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Suture obliteration patterns in wolves and a comparison to dogs

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Age-related patterns in cranial suture and synchondrosis obliteration in 371 known-age North American grey wolves (*Canis lupus*) are examined to assess their utility in estimating the age of archaeological and paleontological wolf crania. Differences in age-related obliteration patterns between these wolves and 576 known-age domestic dogs (*Canis familiaris*) also are explored. Domestication has likely altered the growth and development of dog crania in relation to that of wolves, but these processes remain poorly understood. Wolf total suture obliteration score and age were positively correlated, indicating that the level of suture obliteration can be used to track age to some extent. Wolf sex and dietary patterns had no meaningful effects on this correlation. Mesocephalic or dolichocephalic dogs generally begin exhibiting more extensive suture obliteration than wolves during early adulthood, at about 2–4 years of age. This pattern of more extensive obliteration persists throughout the lifespan, with dogs tending to experience more obliteration in the observed sutures and synchondroses. Several interrelated factors may contribute to this pattern, all outcomes of domestication, including differences in physical strains in the cranium, alteration of development and ageing, and the emergence of diverse head shapes that relate in part to suture closure timing.

Keywords Ageing methods, Suture obliteration, Dogs, Wolves, Zooarchaeology

This paper examines patterns in cranial suture and synchondrosis obliteration in North American grey wolves (*Canis lupus*) to address two primary questions. First, can patterning in suture and synchondrosis obliteration be utilized for ageing wolf crania? Such a method would be particularly useful for estimating the ages of archaeological and paleontological wolf crania, which often cannot be destructively sampled (for cementum ageing, for example). Reliable age-at-death estimations are crucial for understanding how humans engaged with wolves in the past, including during the domestication of a subset of wolves that led to the emergence of dogs (*Canis familiaris*). For example, one might expect increases in average life expectancy through the domestication process, as shelter and provisioning provided by humans likely increased the likelihood of some individuals reaching advanced ages. Second, does the patterning in wolf suture and synchondrosis obliteration by age differ from that in domestic dogs? Domestication has altered developmental timing and patterning in many mammals, and some of these changes likely manifest in suture and synchondrosis closure and obliteration patterning. Documenting any such changes potentially provides additional insights into the complex developmental and morphological outcomes of domestication, many of which remain poorly understood.

Adjacent bones of the cranium join together by fibrous articulations known as sutures and cartilaginous articulations termed synchondroses. Cranial bones primarily grow along these articulations, and some close (join together) and then partially or entirely obliterate (become no longer visible) as individuals age^{1–4}. Open (patent) and unobliterated sutures allow for short-term deformation, such as during birth, and perhaps also the redistribution of force associated with heavy mastication and other forceful acts (predation, fighting) involving the skull^{2,4}. Patent sutures are also reservoirs for mesenchymal stem cells, which support bone growth in the cranium⁴. Suture and synchondroses closure marks the cessation of growth of cranial elements, stabilizing their form and articulation with adjacent elements. These closures have protective functions, including encasing the brain. Obliteration occurs when the lines or juncture points between closed sutures or synchondroses are fused and no longer visible due to bone growth and remodelling^{4,5}. Obliteration thus further strengthens surrounding cranial regions and presumably reshapes the distribution of strain within the skull.

For over a century, archaeology and forensic sciences have utilized cranial suture closure and obliteration patterning to assign human remains to general age-at-death categories^{3,6–8}. Such ageing approaches rarely have

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been used with ancient canid remains, largely due to the lack of reliable information on age-related suture closure and obliteration patterning. Methods for ageing dogs and wolves in zooarchaeology, paleontology, and wildlife biology typically involve studies of tooth wear, post-cranial skeletal element fusion, pulp-cavity closure, and cementum annulation, though all have limitations and drawbacks^{9–17}. The extent of tooth wear among wild wolves, for example, shows considerable variation within populations, meaning that it provides somewhat imprecise age estimations⁹. Post-cranial skeletal fusion is completed at roughly 12 months of age¹⁶, providing no useful ageing information among adults. Cementum annulation studies are far more accurate, but most such methods require destructive thin sectioning of teeth, which ideally should be avoided when dealing with archaeological or fossil specimens.

In recognition of some of these challenges, Losey and Nomokonova⁵ developed an ageing method focusing on suture and synchondrosis obliteration patterning among domestic dogs. This method, designed for use with archaeological specimens, relies on visually scoring suture conditions. They found that the extent of suture obliteration in mesocephalic and dolichocephalic dogs was positively correlated with their ages at death. Scoring of these patterns provides an expedient method for differentiating dog crania to some age classes, particularly juveniles and adults. Further, suture obliteration scores allow one to assign adult individuals to somewhat more specific age categories, though with less certainty among middle-aged to older adults. Breed, sex, body size, and cranial shape all introduce some variation to the obliteration patterning. Previous ageing studies using suture closure patterns in fox and wolf populations have unknown reliability due to small sample sizes or focus on a limited number of sutures^{13,18,19}.

Domestication has likely altered suture and synchondrosis obliteration patterning in dogs compared to that in wolves, as this process involves interrelated changes in appearance, behaviour, and ontogenesis^{20–22}. In some dogs, pre/perinatal skull development appears slower than in wolves, but variation in postnatal ontogeny rates results in adults with a range of head shapes, ranging from paedomorphic (juvenile-like) to peramorphic (having additional traits beyond those of typical adulthood)²³. In many modern dogs, sexual maturity is attained significantly earlier than in modern wolves²⁴. In contrast, dental maturity and proximal humerus epiphysis fusion schedules are very similar between modern dogs and wolves²⁴. The extensive phenotypic variation in modern dog breeds, well evidenced by differences in head shape, is also a product of domestication. For example, intensive selection for appearance in some dog breeds has resulted in extreme head forms (brachycephalic crania). Adults with such head shapes tend to have earlier or more extensive closure of cranial sutures and synchondroses than dogs with more wolf-shaped crania; such dogs also have more extensive cranial suture closure than adult wolves^{24,25}.

Here, cranial suture and synchondrosis obliteration patterns are examined in four groups of known-age North American grey wolves ($n=371$) using the scoring method developed for dogs⁵. First, the extent to which obliteration patterns are correlated with age in the overall wolf sample is examined. Other factors that potentially contributed to variation in the patterning of obliteration are explored, including sex and subpopulation. Two of the subpopulations, both from Yellowstone National Park, U.S.A., have well-documented differences in dietary stress, which could have an effect on suture closure and obliteration patterning. Differences in total obliteration scores calculated for seven suture/synchondrosis groups are examined, as well as differences between specific suture/synchondrosis groups. Second, age-related patterning in suture obliteration in the wolves is compared to that in a sample of known-age mesocephalic or dolichocephalic domestic dogs ($n=576$). The identified patterns and differences are then discussed, along with potential causes for them and the overall implications of our findings.

Results

Total obliteration score, age, and sex for wolves

The correlation between wolf total obliteration score and age is shown in Fig. 1 and Table 1, with the overall wolf population ($n=371$) divided by sex. The total obliteration scores for male and female wolves are significantly positively correlated with age, with a Pearson's r value of 0.78, $p=4.59E-06$ for females, and 0.71, $p=9.57E-08$ for males. ANCOVA tests revealed insignificant differences between the regression slopes (Table 1) of the males and females, suggesting no true differences in the relationship between age and obliteration score for male and female wolves ($F(1, 341)=0.95, p=0.33$). Together, the correlation coefficient for the total population of wolves is 0.74, $p=5.82E-14$.

Total obliteration score, age, and wolf subpopulations

All regional wolf populations analyzed (Alberta, Yellowstone (including dietarily stressed and unstressed), and Northwest Territories) (Fig. 2 and Table 2) show significant positive correlations between total obliteration score and age, with a Pearson's r value of 0.70, $p=0.06E-03$ for Alberta, 0.73, $p=3.35E-04$ for Yellowstone Stressed, 0.76, $p=1.89E-03$ for Yellowstone Unstressed, and 0.75, $p=2.13E-08$ for the Northwest Territories. A one-way ANCOVA for four independent samples was significant ($F(3, 356)=7.15, p=0.0001$), indicating that the linear regression of age and total obliteration score for one or more wolf populations are significantly different than the others. To explore this, a one-way ANCOVA for two independent samples was conducted for each population pair. The Alberta wolf population was significantly different from the Yellowstone Stressed, Yellowstone Unstressed, and Northwest Territories populations, being $F(1, 191)=9.27, p=2.66E-03$, $F(1, 202)=18.95, p=2.10E-05$, and $F(1, 203)=12.15, p=1.57E-04$ respectively. All other population comparisons were not significantly different from each other.

Suture specific patterns for wolves

Obliteration occurs rapidly in the basisphenoid-basioccipital synchondrosis, with scores of 0 found only in individuals younger than 1.5 years (mean = 0.68 years) (Table 3). Therefore, an unobliterated basisphenoid-

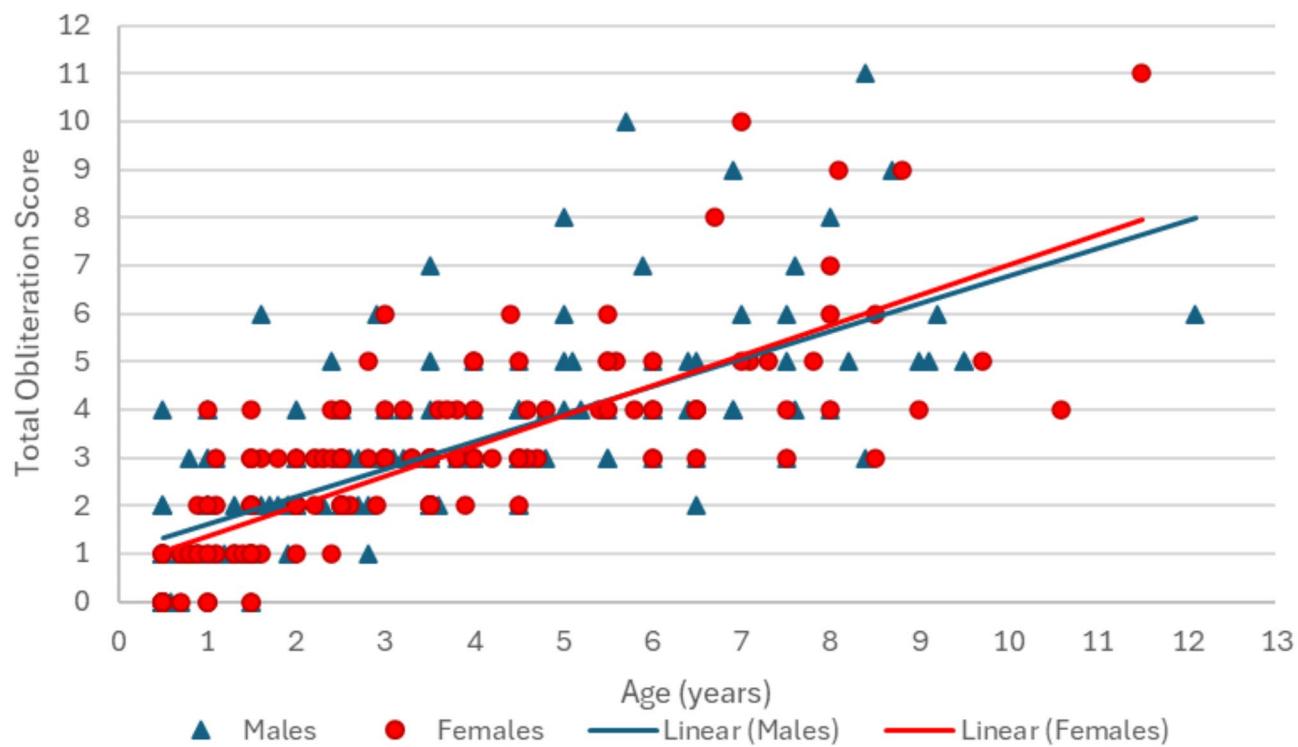


Fig. 1. A scatterplot of the total obliteration score and age by sex with linear regression lines shown.

Group	N	R ²	Constant	Coefficient	p value
Total population	371	0.55	0.91	0.60	5.82E-14
Males	164	0.51	1.05	0.57	9.57E-08
Females	180	0.60	0.73	0.63	4.59E-06

Table 1. Linear regression statistics for total obliteration scores and ages for the total wolf population and the identified males and females.

basioccipital synchondrosis is a reliable indicator of a juvenile wolf. However, full obliteration of the basisphenoid-basioccipital synchondroses occurs in wolves aged 0.5 years and up. All other suture groups tend to begin obliteration at a much older mean age, with scores of 1 (marking at least some obliteration, see Methods) beginning at mean ages of 4.26, with the highest mean age (8.03 years) for the initiation of obliteration occurring in the internasal (Table 3). Scores of 2, which mark more extensive or full obliteration, show higher mean ages across all suture/synchondrosis groups, except for the internasal, where no individuals exhibited greater than 25% obliteration.

Total obliteration scores for the total wolf population ranged from 0 to 11, with some overlap across all age groups (Fig. 3). Wolves under one year of age show relatively little overlap with those in the other age categories. Individuals from 1.0 to 1.9 years have scores overlapping with many wolves that were 2.0 to 3.9 years of age, but fewer individuals of this age range had scores overlapping with older age groups. Wolves ranging in age from 4.0 to 7.9 years overlapped mostly with wolves that were 8.0 years and older.

Total obliteration score between dogs and wolves

Comparisons of the relationships between total obliteration score and age in dogs and wolves (Fig. 4) reveals that the two variables are more strongly positively correlated among wolves, with the Pearson's r value of 0.74, $p=5.82E-14$. In contrast, the correlation in the dogs has an r value of 0.68, $p=1.14E-10$. ANCOVA tests revealed significant differences for the regression slopes (Table 4) of wolves and dogs ($F(1, 944)=61.48$, $p\leq 0.0001$).

Total obliteration score and age group between dogs and wolves

Examination of total obliteration scores for wolves and dogs by age group better reveals how the pattern and extent of obliteration differ between the two groups (Fig. 5 and Table 5). Divergence in total obliteration scores emerge between dogs and wolves beginning with the 2–3.9 years (young adult) category. The two younger age groups, namely the juveniles (0.5–0.9 years) and juvenile/young adults (1.0–1.9 years), show extensive overlapping scores between the dogs and wolves. Across the young adult (2–3.9 years), prime adult (4–7.9 years), and older

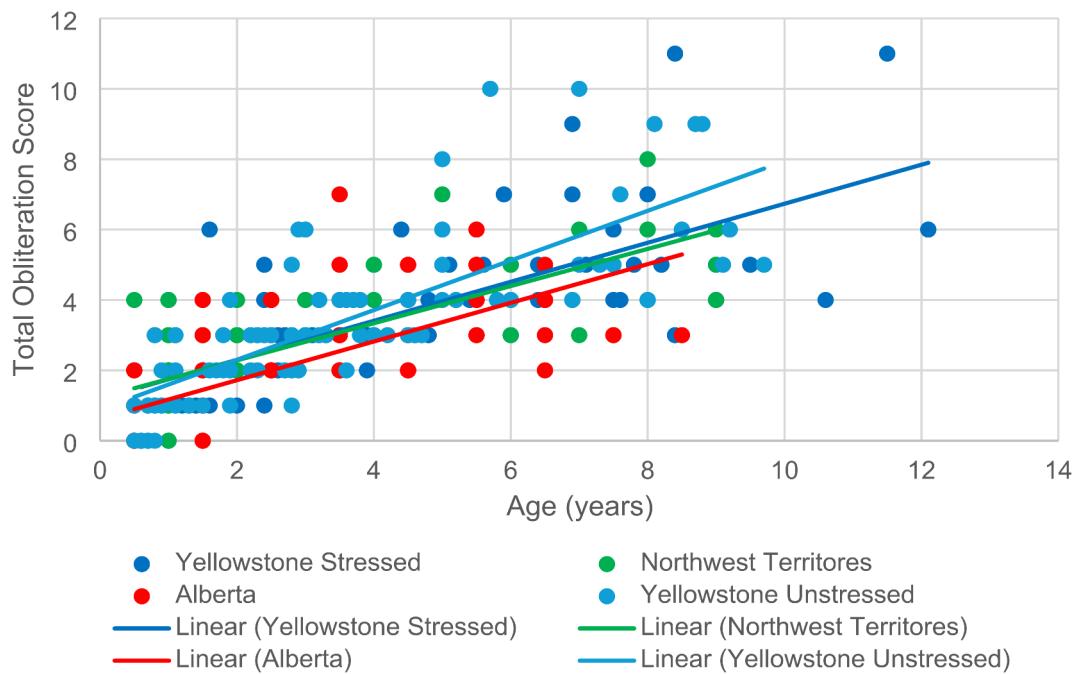


Fig. 2. Scatterplot of the total obliteration score and age for wolves, divided by population with linear regression lines shown.

Group	N	R ²	Constant	Coefficient	p value
Alberta	122	0.49	0.62	0.55	6.03E-04
Yellowstone Stressed	72	0.53	1.19	0.55	3.35E-04
Yellowstone Unstressed	83	0.60	0.89	0.71	1.89E-03
Northwest Territories	84	0.56	1.23	0.53	2.13E-08

Table 2. Linear regression statistics for total obliteration scores and ages for each wolf subpopulation.

Sutures and suture groups	Score 0 mean age (years), range	Score 1 mean age (years), range	Score 2 mean age (years), range
Basispheno-basioccipital	0.68, 0.5–1.5	1.23, 0.5–3.6	4.14, 0.5–12.1
Interpalatine and Intermaxillary	2.66, 0.5–9.0	5.58, 1.0–12.1	7.22, 5.0–9.0
Maxillo-palatine	2.81, 0.5–10.6	5.73, 0.5–12.1	8.20, 8.0–8.4
Premaxillo-maxillary (lateral)	1.73, 0.5–6.5	4.26, 0.5–10.6	7.65, 4.4–12.1
Nasal-premaxilla-maxilla-frontal	3.14, 0.5–12.1	6.40, 2.4–9.5	8.00, 4.5–11.5
Internasal	3.28, 0.5–12.1	8.03, 3.5–11.5	
Interfrontal	3.21, 0.5–12.1	4.26, 1.0–7.3	6.76, 2.9–11.5

Table 3. Descriptive statistics for the total wolf population for individual synchondroses, sutures, and suture groups by total obliteration score, including the mean age and age range for each in years. Note that for the internasal suture group, no wolves achieved a score of 2. Descriptive statistics for the dog population can be found in Supplementary Table S2.

adult (8.0+ years) categories, the total obliteration scores of the wolves are, on average, lower than those of dogs. That is, adult wolves tend to have lower obliteration scores than similarly aged dogs. These differences were assessed using two-tailed, two sample t-tests assuming unequal variance (Table 6). These tests reveal statistically significant differences between the total obliteration scores of wolves and dogs for the young adult ($t(66) = 4.54$, $p = 2.49E-05$), prime adult ($t(256) = 9.30$, $p = 6.31E-18$), and older adult ($t(29) = 6.39$, $p = 5.44E-07$) categories. Statistically insignificant differences are found between the total obliteration scores of wolves and dogs for the age categories of juvenile ($t(116) = 0.10$, $p = 0.92$) and juvenile/young adult ($t(62) = 1.39$, $p = 0.17$).

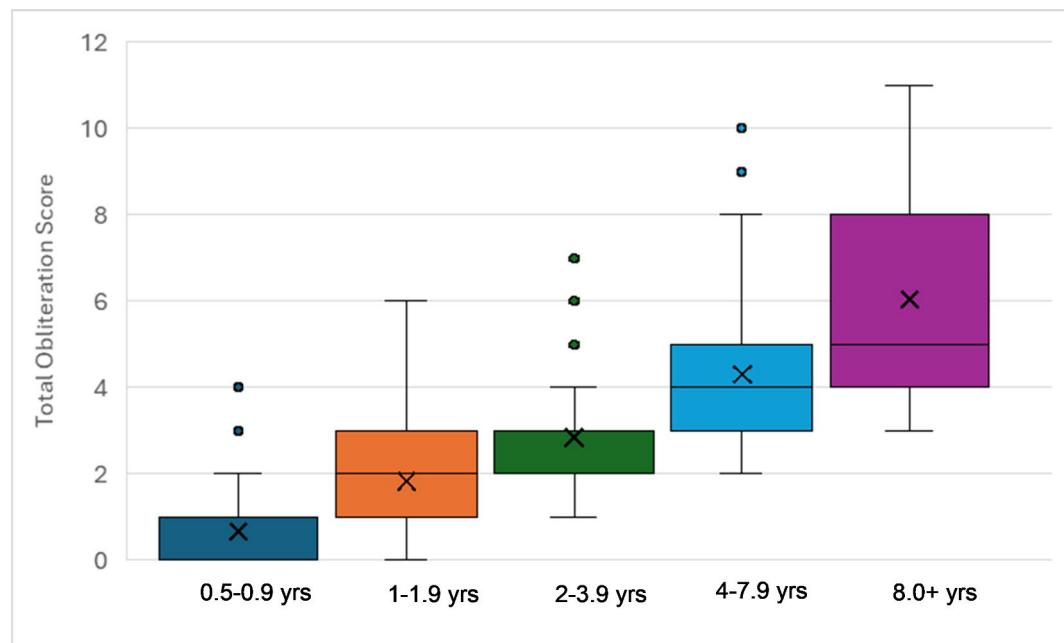


Fig. 3. Boxplots for total obliteration score and age category for wolves. For the boxplots, the bold horizontal lines mark the median scores, the boxes the extent of the upper and lower quartiles, and the whiskers denote the minimum and maximum values within the range. Circles mark outliers, and the X represents the mean value for each category.

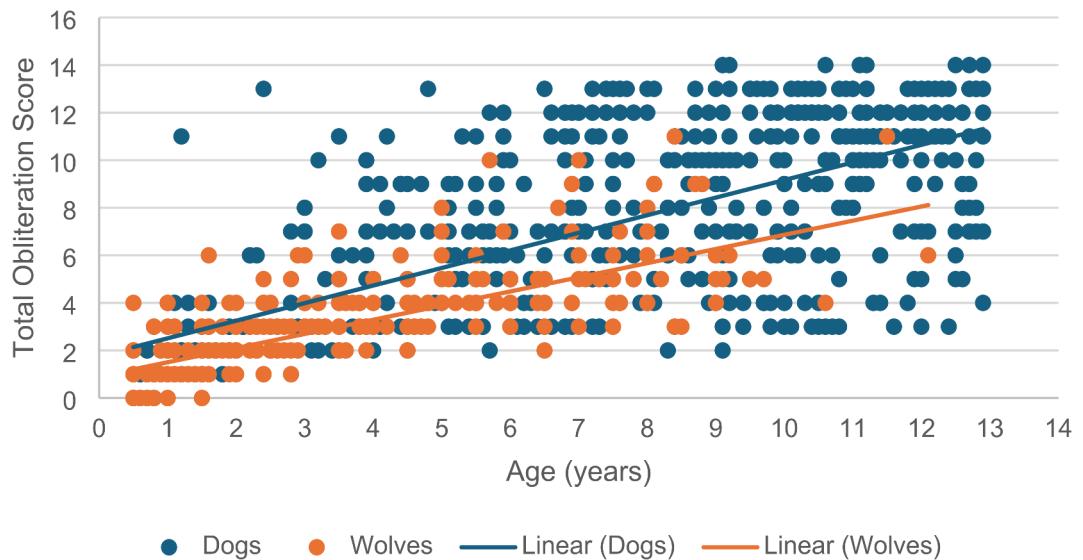


Fig. 4. A scatterplot of the total obliteration score and age for wolves and dogs with linear regression lines shown.

Group	N	R ²	Constant	Coefficient	p value
Wolves	371	0.55	0.91	0.60	5.82E-14
Dogs	576	0.47	1.77	0.74	1.14E-10

Table 4. Linear regression statistics for total obliteration scores and ages for the total wolf population the total dog population.

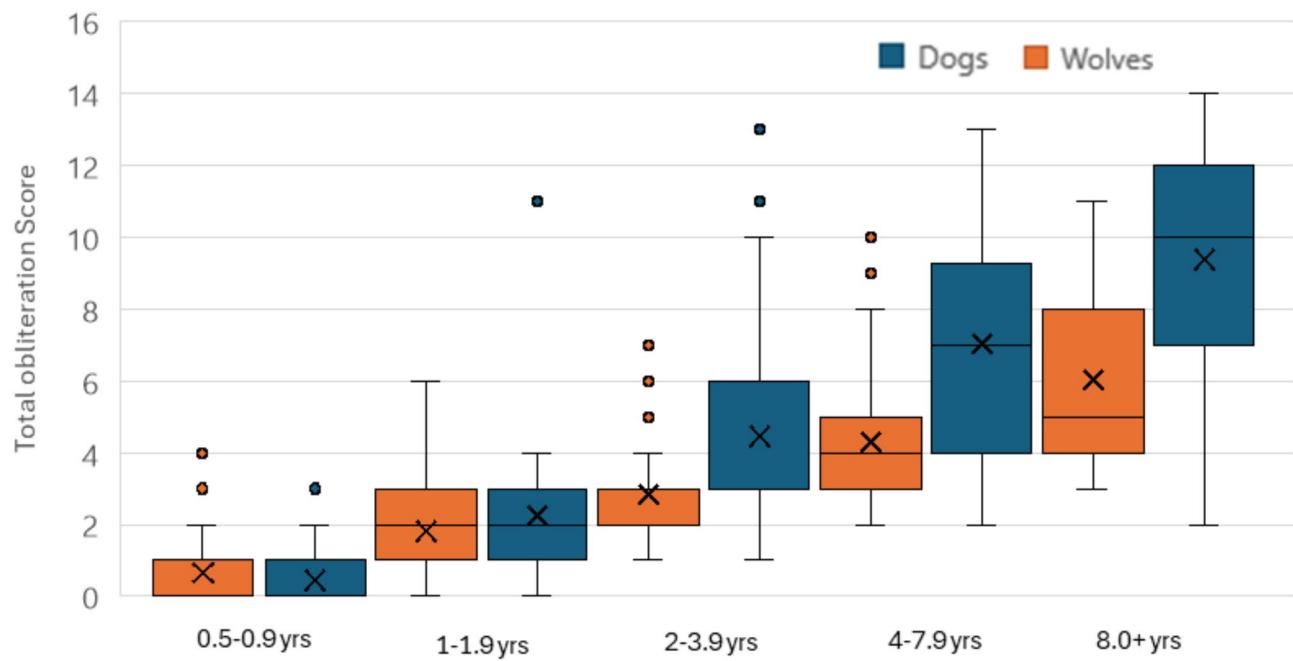


Fig. 5. Boxplots for total obliteration score and age category for the total population of wolves (orange) and dogs (blue). For the boxplots, the bold horizontal lines mark the median scores, the boxes the extent of the upper and lower quartiles, and the whiskers denote the minimum and maximum values within the range. Circles mark outliers, and the X represents the mean value for each category.

Age category (years)	N	Mean	Std. Dev.	Median	Min.	Max.
Wolves						
Juvenile (0.5–0.9 years)	58	0.66	0.89	0	0	4
Juvenile/young adult (1–1.9 years)	68	1.82	1.25	2	0	6
Young adult (2–3.9 years)	121	2.83	0.99	3	1	7
Prime adult (4–7.9 years)	101	4.30	1.59	4	2	10
Older adult (8.0+ years)	23	6.04	2.34	5	3	11
Dogs						
Juvenile (0.5–0.9 years)	33	0.45	0.79	0	0	3
Juvenile/young adult (1–1.9 years)	39	2.26	1.70	2	0	11
Young adult (2–3.9 years)	59	4.46	2.66	3	1	13
Prime adult (4–7.9 years)	166	7.04	3.20	7	2	13
Older adult (8.0+ years)	279	9.39	3.12	10	2	14

Table 5. Descriptive statistics for the total obliteration scores of the five age categories of the total wolf and dog populations.

	Test stat.	Deg. freedom	p value
Juvenile (0.5–0.9 years)	0.10	116	0.92
Juvenile/young adult (1–1.9 years)	1.39	62	0.17
Young adult (2–3.9 years)	4.54	66	2.49E–05
Prime adult (4–7.9 years)	9.30	256	6.31E–18
Older adult (8.0+ years)	6.39	29	5.44E–07

Table 6. Two sample t-test assuming unequal variance between the total obliteration score of dogs and wolves for each age category ($P(T \leq t)$ two-tail).

Individual suture obliteration score differences between dogs and wolves

Statistically significant differences were found between dog and wolf obliteration scores for each of the individual suture/synchondroses groups (Table 7). These results should be evaluated cautiously given the relatively small number of individuals from each age group (Table 5). Significant differences in the obliteration of the maxillo-palatine, premaxillo-maxillary (lateral), and nasal-premaxilla-frontal groups first appear in the young adult age category (2–3.9 years), a pattern which is mirrored in the total obliteration scores (Fig. 5). In the interfrontal group, obliteration scores diverge earlier between dogs and wolves, namely during the juvenile/young adult age category (1–1.9 years). The internasal, however, shows obliteration timing differences occurring later, during the prime adult age category (4–7.9 years). Both the basispheno-basioccipital and interpalatine and intermaxillary suture groups show variability in obliteration scores, with differences observed intermittently across the age categories.

Discussion

Wolf suture obliteration

This study had two primary findings. First, wolf total obliteration score and age were positively correlated, indicating that the extent of suture obliteration can be used to track age. Sex had no meaningful effect on this relationship, unlike in dogs, where males tended to have slightly higher obliteration scores than similarly aged females⁵. Subpopulation differences in patterning, including between groups with well-documented differences in diet, also were minimal and had no meaningful effect. The only wolf group exhibiting a statistically different relationship between age and suture obliteration score is the Alberta sample. The reasons for this are unclear. A nearly identical sample of the same Alberta wolves previously showed a significant relationship between age and tooth wear compared to essentially the same three wolf samples⁹. It is possible the Alberta wolves have slight errors in their age estimates, which were made decades before those of the other three wolf groups. Unfortunately, we have no data to test this possibility. Sample size may have some effect, as the Alberta sample ($N=122$) is considerably larger than those from Yellowstone (stressed and unstressed) and the Northwest Territories ($N=72$, 83, and 84, respectively). Regardless, removing the Alberta wolves from consideration had no statistically significant impact on the correlation between total obliteration score and age (see supplementary Fig. S1).

Total obliteration scores and age were more strongly correlated in wolves than in dogs, and the correlation coefficient for this relationship matches or exceeds that of most suture ageing methods for human remains³. Scoring of suture obliteration thus offers an expedient and non-destructive approach for ageing North American gray wolf skulls from modern or ancient contexts. This method will be most reliable for differentiating juveniles from adults, and it also provides some resolution in distinguishing younger adults from older adults. Our recommendation is to use this method in combination with other age estimation methods, such as cementum annulation or tooth wear ageing methods, to achieve the most dependable results^{9,11,12,14,17}. Ancient crania are often poorly preserved and recovered as fragments. This may limit the applicability of suture and synchondrosis patterning in that context. However, when teeth are absent or damaged in isolated crania (a common occurrence in archaeology and paleontology), cranial suture and synchondrosis obliteration patterning will be the only applicable age estimation method.

The ageing method developed in this study should be widely applicable to North American grey wolf crania, and likely grey wolf remains from other regions. However, care should be exercised if the wolf crania under examination come from animals with extremely small body sizes or unusual morphologies. Additional care needs to be taken when the taxonomic status of archaeological and paleontological specimens is unclear. For example, on the Northern Plains of North America, Indigenous dogs are historically described primarily as large and wolf-like^{26,27}. In many cases, morphological identification of archaeological canid remains from this region, even from recent periods, is particularly challenging^{28,29}. Suture obliteration methods for ageing both dogs and wolves might be cautiously applied in such cases. It also remains unclear when, during the evolution of domestic dogs, their suture obliteration patterns began to differ from those of wolves. In some cases, perhaps

	0.5–0.9 years	1–1.9 years	2–3.9 years	4–7.9 years	8.0+ years
Basispheno-basioccipital	$(t(69)=1.08, p=0.29)$	$(t(96)=-2.44, p=0.02)$	$(t(107)=-1.02, p=0.31)$	$(t(158)=-6.95, p=9.05E-11)$	$(t(286)=-13.35, p=6.27E-32)$
Interpalatine and Intermaxillary	$(t(32)=-2.65, p=0.01)$	$(t(101)=0.31, p=0.76)$	$(t(88)=-3.15, p=0.00)$	$(t(223)=-2.03, p=0.04)$	$(t(29)=-0.85, p=0.40)$
Maxillo-palatine	$(t(57)=-1.90, p=0.06)$	$(t(67)=0.31, p=0.76)$	$(t(68)=-4.35, p=4.67E-05)$	$(t(254)=-4.05, p=6.69E-05)$	$(t(32)=-3.45, p=0.00)$
Premaxillo-maxillary (lateral)	$(t(57)=0.57, p=0.57)$	$(t(72)=-0.38, p=0.70)$	$(t(112)=-5.07, p=1.57E-06)$	$(t(215)=-3.70, p=0.00)$	$(t(30)=-0.60, p=0.55)$
Nasal-premaxilla-maxilla-frontal	NA, insignificant differences	$(t(38)=-1.98, p=0.06)$	$(t(63)=-2.39, p=0.02)$	$(t(230)=-8.04, p=4.68E-14)$	$(t(33)=-6.41, p=2.92E-07)$
Internasal	NA, insignificant differences	$(t(38)=-1.00, p=0.32)$	$(t(64)=-1.11, p=0.273)$	$(t(169)=-7.84, p=4.88E-13)$	$(t(49)=-8.55, p=2.79E-11)$
Interfrontal	$(t(32)=-1.00, p=0.32)$	$(t(42)=-2.33, p=0.02)$	$(t(64)=-4.66, p=1.64E-05)$	$(t(257)=-13.21, p=9.44E-31)$	$(t(29)=-7.61, p=2.15E-08)$

Table 7. Two sample t-test assuming unequal variance between individual suture group scores for dogs and wolves for each age category ($P(T \leq t)$ two-tail). Significance is denoted by bold characters.

with the remains of the earliest domestic dogs, wolf obliteration patterning may be more useful for ageing than such patterns in modern domestic dogs⁵.

Comparisons of wolf and dog suture obliteration

Second, this study demonstrated that medium to large-size mesocephalic or dolichocephalic (klinorhynch) dogs begin exhibiting more extensive suture closure than wolves during early adulthood, at about two to four years of age. These differences, scored as a total obliteration score, persist through the remainder of the adult lifecycle, but vary somewhat in extent and timing when individual suture groups are examined. Several potential factors likely contribute to creating these differences, including differences in physical stresses in the cranium, as well as alteration of development, ageing, and head shape in dogs through domestication.

It is possible that the extent of cranial stress experienced during life could manifest in dog and wolf suture obliteration patterning. As mentioned, open and unobliterated sutures can help redistribute biomechanical strain in the skull resulting from heavy mastication and behaviours such as predation and fighting^{2,4,30}. Closed and obliterated sutures would produce a more rigid structure, presumably less effective at redistributing such strains. Divergence in behaviours and feeding practices between dogs and wolves could contribute to the more extensive suture obliteration observed here in dogs. The diets of grey wolves in Alberta, Yellowstone National Park, and the Northwest Territories are primarily centred on large ungulates such as elk (*Cervus elaphus*), moose (*Alces alces*), caribou (*Rangifer tarandus*), and bison (*Bison bison*)^{9,31–34}. They are social hunters who compete with others for food, social dominance, and mates, and extract within-bone nutrients from carcasses when necessary^{35–38}. Conversely, all dogs analyzed were pet or working dogs fed by their human keepers, meaning they likely did no hunting, little scavenging, and relatively little fighting with other dogs. Most were likely fed soft foods, but we have no dietary data to assess this. In general, we should expect these modern dogs to have experienced less strain in their skulls than the free-ranging wolves.

Experimentation with rats indicates that switching to a softer diet can result in facial sutures that are simpler, narrower, and at times, more extensively obliterated³⁹. Conversely, research on mice has found that increased masticatory muscle mass resulted in decreased suture stiffness, seemingly allowing mechanical loads to dissipate better⁴⁰. In previous studies, Yellowstone National Park wolves with abundant prey (when first reintroduced to the park; our unstressed group) were shown to have experienced somewhat lower rates of tooth fracture and tooth wear than those inhabiting the park during a period of lower prey availability^{9,34}. This presumably resulted from the latter wolves more fully processing each carcass attained—they more extensively gnawed skeletal elements than wolves with high prey availability. When the two Yellowstone wolf groups were compared in this study, no statistically significant relationships were found between the extent of cranial suture obliteration and age. Perhaps the differences in masticatory stress experienced by these two wolf groups were of too low magnitude to noticeably affect these patterns.

It seems more likely that differences in the extent of suture obliteration between dogs and wolves were largely genetically encoded and emerged during domestication. Masticatory strain probably began to decline in dogs millennia ago through the relaxation of selection provided by living with humans. Stable isotope analysis of archaeological dog remains demonstrates that dietary differences were present between many dogs and wolves by the Middle Holocene, and possibly earlier⁴¹. At least in Siberia, many early dogs had diets that paralleled those of the people who kept them, while wolf diets generally continued to focus on large-bodied ungulates. These early dog diets were variable but at times included freshwater and marine foods such as fish and sea mammal blubber, as well as cultivated crops and other human food waste in some settings⁴¹. Body sizes also declined over the Holocene in many domestic dogs in Eurasia, meaning that their abilities to function as large mammal hunters decreased (i.e., they had reduced bite strength), likely resulting in increased reliance on small game, human provisioning, and scavenging⁴¹. These longstanding patterns likely decreased the need for cranial element deformation in domestic dogs, potentially allowing for a diachronic increase in individuals with more extensive suture obliteration.

Changes in the timing and rate of ontogeny and ageing that accompanied dog domestication may be even more critical to the differences seen between the total obliteration scores of dogs and wolves as they age. Modern breed dogs have remarkably diverse head shapes, far more so than wolves⁴², and some of this variation is present in our dog sample. Such differences in head shape between dogs and wolves emerge in prenatal and early postnatal development and are both neomorphic (unique in dogs) and paedomorphic—juvenile dogs of a given age are shaped like younger wolves²³. The timing of suture closure should correlate with adult cranium morphology and size to some degree, although these relationships are variable, complex, and poorly documented in most species, including canids^{4,21,30,43}. If some sutures in dogs close earlier than those in wolves while developing paedomorphic and neomorphic shapes, this should allow for earlier initiation of suture obliteration and a greater extent of suture obliteration over a lifetime.

Finally, it is worth considering other factors that might have contributed to the differences in the extent of suture obliteration between dogs and wolves. Nearly all the dogs examined for this study were modern breed animals, characteristically produced through strict selection (narrow breeding stock) for appearance and sometimes behaviour⁴⁴. Utilizing very limited breeding pools to achieve discrete appearances in dogs could have fixed deleterious patterns of extensive suture obliteration in some breeds. Some skull rigidity also may have become fixed in breed-specific dogs unintentionally through selection for behavioural traits. For example, Geiger and Haussman²¹ suggest that dogs bred for fighting or holding prey may have inadvertently developed increased rigidity in the cranium through suture obliteration as a means of preventing injury to the brain. Some modern dogs also have markedly different facial muscle morphology and physiology than wolves^{45–47}. The influences of such differences on suture obliteration extent remain unknown but point to the complexity of the changes dogs have undergone over the course of their domestication history.

Suture and suture groups, portion scored	Scoring of obliteration extent
Basispheno-basioccipital, entire	0 = none; 1 = partial; 2 = complete
Interpalatine and Intermaxillary, entire	0 = none; 1 = partial; 2 = complete
Maxillo-palatine, entire	0 = none; 1 = partial; 2 = complete
Premaxillo-maxillary (lateral) entire most affected side	0 = none; 1 < 50%; 2 > 50%
Nasal-premaxilla/maxilla/frontal, entire most affected side	0 = none; 1 < 25%; 2 > 25%
Internasal, entire	0 = none; 1 < 25%; 2 > 25%
Interfrontal, entire, except caudal-most 10%	0 = none; 1 < 25%; 2 > 25%

Table 8. Synchondroses, sutures, and suture groups analyzed in the study and their associated scoring schemes.

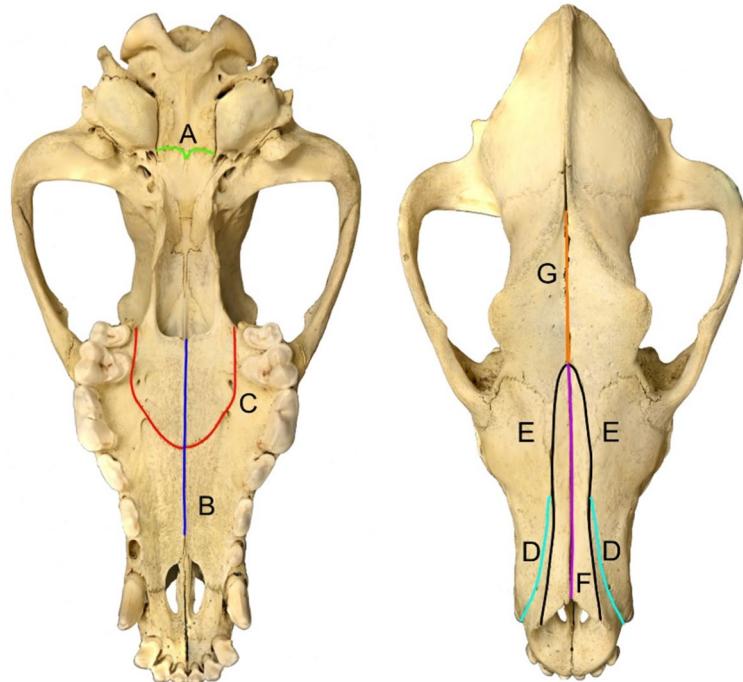


Fig. 6. Sutures scored in the study. (A) Basispheno-basioccipital synchondrosis (green); (B) Interpalatine and Intermaxillary suture group (dark blue); (C) Maxillo-palatine suture (red); (D) Premaxillo-maxillary lateral sutures (light blue), both sides shown; (E) Nasal-premaxilla/maxilla/frontal suture group (black), both sides shown; (F) Internasal suture (purple); (G) Interfrontal suture (orange).

Materials and methods

A total of 371 modern, known-age wolves and 576 known-age pedigree dogs were examined in this study. The wolf population stemmed from collections curated at the University of Alberta (with permission from R. Losey), Royal Alberta Museum (with permission from Sean McFadden), and the Yellowstone Heritage and Research Center (with permission from Miriam Watson), and includes individuals from the boreal forests and Rocky Mountains of Alberta, Canada, the boreal forest or tundra ecozones of the Northwest Territories, Canada, and from Yellowstone National Park, U.S.A. The individuals from Yellowstone National Park were divided into two populations, dietarily stressed and unstressed, following Van Valkenburgh et al.³⁴. Both the Alberta and Northwest Territories wolves were age estimated (the Alberta wolves in the 1980s, likely by Alberta Fish and Wildlife; the Northwest Territories wolves in the late 2010s and 2020s by Matson's Laboratory, Montana, U.S.A.) using cementum annulation, which is currently the most reliable and expedient method of ageing canids outside of having known-aged individuals^{9,13,48}. The wolves from Yellowstone National Park were collared individuals, most of which were tracked year-round since birth, whose age at death was recorded in years and months. The total wolf sample includes individuals aged 0.5–12.1 years.

The dog sample was adapted from Losey and Nomokonova⁵ and was curated at the Albert Heim Collection at the Natural History Museum of Berne, Switzerland (with permission from Dr. Anne-Claire Fabre). The dog sample included breeds which are mesocephalic or dolichocephalic and are of similar size to the wolves analyzed (see supplementary Table S1). Additionally, only individuals whose ages overlapped with those of the wolves were included in this study, as the lifespan of dogs typically exceeds that of wild wolves^{49,50}. Specifically, the

analyzed dog sample included individuals aged 0.5–12.9 years. Due to the nature of the modern dog sample, the age profile was skewed to favour older individuals (mean = 7.36 years), whereas, in the wolf populations, younger individuals are more numerous (mean = 3.35 years) (see supplementary Fig. S2). This appears to have little meaningful effect on our results, as differences in the extent of suture obliteration between dogs and wolves emerged early in the lifecycle. For both wolves and dogs, individuals with pathological or traumatic lesions were excluded from this study as trauma and disease can affect suture conditions in dogs and likely wolves as well^{15,21,25}.

Seven suture groups for each specimen were recorded according to Losey and Nomokonova⁵, including the basispheno-basioccipital, interpalatine and intermaxillary, maxilla-palatine, premaxillo-maxillary (lateral), nasal-premaxilla/maxilla/frontal, internasal, and interfrontal sutures and synchondroses. All specimens analyzed for this study were scored by R. Losey. Obliteration scores of 0 (no obliteration), 1 (partial obliteration), or 2 (complete obliteration) were assigned to each suture group on each of the wolf and dog specimens (Table 8 and Fig. 6). Examples of scoring for the Basispheno-basioccipital and Premaxillo-maxillary (lateral) can be found in Figs. 7 and 8, respectively. Unobliterated suture or synchondrosis sections are defined by visible suture lines (whether they were closed or open). Obliterated sections of sutures and synchondroses were defined by the absence of the suture line—they were not visible due to bone growth that bridged the line. When only a portion of a suture or synchondrosis was obliterated, it was considered partially obliterated. When the total line was obliterated (not visible), it was considered completely obliterated.

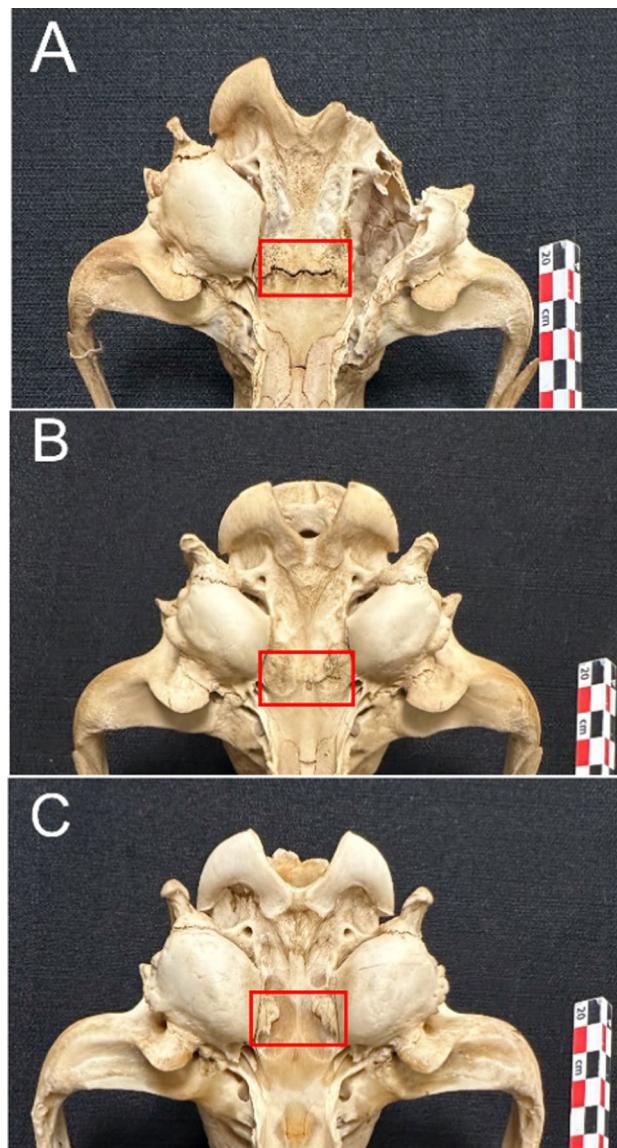


Fig. 7. Sample scoring of the basispheno-basioccipital suture group. (A) shows a score of 0, with no obliteration. (B) shows a score of 1, with partial obliteration. (C) shows a score of 2, with complete obliteration. The red box highlights the suture being examined. Suture obliteration can initiate at any location, and to correctly score obliteration, one should refer to the definitions of scores in Table 8.

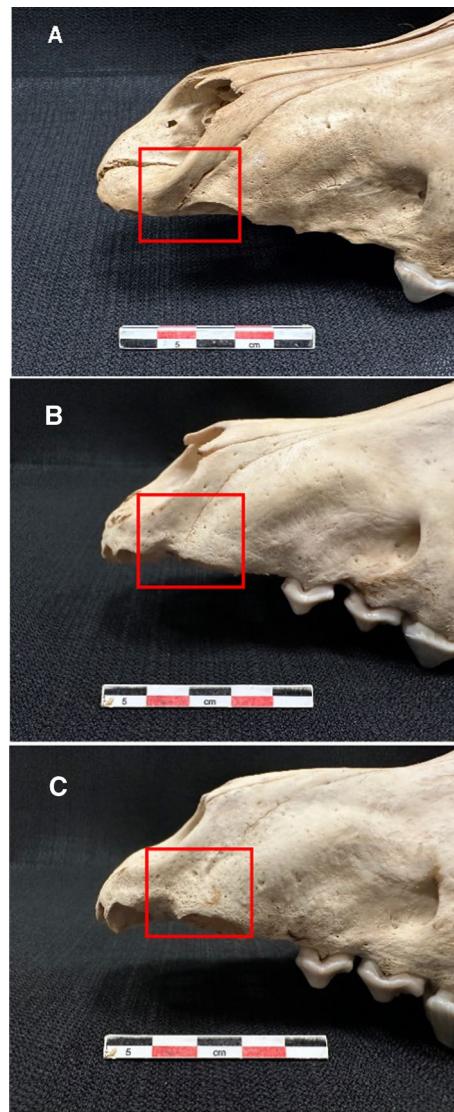


Fig. 8. Sample scoring of the premaxillo-maxillary (lateral) suture group. (A) shows a score of 0, with no obliteration. (B) shows a score of 1, with < 50% obliteration. (C) shows a score of 2, with > 50% obliteration. The red box highlights the suture being examined. Suture obliteration can initiate at any location, and to correctly score obliteration, one should refer to the definitions of scores in Table 8.

All statistical analyses were completed in Microsoft Excel V2410. First, the total wolf population was examined independently to evaluate the relationship between total obliteration score and age in wolves. Scatterplots, linear regressions, and Pearson's correlations were used to determine how sex and individual wolf population affect correlations between total obliteration score and age. An ANCOVA was then used to determine the significance of the difference in slope between sex and population. Second, the wolf population was compared with the dog population to explore the differences in suture obliteration based on species. A scatterplot, linear regression, and Pearson's correlation were employed to explore the relationship between total suture obliteration scores and age, in both canid populations. An ANCOVA was also used here to determine the significance of the regressions. A box and whisker plot was then used to compare the obliteration score of wolves and dogs, with the populations divided into five age categories of 0.5–0.9 years (juvenile), 1–1.9 years (juvenile/young adult), 2–3.9 years (young adult), 4–7.9 years (prime age adult), and 8.0+ years (older adults), following Losey and Nomokonova⁵ age categories for dogs. Two-tailed, two-sample t-tests assuming unequal variances were then used to determine the significance of the observed patterns.

Data availability

All data generated or analyzed during this study is included in this published article.

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Author contributions

M.B. and R.L. wrote the manuscript text, analyzed the data, and prepared the figures. R.L. and T.N. collected the data. H.D.C., N.J., and A.W. edited the manuscript and provided specimens for data. M.B. and R.L. provided funding and designed the project.

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Declarations

Competing interests

The authors declare no competing interests.

Additional information

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