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**Title: Genomic and archeological evidence for a dual origin of domestic dogs**

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39 **Abstract:** The geographic and temporal origins of dogs remain controversial. Here, we generated  
40 genetic sequences from 59 ancient dogs and a complete (28x) genome of a late Neolithic dog  
41 (~4,800 calBP) from Ireland. Our analyses revealed a deep split (early Bronze Age or late  
42 Neolithic) separating modern East Asian and Western Eurasian dog populations. In addition,  
43 analyses of ancient and modern mitochondrial DNA revealed a sharp discontinuity in haplotype  
44 frequencies in Europe. These results suggest that dogs in Eastern and Western Eurasia were  
45 domesticated independently from distinct wolf populations. East Asian dogs were then likely  
46 transported alongside people during the late Neolithic or early Bronze Age, potentially  
47 coincident with the recently described major human migration of pastoralists into Europe, where  
48 they replaced the indigenous Upper Paleolithic European dogs.

49 **One Sentence Summary:** Genomics and archeology reveal both a dual origin of domestic dogs  
50 and a subsequent translocation of East Asian dogs into Europe.

51 **Main Text:** Dogs were the first domestic animal and the only animal domesticated prior to the  
52 advent of settled agriculture(1). Despite their importance in human history, no consensus has  
53 emerged with regard to their geographic and temporal origins, or whether dogs were  
54 domesticated just once or independently on more than one occasion. Though several claims have  
55 been made for an initial appearance of dogs in the early Upper Paleolithic (~30kya; e.g. 2), the  
56 first remains confidently assigned to dogs appear in Europe ~15,000 years ago and in Far East  
57 Asia ~12,500 years ago (1, 3). While archaeologists remain open to the idea that there was more  
58 than one geographic origin for dogs (e.g. (4, 5), most genetic studies have concluded that dogs  
59 were likely domesticated just once (6) – disagreeing on whether this occurred in Europe (7),  
60 Central Asia (8), or East Asia (9).

61 Recent palaeogenetic studies have had a tremendous impact on our understanding of  
62 early human evolution (e.g. (10, 11)). Here we apply a similar approach to reconstruct the  
63 evolutionary history of dogs. We generated 59 ancient mtDNA sequences from European dogs  
64 (from 14 to 3Kya) as well as a high coverage nuclear genome (~28x) of an ancient dog ~4,800  
65 calBP (12) from the Neolithic passage grave complex of Newgrange (Sí an Bhrú) in Ireland. We  
66 combined our ancient sample with 80 modern publically available full genome sequences and  
67 605 modern dogs (including village dogs and 48 breeds) genotyped on the 170k HD SNP array  
68 (12).

69 We firstly assessed characteristics of the Newgrange dog by typing SNPs associated with  
70 specific phenotypic traits and by assessing the level of inbreeding. Our results suggest that the  
71 degree of artificial selection and controlled breeding during the Neolithic was similar to that  
72 observed in modern free-living dogs. In addition, the Newgrange dog did not possess variants  
73 associated with modern breed-defining traits including hair length or coat color. And though this  
74 dog was likely able to digest starch less efficiently than modern dogs, it was more efficient than  
75 wolves (12).

76 A phylogenetic analysis, based on 170k SNPs revealed a deep split separating the modern  
77 Sarloos breed from other dogs (Fig. 1a). This breed - created in the 1930s in the Netherlands -  
78 involved breeding German Shepherds with captive wolves (13), thus explaining the breed's  
79 topological placement. Interestingly, the second deepest split (evident on the basis of both the  
80 170K SNP panel – Fig 1a - and genome-wide SNPs - Fig. S4) separates modern East Asian and  
81 Western Eurasian (Europe and the Middle East) dogs. Moreover, the Newgrange dog clusters  
82 tightly with Western Eurasian dogs. We used Principal Component Analysis (PCA), D-statistics

83 and *TreeMix* (12) to further test this pattern. Each of these analyses unequivocally placed the  
84 Newgrange dog with modern European dogs (Figs. S5, S6, S7). These findings demonstrate that  
85 the node separating the East Asian and Western Eurasian clades is older than the Newgrange  
86 individual; directly radiocarbon dated to ~4,800 years ago.

87 Other nodes leading to multiple dog populations and breeds (including the basal  
88 breeds(1) such as Greenland Sledge dogs or Siberian Husky; Fig. 1a) are poorly supported,  
89 suggesting that these breeds likely possess mixed ancestry from both Western Eurasian and East  
90 Asian dog lineages. To further assess the robustness of the deep split and those nodes associated  
91 with the potentially admixed lineages, we defined Western Eurasian and East Asian “core”  
92 groups (Fig. 1a) supported by the strength of the node leading to each cluster (12). We then used  
93 D-statistics to assess the affinity of each population to either Western Eurasian or East Asian  
94 core groups (12). The results of this analysis again revealed a clear East-West geographic pattern  
95 across Eurasia associated with the deep phylogenetic split (Fig. 1b). Breeds such as the Eurasier,  
96 Greenland Sledge dogs and Siberian Huskies (all basal breeds from Northern regions(1)),  
97 however, possess strong signatures of admixture with the East Asian core samples (Fig. S11), as  
98 do populations sampled in East Asia that clustered alongside Western Eurasian dogs (e.g. Papua  
99 New Guinean village dog; Fig. 1a).

100 The existence of such a deep phylogenetic split between modern East Asian and Western  
101 Eurasian lineages suggests that dogs were derived independently from geographically and  
102 genetically differentiated wolf populations in different regions of Eurasia. To address this  
103 hypothesis we reconstructed their population history through time using the Multiple  
104 Sequentially Markovian Coalescent (*MSMC*)(12, 14). A reconstruction of effective population  
105 size from single high coverage genomes demonstrated a long, shared population history between  
106 the Newgrange dog and modern dogs from both Western Eurasia and East Asia (Fig. S15). A  
107 reconstruction using two genomes per group improved the resolution for recent time periods  
108 (Fig. 2a) and revealed a bottleneck in the Western Eurasian population, following its divergence  
109 from the East Asian core. A similar bottleneck observed in non-African human populations has  
110 been interpreted as a signature of a migration out of Africa (15). We therefore speculate that the  
111 analogous bottleneck observed in our dataset could be the result of a divergence and subsequent  
112 migration from east to west; supporting suggestions drawn from recent analyses of modern dog  
113 genomes (8, 9, 16).

114 To further assess the possibility that dogs were independently domesticated from two  
115 separate wolf populations, we computed the divergence time between Eastern and Western  
116 populations using *MSMC*. To obtain reliable time estimates, we used the radiocarbon age of the  
117 Newgrange dog to calibrate the mutation rate for dogs (12)(Fig. S16). This resulted in a mutation  
118 rate estimate of between  $0.3 \times 10^{-8}$  and  $0.45 \times 10^{-8}$  per generation - similar to that obtained with an  
119 ancient grey wolf genome (17). Using this mutation rate, we calculated the divergence time  
120 between the two modern Russian wolves (18) used in this study and the modern dogs to be 60-  
121 20Kya (Fig. S17; Fig. 2b). Importantly, this date should not be interpreted as a time frame for  
122 domestication, since the wolves we examined may not have been closely related to the  
123 population that gave rise to dogs (6).

124 This analysis also suggested that the divergence between the East Asian and Western  
125 Eurasian core groups (~14,000-6,400 years ago) occurred commensurate or several millennia  
126 after the earliest known appearance of domestic dogs in both Europe (>15,000 years) and East  
127 Asia (>12,500 years) (1) (Figs. S17, 2b). In addition, admixture signatures from wolves into

128 Western Eurasian dogs most likely pushed this estimated time of divergence deeper into the past  
129 (*12*) meaning that the expected time of divergence between East and Western cores is likely  
130 younger than our estimate. These results imply that indigenous populations of dogs were already  
131 present in Europe and East Asia prior to this genomic divergence. As a result, the early  
132 indigenous dog population in Europe was most likely replaced by the arrival of East Eurasian  
133 dogs.

134 To investigate the likelihood of this replacement, we sequenced and analyzed 59 hyper-  
135 variable mtDNA fragments from ancient dogs spread across Europe and combined those with  
136 167 modern sequences (*12*). Each sequence was then assigned to one of four major well-  
137 supported haplogroups (A-D) (*19*). While the majority of ancient European dogs belonged to  
138 either haplogroup C or D (63% and 20%, respectively), most modern European dogs possess  
139 sequences within haplogroups A and B (64 and 22% respectively) (Fig. 2c, d, e). Using  
140 simulations, we showed that this finding cannot be explained by drift alone (*12*). Instead, this  
141 pattern arose from clear turnover in the mitochondrial ancestry of European dogs, most likely as  
142 a result of an arrival of East Asian dogs. This migration led to a replacement of ancient dog  
143 lineages in Europe that were present by at least 15,000 years ago (*1*).

144 Though the mtDNA turnover is obvious, the nuclear signatures reveal an apparent long-  
145 term continuity. Assessments of ancestry in humans have demonstrated that major (nuclear)  
146 turnovers can be difficult to detect without samples from the admixing population (*11*). A  
147 genome-wide PCA analysis revealed that PC2 clearly discriminates the Newgrange dog from  
148 other modern dogs (Fig. S8), suggesting that this individual possessed ancestry from an  
149 unsampled population.

150 Our MSMC analysis reveals that the population split between the Newgrange dog and the  
151 East Asian core (as measured by cross coalescence rate [CCR]) is older (on average) than the  
152 split between modern Western Eurasian and East Asian lineages (Fig. 2b). Simulations suggest  
153 that this pattern could be explained by a partial replacement model in which the Newgrange dog  
154 retained a degree of ancestry from an outgroup population (Fig. S20a,b), that was different from  
155 modern wolves (*12*). Alternatively, this pattern could also be explained by secondary gene flow  
156 from Asian dogs into modern European dogs (Fig. S20c). Nevertheless, simulations show that  
157 secondary gene flow has a smaller effect on CCR than the partial replacement model (Fig.  
158 S20b,d). Moreover, secondary gene flow cannot explain the placement of the Newgrange dog on  
159 our genome-wide PCA (Fig. S8). Overall, these observations are consistent with a model in  
160 which the Newgrange dog retained a degree of ancestry from an ancient canid population that  
161 falls outside of the variation of modern dogs, but that is also different from modern wolves.

162 The evidence for a human-mediated East-West translocation of dogs, during the late  
163 Neolithic/early Bronze Age, is consistent with recent genetic evidence from both dogs (*9, 16*)  
164 and humans (*10, 11*). Thus, the arrival of Eastern dogs likely resulted in the replacement of an  
165 indigenous population that inhabited Europe during the Paleolithic (Fig. 2c,d,e). The overall  
166 genomic pattern presented here, supporting the existence of two populations of dogs during the  
167 Paleolithic in the East and West of Eurasia, is consistent with two scenarios. Either two wolf  
168 populations were domesticated independently (Fig. 3a), or dog domestication occurred once  
169 (more than 12,000 years ago) followed by a Paleolithic dispersal across Eurasia. In the latter  
170 scenario, a temporal cline across Eurasia of the first appearance of dogs should be evident in the  
171 archaeological record. Instead, current archaeological evidence (*12*) reveals that no dogs

172 predating 8,000 years ago are present in central Eurasia (Fig. 3b; Table S7), countering the  
173 hypothesis that dogs were transported across Eurasia during the Paleolithic.

174 Our combined results support the following hypothesis: two genetically differentiated and  
175 potentially extinct wolf populations in Eastern (8, 9) and Western Eurasia (7) were independently  
176 domesticated prior to the advent of settled agriculture (Fig. 3a). The eastern dog population then  
177 dispersed westward alongside humans during the recently described late Neolithic and Early  
178 Bronze Age human migrations (Yamnaya culture) into Western Europe (10, 11), including  
179 Ireland (20) whereupon they replaced an indigenous Paleolithic dog population. For numerous  
180 reasons, the null hypothesis should be that individual animal species were domesticated just once  
181 (21). The combined genetic and archeological results presented here, however, suggest that dogs,  
182 like pigs(22), were domesticated twice. Additional studies incorporating larger numbers of  
183 prehistoric samples, as well as further archeological investigation, will allow us to more firmly  
184 establish the temporal and geographic origins of domestic dogs.

185

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211  
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213 Nucleotide Archive (ENA) with project number: PRJEB13070. Mitochondrial sequences as well  
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229 interest.

230

231 **Fig. 1: Deep split between East Asian and Western Eurasian dogs.** *a.* A neighbour-joining  
232 tree (with bootstrap values) based on Identity by State (*I*<sub>2</sub>) of 605 dogs. Red and yellow clades  
233 represent the East Asian and Western Asian core groups respectively (*I*<sub>2</sub>). *b.* A map showing the  
234 location and relative proportion of ancestry (mean D-values) of dogs (Fig. S10). Positive values  
235 (red) indicate that the population shares more derived alleles with the East Asian core while  
236 negative values (yellow) indicate a closer association with the Western Eurasian core.

237 **Fig. 2: Effective population size, divergence times and mtDNA.** *a.* Effective population size  
238 through time of East and Western Eurasian dogs and wolves with MSMC. *b.* Cross-coalescence  
239 rate (CCR) per year for each population pair in Fig. 2a. The CCR represents the ratio of within  
240 and between population coalescence rates (CR). The ratio measures the age and pace of  
241 divergence between two populations. Values close to 1 indicate that both within and between CR  
242 are equal meaning the two populations have not yet diverged. Values close to 0 indicate that the  
243 populations have completely diverged. *c.* Bar plot representing the proportion of mtDNA  
244 haplogroups at different time periods. *d.* Locations of archaeological sites with haplogroup  
245 proportions. *e.* Location of modern samples with haplogroup proportions.

246 **Fig. 3: Model of dog domestication and archeological evidence for a dual origin of dogs. a.**  
247 Most likely model of dog domestication suggested by our data. An initial wolf population split  
248 into East and West Eurasian wolves that were then domesticated independently before going  
249 extinct (as indicated by the † symbol). The Western Eurasian dog population (European) was

250 then partially replaced by a human-mediated translocation of Asian dogs during the late  
251 Neolithic / early Bronze Age, a process that took place gradually after the arrival of the eastern  
252 dog population. **b.** Map representing the geographic origin and age of the oldest archeological  
253 dog remains in Eurasia (12).

254

255 **Supplementary Materials:**

256 Materials and Methods

257 Figs. S1-S29

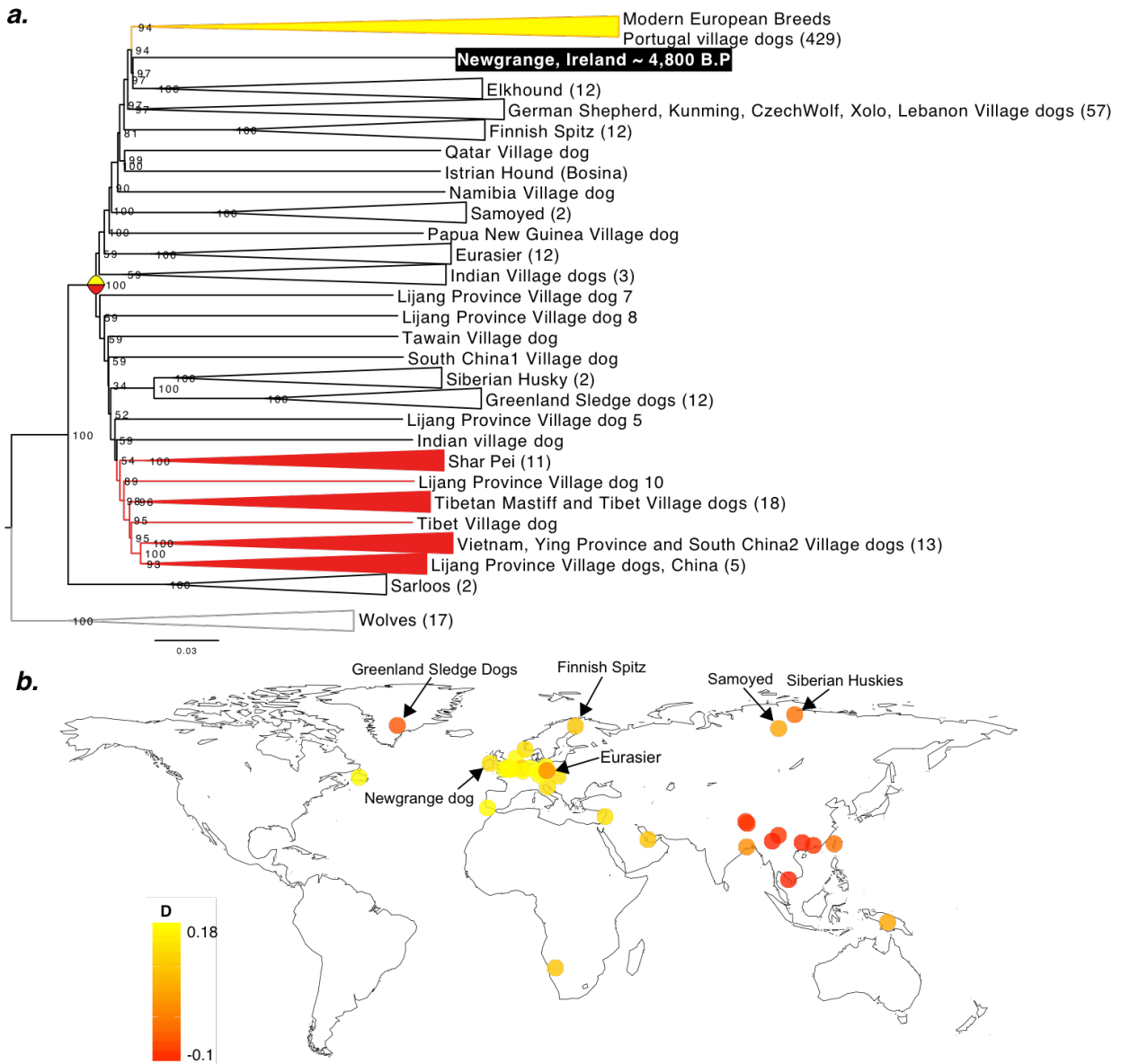
258 Tables S1-S7

259 References (22-110)

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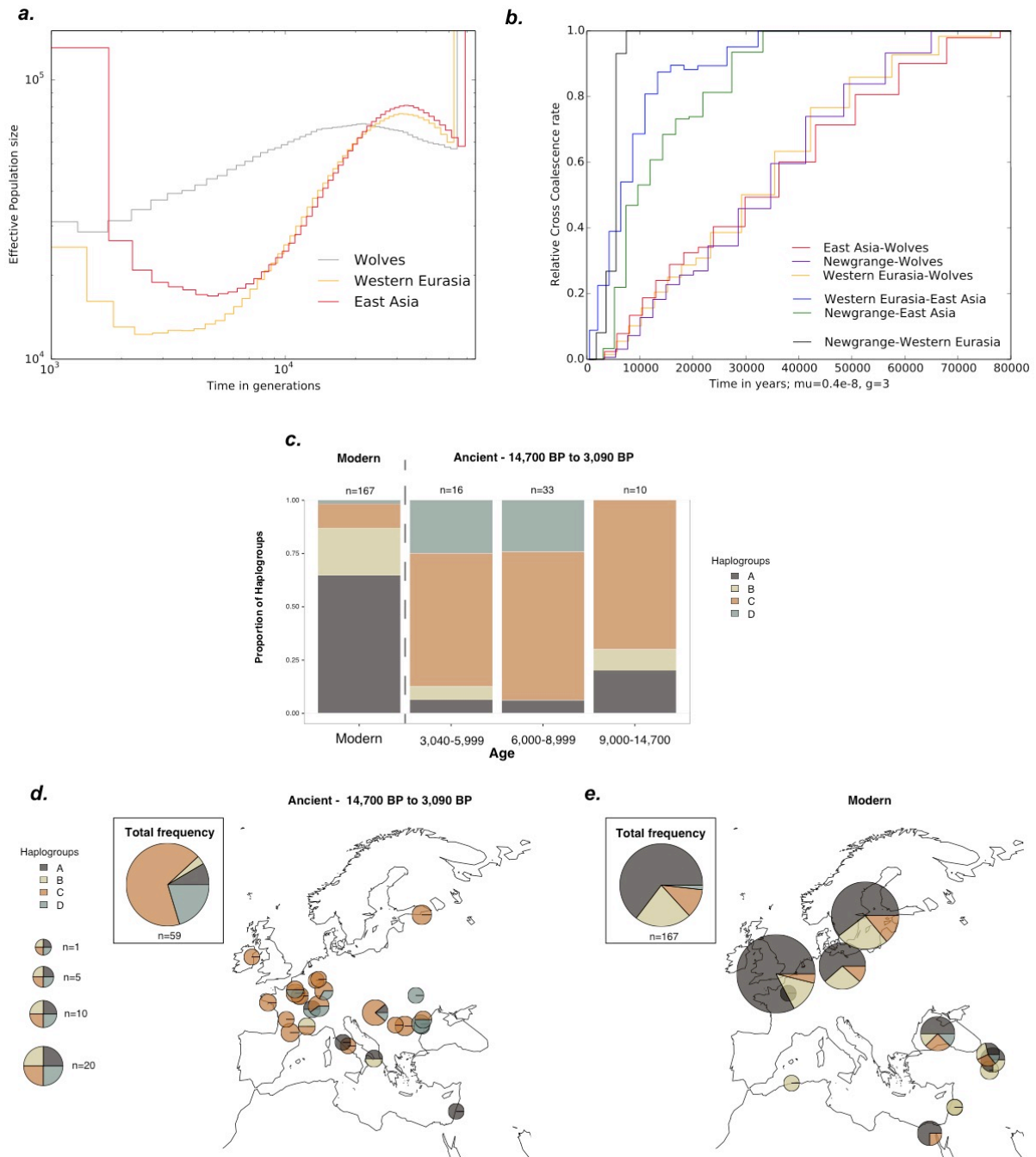
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264

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 269 negative values (yellow) indicate a closer association with the Western Eurasian core.  
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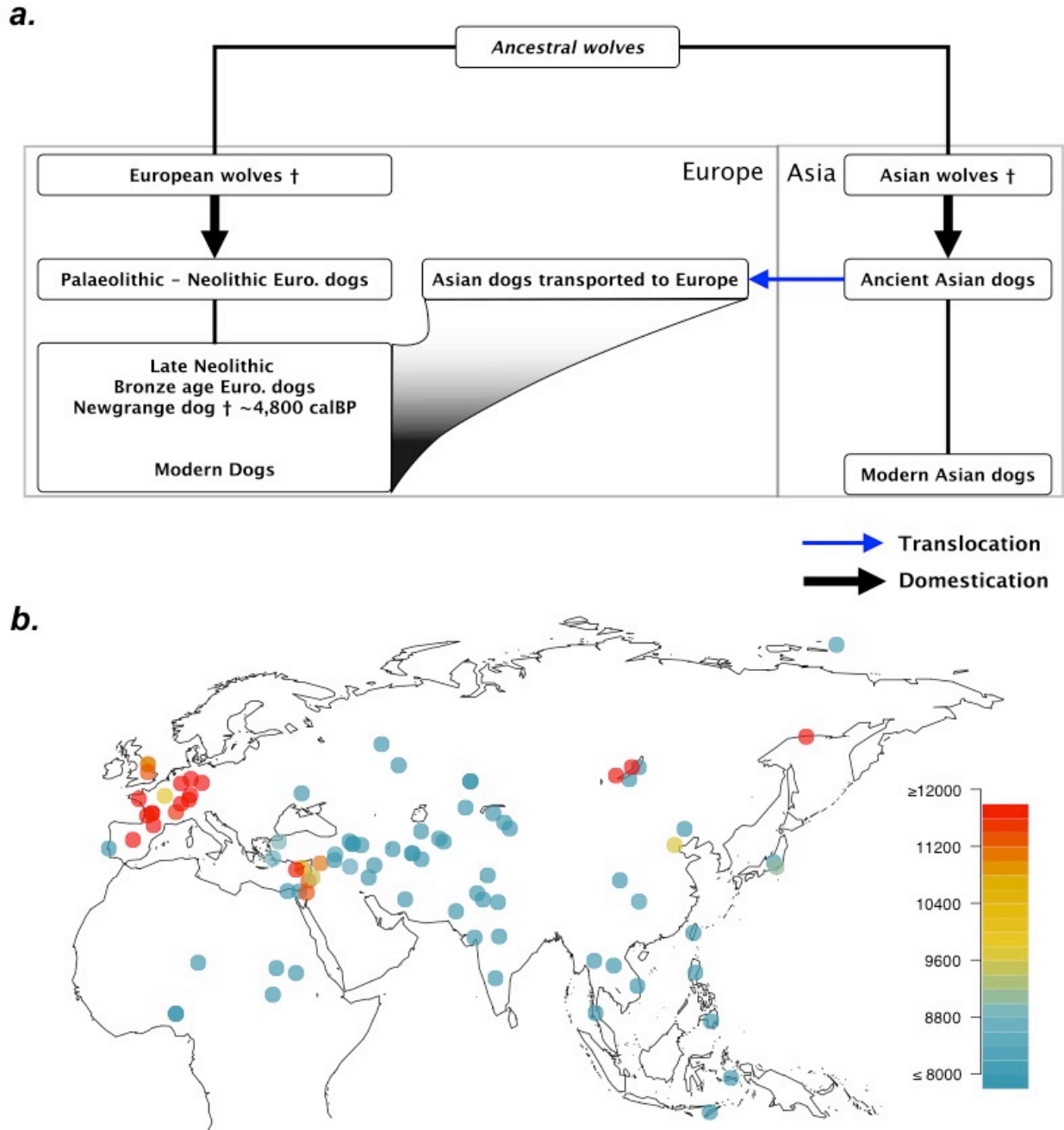




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