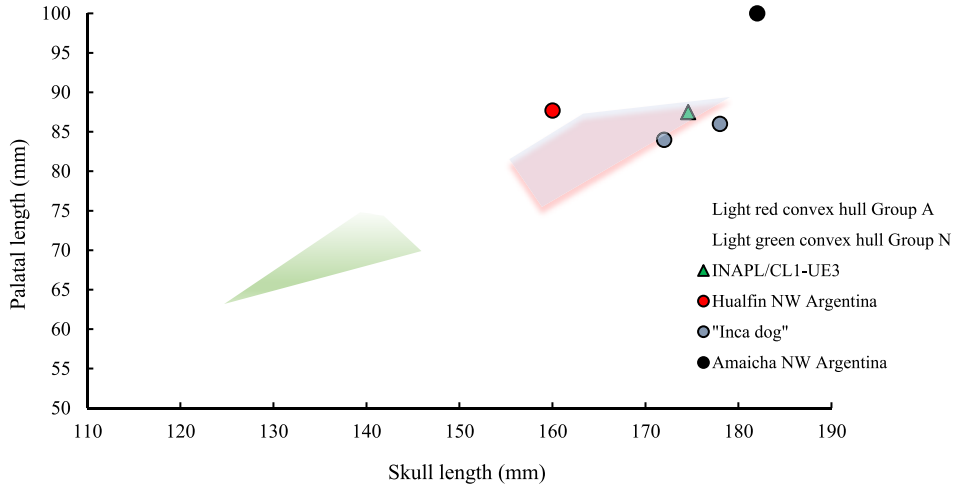

Figure 8. Biplot of Andean dogs and adult specimen INAPL/CL1-UE3. Values of Groups N and A are estimated and modified from Brothwell, Malaga, and Burleigh (1979, Figure 7) (outliers and 'hybrid' values were not included). Values of Amaicha and Hualfin dogs were taken from Cabrera (1934); values of Inca dogs (specimens 176386 and 176309) were taken from Allen (1920).

recognised. One of which is the Amaicha's dog, a morphotype of a large dog; there were also smaller dogs closer to Brothwell's Group N (Figure 8), but their skulls are incomplete, preventing their inclusion in the bivariate plot or this figure (see Cabrera 1934). This variability highlights the presence of different dog-types in the Argentine Andean area, which is not recorded in the South-eastern lowlands.

Withers Height

Based on the average of the long-fused bones, the withers height of four adult specimens (INAPL/CL1-UE3; CH2D01-II; Chenque 1; CS 49133) were calculated using Harcourt´s (1974) formulae, ranging in-between 44.5 and 48.4 cm ($\bar{x}$ 46.4 ± 1.7 cm) (Supplemental Table 1). Similar values (from 43.2 to 47.3 cm; $\bar{x} \sim 45$ cm) are obtained using the Blanco Padilla, Rodríguez Galicia, and Valadez Azúa (2009) formula, developed from pre-Columbian Mexican dogs (based on tibia length). In immature specimens CH2D01-B and PST, we obtained a range from 40 to 42 cm height. Since medium-sized dogs reach full maturation between 8 and 18 months (Lewis 2019; Sisson and Grossman 2000), it is expected that the size of the specimens aged between 12 and 15 months will be slightly smaller than the fully developed specimens (Supplemental Table 1, Figures 9 and 10).

We can also estimate the withers height of other local dogs based on isolated ulnas, because the trochlear notch length (measure M1 after Loponte and Acosta 2016a, 244) has a positive correlation ($p = 1$)

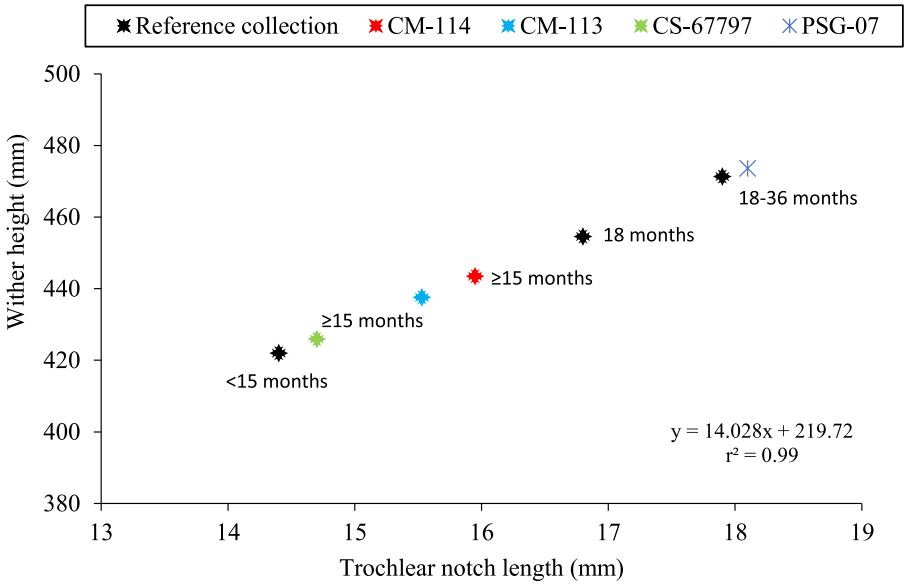

Figure 9. Relationship between the ulnar trochlear notch length and withers height in local *Canis lupus familiaris*. The correlation and the linear equation were obtained for the reference collection INAPL-CL1-UE3, CH2D01-II and CH2D01-B, in which withers heights were obtained independently from long complete bones following Harcourt´s (1974) formulae.

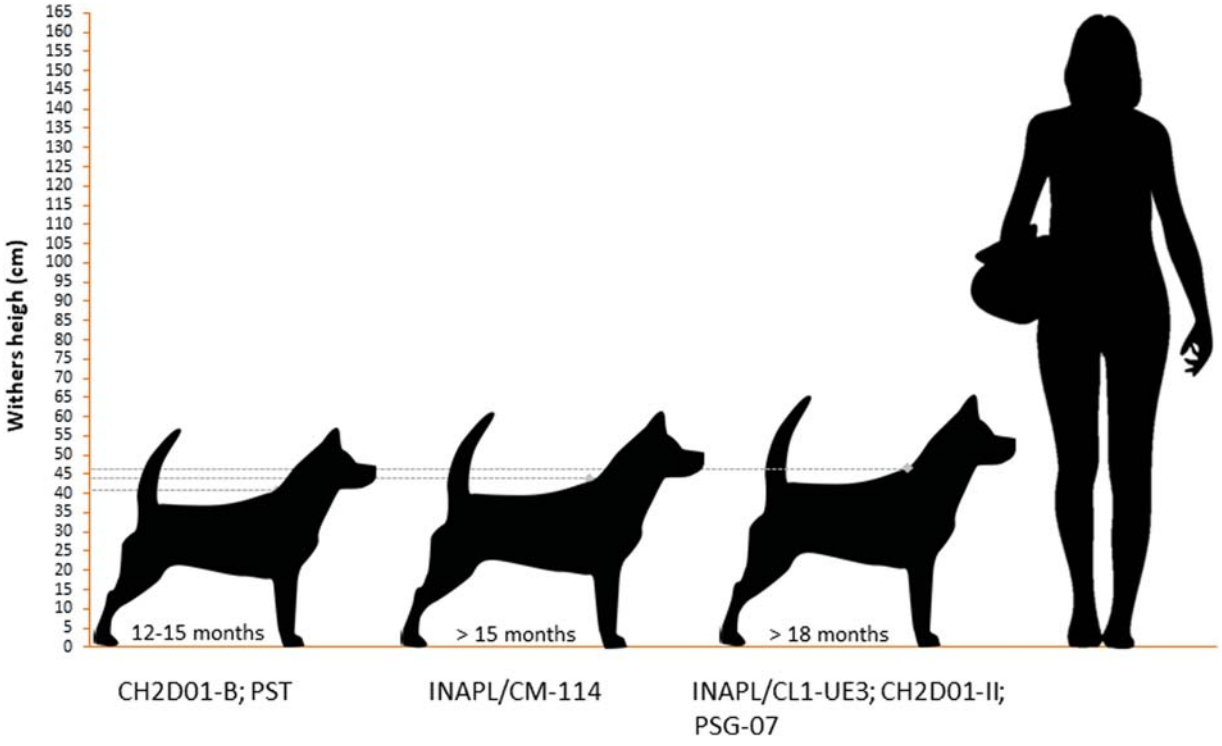

Figure 10. Withers height of local dogs compared to a human 165 cm tall.

with the withers height of the adult dogs ($y = 14.082x + 219.72$). However, this statistical relationship is not strong due to the small sample size of the reference collection (Figure 9). If its statistical significance is verified, there is also no certainty that it could be used for other morphotypes of dogs. By applying this regression equation to the isolated ulnae INAPL/CM-113, INAPL/CM-114, CS 67797 and PSG-07 (see Supplemental Table 1), a range from 42.6 to 47.3 cm height is obtained (Figures 9 and 10), similar to the withers height calculated for the other dogs using the length of the bones. It must be noted that two of these isolated ulnae (INAPL/CM-114 and CS-67797) have both epiphyses fused, corresponding to individuals of 15 months at least, but we don't know if they reached 18 months, when the dogs end their growth process (cf. Sisson and Grossman 2000). The epiphysis of INAPL/CM-113 lacks the olecranon, therefore the age of this specimen cannot be determined.

This brief review of measurements clearly suggests the limited variability in the size of the skulls, teeth and long bones (see Supplemental Table 1), suggesting the presence of a single dog morphotype with mesocephalic skull, with adult specimens ranging from ~45 to ~47 cm height (intervals of confidence between 44.5 and 48.8 cm), similar to Andean type 3 (Venegas Gutiérrez 2019). This low variability is also seen in axial skeleton bones such as the axis (measure M1 $x_3 = 33.9 \pm 0.4$ mm, CV = 1.2%; measure M2 $x_3 = 47.3 \pm 2.6$; CV = 6.6%, see Supplemental Table 1).

Body Mass

The weights of the dogs from the core area were reconstructed using the Losey's et al. (2015, 2017) formulas (see supplemental Table 2). The weight of adult dogs with more than five measures corresponds to three specimens, both from Cerro Lutz and the other from CH2D01-II, which are in-between 15.0 and 15.8 kg (Supplemental Table 2), being the most reliable range for the local dogs with the current state of the sampling. The body mass of two other adult dogs from Cañada Saldaña, based on three dentocranial measures (CS 38342 and CS 49136), yielding 15.6 and 16.5 kg respectively, quite similar to the previous. The isolated complete tibia from the same site (CS49133), a bone that when complete allows us to obtain a reliable weight (see Supplemental Table 2), corresponds to a 15.3 kg dog. Thus, the better estimation for the weight of the adult dogs of the core area shows a narrow range from 15 to 16.5 kg, which is a parsimonious result with the existence of a single supposed morphotype. Other estimates of adult dogs' range between 12.6 and 19 kg, but it is a range mostly based on two dentocranial or epiphyses measures for each specimen, and some of these measures tend to overestimate the weight (*i.e.* m1 and M1 width), or underestimate (*i.e.* distal tibia Dd) (see Supplemental Table 2), being unreliable when used as the only data to reconstruct the weights. Regarding the subadults, for the same reasons we stated previously, the most confident weights correspond to PST and CH2D01-B dogs, in-between 14.8 and 13.3. kg respectively (see Supplemental Table 2), which are in

accordance with the weight of the adults previously obtained.

Post-Cranial Morphological Features

In addition to the morphometric similarities noted in the previous sections, dogs from the core area shared some particular postcranial features. Among them is the dome-shaped design of the neural spine, observed in those specimens whose axis morphology was analysed and published (INAPL/CL1-UE3, INAPL/LB2-CF-2 and CH2D01-II; Loponte and Acosta 2016a, and Figure 11 of this study). European dog specimens available at the Instituto Nacional de Antropología (Buenos Aires) and Museo Argentino de Ciencias Naturales (Buenos Aires) do not show this particular pattern, although it is a very small sample ($n = 3$). There is no published data on the morphology of this feature of the axis of pre-Columbian dogs. This particular design, for instance, has not been noticed in the axis of Mesoamerican pre-Hispanic dogs (Figure 11). Thus, this dome-shape could be part of the phenotypic expression of the dog morphotype from the core area, with a potential geographical/temporal significance (*cf.* Margalef 1974; Pianka 1999), as has been proposed for other features for the Andean area related to micro-evolutionary processes (Brothwell, Malaga, and Burleigh 1979). A robust olecranon displaying a 10° – 16° inclination with respect to the ulnar axis has also been observed, which clearly differentiates the ulnas of dogs from local foxes of a similar size (Loponte and Acosta 2016a, Figure 3).

Sex and Demographic Patterns. So far, sex could be inferred in just two dogs. One corresponds to the female INAPL/CL1-UE3 (sex index IV = 146.4, cf. Trouth et al. 1977), the other corresponds to the male CH2D01-B (sex index IV = 124). This last specimen has been considered a female by other authors (López Mazz et al. 2018) because the bacular bone was not recovered; however, this bone generally is not preserved in archaeological contexts (Blanco Padilla, Rodríguez Galicia, and Valadez Azúa 2009), and in addition, this dog also lacks other bones, so its absence could be a taphonomic or sampling issue. Based on bone fusion and Horard-Herbin's (2000) wear stages, most of the individuals of the core area are not older than 36 months (INAPL/CL1-UE3; both CH2D01, PST, MRA-LZA-D7-130, PSG-07, Supplemental Table 1). Isolated remains also show the same range in the death profile. For instance, mandibular fragment CS 49136 is between 24–36 months, hemimandible CS 38342 from 36 to 48 months, the m1 CS 49019 in-between 36–48 months, and the m1 INAPL/CL1-UE20 below 36 months. The isolated m1 code CS 17-118-1 could be a worn-out tooth, but the enamel is fractured preventing a clear interpretation. Only two loose pieces of the core area have a somewhat more advanced degree of wear. The first corresponds to the M1 INAPL-LB2-CF1, whose metacone and paracone have slight wear flattening, suggesting that this individual was older than 36 months or it had a very different diet (Loponte and Acosta 2016a). The second corresponds to the m1

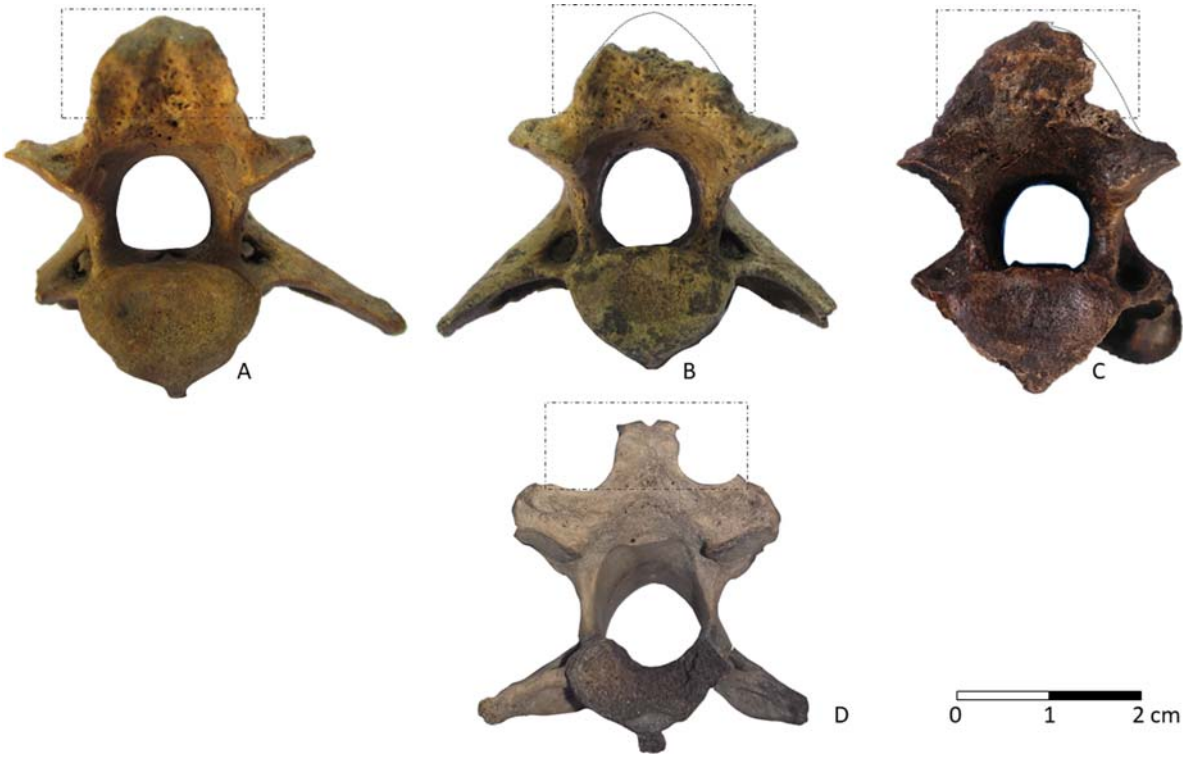

Figure 11. Axis caudal view. A: INAPL/CL1-UE3. B: INAPL/LB2-CF-2. C: CH2D01-II. D: Mesoamerican dog M10-m1 (courtesy of Raúl Valadez Azúa).

INAPL/CM-111, whose hypoconid is flattened showing in parallel a significant separation between the protoconid and the paraconid (Loponte and Acosta 2016a, 440) approaching the Horard-Herbin's stage F (up to 48 months). Castro et al. (2020) suggested that the mandible MAMA-SPL-A from Sambaquí Puerto Landa would correspond to a specimen of 8 years or older. The observed trend, with the few exceptions noted, shows a relatively early age of death of the dogs in the area.

Post-Mortem Treatment. Some dogs were intentionally buried in human mortuary areas. This is the case for INAPL-CL1-UE3, CH2D01-II, CH2D01-B, PST, Cráneo Marcado-B, and probably INAPL/CM-113 and MRA-LZA-D7-130 (Acosta, Loponte, and García Esponda 2011; Castro et al. 2020; Loponte and Acosta 2016a; López Mazz et al. 2018). Also, several disarticulated but clustered bones grouped as INAPL/CL1-UE20 were also recovered in a human mortuary area (Acosta, Loponte, and Buc 2021). In Cañada Saldana, there is no related information regarding the way in which dog remains were found (pioneering excavations of the past century without adequate stratigraphic control). Here, the bones were mixed with the rest of the fauna, but without fresh fractures, cut-marks or scraping as they are present in the latter. The same high integrity with some taphonomic deterioration is also observed in the isolated humerus INAPL/LB2-CF-3 from La Bellaca 2 site (Figure 12). However, in this site the axis INAPL/LB2-CF-2 shows cut-marks (Figure 11). The use of dog bones to manufacture instruments is also evident in the femur of the specimen of Cerro Lutz INAPL/CL1-UE20 (Figure 12), which is a typical by-product of the preparation of bone artefacts in the region (Buc 2012). Other evidence of post-mortem manipulation corresponds to the canines transformed in pendants or blanks to produce them (e.g. INAPL/A81; INAPL/A80; INAPL/AR8) (Figure 12).

Phenotype Reconstruction

In the previous sections we reconstructed for the core area a medium sized mesocephalic morphotype, metrically indistinguishable from the Andean morphotype 2 of Cornejo et al. (2012), or Type 3 from Venegas Gutiérrez (2019). The mummies of this morphotype had short ears, slightly drooping lower lip, and 2.5–3 cm long dark brown hair and yellowish spots. Due to the humid characteristics of the Lowlands, neither hairs nor soft tissue were conserved, but we can approach a 3D reconstruction, based on the skull INAPL/CL-UE3 using the ZBrush 4R7 software (Pixologic, Inc.; for more details see Supplemental information text 1). Of course, hair colour and length are analogies with Andean medium dogs, so we also present a hairless reconstruction (Figure 13).

Iconography

In some archaeological contexts of the lowlands of the Paraná-Uruguay Rivers (Sector II, Figure 11), a fraction of the local fauna was represented as modelled appendages on the vessels. The animals selected were not the typical prey, but those that had a special

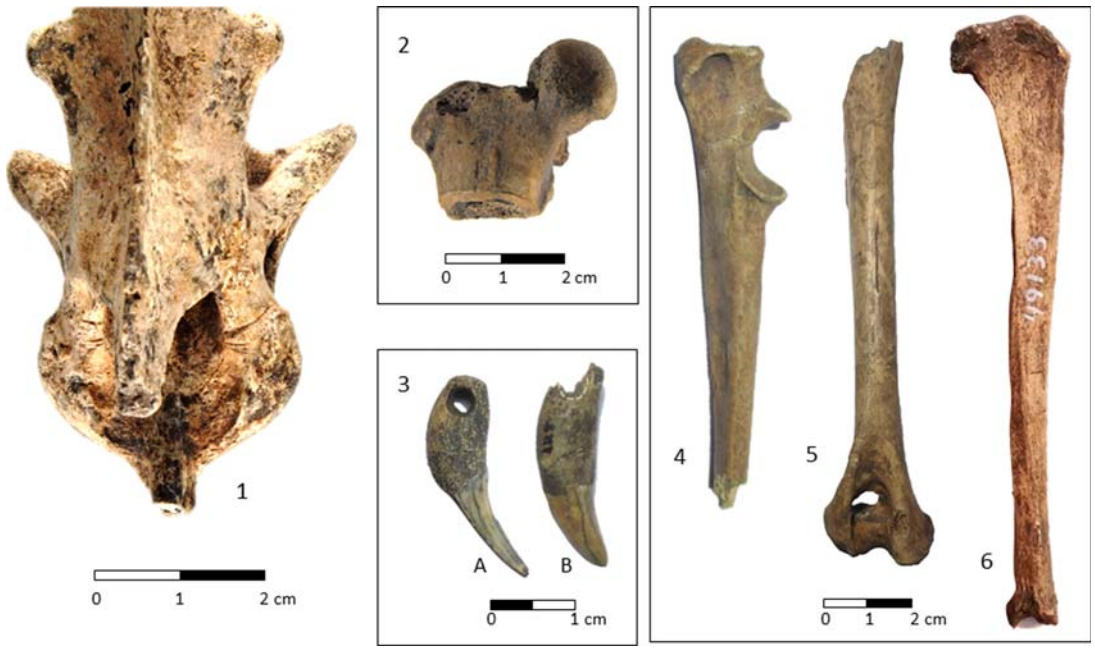

Figure 12. Piece 1 Axis INAPL/LB2-CF-2 with cutmarks in both sides of the neural canal. Piece 2: distal femur INAPL/ CL1-UE20 with perimetral sawing. Piece 3A: upper canine INAPL/A80 (the crown is fragmented). Piece 3B: lower canine INAPL/AR8 both used as pendants. Piece 4: ulna INAPL/CM-114. Piece 5: humerus SINAPL/LB2-CF-3. Piece 6: tibia CS 49133. Scales are approximate.

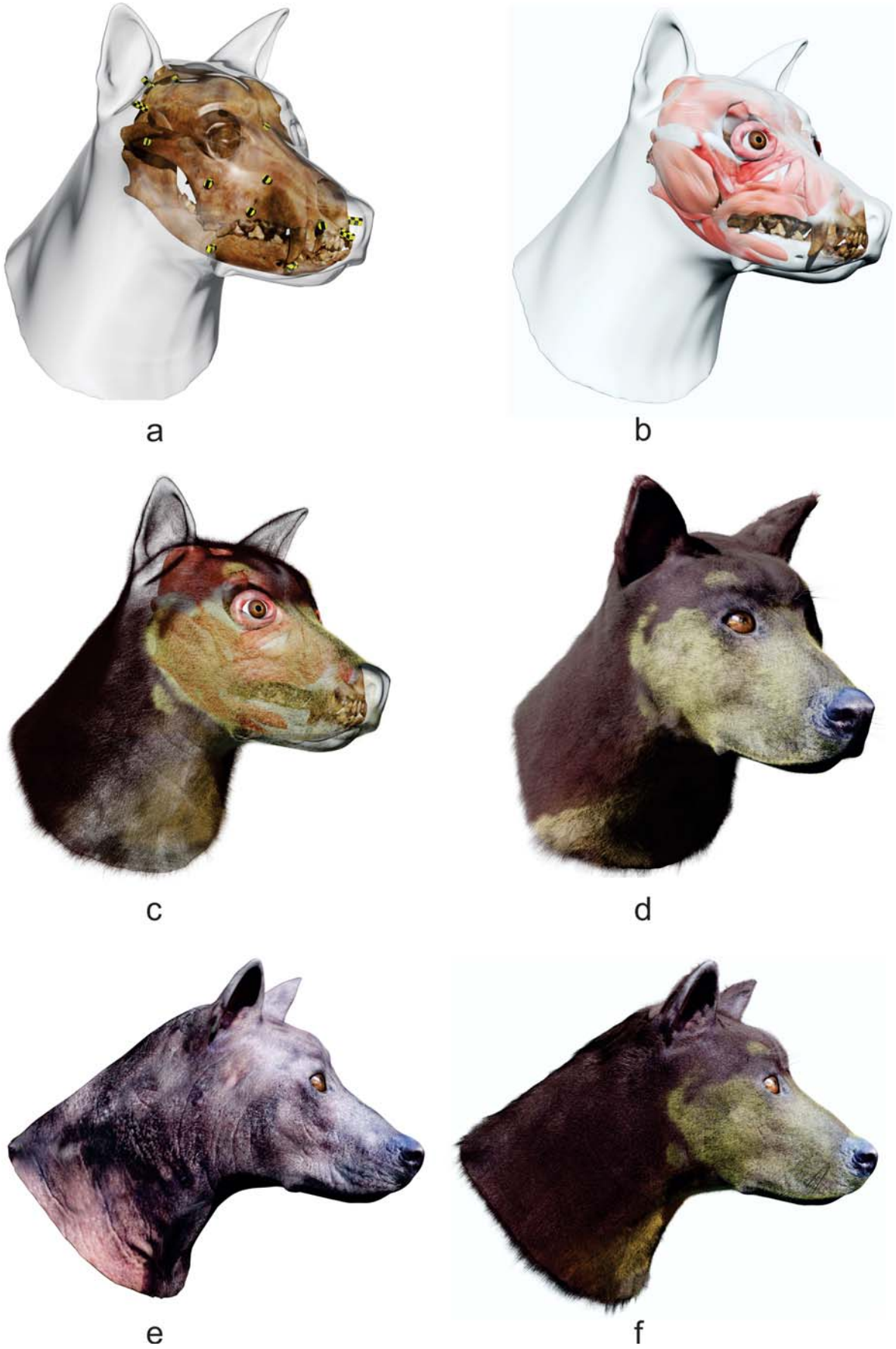

Figure 13. Head reconstruction based on skull INAPL/CL1-UE3. a-d: Perspective view of the reconstruction stages; e: Side view without hair, and (f) with hair. The shape of the ears, colour and hair type adapted from Cornejo et al. (2012).

Figure 14. Zoomorphic appendage recovered at Las Tejas San Nicolás 1 site, representing a canid (probably a dog), compared with the reconstruction of Figure 13. The scale is approximate.

symbolic relationship with humans. The representations of mammals in general and the canids in particular are little known, since these contexts have scarcely been investigated. Nevertheless, one of these plastic representations has enough morphological attributes to be considered as a canid (Figure 14). Given the morphological similarity between them, it could be a native fox species or a dog. The ears are typical (like those) of a fox, short and pricked, but so are the ears of many of the iconographic dog reproductions in the Andean pottery and historical sources (Allen 1920; Gallardo 1964-1965; Mendoza España and Valadez Azúa 2006), also sustained by dogs mummies (Cornejo et al. 2012; Venegas Gutiérrez 2019). Zoomorphic appendages are mediated by human symbolism, of course, and supposed representations of dogs in the vessels that are presented in some local studies are absolutely conjectural. However, the animal in Figure 14 presents a combination of morphological characteristics that are typical of a dog, such as the broad incisive bone between the line of the mouth and the nostrils, the broad development of the latter and a snout that tends to be more robust than that of foxes. The image also shows a moderately elongated snout, suggesting a mesocephalic/dolichocephalic skull type (Figure 14).

Historical Sources

For the plains of South Brazil and Uruguay, there are no early chronicles available from the European exploration phase (early middle of sixteenth century). On the contrary, for the lower Paraná-Uruguay wetland, there are several mentions of the local fauna, the subsistence and aboriginal lifestyle, including hunting episodes. However, there are no references to local dogs (see chronicles in Madero 1939; Schmidl 1948; Lopes de Sousa 1927, among others). Given that the existence of pre-Columbian dogs in the region has been proven, their historical 'absence' is just one more example of why chronicles cannot be taken as sources of validation. To explain their observational absence, we hypothesised elsewhere a low dog demography (Loponte and Acosta 2016a), but also a symbolic and restricted use of them, or just simply for chroniclers their presence was just not noticeable. In fact, the two exceptions correspond to a professional historian who had the official charge from the crown to describe the New World. Indeed, Fernández de Oviedo y Valdés (the first 'Chronicler of the Indies'), although he never stayed our region of study, he interviewed numerous travellers who had been there, and he transcribes the accounts of 'several and reliable witnesses' (which means officers and noble Spaniards). This author indicates the existence of 'large and small' dogs of European origin, left by the expedition of Sebastiano Caboto (Sebastian Gaboto or Cabot) only a few years before (1527–1529 CE). He explicitly stated that before the arrival of the Europeans there were no dogs. These 'introduced' dogs among the 'Mecoretaes' (a local hunter-gatherer group identified by the Spaniards) were used in hunting activities (Fernández de Oviedo y Valdés 1944, V, 156). Since we know without doubt that pre-Hispanic dogs existed in this area, it is possible that this description by Oviedo of European like-dogs is the consequence of a low demography of aboriginal dogs and a rapid reproduction of European forms, or a hybridisation with them.

The second mention is related with an imprecise area of the same Paraná basin, somewhat further north of the aforementioned, where this author points out the existence of small and native dogs which could not bark, tamed by the local population, and used as food (Fernández de Oviedo y Valdés 1944, V, 155). The inability to bark has been recognised in other dogs from different regions of the Spanish Empire in America (Gallardo 1964-1965). In fact, some current dog breeds do not bark or they do so rarely (Gallardo

1964-1965; Scott and Fuller 1965). Due to Fernandez de Oviedo's description that they appeared externally as foxes but actually were dogs, also describing a behaviour identical to the latter, it has been ruled out that it corresponds to foxes (Gallardo 1964-1965; see also Gilmore 1950 and Stahl 2013 for a different position). Allen (1920) suggests that the 'Techichi' dog-type (small, light-limbed dog, hair from black to yellow) could correspond to these fox-like dogs. It should be noted that in three of these regions with historical references of dogs that did not bark (Central Andes; the Antilles and the Paraná basin), there is no evidence (for now) of tamed foxes, and on the contrary, the existence of pre-Columbian *Canis lupus familiaris* has been proven (Acosta, Loponte, and García Esponda 2011; Laffoon et al. 2019; Loponte and Acosta 2016a; Wing 1989, 2008; this study). Nevertheless, this possibility, as well as hybridisation between dogs and foxes should be left open (Petrigh and Fugassa 2013; Stahl 2013, 2020).

Diet and Mobility of Dogs Based on Stable Isotopes

Supplemental information text 1 provides methodological aspects of isotopic analyses, laboratories, the respective cautionary tales, and the oxygen ecozones identified in the Paraná-Uruguay Lowlands. Regarding the $^{87}Sr/^{86}Sr$ values obtained in some dogs, it should be noted that the Paraná and Uruguay rivers run through areas with different and complex geologies, resulting in significant variations even in small geographic areas. In this study, we use strontium isotope data to evaluate life-history changes of the dogs by comparing their values with the humans with which they lived in the same sites.

Dogs Diet

The dog diets were based on C_3 resources (x_7 δ^{13}Cco – 20.5 ± 1.4 ‰; δ^{13}Cap – 13.4 ± 1.3 ‰), whose original source had an average of δ^{13}C −23.2 ± 1.3 ‰ (Table 2). The C_3 photosynthetic pattern is the most frequent in local plants and fauna, as well as in the sources of energy in the regional fluvial systems (Madanes, Kalesnik, and Vargas 2013; Marchese et al. 2014; Saigo et al. 2015; Loponte, Acosta, and Corriale 2016c). The average value of δ^{15}N is 8.2 ± 1.7 ‰, and the spacing between both carbon sources is Δ^{13}C 7.0 ± 1.4 ‰. Both magnitudes are typical of the local omnivory (Loponte, Acosta, and Corriale 2016c; Loponte 2020). However, the dogs show a significant individual variability reflecting a wide effective niche, which ranges between more carnivorous diets to others with a significant plant intake (Table 2 and Figure 15). The PSG-07 dog was excluded in Table 2 because the site where this individual was recovered is located in a marine lagoon, and this dog shows precisely this marine influence mixed with some continental resources (δ^{13}C −11.4; δ^{15}N 10.6 ‰). In the plot of Figure 15 this specimen is included.

Dogs in Human Contexts: Cerro Lutz

Isotopic diets of dogs have been considered as a proxy to that of humans (Cannon, Schwarcz, and Knyf 1999; Guiry 2012, 2013; Laffoon et al. 2019; Grandal-d'Anglade et al. 2019, among others), but there are also opposed examples (Eriksson and Zagorska 2003; Tsutaya et al. 2014; Ames et al. 2015; Grandal-d'Anglade et al. 2019, among others). The latter occurs in the specimen of Cerro Lutz INAPL/CL1-UE3. Its $\delta^{13}C_{collagen}$ (−22.3 ‰) is more negative than in humans (x_5 −19.9 ± 0.6 ‰), and its δ^{15}N (8.0 ‰) is a trophic step lower than adult humans of the same site (x_5, δ^{15}N 11.1 ± 0.67 ‰) (See Figure 16). Human diet was based on local fish that have high levels of δ^{15}N (Marchese et al. 2014; Saigo et al. 2015; Loponte, Acosta, and Corriale 2016c), while dogs seem to have had no access to them. The humans also incorporated freshwater molluscs, ungulates (range 150–20 kg) and medium and small rodents (range 8–0.4 kg). However, the bones of these prey in the archaeofaunal collections recovered in the area, including those where the dog remains were recognised, do not show traces of carnivore action (Acosta 2005; Arrizurieta, Mucciolo, and Musali 2010; Loponte 2008). This suggests that dogs may not have consumed soft tissues attached to the bones of the main prey, or at least not on a daily basis. In fact, the nitrogen values indicate the intake of proteins with low level δ^{15}N and carbs. In relation to the latter, the apatite values of humans and dogs

Table 2. Isotopic values of continental diet of dogs from Southeast South America.

Site	Site ecozone (δ^{18}O)	Code sample	Lab. Code	Sample	$\delta^{13}C_{co}$‰	$\delta^{13}C_{ap}$‰	Diet[c]	$\Delta^{13}C_{ap\text{-}co}$	δ^{15}N‰	δ^{18}O‰
Anahí	Paraná River	INAPL/A81	EIL 902	canine[a]	−21.5	−14.4	−24.2	7.1	10	−1.82
La Bellaca site 2	Paraná River	INAPL/LB2-CF-2	EIL 903	Axis	−21.4	−15.5	−25.3	5.9	8.6	−1.89
Cerro Mayor	Uruguay River	INAPL/CM-113	EIL 904	ulna	−20.1	−13.9	−23.7	6.2	5.2	−1.72
Cañada Saldaña	Uruguay River	CS 49047	EIL 4088	Maxilla	−19.9	−12.1	−21.8	7.8	9.1	−2.33
Cañada Saldaña	Uruguay River	CS 38339	EIL 4089	incisive[a]	−19.5	−13.6	−23.3	5.9	8.9	−1.13
La Yeguada	Uruguay River		EIL 5032	canine[b]	−18.4	−12.1	−21.7	6.3	7.1	−1.34
Cerro Lutz	Transition zone	INAPL/CL1-UE-3	EIL 901	rib	−22.3	−12.5	−22.2	9.8	8	−2.76
Mean					−20.5	−13.4	−23.2	7	8.2	−1.85
SD					1.4	1.3	1.3	1.4	1.7	0.6
CV					6.6	9.6	9.6	20.1	20.5	30

[a]Enamel. [b]Whole tooth. [c]Whole diet based on Kellner and Schoeninger (2007, 1120, Equation 1).

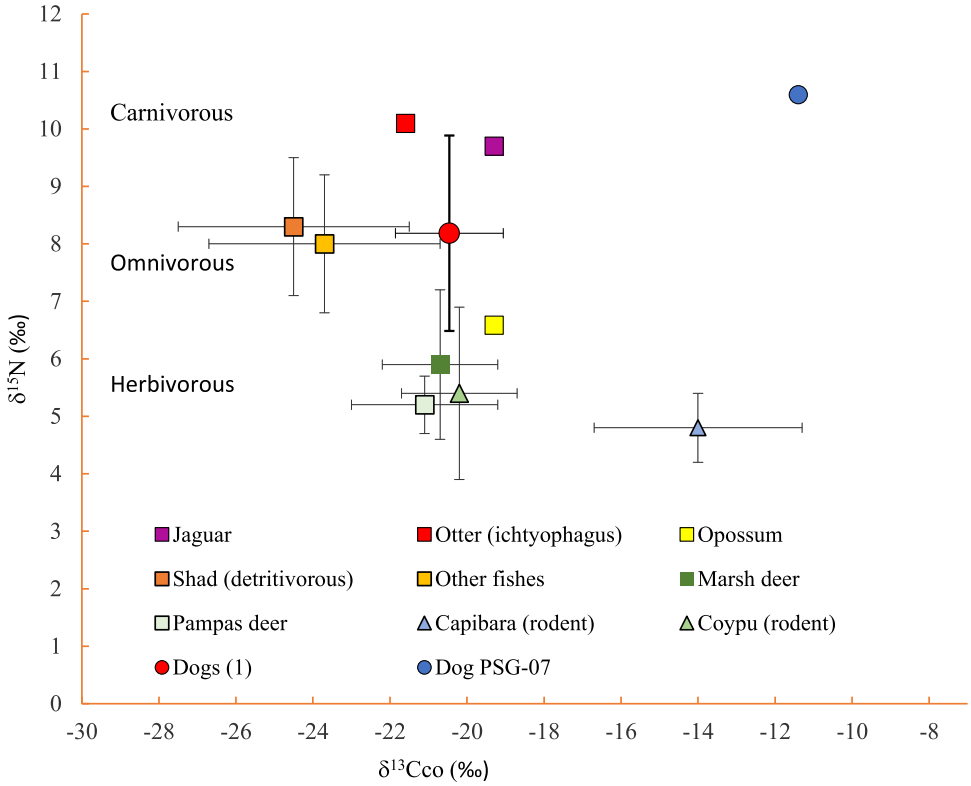

Figure 15. Mean values (±1 SD) of $\delta^{13}C_{co}$ and $\delta^{15}N$ of local trophic chain (taken from Loponte, Acosta, and Corriale 2016c). The values of 'Dogs (1)' were taken from Table 2.

show similar values (Figure 16), suggesting a similar biochemical source of carbohydrates.

Cerro Lutz is located in an area where today (and presumably when the site was occupied), different branches of the Paraná River flow into the Uruguay River, generating a vast space with mixed waters of both rivers, and intermediate isotopic values of $\delta^{18}O$ (Loponte et al. 2016b). Dogs and humans of Cerro Lutz show these mixed magnitudes (see Figure 16), supporting a life-cycle developed mostly in this area (Loponte and Ottalagano 2021). The $^{87}Sr/^{86}Sr$ value of the dog is 0.711934 in dentin, and 0.711332 in enamel. The small difference between the two (<0.000 ppm), suggests that it did not undergo significant diagenesis, and that the breeding and the life-cycle areas were not different. The samples corresponding to humans also do not show signs of diagenesis, but there is an important dispersion of inter-individual values. The dentin varies between 0.711550 and 0.713083, while the enamel between 0.710808 and 0.713026. Beyond the dispersion of humans, these are grouped (with a single exception) in a different way than the value obtained in the dog (Figure 16). It should be noted that human diets were based on fish (most of them with migratory patterns), which cannot be ruled out as one of the sources of variation among the humans, and between them and the dog (Figure 16). Considering both isotopic results (^{18}O and $^{87/86}Sr$), the dog seems to have been born and lived in the same oxygen ecozone as humans, but in a sector with a slightly different Sr isotopic signature. Ongoing $^{87/86}Sr$ analysis of several sites in the area of the fauna and plants will provide new data for this discussion.

Dogs in Human Contexts: The Rest of the Sites

The values of collagen and apatite in the dogs of the other sites are, in general, more negative than humans of the same sites, with mixed results at Cañada Saldaña (Figure 17). As observed in Cerro Lutz, the trophic level in dogs is lower than humans, with the exception of the Anahí site. This happened because the Anahí´s dog had the most carnivorous diet of all of them, and the only human analysed from this site had the highest incidence of plants in the whole region (see discussion in Loponte, Acosta, and Corriale 2016c). While there are no human values to compare for the La Yeguada site, the dog recovered there also has a low level of $\delta^{15}N$.

Oxygen values in all these dogs range between –2.33 ‰ and – 1.13 ‰ (Table 2), which are compatible with the Uruguay River ecozone and with the mixed fluvial waterfront of both rivers, including dogs from Anahí and Bellaca 2 sites, which are located in the Paraná River ecozone (see Table 2). This means that these last two specimens probably lived most of their lives in the ecozone of the Uruguay River and were moved to the Paraná river shortly before their death, given the null influence of its water in the oxygen values. This fact is reinforced by the $^{87}Sr/^{86}Sr$ values

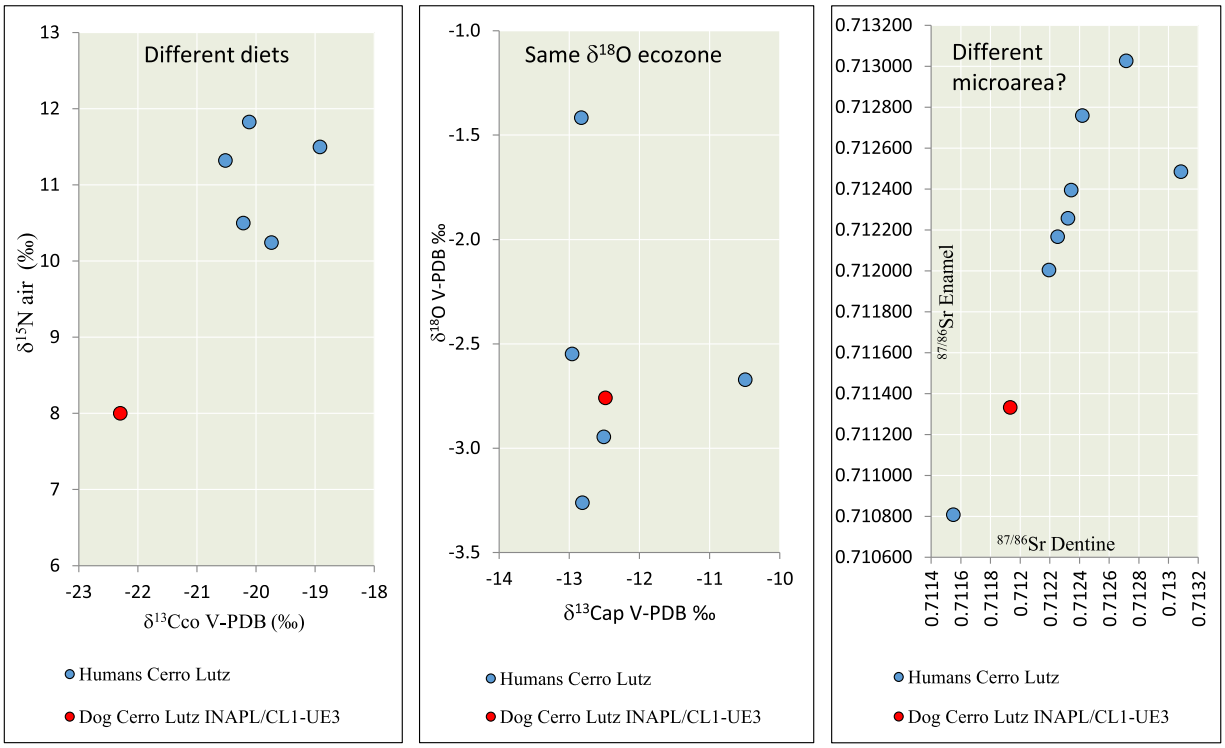

Figure 16. Isotopic values of dog INAPL/CL1-UE3 and humans from Cerro Lutz site. $\delta^{13}C$ (collagen and apatite) and $\delta^{15}N$ from humans taken from Loponte, Acosta, and Corriale (2016c). Values of $\delta^{18}O$ and $^{87/86}Sr$ this study.

in the dentin of the Anahí dog (0.711052) which differs only 0.000882 with the dentin of the dog of Cerro Lutz; whereas its enamel value of 0.711303 hardly differs by 0.000029 from that of the Cerro Lutz specimen. It is important to note that at Anahí, dog remains are only teeth, so that there is always the possibility that they have been subject to a post-morten exchange as blanks or pendants. This is not the case of the dog from La Bellaca site 2, where there are postcranial elements, and the analysis of $\delta^{18}O$ was performed on an axis (Table 2).

Genetics. DNA extraction and pre-amplification steps of all samples reported in this study were performed at the University of Tübingen. Data processing was performed using the bioinformatics tool Efficient Ancient

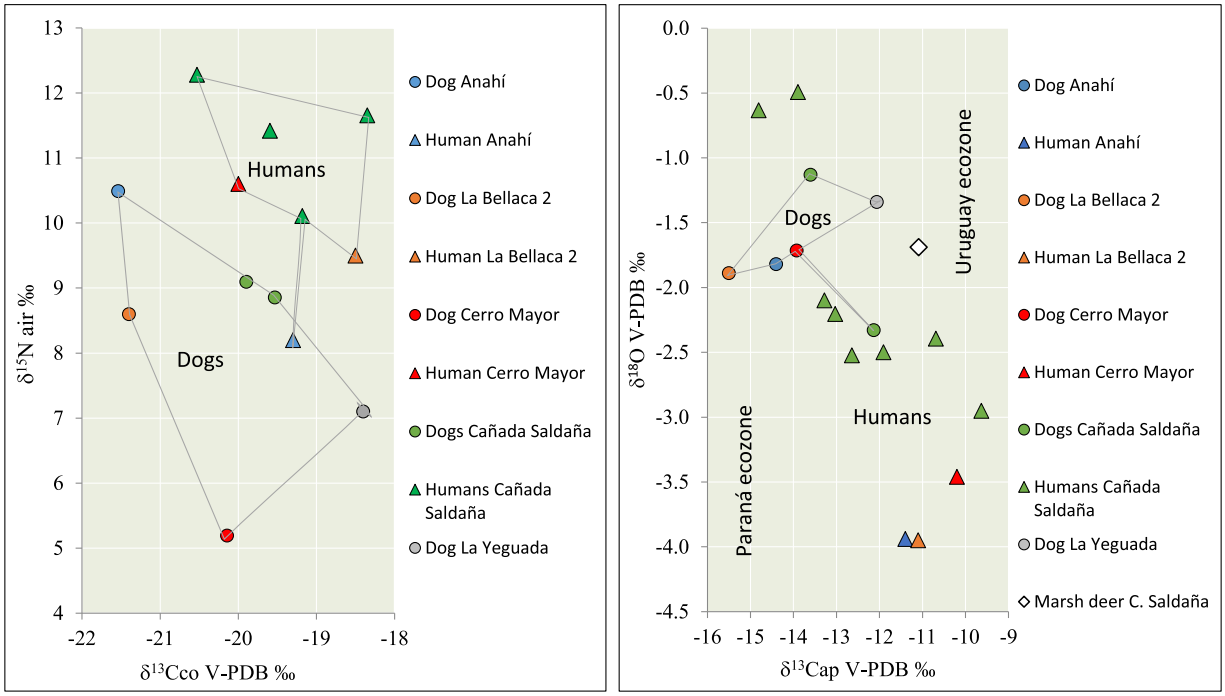

Figure 17. Human values correspond only to adult individuals ($\delta^{13}C$ collagen and apatite, and $\delta^{15}N$ values taken from Loponte, Acosta, and Corriale (2016c); $\delta^{18}O$ values of humans and all the Cañada Saldaña isotopic values, this study).

Genome Reconstruction (EAGER) pipeline (Peltzer et al. 2016). The quality of the sequencing data was shown by EAGER using the FastQC tool (Andrews 2010) and duplicate reads were removed, using Mark Duplicates v2.15.0 (Picard Tools), for read mapping against the reference genome (Peltzer et al. 2016). For demonstrating the authenticity of the ancient DNA reads the program MapDamage (Ginolhac et al. 2011) is integrated in the EAGER pipeline to estimate distribution and frequency of the deamination substitutions of DNA sequencing reads. The laboratory workflow and data processing are described in more detail in Supplemental information text 2. Due to poor DNA preservation, we were only able to reconstruct three almost complete mitochondrial genomes (Supplemental Table 3) out of seven analysed specimens (Supplementary Table 4). In our study we obtained a five-fold coverage higher than 90% for the specimens LB2-CF-1 (La Bellaca 2) and PSG-07 (Pontal da Barra) (Supplemental Table 4). For the specimen CS 49136 (Cañada Saldaña) we obtained a 1-fold coverage of around 70% (Supplemental Table 4). We reconstructed the mitochondrial genome of these three individuals and used them for further analysis.

Phylogenetic and F_{st}-analysis

Initially the reconstructed mitochondrial genomes with a 1-fold coverage of at least ~70% were aligned with 224 mitochondrial canid genomes (Thalmann et al. 2013; Frantz et al. 2016; Botigué et al. 2017; Ní Leathlobhair et al. 2018) by MAFFT (Katoh and Standley 2013). The multiple sequence alignment was then used for phylogenetic tree reconstruction to infer the relationships between the individual genomes. The phylogenetic tree was generated by IQ-TREE (Nguyen et al. 2014) using maximum likelihood approach with an estimation of 10,000 bootstrap. Regarding F_{st}-analysis, genetic variations between the three mitochondrial genomes presented in this study and previous published mitochondrial genomes (Thalmann et al. 2013; Frantz et al. 2016; Botigué et al. 2017; Ní Leathlobhair et al. 2018) were estimated (Supplemental Figures 1 and 2 and Supplemental Tables 5a, 5b, 6a, 6b) using F_{st}-analysis performed by Arlequin (Excoffier and Lischer 2010). To investigate the genetic variations between South-American, North-American, Eurasian ancient and modern dogs and wolves, the 224 previously published genomes (Thalmann et al. 2013; Frantz et al. 2016; Botigué et al. 2017; Ní Leathlobhair et al. 2018) used for the phylogenetic analysis and the newly reconstructed genomes were assigned to different population groups manually and the genetic variance was calculated (Supplemental Figure 1; Supplemental Tables 5a and 5b). These population groups are namely modern coyotes (mCoyotes), modern Eurasian wolves (mEA_Wolves), modern American Wolves (mA_Wolves), ancient Eurasian Wolves (aEA_Wolves), ancient North-American wolves (aNA_Wolves), modern Eurasian dogs (mEA_Dogs), modern North-American Dogs (mNA_Dogs), ancient Eurasian dogs (aEA_Dogs), pre-Columbian North-American dogs (PC_NA_Dogs), pre-Columbian South-American dogs (PC_SA_Dogs), and the pre-Columbian South-American dogs of this study (PC_SA_Dogs), defined by different population group sizes. Due to the small sample size of our studied pre-Columbian dog mitochondrial genomes, an additional F_{st}-analysis was performed for which the newly reconstructed genomes were grouped together with previous published ancient pre-Columbian dog genomes (Thalmann et al. 2013; Ní Leathlobhair et al. 2018) from South- and North-America, and named pre-Columbian American dogs (PC_A_Dogs). The population groups formed for this purpose are represented in Supplemental information Table 6a. All pairwise F_{st}-Analysis were performed with the following settings, number of permutations = 100, significance level (p-value) = 0.05 and gamma value = 0.

Due to the possibility, that F_{st} analysis is biased by a low sample size of the defined population groups, additionally the pairwise genetic distance of mitochondrial DNA sequences was calculated by MEGA X (Kumar et al. 2018). Analyses were conducted using the Tajima-Nei model (Tajima and Nei 1984), including all nucleotide substitutions. Ambiguous positions were excluded pairwise. The pairwise distance matrix was then visualised in a multidimensional scaling (MDS) plot using the *cmdscale* command in R (R Core Team 2013). For this purpose, the first two dimensions describing the dissimilarities between the sequences were calculated. Hence, the distance of the data points in the MDS plot are equal to the genetic distance of the samples.

In the phylogenetic tree, including all mitochondrial genomes of modern and ancient wolves and dogs published so far (Thalmann et al. 2013; Frantz et al. 2016; Botigué et al. 2017; Ní Leathlobhair et al. 2018), our three mitochondrial genomes (La Bellaca 2; Cañada Saldaña, and Pontal da Barra PSG-07) cluster with five previously published pre-Columbian South American dog mitochondrial genomes (Thalmann et al. 2013; Ní Leathlobhair et al. 2018) (Figure 17). Furthermore, all pre-Columbian South American dog mitochondrial genomes form a sub-branch with the other pre-Columbian mitochondrial genomes from America (Figure 18). This indicates a high genetic relatedness of pre-Columbian dog populations from North- and South America. All pre-Columbian dogs are located in a sister clade to modern dogs with the dog haplogroup A. Besides the pre-Columbian dogs and ancient European wolf genome, Switzerland_2 (Thalmann et al. 2013) is located basal to the clade of dog haplogroup A.

Regarding the Fst-analysis, the determination of the genetic variance between the single groups by the calculation of their *p*-values (Supplemental Tables 5b and 6b) is visualised in a pairwise distance matrix (Supplemental Figures 1 and 2). A high genetic differentiation of the pre-Columbian dogs and modern American dogs can be observed whereas the genetic distance of modern American dog population group and modern Eurasian dog population group is less but not significant. The group encompassing the pre-Columbian dogs has the smallest genetic distance to the group of ancient Eurasian dogs, but this value is also not significant.

For the estimation of the pairwise genetic distance of all mitochondrial genomes, the mitochondrial DNA sequences of the coyotes, two modern Chinese (China 1 and China 2) wolves as well as of one ancient North-American dog (ISM21C) were excluded. The four coyotes and the two modern Chinese wolves were excluded because all six specimens were either *C. lupus lupus or C. lupus familiaris*. The mitochondrial genome of the specimens ISM21C was excluded due to its close position to the coyotes in the phylogenetic tree (Figure 18) and missing background information about this sample. The average calculated pairwise distance of all mitochondrial DNA sequences is 0.00438. The genetic distances are visualised in an MDS plot (Supplemental Figure 4). In this plot our three pre-Columbian South-American dogs are clustering with the previous published pre-Columbian dogs' mitochondrial genomes.

Overall our results indicate a high genetic similarity of the pre-Columbian dogs on the maternal lineage. The maternal relatedness of all pre-Columbian dogs is demonstrated by the clustering of their mitochondrial genomes in the phylogenetic tree (Figure 18). This observation is also supported by the investigation of the genetic variance and distance of our dogs and

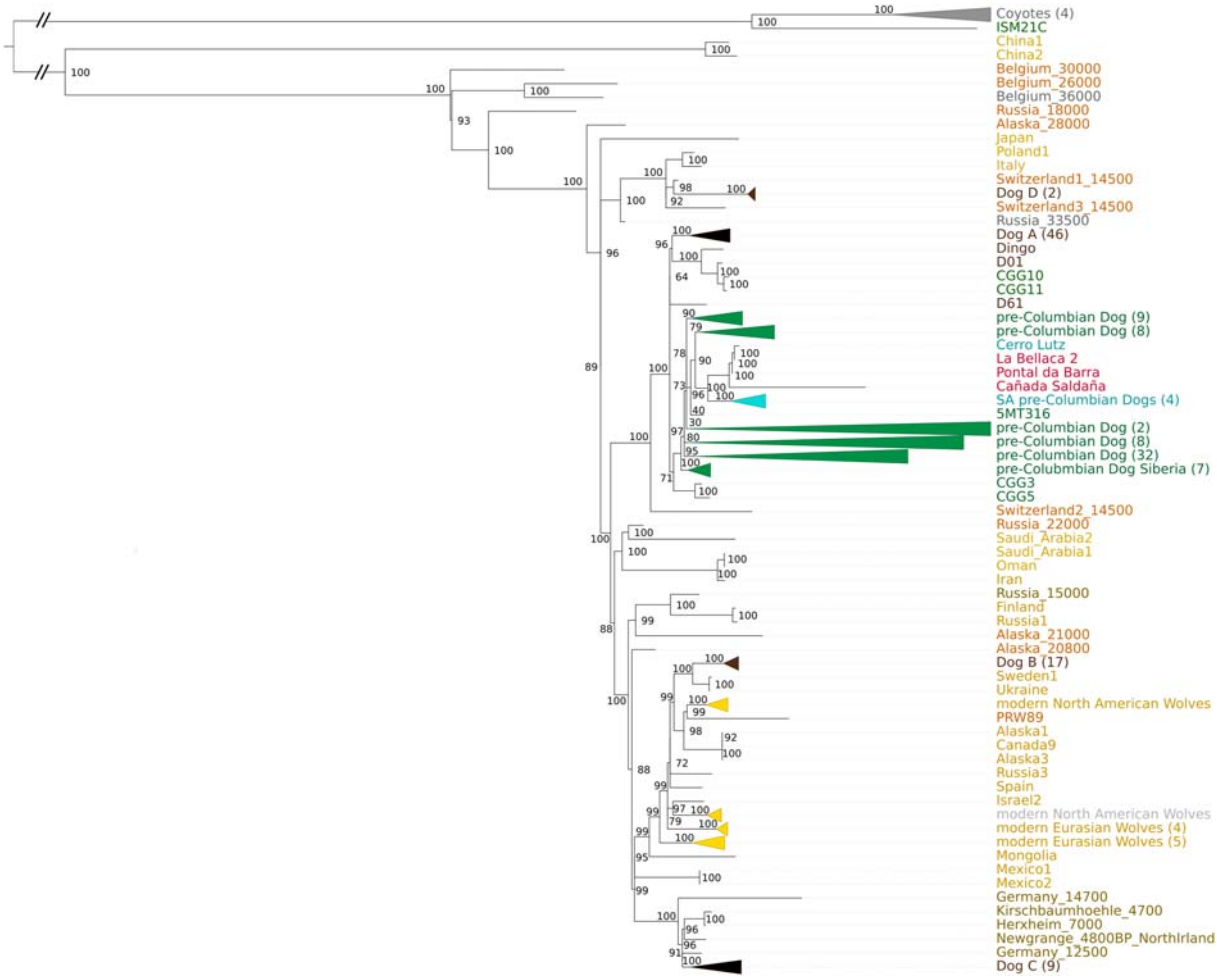

Figure 18. Phylogenetic tree. For visibility reasons, the branches containing only modern dog or wolf mitochondrial canid genomes are collapsed. Statistical support was evaluated with 10000 bootstrap steps and is indicated at each node. The colour patterns of the phylogenetic tree are the following: the mitochondrial genomes reconstructed in this study are represented in red, previous published South-American pre-Columbian dog genomes (Ní Leathlobhair et al. 2018; Thalmann et al. 2013;) are coloured in turquoise, all other pre-Columbian dog genomes (Ní Leathlobhair et al. 2018) are coloured in green. Previously published modern dog genomes are represented in dark brown, ancient dog genomes in olive-green, modern wolf genomes originated from previously published data are coloured in dark-yellow and the ancient wolf genomes are coloured in orange (Botigué et al. 2017; Frantz et al. 2016; Thalmann et al. 2013). Sequences coloured in grey are mitochondrial genomes from previous published study not clearly assigned to dog or wolf species (Thalmann et al. 2013).

previously published dogs from pre-Columbian South- and North America (Ní Leathlobhair et al. 2018; Thalmann et al. 2013). Calculating the genetic variance by F_{st}-analysis, these three population groups have a low calculated genetic distance estimated by the p-values (Supplemental Table 5b) compared to each other (Supplemental Figure 1). However, the *p*-values are not significant. The absence of significance can be explained by the low number of samples forming the population groups of the South-American pre-Columbian dogs. The sample of previous South American pre-Columbian dogs ($n = 5$) and the population group formed by our pre-Columbian dogs (sample size $n = 3$) are represented by less than six individuals. To exclude a potential bias caused by the low sample size, the genetic distance of all mitochondrial sequences was calculated and visualised in an MDS plot. In this plot the pre-Columbian dogs of our study show also minimal genetic distance to previously published pre-Columbian dogs from South- and North-America (Ní Leathlobhair et al. 2018; Thalmann et al. 2013) on the maternal lineage. Furthermore, the observed close maternal relationship between our pre-Columbian dogs and the pre-Columbian ones from previous studies (Ní Leathlobhair et al. 2018; Thalmann et al. 2013) demonstrated by the reconstruction of a phylogenetic, F_{st}-analysis and pairwise distance analysis is consistent with the suggestion of an autonomous pre-Columbian dog population in the Americas (Ní Leathlobhair et al. 2018; Thalmann et al. 2013). On the contrary, all pre-Columbian dog population groups have a higher genetic distance to all other modern-day canid population groups or ancient wolf populations as well as to ancient Eurasian dogs than the genetic distance between the pre-Columbian groups (Supplemental Figure 4, Supplemental Figures 1 and 2, Supplemental Tables 5b and 6b). In addition, the results show that the pre-Columbian dogs have less genetic distance to the Eurasian modern and ancient dog populations than to the modern American dogs. This result supports the hypothesis of an almost complete replacement of the autonomous pre-Columbian dog population starting with the arrival of European settlers in the fifteenth century, which was established by previous studies investigating the evolutionary history of American dogs by analysing haplotypes, mitochondrial and nuclear DNA (Ní Leathlobhair et al. 2018; Castroviejo-Fisher et al. 2011).

The clustering of pre-Columbian dogs and modern dogs of the haplogroup A in the phylogenetic tree (Figure 18) suggests a maternal relationship between both dog lineages, presumably resulting from shared common ancestry (see also Ní Leathlobhair et al. 2018; Thalmann et al. 2013). Thereby, our results further support the assumption that both dog lineages could be descendants of Eurasian canid populations, which probably migrated to the Americas together with the first hunter-gatherers, at least before the Bering land bridge was flooded (Ní Leathlobhair et al. 2018).

Conclusions and Perspectives

The archaeological record shows the presence of medium-sized dogs with mesocephalic skulls in the southeastern South America Lowlands from southern Brazil to the lower Paraná-Uruguay wetland from the III millennium BP. There is no evidence of bigger/smaller or brachycephalic/dolicocephalic dogs, nor with ectodermal dysplasia. The phenotypic reconstruction shows a remarkable homogeneity, which does not seem to result, at the moment, from a sampling defect, although we cannot rule out the existence of other morphotypes. If there were, they appear to have eluded identification for now.

The absence of pre-Columbian dogs in the southern Pampa (sector III of Figure 1), and in practically all of Patagonia, does also not seem to be the result of a sampling defect. Years of research with redundant results in zooarchaeological analyses of both areas suggest that the hunter-gatherers who inhabited these regions did not breed dogs before the sixteenth century, following in some way the observation of Hayden and Schulting (1997), which points out the more generalised absence of these mammals among simple hunter-gatherers, and their presence in complex hunter-gatherers. The rapid expansion of the dog of European pools in sector III (and also in sector IV and in much of Patagonia) could be related to the sudden ecological changes ensuing from the biological invasion of the exotic species. In less than two centuries, those simple hunter-gatherers were subjected to a remarkable process of social and economic complexity which included breeding horses, cattle and even the adoption of agricultural practices, with more or less close contact with the capitalist system of the Spanish empire (Mandrini 1992; Palermo 1988). On the opposite geographic border, in the Highlands of the Brazilian plateau (north of sector I of Figure 1), few archaeofaunal reports are available, but it is certainly an area of active archaeological research, and it is expected that in the medium term there will be new information to discuss if there was a continuous distribution of the dog from sector I (Figure 1) to the north.

The local morphotype of the lowlands identified in this study appears metrically similar to the Venegas Gutiérrez's Andean type 3 (and others related with it), although more research is required in this regard. These similarities quickly evoke the hypothesis of the exchange between the Andean area and the South eastern Lowlands, a trade system which included dogs, metals, and perhaps green rock beads (see above).

However, this hypothesis is less supported by the new facts. Processes such as point-to-point exchange can be ruled out, that is, from the Andes directly to the Lowlands of the lower Paraná and Uruguay rivers and south Brazil, which is a huge area. This type of exchange would have produced a broader record of Andean objects (pottery, raw materials, humans, etc.), which in fact did not happen. Moreover, green rock pendants are scarce, and metal objects definitively are extremely uncommon, nor is there any mention in the sixteenth century chronicles of direct trade with the Andean area, even for late moments. To explain some metal objects of undoubtedly Andean origin (and probably pendants of green rocks), it is more feasible to consider a slow flow process through successive stages of exchange in the geographic space that separates the Andes from the Lowlands as previously proposed. A second issue is that in this 'middle earth' of about 700 km from the Amaicha and Hualfin dogs (the closer findings on the northwest Argentina) to the Paraná wetland (Sector II of Figure 1), there is no record of dogs that supports the idea of transport of dogs from the Andean area. Although this may be a sampling defect, given that this intermediate sector is an extensive area with little archaeological information.

Isotopic evidence does not support a direct Andean exchange to explain the presence of the dogs. All the lowlands specimens included in Table 2, show no trace of maize consumption in the bones nor in the enamel of the canines and incisors that, although they erupt around the fourth month of life, begin to form before birth. Moreover, the $\delta^{18}O$ values obtained in the bones and teeth of these dogs suggest that they were locally bred, possibly in the ecozone that extends from the Uruguay River valley to the east, although other or multiple origins cannot be ruled out yet. While there are no extensive archaeological studies of $\delta^{18}O$ values in Northwest Argentina (see Dapeña and Panarello 2011), the meteoric water of that region is expected to be lighter due to the concurrence of both higher altitude and the continental effect (Dansgaard 1964; see some values in Dapeña and Panarello 2011). In addition to all these data contrary to the exchange hypothesis, it should be explained that, within all the phenotypic variability that we know of Andean dogs, including those from north-western Argentina (Belotti López de Medina 2017; Cabrera 1934; Zetti 1973), only one morphotype was introduced in the lowlands during ~2000 years (from ~2.5 ka to ~0.5 ka BP). Thus, although the Andean exchange hypothesis (or other origins) cannot be discarded (for instance, as neonates that did not average maize intake due to their short life cycle in the Andean zone, and were selected according to a particular morphotype destined for exchange), it remains for now as a weak explanation for the presence of the Lowlands dogs. In the semi-arid sector of central Argentina (sector IV of Figure 1), where the record of dogs is extremely scarce, their presence has also been related to exchange processes of long distances (Prates, Prevosti, and Berón 2010). However, more information is needed from the individual of this sector to include them in this discussion.

While metric similarity between Venegas Gutiérreźs Andean type 3 and Lowlands dogs cannot be ignored, this does not imply a direct relationship, since, for example, there are also notable similarities with some specimens recovered from archaic sites in North America (Darwent and Gilliland 2001; Perri et al. 2019; Walker, Morey, and Relethford 2005) (see also Thalmann et al. 2013). If we leave aside the Andean exchange, other options arise. One is that these dogs could represent a single founder population which arrived early, and successfully adapted to the plains of south-eastern south America, which predate or arose independently of the process of generation of morphological variability associated with Andean dogs. Whatever the process that generated a local single morphotype, these dogs could have been reproductively isolated from other South American forms, and have undergone endogamous reproduction since the middle of the third millennium BP at least. This process could, eventually, have led to an accumulation of deleterious alleles, loss of genetic diversity, and a reduction in the survival rate of the offspring (Donner et al. 2016; Keijser et al. 2018; Wiener et al. 2017; Wayne and vonHoldt 2012). In turn, this could have led to a population with low demographic density, generating an Allee effect (Fowler and Baker 1991; Stephens, Sutherland, and Freckleton 1999), where individuals do not mate because they fail to bond with other individuals of the same species, facilitating a fast replacement by European pools after the sixteenth century.

However, this view of a low demographic density may be influenced by an inadequate spatial coverage of the investigations, and bias in the faunal analysis. For example, the review of the La Yeguada and Cañada Saldaña collections, resulted in the identification of at least four dogs (Table 1). The increase in the sample analysed from the Cerro Lutz site facilitated the identification of a second specimen. Of thousands of mounds in eastern Uruguay, which seem to have a significant record of dogs, only around 15 have been excavated (Bracco and Duarte 2020), from which five dog specimens have been recovered; the sampling situation is not any better for the mounds of southern Brazil, where zooarchaeological analysis are still in an initial stage. Thus, the number of dogs recovered in these mounds in relation to the few that have been sampled and analysed, suggests that here they could be more prevalent. In the lower Paraná, the excavations and systematic analysis of faunal assemblages began timidly around the year 2005, and much later for the middle Paraná, all of them

with irregular intensity due to the fluctuations of financial resources.

Throughout the region, some dogs were buried in human mortuary areas. It is noteworthy that these specimens were buried complete or with high integrity. Their canines were not removed to make pendants, nor were their bones used to make instruments; on the contrary, care and interest were taken to bury complete bodies. This could reflect an affective relationship of humans with their dogs in the moment of the death of their pets, or because dogs were considered or socially conceived as humans (Viveiros de Castro 1998). However, other symbolic meanings could be involved. We have seen in the core area that in at least three cases of Uruguayan mounds (Cráneo Marcado, PST and probably CH2D01-II), dogs were directly associated with human burials, and probably the same happened in the case of INAPL/CL1-UE3. In sector IV of this study, outside the core area, the dog of Chenque 1 was recovered in a double human-dog burial. Thus, there seems to be a very close relationship between the deaths of humans and the deaths of these dogs, meaning a human induced death of dogs. The double burials could be associated with a human owner's death, or as accompaniment into an afterlife (Kretschmar 1938; Schwartz 1997). These eventual sacrifices could be related in some way to the almost complete absence of dogs >48 months in age (Supplemental Table 1). It should be noted that the number of human burials is much higher than the few dogs found. For instance, in Cerro Lutz, numerous mortuary structures have been recovered but only one dog burial was identified (Mazza and Loponte 2012). Therefore, it is worth asking why some individuals were buried with dogs and others were not. No mortuary objects clearly associated with these burials of the core area were found. Therefore, are these dogs reflecting the social status and representing in this way evidence of social inequality (*cf.* Hayden and Schulting 1997), which has up to now been elusive? Thus, one of the questions we must ask now is who are those humans buried with these dogs; this implies a new agenda of analysis of these individuals in particular (death profiles, diet, health, mobility, etc.), as well as other burials with bones of other associated species (Acosta and Mazza 2016).

Unlike the careful burials noted above, other dogs were subjected to post-mortem manipulation. The evidence of skull disarticulation observed at the La Bellaca 2 site could be related to the handling of parts of the dog for symbolic or technological purposes, consumption, or even with mortuary feasts (*cf.* Prentiss and Kuijt 2012). It should be noted that the byproduct made of a dog's femur at Cerro Lutz (Figure 12) probably indicate the use of the bones as blanks to produce tools or ornamental artefacts, and extend their temporal presence within the systemic contexts. These differences in human behaviour related with dead dogs indicate the complexity of the relationship between both, where affection, social status, and/or the symbolic meaning of some of them (hunting dogs, common pets, trade goods, etc.) should not be discarded (*cf.* Koster 2009).

The humans who lived with these dogs were complex hunter-gatherers intensifying environmental exploitation in the lower Paraná-Uruguay wetland (sector II, Figure 1). Most of the faunal resources probably were boiled to maximise the nutrient extraction, and discarded without soft tissues or marrow. This scenario suggests that the food rejected by humans may have been unavailable, leaving few options for dogs like hunting of small rodents (cf. Beisiegel and Ades 2002), or scavenging prey entrails (Montiel Ortega, Arias-Reyes, and Dickinson 2000), garbage, and direct consumption of C_3 vegetables, which would also help explain the most negative values in δ^{13} and the lower $\delta^{15}N$ in relation to humans. The dispersion of the isotopic values of their diets indicates, precisely, an opportunistic strategy and broad-spectrum diet. Therefore, the diet of these dogs does not reflect the human diet.

Regarding DNA results, combining our generated mitogenomes of pre-Columbian dogs from South-America with published canid mitogenomes, we were able to reinforce two hypothetical assumptions concerning the history of American dogs. First the phylogenetic analysis illustrates the maternal relatedness of pre-Columbian dog populations and modern dogs belonging to the haplogroup A, thus results support a possible common ancestry of both dog lineages (Ní Leathlobhair et al. 2018; Thalmann et al. 2013). Second, the pairwise distance analysis of present-day American dogs and pre-Columbian dogs estimates a high genetic distance between them, supporting the hypothesis of an almost complete replacement of the pre-Columbian dogs by other dog populations from Europe after the arrival of Columbus (Castroviejo-Fisher et al. 2011; Ní Leathlobhair et al. 2018;). Finally, the results of our study coincide with those obtained in research related to the evolutionary history of America dogs (Castroviejo-Fisher et al. 2011; Ní Leathlobhair et al. 2018; Thalmann et al. 2013).

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