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1 **Can we identify the Mexican hairless dog in the archaeological record?**

2 **Morphological and genetic insights from Tizayuca, Basin of Mexico**

3
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27 **Declaration of interest: The authors declare no conflicts of interests.**
28

29 **Abstract:** The Mexican Hairless dog, or Xoloitzcuintle, is a breed characterised by a
30 sparse hair coat and a severe oligodontia. This phenotype is a consequence of Canine
31 Ectodermal Dysplasia (CED) caused by a mutation on the FoxI3 autosomal gene. First
32 accounts of hairless dogs in Mexico are dated to the 16th century CE, according to the
33 historical record, but pre-Hispanic dog skeletons presenting missing and abnormally shaped
34 teeth have been interpreted as earlier evidence of hairless dogs. However, several questions
35 remain unanswered regarding the timing of apparition of this phenotype and its relationship
36 with modern hairless breeds. In this paper, we review the morphological characteristics of
37 potential hairless dogs and we apply ancient mitochondrial DNA analyses along with
38 radiocarbon dating to eight archaeological dog mandibles from Tizayuca, Basin of Mexico,
39 presenting anomalies that could be attributed to a CED. The archaeological dogs were dated
40 between 1620 and 370 years BP. Among these eight individuals, we identify four different
41 mitochondrial haplotypes including two novel haplotypes. The dogs from the Basin of Mexico
42 display a very high genetic diversity and continuity from the Classic to the Postclassic.
43 However, our attempt at amplifying the FoxI3 mutation was unsuccessful. Finally, we show
44 that some haplotypes are present in both archaeological dogs and modern hairless breeds,
45 perhaps reflecting their maternal ancestry.

46

47 **Keywords:** Mesoamerica; Xoloitzcuintle; Zooarchaeology; Domestication; Ancient DNA;
48 Canine Ectodermal Dysplasia; Radiocarbon Dating;

49

50 **Highlights**

- 51 - We studied the mitochondrial DNA from eight ancient Mexican dogs
- 52 - The dogs show dental anomalies usually associated with Canine Ectodermal Dysplasia
- 53 - Some haplotypes are present in both archaeological dogs and modern hairless breeds
- 54 - Mexican dogs display a high genetic diversity and continuity for ca. 1000 years

55

56

57

58 **1. Introduction**

59 While dog (*Canis familiaris*) domestication would have started during the Palaeolithic,
60 breed formation is a recent phenomenon that occurred mostly during the last 200 years (e.g.
61 Larson et al., 2012; Lindblad-Toh et al., 2005; Parker et al., 2017a; Vilà et al., 1997). Some
62 morphotypes were then genetically isolated by reproductive rules to enable the formalisation
63 of breed standards and many breeds that were thought to be of ancient origin (also called
64 primitive breeds) appear to be recent creations (Parker et al., 2004). In Latin America, the
65 Mexican Hairless Dog (also named Xoloitzcuintle) and the Peruvian Hairless Dog are
66 recognised by the World Canine Organisation (FCI) as “Primitive breeds” (<http://www.fci.be>,
67 Group 5 Section 6) although many questions remain unanswered regarding their antiquity
68 (Parker et al., 2017a; van Asch et al., 2013).

69 American dog populations have been created by two major migration events. The first one
70 occurred about 10,000 years ago when domesticated dogs were first introduced to the
71 continent following human migrations (Leonard et al., 2002; Ní Leathlobhair et al., 2018;
72 Witt et al., 2015). Then, about 500 years ago, European exploration and colonisation of
73 America lead to the introduction of numerous dogs from Western Europe and the progressive
74 vanishing of indigenous maternal lineages (Castroviejo-Fisher et al., 2011). However, some of
75 them may have survived among the modern breeds of American origin (van Asch et al.,
76 2013). Yet, these assertions are mostly based on modern genetic data with limited
77 contribution of archaeological evidence.

78 The Xoloitzcuintle is one of the Native American breeds with a long-running history. Its
79 first naturalistic description arises from the 16th century (Dibble and Anderson, 1975: 16;
80 Hernández, 1959). At the beginning of the 20th century, hairless dogs are still present in
81 Mexico, although they are uncommon (“The hairless dog,” 1917). The first standard of the
82 breed is established in 1956 from those residual populations (Blanco et al., 2008) and the

83 Xoloitzcuintle is definitively recognised by the FCI in 1961¹. The breed presents sparse or
84 absent hair coat along with a severe oligodontia and abnormally shaped teeth, both
85 consequences of Canine Ectodermal Dysplasia (CED) of autosomal dominant monogenic
86 inheritance caused by a mutation of the FoxI3 gene (Drögemüller et al., 2008; Kupczik et al.,
87 2017; Robinson, 1985). Whereas the dental anomalies were not mentioned by the 16th century
88 naturalists, Darwin (2008, p. 58) notices, by the first half of the 19th century, the correlation
89 between the absence of hair and absence of teeth.

90 Because skin and fur are usually not preserved, archaeologists have used oligodontia and
91 abnormally shaped teeth as an evidence for the presence of hairless dogs in pre-Hispanic sites,
92 along with iconographic depictions of wrinkled and naked dogs (Valadez Azúa et al., 2009;
93 Vásquez Sánchez et al., 2016, 2009). Dogs with missing premolars and teeth of simplified
94 form were identified as hairless dogs and a direct lineage between these and modern hairless
95 breeds has been claimed (Blanco et al., 2008; Valadez Azúa et al., 2013; Vásquez Sánchez et
96 al., 2016) (SI text 1). It is assumed that this morphotype appeared in Western Mexico at the
97 beginning of our era, the first ceramic representations of hairless dogs being found in the
98 region of Colima during the Preclassic (ca. 1500 BCE – 200 CE); from the 6th century CE,
99 they would have spread across Mesoamerica until reaching the Andean region during the 14th
100 century CE (Carot and Hers, 2016; Valadez Azúa et al., 2010, 2009; Vásquez Sánchez et al.,
101 2016) (Figure 1).

¹ <http://www.fci.be/en/nomenclature/XOLOITZCUINTLE-234.html>, consulted on the 21/01/2018.

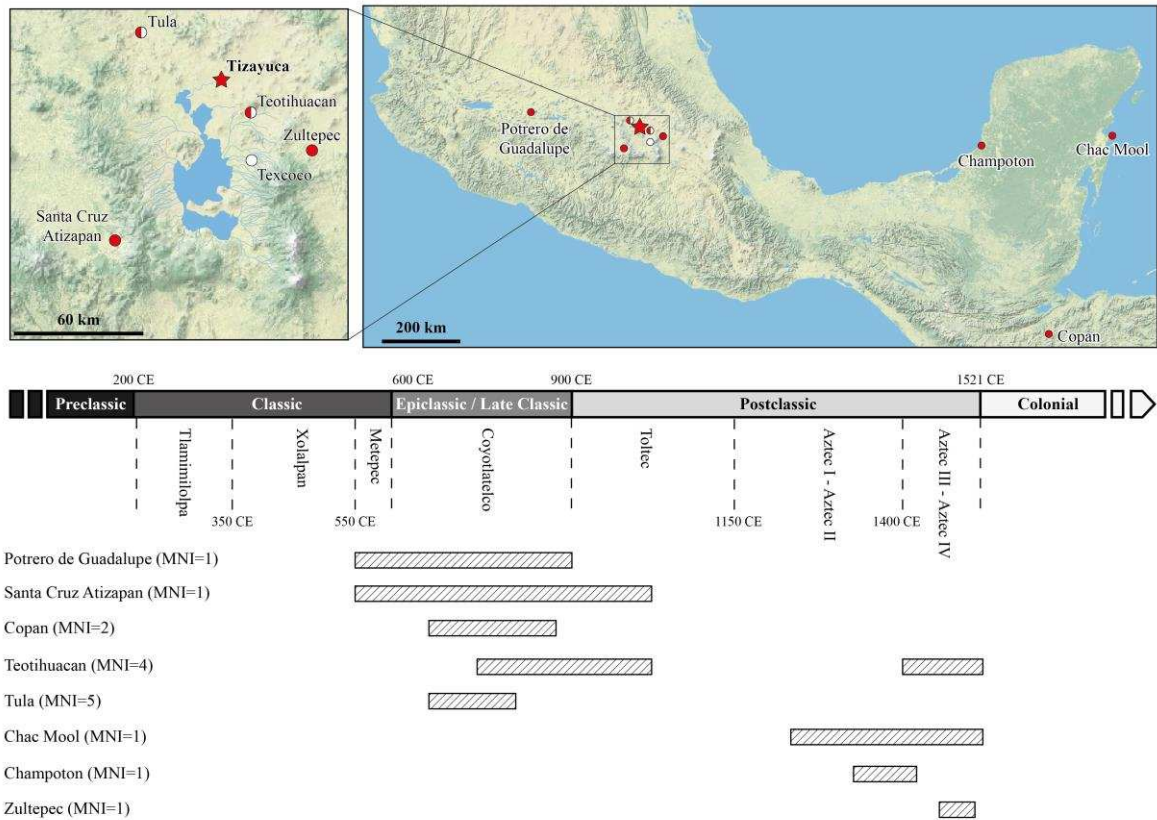


Figure 1 - Top: location of Tizayuca (red star) and other Mesoamerican sites that have yielded remains of dogs identified as hairless (red dots) and aDNA references (white dots). Bottom: chronology of the Basin of Mexico and distribution of the archaeological remains described as hairless dogs in Mesoamerica with the minimum number of individuals (MNI), according to Collins (2002) and Valadez et al. (2009).

113

114 However, no genetic study confirms the relationship between this archaeological
 115 morphotype and modern hairless breeds. Indeed, aDNA analyses of archaeological dogs are
 116 scarce in Latin America, with only 17 individuals published so far including one possible
 117 hairless dog from Tula, Hidalgo (Leonard et al., 2002; Ní Leathlobhair et al., 2018; Valadez et
 118 al., 2003) and past genetic diversity remains mainly unknown. Moreover, missing teeth have
 119 been observed in several modern dog breeds as well as in wild carnivores (Buchalczyk et al.,
 120 1981; Knyazev et al., 2003; Losey et al., 2014; Miles and Grigson, 1990; Szuma, 1999; Vilà
 121 et al., 1993), although there is no quantitative estimation of their proportion in the canine
 122 population (see SI text 1 for a discussion). Indeed, both a low selective pressure on the
 123 number of premolars and a high potential for evolutionary plasticity to diet change on the

124 molars could contribute to this variability (Asahara, 2013; Vilà et al., 1993). Therefore, the
125 identification of hairless dogs through their phenotype needs to be clarified and further
126 genetic analyses are essential to support affinity between modern hairless breeds and ancient
127 dogs. Finally, accurate dating of each sample is crucial to ascertain their origin and
128 chronological distribution.

129 Here we apply genetic analyses along with direct radiocarbon dating to eight
130 archaeological dogs from Central Mexico, which show dental anomalies that are similar with
131 modern hairless dogs (referred to here as a “hairless-like” phenotype). Our aims were to
132 clarify the origin of this phenotype and to document the past genetic diversity of dogs from
133 Central Mexico, testing for their relationship with modern breeds, in particular ones of
134 American origin.

135 **2. Material and methods**

136 *2.1. The archaeological site of Tizayuca*

137 All the archaeological elements analysed in this study come from three settlements of the
138 municipio of Tizayuca, Mexico, excavated between 2006 and 2010 (Equihua Manrique et al.,
139 2008). Architectural, lithic and ceramic elements from Tlamimilolpa, Xolalpan (both
140 associated to the Teotihuacan cultural complex), Toltec and Aztec phases as well as some
141 Colonial remains attest to the persistent occupation of the area from the 3rd to the 16th century
142 CE (Figure 1). Located in the vicinity of the powerful settlements of Teotihuacan, Tula and
143 Mexico-Tenochtitlan, the area of Tizayuca would have been under their direct influence.
144 However, the stratigraphy is highly disturbed and prevented a clear chronological attribution
145 of the ecofacts (Equihua Manrique et al., 2008).

146 The archaeological area of Tizayuca yielded a total of 3,327 vertebrate remains, from
147 which more than 25% have been attributed to *Canis* sp. (number of identified specimens,
148 NISP = 877). Osteological identification between dog, Mexican wolf (*Canis lupus baileyi*)
149 and coyote (*Canis latrans*) was based on morphological and morphometrical criteria (Blanco
150 Padilla et al., 2009; Lawrence and Bossert, 1967). Measurements were taken following von
151 den Driesch (1976) and ruled out the presence of wild canids in several cases (SI Text 1). We
152 identified at least six juveniles (neonatal to 6 months; Hilson, 2005) and 36 adults (> 7
153 months; Hilson, 2005), exceeding the presence of any other animal. Canids are followed by
154 leporids (*Sylvilagus* spp., *Lepus* spp., NISP = 271), turkey (*Meleagris gallopavo*, NISP = 144)
155 and large artiodactyls (*Odocoileus virginianus*, *O. hemionus*, cf. *Ovis canadensis*, NISP = 130)
156 (Manin and Lefèvre, 2015). Four dogs (three adults and a juvenile) have been deliberately
157 buried, either as connected or rearranged skeletons, and we also recovered a canine ornament
158 and a tool made from a canid bone. Moreover, burning and butchering marks suggest the
159 consumption of dog meat. These different elements show the importance of dogs to the
160 inhabitants of Tizayuca in both ritual and economic spheres, as was the case in many
161 American cultures (Schwartz, 1997).

162 *2.2. Canid sampling*

163 Among the 36 unpaired canid adult mandibles, several dental anomalies were observed in
164 the premolar row (NISP = 11). The absence of the first premolar (NISP = 3) has been
165 described in many American dog specimens – archaeological and contemporaneous – and is
166 not specifically related to hairless dogs (Allen, 1920: 439; Miles and Grigson, 1990).
167 However, other anomalies have been regularly described as characteristics of hairless dogs
168 (Grouard et al., 2013; Urbano Torrico, 2008; Valadez Azúa, 1995), in particular missing 2nd to
169 4th premolar and abnormal shape (see criteria in SI Text 1). The eight dog mandibles carrying

177 these anomalies (representing 22% of the dog population in Tizayuca) were selected for
178 further investigation (Table 1; Figure 2). In order to perform radiometric and molecular
179 analyses, sections of about 1 cm x 3 cm were opened in the body of each mandible with an
180 electric saw to take samples for aDNA (0.8 – 2.34 g) and collagen extraction (0.6 – 2.13 g).
181 To avoid contaminations, the saw and the working space were bleached between each
182 sampling and a new blade has been used.

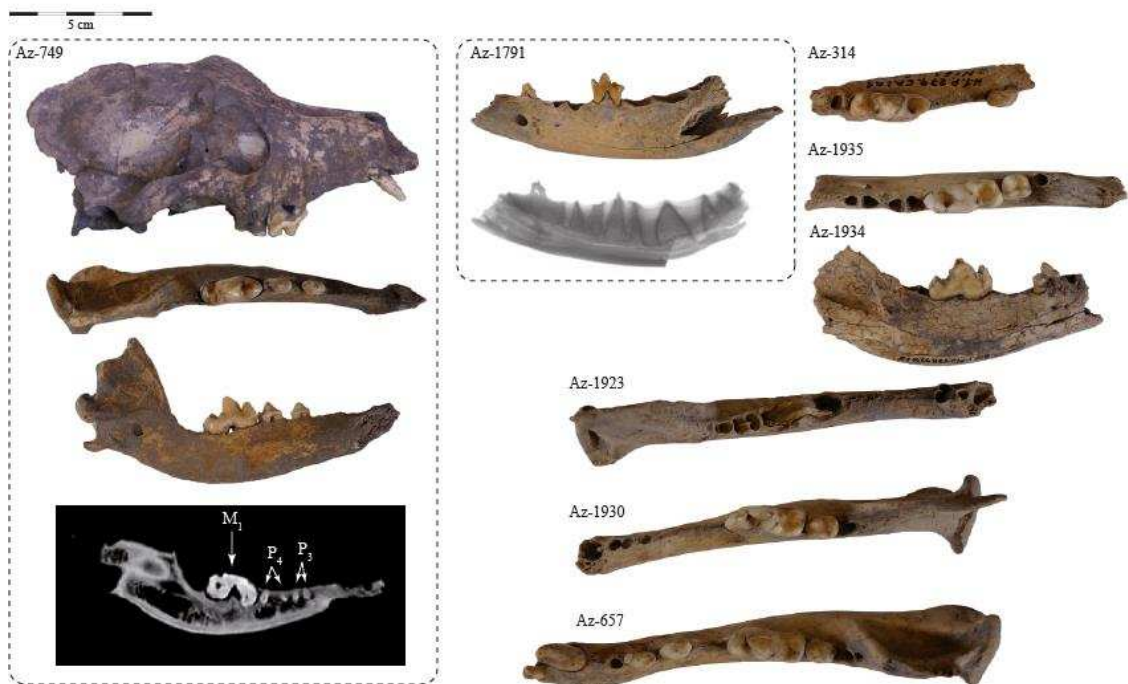


Figure 2 – Illustration of the eight archaeological individuals analysed in this study, including computed tomography (Az-749) and X-ray (Az-1791) images.

183

ID	Dental anomalies
Az-314	P ₄ absent
Az-657	P ₄ absent, supernumerary M ₃
Az-749	Only presence of P ₃ , P ₄ , M ₁ ; P ₁ abnormally shaped
Az-1791	Persistence of dp ₂ (or dp ₃) and dp ₄ on adult specimen
Az-1923	P ₃ and P ₄ absent
Az-1930	P ₃ and P ₄ absent
Az-1934	P ₄ absent
Az-1935	P ₂ absent

Table 1: List of dental anomalies observed on the selected mandibles. P = premolar, M = molar, dp = deciduous premolar.

184 *2.3. Radiocarbon dating*

185 Bone collagen from the eight samples was extracted in the Museum national d’Histoire
186 naturelle of Paris (France) and dated using the compact AMS ECHoMICADAS at Gif-sur-
187 Yvette following the method outlined in SI Text 1. All the samples provided acceptable
188 collagen yield [$>1\%$, (Ambrose, 1990)].

189 *2.4. Ancient DNA analyses*

190 All the aDNA extraction and analyses were carried out in the Palgene facility at the Ecole
191 Normale Supérieure of Lyon (France) with tools dedicated to aDNA and strict protocols of
192 decontamination and control. Ancient DNA was extracted following a silica based method
193 (Bastian et al., 2018, see also method outlined in SI Text 1). DNA of the eight samples has
194 been retrieved in two batches consisting of four Mesoamerican dogs, a fish vertebra that was
195 used as cross-contaminant and a blank extraction to rule out aerosol and reagent
196 contaminations.

197 We used two pairs of published PCR primers (Leonard et al., 2002) to target two
198 overlapping fragments of Canis mtDNA control region (CR) producing a 173 bp fragment
199 (position 15515-15687 on the complete mitogenome, Kim et al., 1998). This fragment was
200 chosen as it was short enough to be retrieved even in highly degraded samples, and allows

201 enough resolution for haplogroup attribution (Frantz et al., 2016), detection of the Latin
202 American clade 1a (Leonard et al., 2002) and individualisation of the American private
203 haplotype A185 (van Asch et al., 2013). Positive amplicons were sequenced on a Ion PGM
204 System (Ion Torrent, Thermofisher).

205 The sequences were visualised and aligned using Seaview software v.4.6 (Gouy et al.,
206 2010) and the MUSCLE algorithm (Edgar, 2004). Authentic sequences were determined by
207 analysing the reads obtained for each product (218 to 157,669 reads per amplicon) and by
208 considering three independent amplifications for each gene and sample. New SNPs were
209 confirmed by their presence in more than 50% of the reads. Haplotypes were compared
210 through the NCBI BLAST (<https://blast.ncbi.nlm.nih.gov>) to identify matching sequences.
211 Novel haplotypes were described following the recommendations from Pereira et al. (2004).
212 Briefly, the sequences were aligned to the reference genome (Kim et al., 1998) and the
213 position of the polymorphisms was listed unambiguously from this alignment. Position
214 numbers without superscripts denote transitions (e.g., A to G or C to T) whereas other base
215 changes are explicitly indicated.

216 The sequences produced in this study were then compared to 339 published sequences
217 (Table S1) from American archaeological dogs (Ames et al., 2015; Barta, 2006; Brown et al.,
218 2013; Kemp et al., 2017; Leonard et al., 2002; Thalmann et al., 2013; Witt et al., 2015),
219 American dogs of indigenous origin (Castroviejo-Fisher et al., 2011) selected according to
220 van Asch et al. (2013) and modern dogs from four breeds of presumed American origin:
221 Carolina Dog, Chihuahua, Xoloitzcuintle and Peruvian Hairless Dog (van Asch et al., 2013;
222 Vilà et al., 1999). Multiple alignments of these sequences, number of segregating sites (S),
223 haplotype diversity (H_d), nucleotide diversity (π), Watterson's estimator per sequence (θ_w)
224 and Tajima's D test were assessed using DnaSP v.5.10 (Librado and Rozas, 2009). Analysis
225 of molecular variance (AMOVA) and pairwise F_{ST} population comparison (using the

226 Reynold's distance and Jukes and Cantor computation of the distance matrix, with a threshold
227 of 0.05) were implemented in Arlequin v.3.5.2.2 (Excoffier et al., 1992; Excoffier and
228 Lischer, 2010). Relationships between the sequences were visualised by constructing
229 phylogenetic trees and median-joining networks (Bandelt et al., 1999).

230 In order to evaluate past diversity of American dogs, ancient sequences were grouped in
231 six regions according to cultural similarities and geographic proximity: Alaska, North Pacific
232 Coast, Illinois, Florida, American South West, Mesoamerica and South America. Overall
233 archaeological diversity was also compared to modern diversity in the selected sample.

234 *2.5. Modern DNA analyses*

235 In order to amplify the mutation on the first exon of the FoxI3 gene responsible for the
236 hairless phenotype in modern hairless breeds, we designed a pair of PCR primers targeting a
237 58-65 bp fragment including the 7 bp duplication previously described (Drögemüller et al.,
238 2008). Modern DNA of different breeds (including hairless and coated ones) was obtained
239 through the Antagene laboratory (France). Amplifications were carried out following the
240 protocol outlined in SI Text 1 §6 and positive amplicons were sequenced on a Ion PGM
241 System (Ion Torrent, Thermofisher). The sequences (0 to 175 reads per amplicon) were
242 visualised and aligned to the first exon of the FoxI3 gene using MUSCLE (Edgar, 2004)
243 through Seaview software v.4.6 (Gouy et al., 2010). However, none of them matched the
244 targeted sequence (see detailed results in SI Text 1 §6).

245 **3. Results**

246 *3.1. Morphological description of the archaeological dogs*

247 From the eight individuals selected for this study (Table 1; Figure 2), seven are isolated
248 mandibles, often fragmented, limiting the reconstitution of the morphotype. The last one (Az-
249 749) is a complete dog that was buried in a Teotihuacan compound (Tlamimilolpa or
250 Xolalpan phase), allowing a more accurate description of the animal.

251 In Az-749, incisors and canines are missing, but remodelled bone indicates the teeth were
252 lost during the life of the animal. This scar tissue is not present at the location of the P₁, P₂,
253 M₂ and M₃, however, suggesting an agnosis of these dental pieces. The M₁ is present but it
254 displays a reduced talonid. All these anomalies were observed on both left and right
255 mandibles. Computed tomography scanning showed the absence of dental bud inside the
256 mandible. On the skull, only the canine, P⁴ and M¹ are present on both sides but remodelled
257 bone on the dentary indicates the incisors were lost. P¹, P² and P³ would have never erupted,
258 considering the absence of scar tissue. The canines are thin and slightly curved and the P⁴
259 misses the protocone on both left and right side (Figure 2). Overall, the dog was of medium
260 size, with an estimated shoulder height of 36 to 40 cm (Harcourt, 1974) (Table S2). The
261 presence of a baculum indicates it was a male that died after 6 years according to the pelvis
262 suture (Barone, 1976; Piérard, 1967).

263 Az-1791 shows the presence of deciduous dp₄ and dp₂ (or dp₃) simultaneously with the
264 alveoli of fully erupted P₃ (or P₄) and M₁. X-ray images indicate the dental buds of the
265 missing permanent premolars never developed (Figure 2). Both Az-1923 and Az-1930 show
266 missing P₃ and P₄ while all the other teeth are present, in particular the P₁ and M₃. On Az-
267 1935, there is no P₂ and despite the breakage pattern it seems P₁ is also missing. P₄ is also
268 missing on Az-657 but two alveolar cavities behind the M₂ suggest an uncommon M₃ with
269 two roots or a supernumerary molar. Finally, Az-314 and Az-1934 show missing P₄ but the
270 fragmentation limits further observations.

271 *3.2. Chronology*

272 The radiocarbon dates of the eight samples range from the 4th-6th c. CE to the 15th-17th c.
 273 CE. This age range matches the archaeological occupation of Tizayuca, even for the elements
 274 found in superficial or disturbed layers (Table 2; Figure 3). The oldest sample (Az-749) is
 275 dated from the Classic Period (phase Xolalpan) and is consistent with the context of its
 276 discovery, in an architectural complex strongly influenced by the Teotihuacan culture. Four
 277 specimens cluster in an Epiclassic – Early Postclassic group and three specimens in a Late
 278 Postclassic one. The two more recent samples (Az-1923 and Az-1930) could also pertain to
 279 the Colonial period, albeit with a reduced probability.

Lab ID	Sample	¹⁴ C age (year BP)	Calibrated age (2σ) ^a	Chronological period
ECHo-1528	Az-749	1620 ± 25	386 – 536 CE	Classic
ECHo-1236	Az-657	1170 ± 25	772 – 951 CE	Epiclassic – Early Postclassic
ECHo-1242	Az-1935	1170 ± 25	772 – 951 CE	Epiclassic – Early Postclassic
ECHo-1241	Az-1934	1135 ± 25	777 – 984 CE	Epiclassic – Early Postclassic
ECHo-1235	Az-314	1080 ± 25	895 – 1018 CE	Early postclassic
ECHo-1238	Az-1791	545 ± 25	1318 – 1432 CE	Late Postclassic
ECHo-1240	Az-1930	400 ± 25	1439 – 1619 CE	Late Postclassic – Colonial
ECHo-1239	Az-1923	370 ± 25	1449 – 1631 CE	Late Postclassic – Colonial

Table 2: Results of the radiocarbon dating. ^a Calibrated ages were obtained using the OxCal online program v4.2.4 (Bronk Ramsey, 1994) and the IntCal 13 calibration curve.

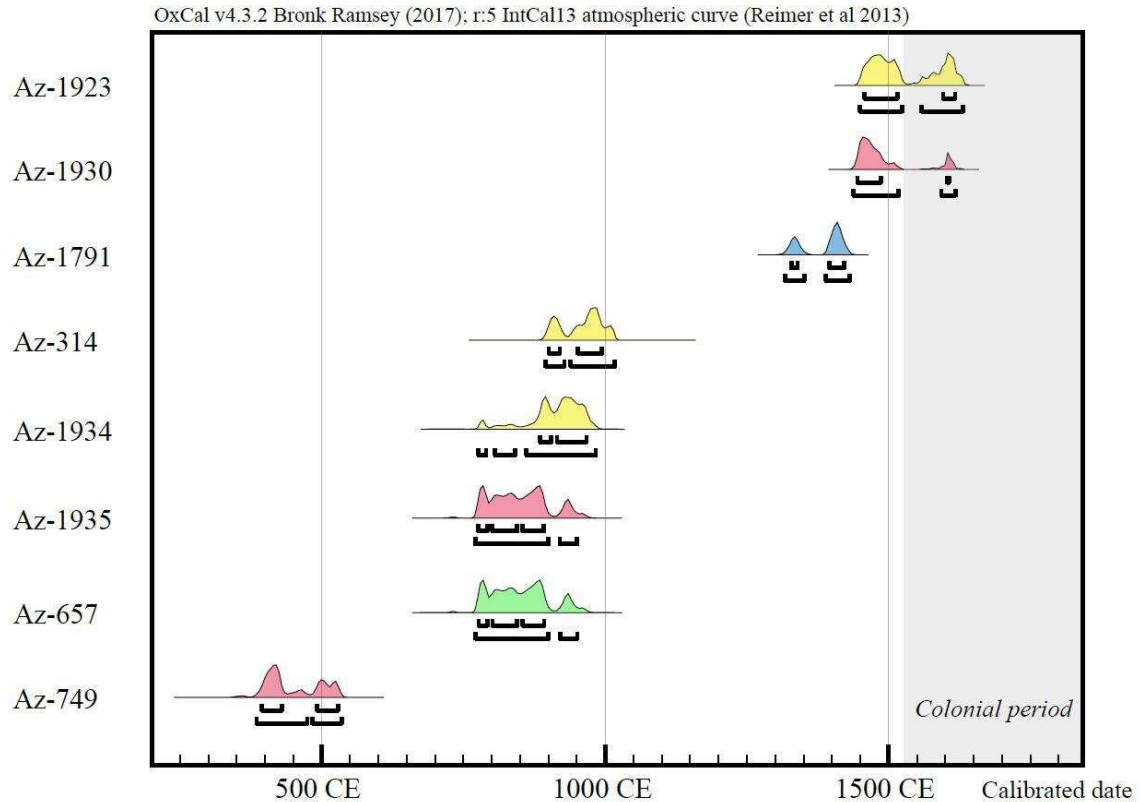


Figure 3: Chronological distribution of the samples with the representation of the haplotypes involved. Age probability is presented with 1 and 2 σ . Calibration was obtained using the OxCal online program v4.2.4 (Bronk Ramsey, 1994) and the IntCal 13 calibration curve. Haplotypes are coloured as follow: red = Xol-H1; green = Xol-H2; Yellow = A11-15-65; blue = A165 (see colours in online version).

Lab ID	Sample	Haplotype	GenBank accession match	Novel haplotype definition
1618	Az-1791	A176	KF002258.1	
1619	Az-1923	A11-15-65	KT321361.1	
1620	Az-1934	A11-15-65	KT321361.1	
1621	Az-1935	(Xol-H1)		15621 15639 ^{T/A} 15651
1622	Az-749	(Xol-H1)		15621 15639 ^{T/A} 15651
1623	Az-1930	(Xol-H1)		15621 15639 ^{T/A} 15651
1624	Az-314	A11-15-65	KT321361.1	
1625	Az-657	(Xol-H2)		15633 15639 ^{T/A}

Table 3 – Results of the mitochondrial aDNA amplification (173 bp fragment of the DLoop). Haplotype names are given after Angleby et al. (2014); when multiple entries were matching identically on GenBank, one only has been given. Novel haplotypes are defined according to Pereira et al. (2004), based on Kim et al. (1998) dog complete mitochondrial genome.

281 The eight specimens analysed yielded positive amplification of the 173 bp targeted in this
282 study, allowing the identification of four different sequences. Comparison with the NCBI
283 standard nucleotide BLAST for highly similar sequences indicates two corresponding
284 sequences and two novel haplotypes: Xol-H1 and Xol-H2 (Table 3). All the sequences have
285 been submitted to GenBank under accession number MH175494-MH175501.

286

287 Three individuals carry a sequence identical to haplotypes A11, A15 and A65 on the
288 targeted 173 bp (Angleby et al., 2014). While A15 and A65 are rare, A11 is a Universal Type
289 (UT) highly frequent in all dog populations (Angleby et al., 2014; Pang et al., 2009; van Asch
290 et al., 2013). One dog carries a sequence identical to haplotype A176, which has only been
291 recognised in a Swedish Dalmatian so far (Angleby et al., 2014), but varies from A11-15-65
292 of only one mutation on the sequence considered here (T>C, position 15650 on the complete
293 mitogenome, Kim et al., 1998). One novel haplotype (Xol-H1), shared by three archaeological
294 dogs widely separated in time, varies from haplotype A185 (van Asch et al., 2013) by one
295 substitution (C>T, position 15651 on the complete mitogenome, Kim et al., 1998). Haplotype
296 A185 has been considered as a Private Type (PT), only found in the modern Chihuahua breed,
297 and identical sequences have been found in ancient dogs from Central Mexico and North-
298 western America (Ames et al., 2015; Barta, 2006; Leonard et al., 2002). The second novel
299 haplotype (Xol-H2), found in one archaeological dog, differs from A11-15-65 by one
300 substitution (T>C, position 15633 of the complete mitogenome, Kim et al., 1998).

301 Relationships between these archaeological dogs and other American dogs (both modern
302 and ancient) are illustrated on a median-joining network (Figure 4). The four sequences
303 obtained in this study cluster in Haplogroup A, the most diverse and the most common in
304 ancient American dogs (Thalmann et al., 2013), but none cluster with clade 1a, described by

305 Leonard et al. (2002) as characteristic from Latin America. Xol-H1 is also closely related with
 306 a haplotype carried by modern indigenous dogs from Yucatán (Castroviejo-Fisher et al.,
 307 2011) and an ancient Mesoamerican dog from Texcoco (Leonard et al., 2002).

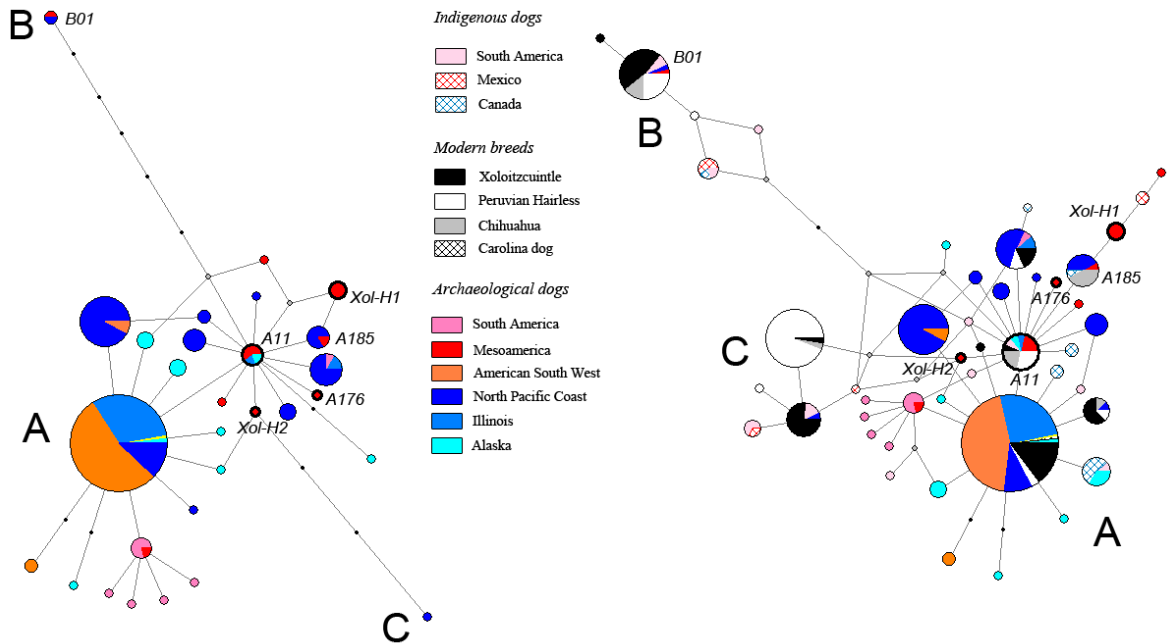


Figure 4 – Median-joining networks displaying the relationships between the obtained sequences (bold circles) and existing archaeological sequences (left; data from Ames et al, 2015; Barta, 2006; Brown et al, 2006; Kemp et al., 2017; Leonard et al., 2002; Witt et al., 2015), with the addition of modern sequences (right; data from van Asch et al., 2013; Castroviejo et al, 2011; Vilà et al. 1999); see colours in online version. Comparative sequences were truncated to the 173 bp analysed in this paper.

308 3.4. Genetic diversity in the Basin of Mexico

309 All four haplotypes identified here are different from the five haplotypes previously
 310 described in archaeological dogs from the Basin of Mexico (Leonard et al., 2002). No other
 311 comparative Mesoamerican samples are available yet, but data from other regions in America
 312 enable large-scale comparison of genetic diversity. We used a set of 339 published
 313 comparative sequences of ancient and modern dogs (Table 4) to perform diversity tests. All
 314 the sequences have been truncated to match the 173 bp fragment targeted in this study.

315 Most of the published ancient American dogs belong to Haplogroup A, but three
 316 individuals belong to Haplogroups B and C. Clade B encompasses one dog from Tula
 317 (Mexico), previously identified as a hairless dog (Valadez et al., 2003), and one dog from
 318 Gaadu Din Cave (British Columbia, Canada) with no specific dental anomalies reported
 319 (Barta, 2006). The last one, in Namu (British Columbia, Canada), pertains to clade C (Barta,
 320 2006).

321 The genetic variation in archaeological and modern dogs is presented in Table 4. The
 322 haplotype diversity H_d is strongly correlated with the nucleotide diversity π ($r = 0.80$, $p =$
 323 0.011) and the Watterson's estimator θ_w ($r = 0.80$, $p = 0.010$), denoting a similar trend
 324 between these different indices. However, and although sample sizes are very dissimilar, none
 325 of these metrics correlate with the number of individuals in each group ($p > 0.05$), indicating
 326 that the diversity observed here is not driven by the sample size and enabling regional
 327 comparisons.

Group	n	S	h	Hd (σ)	π (σ)	θ_w (σ)
TOTAL	347	34	46	0.85 (0.02)	0.0192 (0.00094)	5.29 (2.12)
Modern	153	21	25	0.89 (0.01)	0.0255 (0.00095)	3.75 (1.15)
Archaeological	194	30	29	0.71 (0.71)	0.0087 (0.00083)	5.14 (1.43)
Alaska	13	9	8	0.91 (0.06)	0.0114 (0.00205)	2.90 (1.70)
Illinois	34	2	3	0.17 (0.08)	0.0016 (0.00084)	0.49 (0.36)
North Pacific	66	16	11	0.80 (0.04)	0.0116 (0.00137)	3.36 (1.19)
American SW	58	3	3	0.13 (0.06)	0.0012 (0.00057)	0.65 (0.40)
Mesoamerica	13	14	9	0.92 (0.06)	0.0168 (0.00469)	4.51 (2.02)
South America	9	7	6	0.83 (0.13)	0.0090 (0.00283)	2.58 (1.39)

Table 4 – Measure of genetic diversity among the 347 dogs compared in this study, for a 173 bp sequence of the CR: number of individuals (n), number of segregating sites (S), number of different haplotypes (h), haplotype diversity (H_d), nucleotide diversity (π) and Watterson's estimator (θ_w) with associated standard deviation (σ). Mesoamerican dogs (this study, Leonard et al., 2002) are compared to Alaska (Brown, 2006; Leonard et al., 2002), Illinois (Thalmann et al., 2013; Witt et al., 2015), North Pacific Coast (Barta, 2006; Ames et al., 2015), American South West (Kemp et al., 2017; Witt et al., 2015) and South American (Leonard et al., 2002, Thalmann et al., 2013) archaeological populations, and with modern dogs of American origin (indigenous and pure breed, van Asch et al., 2013; Castroviejo et al, 2011; Vilà et al. 1999). One archaeological dog from Florida (Thalmann et al., 2013) is also included in the archaeological group.

328 Among archaeological samples, those from Mesoamerica show the highest diversity ($H_d =$
 329 0.92 ; $\pi = 0.0168$; $\theta_w = 4.51$). Conversely, ancient dogs from Illinois (Thalmann et al., 2013;
 330 Witt et al., 2015) and from the American South West (Kemp et al., 2017) present an

331 extremely reduced genetic variability ($H_d = 0.17, 0.13$; $\pi = 0.0016, 0.0012$; $\theta_w = 0.49, 0.65$;
332 respectively).

333 An AMOVA performed on archaeological dogs from the different regions indicates that
334 the variation within each population accounts for 74 % of the total variation observed in the
335 sample (Table S4). Conversely, the variation between populations only accounts for 26 % of
336 the variation. F_{ST} pairwise population comparison shows the South American dog population
337 is more closely related to the Mesoamerican population than to the other groups (Figure 5,
338 Table S5).

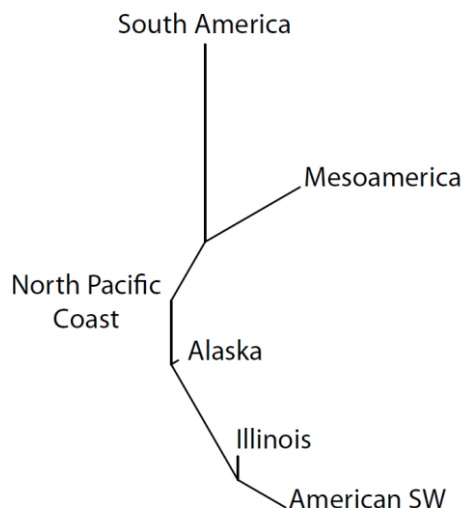


Figure 5 – Unrooted neighbour-joining tree of the F_{ST} pairwise distances showing the relationship between the archaeological populations. Groups follow Table 6.

339 4. Discussion

340 4.1. Origin of the “hairless-like” phenotype and presence of hairless dogs in the 341 Teotihuacan cultural area

342 Direct radiocarbon dating of the eight dogs analysed in this study enable us to clarify their
343 origin. A complete skeleton of hairless-like dog from Tizayuca – Las Golondrinas (Az-749),

344 dated from the Xolalpan phase (350-550 AD) slightly predates former evidence related to
345 Late Classic / Epiclassic in Western Mexico (Rodríguez Galicia et al., 2001), Central Mexico,
346 (Valadez Azúa and Rodríguez Galicia, 2009) or Honduras (Collins, 2002). The settlement of
347 Las Golondrinas would have had direct contacts with the city of Teotihuacan, visible through
348 the architecture (concrete floors and stucco finishing), funerary practices or lithic and ceramic
349 productions, suggesting it was an enclave of the metropolis (Equihua Manrique et al., 2008).

350 The presence of hairless dogs in the city of Teotihuacan has also been suggested through
351 the identification of local Classic zoomorphic effigy pots representing dogs with naked skin
352 (Carot and Hers, 2016). Mesoamerican iconography has often been interpreted in naturalistic
353 terms (e.g. de la Garza, 1995; Saunders, 1994; Seler, 1996; Sharpe, 2014; Stocker et al., 1980)
354 and therefore the identification of ancient dog breeds has often been suggested based on
355 ceramic representations (Guzmán and Arroyo Cabrales, 2014). However, no other skeletal
356 remains of “hairless-like” phenotype has been found yet in the Classic occupation of
357 Teotihuacan, despite extensive investigations (Manzanilla and Valadez Azúa, 2009; Valadez
358 Azúa et al., 2013).

359 *4.2. Genetic diversity in the Basin of Mexico*

360 Results from the analysis of a 173 bp fragment of dog CR show the presence of four
361 different haplotypes in Tizayuca, two of them being present in more than one individual.
362 Regarding their chronological repartition (Figure 3), Xol-H1 appears from the Classic to the
363 Late Postclassic / Colonial period. Haplotype A11-15-65 is present from the Epiclassic / Early
364 Postclassic to the Late Postclassic / Colonial period. Thus, there is an apparent continuity in
365 the dog population from the area of Tizayuca.

366 Compared to other American regions, the Basin of Mexico displays a high genetic
367 diversity. While the extremely reduced diversity observed in Illinois and the American South

368 West was interpreted as an expression of bottleneck caused by artificial selection and
369 breeding (Kemp et al., 2017; Witt et al., 2015), the high diversity in the Basin of Mexico
370 could be explained by several factors, including a selection for multiple morphotypes or the
371 presence of a larger and more stable population of dogs. As dental anomalies (including
372 oligodontia) are recognised as inherited characters (Knyazev et al., 2003), their recurrent
373 presence amongst the Mesoamerican dogs suggests regular inbreeding. Indeed, in the site of
374 Tizayuca, we estimate that 22% of the dogs present dental anomalies in the premolar row. In
375 the meantime the diversity of dogs diet in Mesoamerica, as shown by stable isotopes (eg.
376 White et al., 2001), and a greater dental plasticity on the premolar row (Asahara, 2013; Vilà et
377 al., 1993) would allow the variability of dental phenotypes to persist. However, further
378 analyses of full mitogenomes and nuclear markers are required to improve these hypotheses.

379 Analysis of molecular variance shows there are more differences within the different
380 populations than between them, confirming the low geographic component of domestic dog
381 mtDNA (van Asch et al., 2005; Witt et al., 2015). Interestingly, the neighbour-joining tree
382 built from the F_{ST} pairwise test results indicates clusters differentiating the populations from
383 South America and Mesoamerica from other North American populations (Figure 5). The
384 proximity highlighted between Mesoamerican and South American dogs could be the result of
385 the genetic bottleneck induced by the dispersion of dogs across America, with a loss of
386 genetic variability following the North-South migration. This trend might have been also
387 reinforced by the trade of animals between Mesoamerica and the Andean region. Indeed, eight
388 of the nine South American dogs come from Peru and Bolivia, which is in the heart of the
389 Andean culture. Several archaeological and linguistic evidence point toward continuous,
390 albeit tenuous, exchanges between Mesoamerica and the Andean region during pre-Hispanic
391 times (e.g. Anawalt, 1992; Carot and Hers, 2016; Holser, 1988) and some authors suggested
392 dogs, in particular hairless ones, were part of these movements (Carot and Hers, 2016;

393 Valadez Azúa et al., 2010, 2009; Vásquez Sánchez et al., 2016). However, further
394 comparative analyses will be necessary to address this question.

395 *4.3. Relationship between archaeological “hairless-like” dogs and modern breeds*

396 The Xoloitzcuintle is considered to be a primitive breed and therefore geneticists have
397 tried to find particular markers differentiating it from other modern breeds (Vilà et al., 1999).
398 Nonetheless recent genomic studies have shown that modern Xoloitzcuintle and Peruvian
399 Hairless dog were strongly influenced by European breeds as a result of recent breed
400 selection, and pre-contact traits would have been highly diluted (Ní Leathlobhair et al., 2018;
401 Parker et al., 2017a). The fact that they share the same causal mutation (Drögemüller et al.,
402 2008) sustains the hypothesis of a common origin but it is not clear if it is due to a pre-contact
403 population movement or modern migrations. Yet, the comparison between these two modern
404 American breeds and archaeological “hairless-like” dogs shows two shared haplotypes: A11,
405 found in three dogs from Tizayuca and B01 found in one dog from Tula (Figure 4). Although
406 we cannot discard their European origin due to post-contact interbreeding, these two
407 haplotypes could reflect the American maternal ancestry of these modern breeds.

408 The Chihuahua is another breed showing an American origin (van Asch et al., 2013)
409 carrying a PT (A185) already found in pre-contact archaeological samples from Mexico
410 (Leonard et al., 2002) and Northwest America (Ames et al., 2015; Barta, 2006), albeit none of
411 these present a “hairless-like” phenotype. However, novel haplotype Xol-H1, carried by three
412 “hairless-like” dogs from Tizayuca, is closely related with haplotype A185. Interestingly,
413 genomic data show a close relationship between the Chihuahua and the Chinese Crested dog,
414 another hairless breed carrying the FoxI3 mutation (Parker et al., 2017a). This proximity
415 highlights the complexity of dog history, strengthening the value of aDNA in the analysis of
416 modern breeds and calling for more global studies on the origin of modern breeds.

417 **5. Conclusion**

418 This multidisciplinary analysis of eight dogs with a “hairless-like” phenotype offers new
419 insights into the origin of the American hairless breeds. With direct radiocarbon dating of the
420 samples, we show that “hairless-like” dogs were present in the Basin of Mexico since the
421 Classic, between 386 and 535 CE, and persisted in the archaeological record until 1449 –
422 1631 CE. It is still unclear, however, if these dogs were the hairless specimens observed by
423 the first Spanish arriving to Mexico. First of all, the dental criteria used to identify them might
424 be associated with other developmental anomalies than CED. Also, other mutations exist that
425 lead to hairless dogs without affecting teeth development (Parker et al., 2017b), stressing the
426 difficulties in accurately identifying them in the archaeological record.

427 Nonetheless, we show that the dogs from the Basin of Mexico present a high
428 mitochondrial diversity and genetic continuity across the different cultural periods suggesting
429 the existence of a large and stable population of dogs. Some “hairless-like” dogs from Central
430 Mexico present a similar haplotype as some modern Xoloitzcuintli, Peruvian Hairless Dogs
431 and Chihuahua that could reflect one of the maternal ancestries of the breeds.

432 From the eight specimens analysed, we identified four different haplotypes including two
433 that were never reported before, and all are different from the haplotypes described in ancient
434 Mesoamerican dogs until now. It shows that most of the diversity of ancient American dog
435 populations is still unknown and further studies are required with a larger geographical and
436 chronological sampling to improve our understanding of past and modern dog relationships.
437 Moreover, this study mostly relies on the mtDNA control region whereas complete
438 mitogenome would give a better resolution. On the other hand, mtDNA only represents the
439 maternal half of lineages and plays a limited role in phenotypic expression. Nuclear genomic
440 approaches have been successfully used in ancient dogs to target specific phenotypes (Ollivier
441 et al., 2013), metabolic adaptations (Ollivier et al., 2016), and population history (Botigué et

442 al., 2017; Ní Leathlobhair et al., 2018; Frantz et al., 2016). Therefore, their application to
443 ancient Mesoamerican dogs would allow for a better understanding of past and modern dog
444 relationships.

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