



Morphometric evidence for the differentiation of the Himalayan wolf *Canis lupus chanco* (Canidae; Carnivora)

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Abstract

The taxonomy of wolves (*Canis* sp. complex) is under increasing scrutiny due to molecular evidence revealing the existence of multiple cryptic lineages. Among these, the Himalayan wolf (*Canis cf. lupus chanco*), native to the Tibetan Plateau and the Himalayas, represents one of the most ancient lineages in Eurasia. Its morphological distinction from grey wolf populations remains poorly understood. In this study, we evaluated the morphological differentiation of the Himalayan wolf by analyzing specimens from museum collections using linear and 2D geometric morphometrics. Our comparative analysis included skulls from various wolf populations across Eurasia, grouped according to known genetic lineages. Although linear measurements failed to reveal clear diagnostic features, geometric morphometric analysis indicated that Himalayan wolves possess a shorter muzzle and wider zygomatic arch than other populations. These traits may reflect adaptations to their environment and prey preferences. However, the overlap with other wolf populations was significant, and cross-validation analyses showed low reclassification rates, indicative of morphological conservatism within Canidae. Moreover, several museum specimens previously labeled as Himalayan wolves were misidentified, complicating the taxonomic assessment. Our findings provide support for the subtle morphological distinctiveness of the Himalayan wolf, though further integrative studies incorporating genomic and 3D modeling approaches are required to clarify the taxonomic status of this group.

Keywords Taxonomy · Identification · Museum samples · Linear measurements · Cryptic species

Introduction

Although the family Canidae (Carnivora) includes some of the most charismatic mammals, such as wolves and dogs, its taxonomy remains unresolved. In the 19th century, early taxonomists and explorers described numerous regional species, which were later consolidated into a few large canid species by influential early 20th-century publications

(e.g., Allen 1939; Pocock 1935). With advancements in molecular studies, these species have since been split again, confirming several cryptic or previously lumped canid species (Rueness et al. 2011; Prevosti et al. 2013; Viranta et al. 2017), with others suggesting the existence of even more (Statham et al. 2014; Goddard et al. 2015; Atickem et al. 2018). Accurately describing these species is challenging due to morphological conservatism and intraspecific variation within the family (Prevosti et al. 2013; Machado and Teta 2020). The rarity of these species in museum collections, combined with incomplete data from older records, further exacerbates the potential for misidentification and confusion (Kitchener et al. 2020). In this study, we tackle these challenges by using museum collections to evaluate the morphological differentiation of the Himalayan wolf (*Canis cf. lupus chanco*), a potential cryptic wolf species.

Since Pocock (1935), the Holarctic grey wolf (HW, *Canis lupus*) has largely been considered a single species with a vast distribution across the Holarctic region. However, recent genetic evidence suggests that this group

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actually comprises multiple lineages with distinct evolutionary histories. In North America, genetic and fossil studies have revealed at least two ancient wolf lineages: the red (*Canis rufus*) and Eastern (*Canis cf. lupus lycaon*) wolves (Kurtén 1974; Sacks 2021; VonHoldt and Aardema 2020). In Eurasia, genetic studies have uncovered a deep ancestry and isolation of two Asian wolf subspecies, the Indian wolf (*Canis cf. lupus pallipes*) and the Himalayan wolf, both of which are among the oldest wolf lineages (Aggarwal et al. 2003; Werhahn et al. 2020; Hennelly et al. 2021, 2024).

Despite these deep historical divergences revealed by molecular data, morphological studies within Canidae have lagged significantly behind (Prevosti et al. 2013; Machado et al. 2020). Morphological differentiation is essential for establishing diagnostic features, and no integrative taxonomy effort is complete without a thorough assessment of specimens in natural history museums. Thus, this study has two main objectives: first, to critically evaluate the Himalayan wolf samples in museum collections to identify potential shortcomings, and second, to provide a morphometrical characterization of the Himalayan wolf to further the discussion of its taxonomic status.

Materials and methods

Sample

We took linear measurements and photographed wolf skulls in the following natural history museum collections: Academy of Sciences of the Drexel University, Philadelphia (ANSP); Field Museum of Natural History, Chicago (FMNH); National Natural History Museum of Smithsonian Institution, Washington DC (USNM); Museum of Comparative Zoology, Harvard (MCZ); Museum for Natural History, Berlin (MfN); Natural History Museum, London (NHM); National Museum for Natural History, Paris (NMNH) and Finnish Museum of Natural History, Helsinki (UN). The full list of specimens can be found on Appendix 1. We focused on collecting data on a large sample of confirmed Himalayan wolf skulls but only accepted specimens we could confidently assign to the correct population (see results).

Morphometrics

To test for the morphological differentiation among groups, we employed both linear morphometrics and 2D geometric morphometrics. For linear morphometrics, we utilized 21 measurements taken by digital calipers on the dentition, skull and mandible (Fig. 1). The dental measurements included anteroposterior lengths of the selected teeth (the canines (IC1, lc1), lower carnassial m1 (lm1) and m2 (lm2),

upper P3 (IP3), carnassial (IP4) and M1 (IM1). For the cranium we included the total length (TL) and palatine (PL) length as well as measurements of (mediolateral) widths (intercanine breadth (C: C), intercanassial breadth (P: P), zygomatic breadth (ZB), interorbital breadth (IOB), post-orbital process (POP) and constriction breadths (POC), and occipital intercondylar breadth (OCB). In addition, the length and width of the auditory bullae (ABL and ABW) were measured. For the mandible, the length from condyle to canine (c: cond) and the height behind the carnassial (h: behm1) were measured. For the measurement protocol, see Viranta et al. (2017). We compared each HGW geographical group to the Himalayan wolf sample through pairwise t-tests and applied a Bonferroni correction for multiple tests.

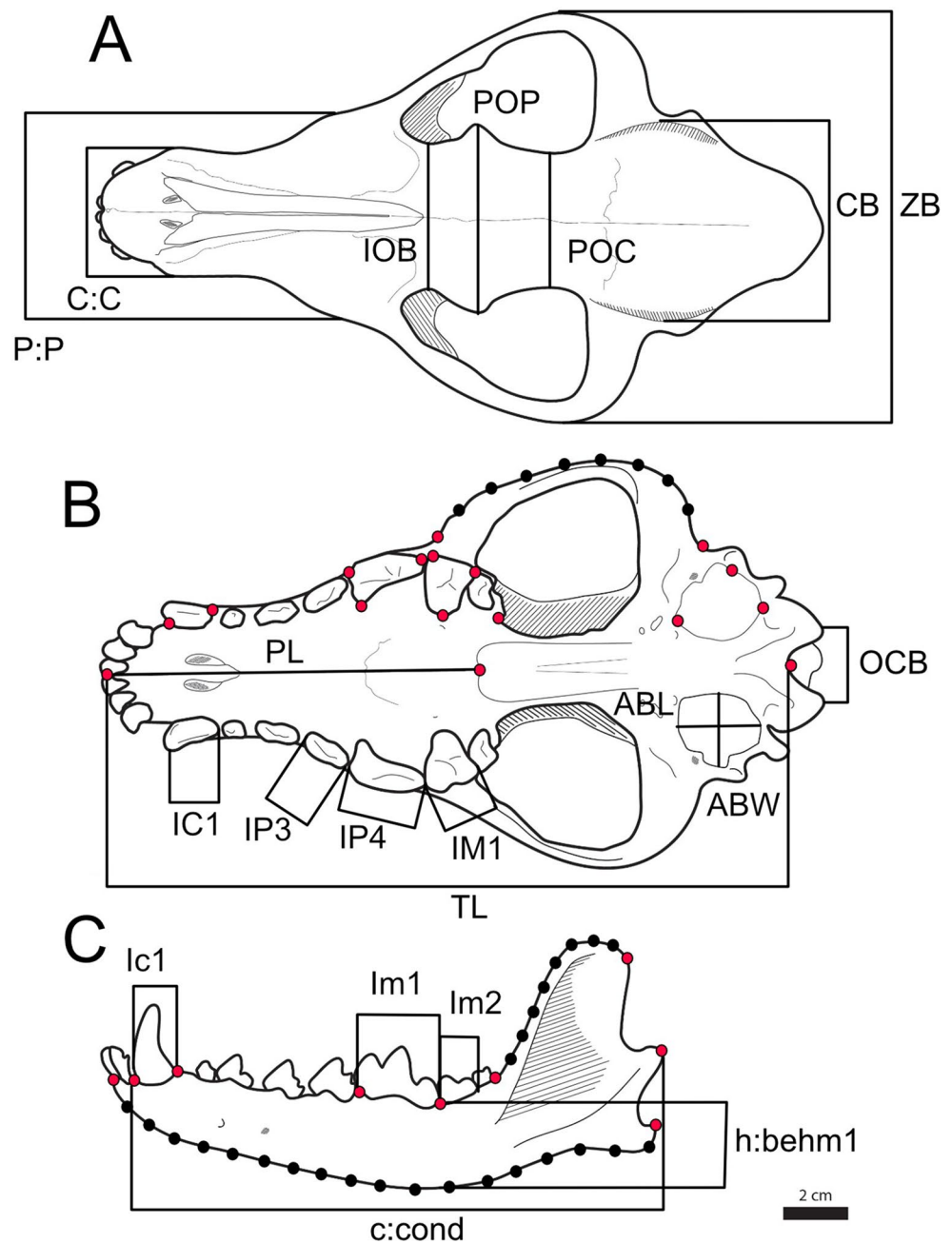
For the 2D morphometrics we utilized standardized photographs in the ventral view of the skull ($n=101$) and the lateral view of the mandible ($n=94$). The plane of the photograph was aligned with the palate and with the body of the mandible, respectively.

We placed landmarks and semi-landmarks on these structures to describe the relative size and shape of different regions of the skull and mandible using the software TpsDig 1.32 (Rohlf 2015). For the ventral view, we digitized 31 landmarks (three along the midline, 14 bilaterally symmetric) and two bilaterally symmetric curves (8 semi-landmarks each; Fig. 1B). For the mandible, we digitized nine landmarks and two curves (with eight and 18 semi-landmarks each; Fig. 1C). Due to the presence of damaged specimens (25 skulls and three mandibles), we employed a thin-plate spline (Bookstein 1989) approach to estimate the missing data from both the mirror image of an individual (for bilaterally symmetric landmarks) or mean shapes of a sample of neighboring specimens (Schlager 2017).

Each dataset was subjected to a general Procrustes alignment (GPA) with a bending.

energy minimization sliding step for the semi-landmarks (Rohlf and Slice 1990; Slice 2001; Gunz et al. 2005). This approach removes the arbitrary effects of orientation, placement, and scale of individuals on the photographs while maximizing individual similarity for landmarks with no clear homology among specimens (semi-landmarks). For the ventral view of the skull, configurations were superimposed to their mirror image and averaged to remove the effect of asymmetry in the data (Klingenberg et al. 2002; Cardini 2016). The resulting residuals of these analyses were then subjected to a non-parametric Multivariate Analysis of Variance (npMANOVA), which allows to test for shape differences among groups globally and in a pair-wise manner (Baken et al. 2021). We then employed canonical variate analyses (CVA) to visualize group differences and to evaluate multivariate overlap using a jackknife (“leave-one-out”) cross-validation approach (Machado and Hingst-Zaher

Fig. 1 Himalayan wolf skull in dorsal (A) and ventral (B) views and mandible in lateral view (C) showing measurements and landmarks used in morphometric analyses. Lines represent linear distances, red dots are fixed landmarks and black dots are semi-landmarks. The landmarks were placed on photographs taken on the specimens using the software TpsDig 1.32 (Rohlf 2015)



2009). All morphometric analyses were implemented with the package Morpho (Schlager 2017) and geomorph (Baken et al. 2021).

Results

Affinity of the samples

For the comparison we used Old World wolf skulls from various localities. We grouped them in populations according to previous genetic analysis (Loog et al. 2020; Pilot et

al. 2019; Wang et al. 2019). Our comparative groups were: Western Eurasia, North Asia, South China, Near East (Arabian wolf) populations and Indian wolf.

For the Himalayan wolf sample we accepted genetically confirmed specimens as well as the ones clearly inside the Himalayan wolf distribution range (shown in orange in Fig. 2) based on the IUCN Red List assessment for the Himalayan wolf (Werhahn et al. 2024). This range includes the Tibetan Plateau of western China, the Himalayas of India, Nepal and Bhutan. Historically also the wolves from Mongolia have been considered to be part of *C. l. chanco*. Recent studies have revealed that the wolves of Mongolia

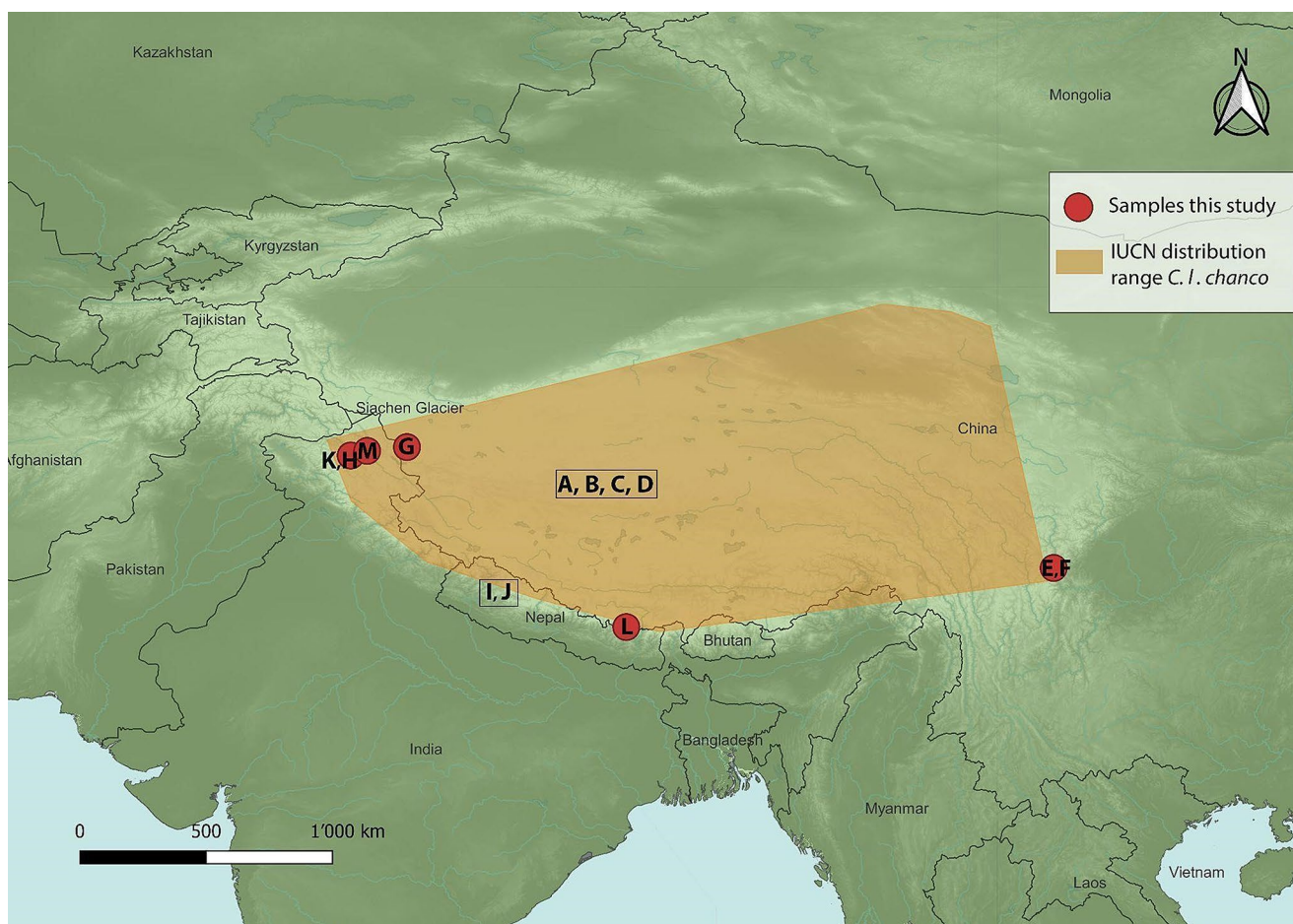


Fig. 2 The map shows the Himalayan wolf samples (red dots show known locations, while for samples marked with boxes only regional location information is available) used in this study with museum identification numbers: (A) ANSP 17496, (B) ANSP 17497, (C) ANSP 17498, (D) NHM 1875.4.10.1, (E) MfN ZMB_Mam_048867,

(F) MfN ZMB_Mam_052523, (G) MfN ZMB_Mam_091078, (H) NHM 25.10.28.1, (I) NHM 35.1.10.1, (J) NHM 58.6.24.61, (K) NHM 36.11.22.1, (L) NHM 59.640.a, and (M) USNM 198457. The orange polygon illustrates the IUCN Red List distribution range for *C. l. chanco*

are not part of the *C. l. chanco* lineage (e.g. Hennelly et al. 2021; Werhahn et al. 2020).

We collected data from three museums in the USA (two of them had Himalayan wolves) and four museums in Europe (two of these had Himalayan wolves). The ANSP catalog lists three Himalayan wolf specimens from Khan Tshumar (Tibet). These were all accepted. The USNM catalog lists five skulls indicated as Himalayan wolves. We accepted two of them and rejected two skulls from Shanxi China and one from Kashmir confirmed as a HGW by mtDNA in Sharma et al. (2004). The MCZ catalog has two Himalayan wolf specimens from Mongolia. As Mongolia is not considered part of the Himalayan wolf range (Werhahn et al. 2024), these were not accepted. In the collections of the NHM eight specimens were accepted as Himalayan wolves. Of these, two were from Ladakh Kashmir (one confirmed by DNA by Hennelly, 2023), three from Tibet, three from Nepal (all confirmed by DNA by Sharma et al. 2004). The MfN has

two specimens from Tibet and one from the Indian Himalayas and these were all accepted.

Morphometrics

Linear morphometrics revealed that no single measurement could distinguish the Himalayan wolf from other wolf groups (Table 1). For instance, lCi and lml were significantly smaller in the Indian wolf (*C. l. pallipes*), lml, Hbehm1, IP4, CC, BW, and PP were smaller in The Arabian wolf (*C. l. arabs*), Ccond, lml, IP4, lM1, TL, CC, ZB, POP, and OCB were larger in Western Eurasian groups and lM1, TL, IOB, POP, POC, and OCC were larger in North Asian samples. No significant differences were observed between South Chinese samples and the Himalayan wolves. When all measurements were considered as a ratio of the total skull length, no comparison yielded a significant difference.

Table 1 Average values for measurements taken on the Eurasian Wolf groups with number of specimens included. Value in parenthesis represents standard deviations. Values in bold were considered significantly different from the Himalayan Wolf (*C. l. chanco*) ($p < 0.05$). Last column contains the values taken from a verified hybrid between the Himalayan Wolf and grey Wolf (Sharma et al. 2004)

	C.l.chanco	C.l.pallipes	C.l.arabs	W Eurasia	N Asia	S China	Hybrid
lCi	13.3(±1.27) (n=8)	11.4(±1.6) (n=20)	10.22(±1.82) (n=4)	14.14(±1.63) (n=26)	12.72(±1.37) (n=5)	12.33(±1.17) (n=10)	14
lm1	27.22(±1.21) (n=11)	25.49(±1.54) (n=21)	23.52(±0.99) (n=5)	28.87(±2.68) (n=30)	26.58(±3.88) (n=5)	25.41(±1.61) (n=10)	28
lm2	11.22(±0.92) (n=11)	10.97(±1.09) (n=21)	9.9(±0.75) (n=4)	11.83(±1.33) (n=30)	12.38(±1.07) (n=5)	11.38(±0.58) (n=10)	13.3
C: cond	167.09(±10.56) (n=11)	159.92(±11.47) (n=21)	151.82(±8.87) (n=5)	182.13(±11.49) (n=31)	184.86(±20.14) (n=5)	160.48(±12.37) (n=10)	152.1
H: behm1	29.24(±4.58) (n=10)	25.52(±1.87) (n=20)	23.58(±2.34) (n=5)	30.15(±3.41) (n=31)	29.42(±3.61) (n=5)	25.2(±2.39) (n=10)	27.5
lCs	12.75(±1.52) (n=11)	12.27(±1.61) (n=20)	10.8(±2.03) (n=5)	14.25(±1.76) (n=28)	14.2(±1.96) (n=6)	12.41(±1.43) (n=10)	9.4
lP3	14.64(±1.3) (n=11)	14.93(±1.99) (n=21)	12.78(±1.31) (n=5)	15.98(±1.55) (n=28)	15.1(±1.32) (n=6)	14.15(±1.06) (n=10)	14.6
lP4	23.32(±1.99) (n=11)	22.23(±3.28) (n=22)	19.78(±1.85) (n=5)	25.39(±1.97) (n=28)	24.77(±2.75) (n=6)	22.4(±1.17) (n=10)	24.8
lM1	14.86(±1.82) (n=11)	15.52(±1.44) (n=21)	13.38(±1.06) (n=5)	16.97(±1.57) (n=33)	17(±0.4) (n=6)	15.47(±1.85) (n=10)	16
TL	213.35(±9.79) (n=11)	210.22(±18.58) (n=20)	195.52(±16.74) (n=5)	238.55(±23.42) (n=31)	234.55(±15) (n=6)	211.9(±13.7) (n=10)	200.5
PL	106.45(±5.43) (n=11)	103.86(±9.55) (n=22)	96.86(±4.25) (n=5)	117.71(±11.06) (n=31)	114.3(±7.89) (n=6)	104.52(±7.41) (n=10)	101.3
C: C	43.74(±4.43) (n=10)	41.54(±4.45) (n=22)	38.08(±3.09) (n=5)	48.02(±4.38) (n=30)	47.05(±4.92) (n=6)	41.84(±3.19) (n=10)	42.5
ZB	123.69(±11.15) (n=11)	120.88(±12.93) (n=22)	114.06(±13.15) (n=5)	140.76(±14.77) (n=29)	143.43(±13.13) (n=6)	115.5(±9.23) (n=10)	111
BW	68.4(±3.68) (n=10)	64.74(±3.51) (n=22)	62.77(±2.35) (n=5)	72.69(±5.38) (n=24)	74.19(±7.5) (n=6)	66.64(±3.18) (n=8)	66
P: P	53.64(±12.88) (n=10)	44.66(±11.61) (n=22)	38.88(±3.13) (n=4)	65.85(±15.98) (n=30)	57.34(±14.04) (n=6)	55.13(±11.78) (n=8)	41.5
IOB	46.47(±5.99) (n=10)	44.11(±7.11) (n=22)	38.44(±8.26) (n=5)	50.69(±6.86) (n=31)	53.64(±3.51) (n=6)	39.33(±5.24) (n=10)	37.8
POP	61.28(±4.95) (n=10)	59.89(±6.76) (n=22)	56.18(±5.66) (n=5)	69.97(±10.35) (n=31)	71.34(±6.11) (n=6)	51.12(±9.3) (n=9)	50.7
POC	43.03(±3.56) (n=10)	42.35(±3.84) (n=22)	42.24(±3.15) (n=5)	46.09(±5.03) (n=31)	48.73(±3.08) (n=6)	42.95(±3.56) (n=10)	43.2
OCB	41.29(±2.15) (n=10)	40.72(±4.83) (n=20)	37.38(±3.95) (n=5)	46.99(±5.9) (n=31)	46.87(±3.94) (n=6)	39.87(±2.19) (n=9)	37
ABL	28.5(±2.65) (n=9)	28.09(±2.48) (n=20)	26.12(±1.05) (n=5)	29.31(±3.14) (n=25)	29.79(±3.21) (n=5)	27.36(±1.65) (n=7)	26.7
ABW	19.96(±1.84) (n=9)	19.9(±1.76) (n=20)	18.48(±1.96) (n=5)	21.35(±3.1) (n=25)	21.27(±1.71) (n=5)	18.77(±0.9) (n=7)	18.8

The npMANOVAs detected a significant effect of group on both the skull ($Df=4$, $SS=0.0135$, $MS=0.003$, $R^2=0.072$, $F=1.713$, $Z=2.413$, $p=0.008$) and the mandible ($Df=4$, $SS=0.028$, $MS=0.007$, $R^2=0.128$, $F=3.055$, $Z=2.959$, $p=0.002$). Pairwise comparison among all groups was able to differentiate *C. l. chanco* from *C. l. pallipes* ($p_{\text{skull}}=0.003$; $p_{\text{mandible}}=0.001$) and West Eurasia ($p_{\text{skull}}=0.036$; $p_{\text{mandible}}=0.034$) populations. *C. l. pallipes* differentiated from South China ($p_{\text{skull}}=0.033$) and West

Eurasian populations ($p_{\text{mandible}}=0.007$). Because no differentiation was detected among the HGW populations (West Eurasia, South China, North Asia, all $p>0.105$), we grouped these populations for the CVA analyses. We kept *C. l. chanco* from *C. l. pallipes* as separate groups due to their morphological and genetic differentiation.

The CVA on the 2D geometric morphometrics was able to differentiate the three groups (*C. l. chanco*, *C. l. pallipes* and HGW) but also revealed considerable morphological

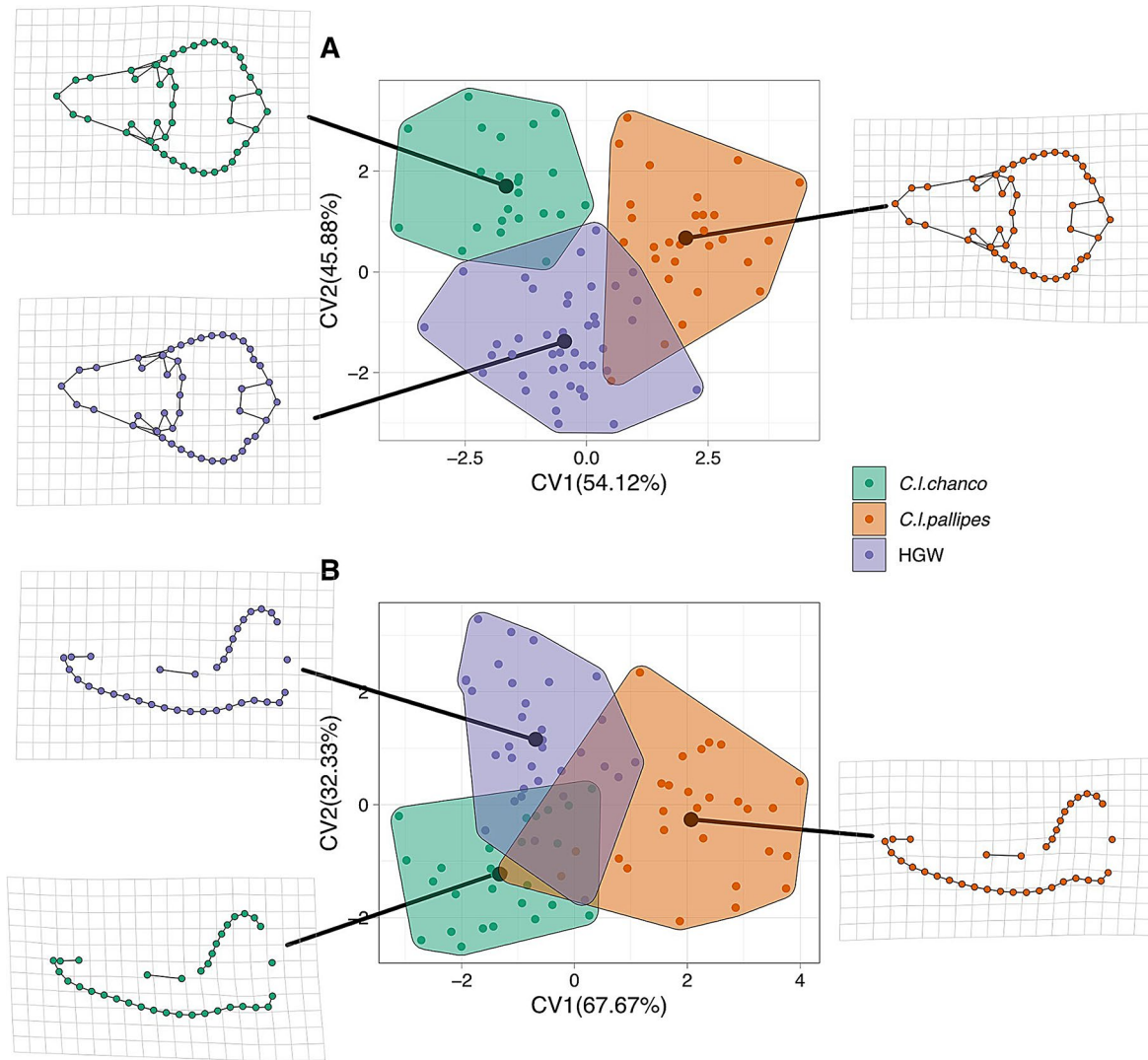


Fig. 3 Canonical analysis of variance for the ventral view of the skull (A) and the lateral view of the mandible (B). Shapes represent the difference between the mean shape and group averages

overlap (Fig. 3). The cross-validation analysis showed relatively low reclassification rates for the entire sample (58.06% and 59.09% for skull and mandible, respectively), reinforcing this idea. Inspection of group mean-shape differences suggests that *C. l. pallipes* is more gracile than *C. l. chanco* and HGWs in both their skulls (relatively longer faces and narrower zygomatic arches) and mandibles (thinner mandibular body and ascending ramus). While both HGWs and *C. l. chanco* are more robust, *C. l. chanco* displays a relatively shorter face and mandible, and a proportionally wider zygomatic arch.

Discussion

The Himalayan wolf lineage is distributed in the Himalayas and the Tibetan Plateau, and presents physiological adaptations to high-altitude ecosystems which are probably the result of long and unique evolutionary history (Zhang et al. 2014; Werhahn et al. 2018). Himalayan wolves are as genetically divergent from the HGW populations as are African wolves (*Canis lupaster*) (Werhahn et al. 2022), with the divergence time of the Himalayan wolf being estimated at 496,000–715,000 years before present (Sharma et al. 2004; Werhahn et al. 2018; Wang et al. 2019; Hennelly et al. 2021). Despite this, their morphological differentiation from remaining HGW has remained elusive. Using geometric morphometrics we were able to show morphological differentiation of the Himalayan wolf from the rest of the

Eurasian wolf populations, while the linear measurements were less conclusive. The Himalayan wolf can be characterized as having a wider zygomatic arch and shorter muzzle than other groups. These may be adaptations to a more powerful bite (Slater et al. 2009; Damasceno et al. 2013), designed to overcome medium and large prey, common to the Himalayan wolf diet (Chetri et al. 2017; Werhahn et al. 2018; Lyngdoh et al. 2020; Shrotriya et al. 2022). Alternatively, these differences might be adaptations to cold and harsh climates as predicted by Allen's rule, which states that mammals in colder climates will evolve shorter extremities to conserve heat (Allen 1877). Irrespective of the fundamental cause of this differentiation, these changes are consistent with the Himalayan wolf ecology and environment.

Despite the geometric morphometrics suggesting some morphological differentiation for the Himalayan wolf, our results are admittedly subtle. Cross-validation classification rates for our Canonical Variate Analyses are low when compared to between-species differences, being compatible with subspecies divergence in canids (Machado and Hingst-Zaher 2009; Machado and Teta 2020). This might stem from the fact that canids are known to be extremely morphologically conservative, with significant between-species variation being due to allometric size differences (Wayne 1986; Morey 1992; Machado and Teta 2020; Prevosti et al. 2013). This is what probably led to the prevalence of cryptic species and taxonomic confusion, despite the long history of knowledge for this group (Prevosti et al. 2013; Statham et al. 2014; Goddard et al. 2015; Koepfli et al. 2015; Viranta et al. 2017; Chemisquy et al. 2019; Machado and Teta 2020; Kitchener et al. 2020). Thus, the finding of extensive morphological overlap observed between Himalayan wolves and HGWs is not unexpected. Despite this, the results from statistical analyses fit with our personal observations of Himalayan wolves being more robust than other HGW. Studies on the internal skull structures (see Green et al. 2012; Curtis and Van Valkenburgh 2014; Suzuki et al. 2024) may help to further explore tentative differences in the brain case and turbinar bones that might be associated with this group's ecology.

One additional hindrance for a comparative analysis for the Himalayan wolf museum specimens is the uncertainty of species identification based on location. For our sample, we only accepted genetically confirmed skulls and those individuals coming from the known population range. We found several museum specimens assigned for the Himalayan wolf, which were unlikely to represent the taxon. Recent molecular studies have redefined the range to exclude the previously included Mongolian wolf population (Hennelly et al. 2021; Werhahn et al. 2020, 2022, 2024). As there are hybridization zones between Himalayan wolf and HGW from neighboring populations (including Mongolia and

China; Sharma et al. 2004; Hennelly et al. 2023; Werhahn et al. 2020), genetic testing might be necessary to evaluate the identity of wolf skulls coming from these regions.

In conclusion, after critically reviewing the identity and origin of all the samples in our study, we found several museum specimens erroneously labeled as *Canis lupus chanco*, despite being from regions unlikely to contain the lineage. By using this revised classification of the museum specimens, we were then able to differentiate the Himalayan wolf crania from nearby HGW populations in 2D morphometric analyses, suggesting the species showcases a more robust cranial morphology. Our results also indicate that the Indian wolf differs from the rest of the HGW by having a more gracile cranial morphology. Despite this, our results are not robust enough to generate definitive diagnostic features for the group, which clearly necessitates more work. The inherent morphological conservatism of wolves and the rarity of geographically representative samples in a single collection probably explains why large-scale taxonomic studies of HGW have rarely been attempted for almost a century (Pocock 1935). Future studies willing to solve this should combine museomics (ancient DNA) and phenomic (3D modeling) approaches of large samples of HGW and of Himalayan wolves.

Appendix 1

Specimens analysed

Canis lupus chanco - ANSP 17496, ANSP 17497, ANSP 17498, MCZ 24870, MCZ 24873, MfN 52523, MfN 91078, MfN 19806, MfN 19807, MfN 48867, MNH 1875.4.10.1, MNH 1939 3592, MNH 52523, MNH 52535, MNH 91078, NHM 1875.4.10.1, NHM 25.10.28.1, NHM 32.4.6.3, NHM 35.1.10.1, NHM 36.11.22.1, NHM 58.6.24.61, NHM 59.640.a, USNM 172654, USNM 172655, USNM 198457, USNM 198458, USNM 19846.

Canis lupus pallipes - MfN 49996, MMfN 49997, MNHN-ZM-AC-1974-121, FMNH 44467, FMNH 44469, FMNH 44470, FMNH 44471, FMNH 46079, FMNH 99417, NHM 35.1.10.3, NHM 35.1.18.1, NHM 35.1.18.2, NHM 35.1.18.4, NHM 35.1.18.5, NHM 35.1.18.6, NHM 35.1.18.7, NHM 35.8.1.52, NHM 35.8.30.1, NHM 35.8.30.3, NHM 35.8.30.4, NHM 56.5.6.42, NHM 56.9.22.24, NHM 61.455, NHM 65.1037, NHM 82.12.2.1, NHM 86.2.1, NHM 98.3.3.1.

Canis lupus (North Asia) - MfN 83452, MfN 93695, MNHN-ZM-AC-1878-395, MCZ 24870, MCZ 24873, NHM 20.7.4.5, NHM 8.8.11.18, NHM 99.6.26.2.

Canis lupus (South China) - MfN 13807, MfN 13810, MfN 16358, MfN 16703, MfN 24319, NHM 9.1.1.12, USNM 172655, USNM 17654.

Canis lupus (West Eurasia) - UN 19426, UN 26215, UN 26471, UN 34354, UN 34390, UN 46762, UN 46763, UN 49398, UN 49629, UN 6364, UN 6735, MfN 22340, MfN 48816, MNHN-ZM-AC-1962-1524, MNHN-ZM-AC-1997-12, MNHN-ZM-AC-1997_445, MNHN-ZM-AC-1997-456, MNHN-ZM-AC-1997-457, NHM 20.1.17.4, NHM 34.8.12.2, NHM 81.8.10.5, NHM 81.8.16.6, NHM 82.9.18.2, USNM 198458.

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Author contributions SV: Data gathering (measurements and photographs), manuscript preparation. GW: Manuscript preparation. FAM: Data gathering (photographs), statistical analysis, manuscript preparation.

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Data availability All data will be made available upon request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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