

Domestication of the dog (*Canis familiaris*) in the light of current palaeogenomic and veterinary knowledge

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Summary

The dog (*Canis familiaris*) is the oldest animal domesticated by humans, and its domestication represents a key stage in the history of human–animal relations. Despite many years of archaeological and genetic research, the course of this process remains a subject of scientific debate. The aim of this article is to present the current state of knowledge regarding the domestication of the dog, with particular emphasis on palaeogenomic data and their significance for veterinary science. The oldest archaeological finds interpreted as early dogs, the main models of domestication, the results of ancient DNA analyses, and demographic processes such as genetic bottlenecks are discussed. Particular attention is paid to genomic adaptations of dogs to the human environment and the significance of the canine transmissible venereal tumour (CTVT) as a unique “living record” of early dog populations. The conclusions indicate that the domestication of the dog was a complex, multi-stage process closely linked to the migrations and cultural changes of human populations. The integration of archaeological, genetic and biological data allows for an increasingly accurate reconstruction of the history of the dog’s origins, whilst having significant implications for modern veterinary medicine.

Keywords: dog domestication, paleogenomics, ancient DNA, genetic bottleneck, canine transmissible venereal tumour (CTVT), archaeozoology

The dog (*Canis familiaris*) occupies a unique position in the history of human–animal relationships as the earliest domesticated species. Its domestication initiated a long-term co-evolutionary relationship between humans and animals, influencing the development of economy, mobility, and social organisation in prehistoric societies. Unlike most livestock species, whose domestication is closely associated with the Neolithic Revolution and the emergence of agriculture, the origins of the dog date to the Late Pleistocene. This makes the dog a useful model for studying the earliest stages of domestication and human–animal interactions. Despite decades of archaeological, morphological, and genetic research, the course of dog domestication remains unresolved and continues to be debated (9, 15). Domestication is now generally interpreted not as a single event, but as a long-term evolutionary process involving multiple populations and repeated interactions between humans and wolves (40). Early morphological studies also highlighted differences

between domestic dogs and wild canids, forming the basis for later discussions on domestication processes (37). Reconstruction of its early stages is hindered by the lack of clear diagnostic criteria distinguishing early dogs from morphologically variable wolf populations, as well as by the fragmentary nature of the archaeological record. Recent advances in palaeogenomics have revised earlier interpretations. The analysis of ancient DNA enables direct investigation of fossil dog and wolf genomes and reconstruction of their population history (8). Current evidence indicates that domestic dogs do not derive directly from any extant wolf population, but from extinct or genetically transformed Late Pleistocene wolf lineages. These findings point to the importance of demographic processes such as population replacement, admixture, and gene flow, and suggest that domestication occurred under conditions of ongoing interaction between wild and human-associated populations. From a veterinary perspective, research on dog domestication has both theoretical and practical

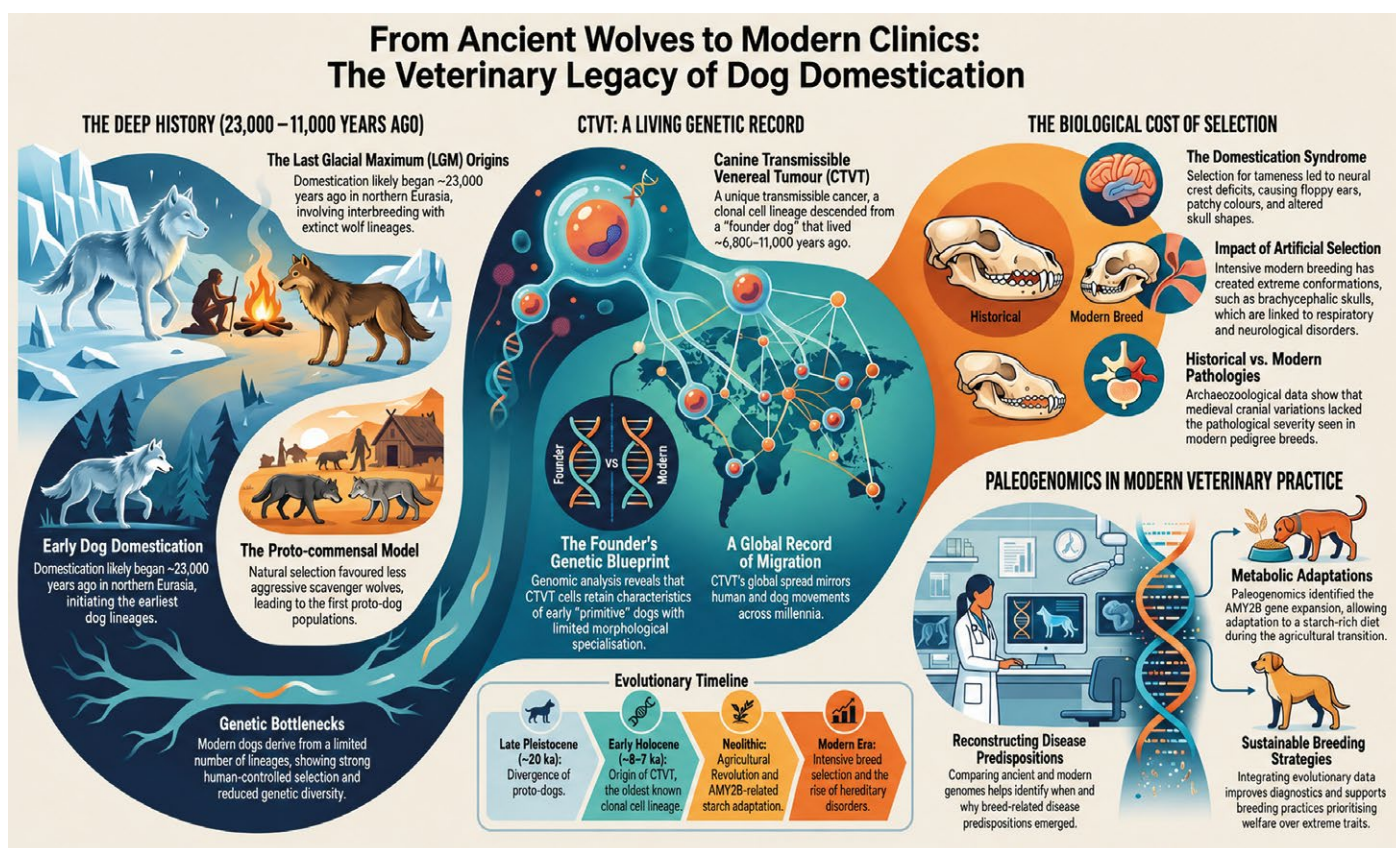


Fig. 1. Paleogenomic and veterinary implications of dog domestication

Illustration of key stages of domestication and their biological consequences. The figure includes early domestication processes, CTVT as a genetic record of early dog populations, and modern veterinary implications such as disease predispositions and effects of artificial selection

relevance. Understanding the evolutionary background of dogs helps interpret morphological diversity, genetic variation, and breed-specific disease predispositions. Many health problems observed in modern dog populations, including hereditary disorders, are linked to processes such as selection and population bottlenecks associated with domestication and subsequent breed formation. Integration of archaeological and palaeogenomic data with clinical knowledge may support improved diagnostics, more accurate risk assessment, and the development of more sustainable and welfare-oriented breeding strategies (Fig. 1).

The aim of this article is to present the current state of knowledge on dog domestication, with particular emphasis on palaeogenomic data and their relevance to veterinary science.

Morphological changes associated with dog domestication (the domestication syndrome)

Morphological changes associated with dog domestication are commonly described within the framework of the so-called domestication syndrome, which encompasses a set of phenotypic traits observed across multiple domesticated species. In dogs, these changes include shortening of the facial region of the skull (reduction of the viscerocranium), decreased tooth size, and increased variability in cranial morphology. In addition, domesticated dogs exhibit a wide range of

coat colour variations, including depigmentation and patchy patterns, which are rare in wild wolf populations. Changes in body size and proportions are also evident, resulting in both dwarfism and gigantism in modern breeds (34, 38). From a behavioural perspective, domestication is associated with reduced aggression, increased tolerance towards humans, and prolonged juvenile traits (neoteny), particularly in social behaviour and communication. These changes are thought to have played a key role in facilitating integration of early dogs into human social environments (20).

A widely discussed explanatory framework for the domestication syndrome is the neural crest hypothesis proposed by Wilkins et al. (2014). According to this model, many traits observed in domesticated animals result from mild deficits in neural crest cell development during embryogenesis. Neural crest cells contribute to the formation of multiple tissues, including craniofacial structures, pigmentation, and components of the nervous system. Subtle changes in their proliferation or migration may therefore produce a wide range of morphological and behavioural effects observed in domesticated species. Similar genomic signals affecting pathways associated with neural crest development have also been identified in comparative analyses of dog and wolf genomes (26). Experimental evidence supporting this concept is provided by long-

term selection experiments in silver foxes (*Vulpes vulpes*), in which selection for tameness alone resulted in correlated morphological changes, including floppy ears, altered coat colour, and cranial modifications (34). These findings suggest that behavioural selection may indirectly drive morphological evolution.

However, recent studies indicate that the domestication syndrome may not represent a uniform or universal set of traits. Comparative genomic analyses suggest that the genetic mechanisms underlying domestication may vary between species, and that not all traits are consistently expressed across domesticated populations (18). In dogs, considerable phenotypic diversity has been further shaped by later, intensive selective breeding, which complicates the distinction between traits associated with early domestication and those resulting from recent artificial selection.

From a veterinary perspective, these morphological changes are of particular importance, as many traits selected during breed formation are associated with increased risk of disease. Examples include brachycephalic skull conformation linked to respiratory disorders, as well as skeletal modifications predisposing to orthopaedic conditions (1, 32). Understanding the evolutionary origins of these traits provides an important framework for interpreting breed-specific pathologies and supports the development of more sustainable breeding strategies.

The earliest evidence of dogs in the archaeological record

The earliest traces of dogs in the archaeological record date to the Late Pleistocene and have been identified at several sites across Eurasia. Among the most frequently discussed are finds from Goyet in Belgium (c. 36,000 years ago), the Altai Mountains (c. 33,000 years ago), and Předmostí in Moravia (c. 27,000-30,000 years ago) (11, 12, 25) (Fig. 2). Additional evidence from Western Europe indicates the presence of small-bodied canids interpreted as early dogs in the Upper Palaeolithic (29). The osteological material from these sites shows features that differ from those of typical wolves, including shortening of the facial region of the skull, changes in cranial proportions, and differences in dentition. These traits have been interpreted as possible indicators of early domestication and may reflect transitional forms between wolves and dogs. However, their interpretation remains debated. Some researchers argue that the observed morphological changes exceed the range of variation in wolf populations and reflect selective processes associated with domestication (11, 12). Under this interpretation, dog domestication may have begun earlier than suggested by more conservative models. In contrast, other authors emphasise that Pleistocene wolves likely exhibited greater morphological variability than modern populations, reflecting broader ecological diversity and less stabilised

From Wolves to Woofs: Three Theories of Dog Domestication

Dog domestication was a complex, multi-stage process involving long-term interactions between humans and extinct wolf lineages during the Late Pleistocene, resulting in significant morphological and genetic changes.

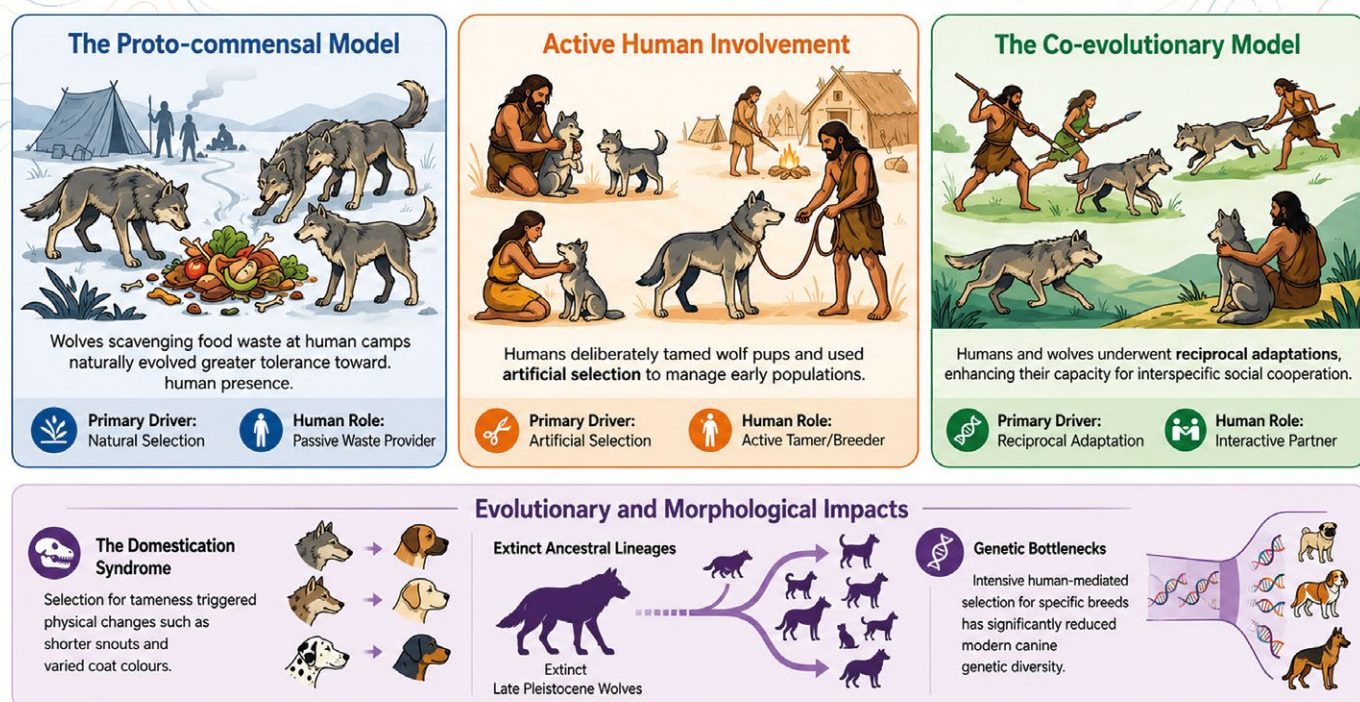


Fig. 2. Main models of dog domestication

Comparison of three principal models: proto-commensal, human-directed, and co-evolutionary. The figure also summarises their evolutionary outcomes, including morphological changes, lineage diversification, and reduced genetic diversity in modern breeds

population structures. This variability complicates the distinction between early dogs and wild forms (15, 27). From this perspective, some specimens may represent specialised local wolf populations adapted to specific environmental conditions rather than products of domestication. This disagreement reflects a broader methodological problem in identifying early dogs in the archaeological record. The difficulty results not only from the fragmentary nature of the material, but also from the lack of widely accepted diagnostic criteria that would allow clear differentiation between early domestic dogs and morphologically variable wolves. Reliance solely on morphological traits may therefore lead to conflicting interpretations, particularly in the case of transitional forms.

For this reason, increasing emphasis is placed on palaeogenomic analyses, which provide a more robust framework for assessing relationships between early dogs and wolf populations (4, 9, 33). These approaches offer independent lines of evidence that complement traditional osteological analyses and allow more consistent interpretation of early canid remains.

Theories of dog domestication

Despite extensive archaeological, genetic, and ethological research, the mechanisms underlying dog domestication remain debated. Several models have been proposed, differing in the role attributed to humans and in the nature of interactions between human and wolf populations (8, 10, 15). Current discussion has shifted from questions of place and timing towards mechanisms and evolutionary pathways. The proto-commensal model, currently the most widely cited, proposes that wolves gradually approached human camps to exploit food waste. Under this scenario, natural selection favoured individuals that were less aggressive and more tolerant of human presence, leading to the emergence of proto-dog populations (10, 15). This model is supported by observations of modern free-ranging dogs and by genomic data consistent with gradual behavioural change (4, 8). However, it does not fully account for the advanced cognitive and social abilities of dogs, particularly their capacity to interpret human communicative signals (20). In addition, the availability of human refuse in Pleistocene environments may have been limited, which challenges the assumption of a stable ecological niche for such interactions (27). An alternative hypothesis emphasises active human involvement, including the taming of wolf pups and deliberate selection (6). While this model highlights human agency, its plausibility remains uncertain. Ethological studies indicate that even hand-raised wolves retain behavioural traits characteristic of wild animals, which restricts their integration into human social structures (20). Moreover, archaeological evidence for early controlled breeding is limited. The multiple domestication hypothesis, based primarily on mitochondrial DNA analyses, initially suggested sev-

eral independent centres of domestication, including in East Asia and Europe (30, 33). More recent palaeogenomic data indicate that these patterns are better explained by admixture and population replacement rather than independent domestication events (4, 9). This model is therefore increasingly interpreted as reflecting complex demographic processes rather than multiple origins.

The co-evolutionary model proposes that domestication resulted from long-term interactions between humans and wolves, leading to reciprocal adaptations (8, 10). Within this framework, selection acted on wolves (e.g. increased tolerance and sociability) as well as on humans (e.g. enhanced capacity for inter-specific cooperation) (Fig. 2). This approach integrates elements of other models and provides a broader explanatory framework. No single model fully accounts for the domestication of the dog. Available evidence indicates that this was a gradual and spatially heterogeneous process, involving different mechanisms depending on ecological and cultural contexts (8, 15). The proto-commensal model likely reflects early phases of domestication, whereas active human involvement may have become more important at later stages. Palaeogenomic data further highlight the role of demographic processes such as migration, introgression, and the extinction of local lineages (4). Current evidence indicates that proto-commensal and co-evolutionary models are not mutually exclusive, but represent complementary frameworks describing different stages and aspects of the domestication process.

Palaeogenomics and the population history of the dog

Advances in palaeogenomics over the past two decades have substantially revised previous interpretations of dog origins (Fig. 3). In contrast to earlier studies based mainly on mitochondrial DNA, recent research includes whole genomes of ancient individuals, which allows more precise reconstruction of the population history of dogs and wolves (8, 10). Current evidence indicates that domestic dogs do not descend directly from any extant wolf population (*Canis lupus*), but from Late Pleistocene wolf populations that either became extinct or underwent significant genetic transformation (4, 9). This is supported by genomic data demonstrating early divergence between dog ancestors and now-extinct wolf lineages (31).

Early genetic studies suggested a much deeper divergence. Vilà et al. (36) estimated the split between dogs and wolves at approximately 100-150 thousand years ago, implying an early onset of domestication. However, these estimates were difficult to reconcile with archaeological data and were later revised in light of more comprehensive genomic datasets. A major advance was the application of ancient DNA analysis, which enabled direct comparison of fossil dogs and

The Evolution of the Dog: A 40,000-Year Evolutionary Timeline

Dog domestication began during the Late Pleistocene and involved a gradual transition from natural human–wolf interactions to intensive human-mediated selection, ultimately producing the diversity of modern dog breeds.

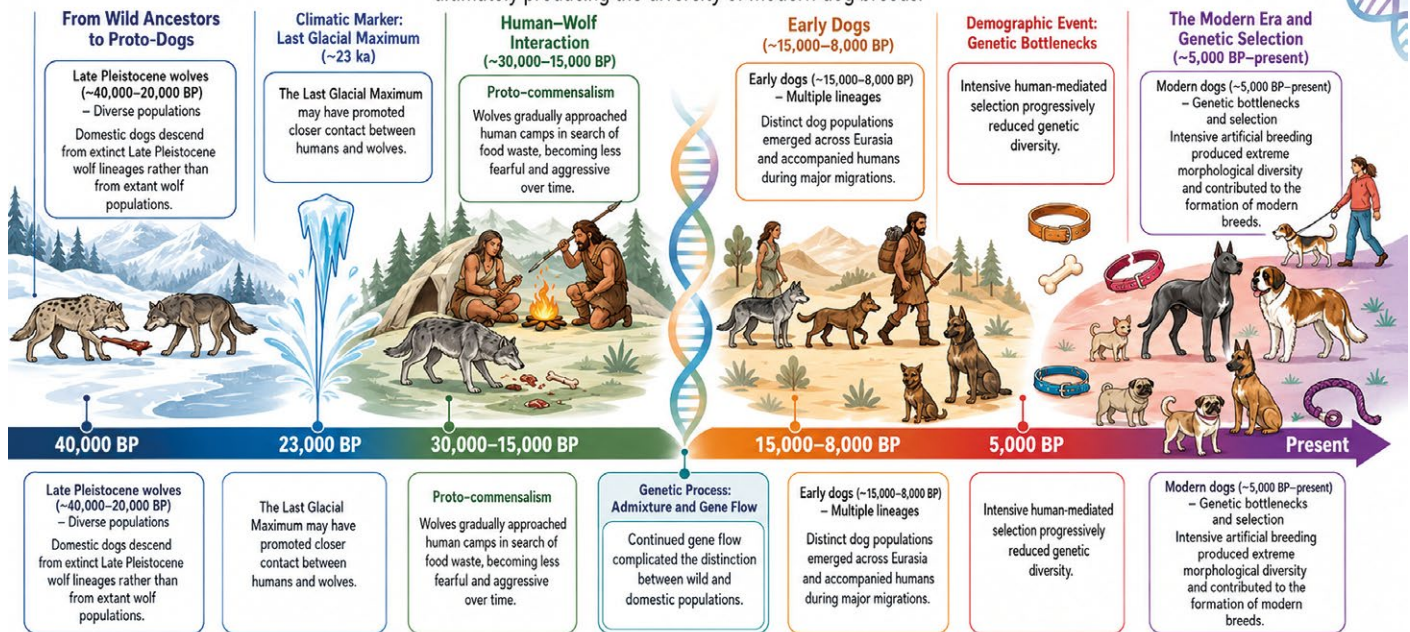


Fig. 3. Timeline of dog domestication

Schematic overview of dog domestication from Late Pleistocene wolf populations (~40,000 BP) to modern breeds. The figure highlights human–wolf interactions, early dog populations, gene flow between lineages, and the impact of recent artificial selection and genetic bottlenecks

wolves. Thalmann et al. (33) proposed a European origin of early dogs; however, subsequent studies indicate a more complex population history. Genomic data show that multiple, genetically distinct dog populations were already present in the Late Pleistocene, many of which did not contribute to modern lineages. Frantz et al. (9) proposed a dual-origin model, whereas Bergström et al. (3) demonstrated the presence of multiple lineages followed by extensive extinction and population replacement. These patterns are further supported by palaeogenomic evidence indicating partial continuity of certain dog lineages from the Early Neolithic to modern populations (5). These findings indicate a population history shaped by repeated episodes of expansion, admixture, and local extinction. Consequently, models assuming a single centre of domestication appear insufficient, and increasing support is given to multi-regional or network-based scenarios involving numerous wolf populations and long-term interactions with humans. Gene flow between dogs and wolves represents a central component of this process.

Multiple studies confirm recurrent introgression after the onset of domestication, resulting in populations of mixed genetic origin (4, 10). This suggests that domestication did not occur under conditions of reproductive isolation, but involved ongoing genetic exchange, which complicates the distinction between wild and domestic populations. Palaeogenomic data also inform on functional adaptations associated with domestication. Axelsson et al. (2) demonstrated

an increased copy number of the *AMY2B* gene in dogs, interpreted as an adaptation to a starch-rich diet associated with the development of agriculture. This indicates that domestication involved not only behavioural changes but also metabolic adaptation, and likely proceeded in successive phases linked to changes in human subsistence strategies. Another key aspect concerns demographic processes such as genetic bottlenecks. Genomic analyses indicate that modern dog populations derive from a limited number of lineages, particularly with respect to the Y chromosome, which suggests strong human-mediated selection (4). Comparable patterns have been observed in other domesticated species. In the domestic horse, modern populations originate from a restricted number of stallion lineages that expanded rapidly during the Bronze Age, reflecting intensive selective breeding (17, 19). Similar processes likely occurred in dogs, where reduced paternal diversity combined with high mitochondrial variability indicates uneven reproductive contribution and increasing human control over breeding. Palaeogenomic data further demonstrate a close relationship between human migrations and the dispersal of dogs. Dogs accompanied humans during the colonisation of Europe and the Americas, as indicated by both genetic and archaeological evidence (16, 28). Recent studies suggest that domestication may have begun in northern Eurasia during the Last Glacial Maximum (c. 23,000 years ago), under conditions that facilitated prolonged interactions between humans and

wolves (28). Current palaeogenomic evidence indicates that dog domestication was not a single event, but a spatially heterogeneous process involving multiple wolf populations and complex demographic dynamics, including migration, introgression, and extinction of local lineages.

Canine Transmissible Venereal Tumour (CTVT) as a record of population history

Canine transmissible venereal tumour (CTVT) constitutes an unusual biological model that provides insight into the population history of dogs. It is one of the few naturally occurring transmissible cancers in mammals, in which tumour cells are transmitted directly between individuals, most commonly during sexual contact (21). Unlike most cancers, which arise independently in each affected individual, CTVT constitutes a clonal cell lineage that originated in a single dog and has been propagated through successive hosts. Genetic analyses indicate that contemporary cases of this tumour share a common origin (23). Genomic studies of this lineage allow partial reconstruction of the phenotypic and genetic characteristics of the founder dog in which the original malignant transformation occurred. Available evidence suggests that this animal belonged to an early dog population and displayed features comparable to those observed in present-day free-ranging or so-called primitive dogs (22). Phylogenomic analyses further indicate that CTVT originated approximately 6,000-11,000 years ago and subsequently spread globally alongside human-associated dog populations (3). It therefore is one of the oldest known continuously propagating cell lineages in mammals. From the perspective of domestication research, CTVT can be treated as an indirect genomic proxy of early dog populations. Analyses of its genome allow inference of past genetic diversity and demographic processes associated with domestication. The inferred genetic characteristics of the founder dog indicate relatively low morphological specialisation, consistent with archaeozoological evidence that early dog populations exhibited moderate phenotypic variability and functioned as semi-managed or loosely controlled groups rather than highly specialised breeds (14). More broadly, CTVT data are consistent with models of domestication that emphasise a gradual, population-level process involving substantial gene flow and limited early morphological differentiation. The absence of traits characteristic of highly specialised breeds in the reconstructed founder profile supports the interpretation that early stages of domestication were not driven by intensive, goal-directed breeding. Instead, they likely involved loosely structured human-animal interactions and relatively weak selective pressures. The global dispersal of CTVT alongside human-associated dog populations further supports a close relationship between dog population history and human mobility.

In summary, CTVT is a distinctive research model that integrates genetic, evolutionary, and veterinary perspectives. Its study contributes to understanding tumour biology and, at the same time, provides indirect evidence for the structure and variability of early dog populations.

The significance of dog domestication for veterinary medicine

Research on dog domestication is highly relevant to modern veterinary medicine, as it helps explain the origins of morphological and genetic variation observed in contemporary dog populations. Domestication, as a stage in human-animal interactions, was closely linked to major economic and social changes in pre-history (15, 35). This process resulted in extensive phenotypic diversity, including both desirable traits and predispositions to numerous diseases (24). Modern dog breeds are often characterised by reduced genetic diversity, largely due to intensive selection and the widespread use of inbreeding. These factors are associated with an increased prevalence of hereditary disorders, including skeletal and joint malformations, neurological conditions, and metabolic diseases (10, 24). Such disorders are frequently linked not only to inbreeding itself but also to selection for extreme conformation traits defined by breed standards (32). From a clinical perspective, domestication can be viewed as a multi-stage process, with later phases – linked to breed-specific selection – being particularly important. Archaeozoological data provide useful context by allowing differentiation between changes associated with early domestication and those resulting from recent selective breeding. Analyses of canine skeletal material from the early medieval period indicate that variation in cranial morphology was already present in historical populations, although it was not consistently associated with pathological changes. In particular, no clear evidence of occipital dysplasia was identified, and the morphology of the foramen magnum remained within the range of normal variation (13).

These observations suggest that some features currently regarded as pathological may represent morphological variants that became clinically relevant only under conditions of intensive modern selection. This is illustrated by variation in cranial morphology and the foramen magnum, which in certain breeds is associated with neurological disorders such as syringomyelia. Historical data indicate, however, that similar variants may have occurred without evident clinical consequences, highlighting the importance of genetic background, population structure, and selective context (7). Palaeogenomic studies further emphasise the role of demographic processes, such as genetic bottlenecks and directional selection, in shaping modern dog populations (4, 8). These processes have direct implications for veterinary practice, influencing disease prevalence, immune variability, and overall susceptibility to dis-

orders. Understanding the evolutionary and genetic background of dog populations therefore supports more accurate diagnostics, improves interpretation of breed predispositions, and contributes to the development of more sustainable and welfare-oriented breeding strategies.

Dog domestication was a complex, multi-stage process that varied geographically and involved long-term interactions between wolf populations and human communities. Archaeological and palaeogenomic data indicate that this was not a single domestication event, but a dynamic process characterised by repeated episodes of migration, admixture, and local adaptation. Recent advances in palaeogenomics have significantly refined our understanding of dog origins, revealing a complex demographic history and highlighting the roles of introgression and genetic bottlenecks in shaping canine populations. These findings emphasise the interplay between environmental factors and human-mediated selection in the formation of modern dogs. From a veterinary perspective, knowledge of the evolutionary background of dogs provides an important framework for interpreting present-day biological variation, disease susceptibility, and breed-specific traits. Domestication should therefore be understood as a series of evolutionary and demographic transformations, the consequences of which are directly reflected in contemporary canine health.

The integration of archaeological, genetic, and clinical data offers a comprehensive approach to understanding canine diversity and supports the development of improved diagnostic strategies and more responsible breeding practices. Future research should focus on refining the temporal and spatial pathways of domestication and identifying the genetic mechanisms underlying key adaptive traits (39). From the authors' perspective, combining palaeogenomic data with insights from CTVT research supports a view of dog domestication as a gradual, population-level process involving gene flow and limited early morphological specialisation. This approach also suggests that some traits currently regarded as pathological may represent variants that became clinically relevant only under conditions of recent intensive selection, which has important implications for veterinary practice and breeding strategies.

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