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TOOTH VARIABILITY IN PLEISTOCENE AND RECENT DHOLE, *CUON ALPINUS* (CARNIVORA, CANIDAE)

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Abstract: The morphometric variability of the canines and cheek teeth of the fossil and modern dhole (*Cuon alpinus*) is considered. It was not possible to detect sexual size dimorphism in the species. Geographical variability of dental parameters established two taxon groups: northern, which included two subspecies (*C. a. alpinus*, *C. a. hesperius*), and southern, which includes all other recent subspecies. Within the southern group, animals of Southeast Asia (Malacca, Sumatra, and Java) are distinguished by their smaller size. The dhole from the Late Pleistocene of Europe (*C. a. europaeus*) is close in dental characteristics to representatives of the northern group, and the Late Pleistocene fossil dhole from North America (Mexico) is close to the modern nominotypic subspecies *C. a. alpinus*. A hypothesis of early, mid-Pleistocene divergence between dholes from the north and north-west of the range and dholes from Southeast Asia is formulated.

Key worlds: *Cuon alpinus*, teeth, palaeontology, geographic variability

Introduction

The dhole *Cuon alpinus* (PALLAS, 1811) is a resident of the mountain and lowland, mainly of forest regions of South and East Asia, and is an important gregarious predator in its ecosystems. Over the past 100 years, its distribution has decreased significantly. The northern border of the range ran along the Tien-Shan, southern Siberia (Altai, Sayan Mountains, Transbaikalia) and the southern part of the Russian Far East (Sikhote-Alin Mountains and adjacent plains), but now the species has completely disappeared there (Aristov and Baryshnikov 2001).

Over this vast territory, *Cuon alpinus* shows taxonomic variability. Eleven nominal taxa of subspecies rank were described (Pocock 1936, Cohen 1978, Ellermann and Morrison-Scott 1951, Wozencraft 2005): *C. a. alpinus* (south of Siberia, Manchuria and Primorskii Territory), *C. a. javanicus* (DESMAREST, 1820) (Java), *C. a. sumatrensis* (HARDWICKE, 1821) (Sumatra), *C. a. dukhunensis* (SYKES, 1831) (India, south of the Ganges), *C. a. primaevus* (HODGSON, 1833) (Kumaon, Nepal, Sikkim, Butan), *C. a. lepturus* HEUDE, 1892 (south of China near Yangtze), *C. a. hesperius* (AFANASJEV et ZOLOTAREV, 1935) (Altai and Tien-Chan), *C. a. infuscus* POCOCK, 1936 (Tenasserim, Indo-China), *C. a. fumosus* POCOCK, 1936 (Szechuan, China), *C. a. laniger*, POCOCK,1936 (Southern Tibet), and *C. a. adustus* POCOCK, 1941 (Upper Burma, Indo-China).

Two northern subspecies, *C. a. alpinus* and *C. a. hesperius*, differ in fur colour and skull proportions (Aristov and Baryshnikov 2001). Also noted is the peculiarity in the structure of the auditory bulla in *C. a. hesperius* (Ivanoff 2007). These subspecies most likely no longer exist in nature.

Molecular genetics data (mtDNA) place the genus *Cuon* as a sister clade to the genus *Canis*, and date their divergence to the Late Miocene (about 6.2 Ma) (Hassanin et al. 2021). Mitochondrial phylogeography of *C. alpinus* revealed two clades in the tropical part of the species range. One includes populations from India southwards of the Ganges and Myanmar, the second includes populations from India north of the Ganges and Indo-China (Iyengar et al. 2005). Animals from the northern part of the range were not included in this analysis.

In the Pleistocene, the dhole's range was larger and extended much further to the west. It included Europe and

the Caucasus; one finding is known from the Southern Urals (Kurtén 1968, Baryshnikov 1996, Gimranov et al. 2015). Fossil *C. alpinus* also recorded in North America (Tedford et al. 2009).

In Europe, the earliest representative of the genus *Cuon* is considered to be *C. a. priscus* Thenius, 1954, from the early Middle Pleistocene. In the late Middle Pleistocene, the subspecies *C. alpinus fossilis* Nehring, 1890 was recorded, which was replaced by the subspecies *C. a. europaeus* Bourguignat, 1875 in the Late Pleistocene (Pérez Ripoll et al. 2010, Petrucci et al. 2012, Brugal et al. 2020, Marciszak et al. 2021). For the Late Pleistocene of the Caucasus, the fossil subspecies *C. alpinus caucasicus* Baryshnikov, 1978 has been established (Baryshnikov 1996). In southern regions of Siberia, two fossil taxa were described: *Canis nischneudensis* Tschersky, 1879 (Eastern Sayan Mountains) and *Cuon gebleri* Ovodov, 2007 (Altai) (Slodkewitsch 1932, Ovodov 2007), which we consider as a subspecies of *Cuon alpinus*.

Slodkewitsch (1932) was probably the first to note the similarities between dholes from Late Pleistocene in Europe and Siberia. European subspecies were considered as taxa that succeeded each other in time (Adam 1959), but then they began to be associated with different waves of immigration of dholes to Europe from Asia (Bonifay 1971, Argant 2010, Brugal and Boudadi-Makigne 2011).

Preliminary results from the analysis of ancient DNA extracted from fossil specimens of *Cuon alpinus* in Europe revealed the presence of at least two haplotypes and significant differences between ancient and modern dhole sequences (Taron et al. 2021). The genetic diversity of fossil dholes was higher than that of recent ones.

The distribution of *C. alpinus* as described above allows in general for the study of its evolution in space and time. The tooth parameters of modern skulls from across the species' range were studied, as well as the metric characteristics of fossil teeth from habitats in Europe, the Caucasus and southern Siberia. The present study aims to compare the metric characteristics of modern and fossil dhole canines and several cheek teeth (P4, p2, p4, and m1).

Materials and methods

Sample collection and measurements

The upper (C1, P4) and lower (c1, p2, p4, m1) teeth of 74 skulls of extant *Cuon alpinus* were measured using a digital sliding caliper to the nearest 0.1 mm (Text-fig. 1, Tab. 1). The skulls belong mainly to adult animals and only a few to subadult ones. The animal remains were collected over the past two centuries. In addition, a number of relationships (indices) between measurements were considered: CW/CL, cW/cL, P4W/P4L, P4Lp/P4L, p2L/m1L, p4L/m1L, m1W/m1L, and m1tal/m1L.

A total of 59 fossil dhole teeth were measured with data obtained from 10 European and Asian Early, Middle and Late Pleistocene (~MIS 13 – MIS 2) sites (Text-fig. 2, Tab. 1, Suppl. Tab. S1a–g): Caune de l'Arago, Orgnac 3, Lunel-Viel, Kudaro 1 and Kudaro 3 caves, Denisova Cave, Kurtak, Nizhneudenskaya Cave, Geographic Society
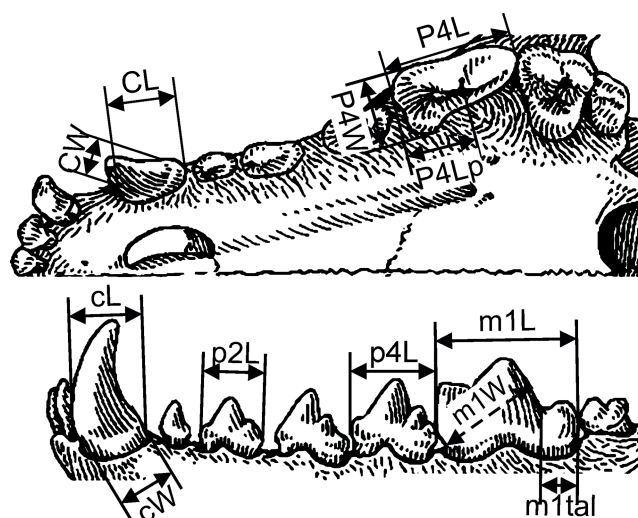
Text-fig. 1. Measurements of *C. alpinus* teeth used in this study: CL, CW – longitudinal length and transverse width of upper canine; P4L, P4W – length and width of upper carnassial tooth (P4); P4Lp – length of paracone; cL, cW – longitudinal length and transverse width of lower canine; p2L, p4L – length of 2nd and 3rd lower premolars; m1L, m1W – length and width of lower carnassial tooth (m1); m1tal – length of talonid of first lower molar (m1).

(= "Geograficheskogo Obshestva") Cave, Bliznets Cave (approximately dated from the end of the Pleistocene to the beginning of the Holocene: Older Dryas – Preboreal; Baryshnikov and Alekseeva 2017, Alekseeva and Baryshnikov 2020).

In addition to our own data, we used measurements of teeth of Pleistocene *Cuon* sp. from literature sources (Adam 1959, Altuna 1973, 1981, Malez and Turk 1990, Cardoso 1992, Tedford et al. 2009, Pérez Ripoll et al. 2010, Bacon et al. 2008, 2011, Petrucci et al. 2012, Ghezzo and Rook 2014, Tong et al. 2019, Volmer et al. 2019, Fan et al. 2022) (Tab. 1, Text-fig. 3).

The combined sample size of modern and fossil teeth, including literature data, was 502 specimens (Suppl. Tab. S1).

The material studied is held in the collections of the Museum of Natural History, London (NHM); Laboratoire de Geologie du Quaternaire, Marsel – Lumine; Muséum National d'Histoire Naturelle, Institut de Paléontologie Humaine, Paris; Museum für Naturkunde, Humbold-Universität zu Berlin; Institute of Archaeology and Ethnography, Siberian Branch of Russian Academy of Sciences, Novosibirsk; Sobolev Institute of Geology and Mineralogy, Siberian Branch of Russian Academy of Sciences, Novosibirsk; Zoological Museum of Lomonosov University, Moscow and Zoological Institute, Russian Academy of Sciences, Saint Petersburg (ZIN).

Sexual size dimorphism (SSD)

The sample of teeth from present-day animals with known sex (according to museum labels) was relatively representative (Suppl. Tab. S2): upper and lower canines – 5 females, 3 males, P4 – 14 females, 24 males, p2 – 12 females, 25 males, p4 – 11 females, 26 males, m1 – 12 females, 27 males. The sample size allows us to use non-

Table 1. Number of teeth of dholes (*Cuon* sp.) from different Pleistocene localities used in this study (see Text-fig. 1).

N	Locality	Name of subspecies	Tooth (number)	Geological age	Country	Reference
1	Große Ofenbergerhöhle	*europaeus*	c(1), p2(1), p4(1), m1(1)	MIS 2	Austria	Fladerer and Reiner 1996
2	Repolusthöhle	*europaeus*?	m1(1)	MIS 10–7	Austria	Adam 1959, Pacher 2003
3	Hundsheim	*fossilis*	P4(2), c(2), p2(2), p4(3) m1(3)	MIS 13	Austria	Adam 1959
4	Bacho Kiro	*europaeus*	m1(1)	MIS 3	Bulgaria	Malez and Turk 1990
5	Mocun Cave	?	p2(1)	MIS 5–2	China	Fan et al. 2022
6	Bailong Cave	*antiquus*	P4(1), m1(1)	MIS 13	China	Tong et al. 2019
7	Zhoukoudian 1	*javanicus/antiquus*?	m1(1)	MIS 13	China	Pei 1934
8	Čertova díra Cave	*europaeus*	p2(1), p4(1), m1(1)	MIS 3	Czechia	Adam 1959
9	Šipka Cave	*europaeus*	p4(1), m1(1)	MIS 3	Czechia	Adam 1959
10	Fontéchevade	*europaeus*	m1(1)	MIS 3	France	Arambourg 1958
11	Grotte de Malarnaud	*europaeus*	m1(1)	MIS 3	France	Bouchud 1951
12	Grotte de Mars	*europaeus*	c(1), p2(1), p4(1), m1(1)	MIS 5–2	France	Boule 1906
13	Isturitz Cave	*europaeus*	m1(1)	MIS 3	France	Bouchud 1951
14	Lunel-Viel	*europaeus*	P4(1), p2(1), P4(5), m1(6)	MIS 13, 11–9	France	Brugal et al. 2021
15	Orgnac 3	*europaeus*	p2(2), p4(1), m1(3)	MIS 11–8	France	Hanquet 2011
16	Arago	*europaeus/priscus*	c(2), p2(1), p4(1), m1(1)	MIS 13–11	France	Moigne et al. 2006
17	Kudaro Caves	*caucasicus*	C(8), P4(4), c(6), p2(2), p4(6), m1(6)	MIS 3	Georgia	Baryshnikov 1996
18	Mosbach 2	*fossilis*	m1(1)	MIS 15–14	Germany	Kahlke 1961
19	Gutenberg Cave (Heppenloch)	*fossilis/priscus*	P4(1), c1(1), p4(1), m1(7)	MIS 11	Germany	Adam 1959
20	Pandejan	*crassidens = alpinus*	m1(1)	Middle Pleistocene	Indonesia	Volmer et al. 2019
21	Sangiran	*priscus*	m1(1)	~MIS 20	Indonesia	Bouteaux and Moigne 2010, Volmer et al. 2019
22	Bucca del Tasso	*europaeus*	p4(1)	MIS 4, 3	Italy	Petrucci et al. 2012
23	Equi Cave	*europaeus*	m1(1)	MIS 3	Italy	Ghezzo and Rook 2014
24	Valserra	*europaeus*	p2(1), p4(1), m1(2)	MIS 5–2	Italy	Petrucci et al. 2012
25	Melpignano-Cursi and San Sidero area	*europaeus*?	m1(1)	MIS 9–3	Italy	Petrucci et al. 2012
26	Tam Hang	*antiquus*	p4(1)	MIS 5, 4	Laos	Bacon et al. 2011
27	San Josecito Cave	?	p2(2), p4(2), m1(4)*	MIS 3?	Mexico	Tedford et al. 2009
28	Grotte de l'Observatoire	*europaeus*	P4(4), m1(3)	MIS 3	Monako	Adam 1959
29	Crvena Stijena	*europaeus*	m1(2)	MIS 3	Montenegro	Malez 1975
30	Biśnik Cave	*europaeus*	p4(1)	MIS 5, 3	Poland	Marciszak et al. 2021
31	Wschodnia Cave	*priscus/fossilis*	m1(1)	MIS 8, 7	Poland	Marciszak et al. 2021
32	Rogóźka Cave	*europaeus*	m1(1)	MIS 3	Poland	Marciszak et al. 2021
33	Escoural	*europaeus*	p4(1)	MIS 3, 2	Portugal	Ripoll et al. 2010
34	Denisova Cave	*gebleri***	p4(1), m1(1)	MIS 10–2	Russia	Malikov and Baryshnikov in press
35	Bliznets Cave	*nizhneudensis*?	C(1), P4(2), c(1), p2(1),	MIS 2–1	Russia	Alekseeva and Baryshnikov 2020
36	Geographical Society Cave (Geographicheskogo Obshestva Cave)	*nizhneudensis*?	p4(1), m1(1)	MIS 3	Russia	Baryshnikov 2015
37	Nizhneudinskaya Cave	*nizhneudensis*	p2(1), p4(1)	MIS 3	Russia	Turner II et al. 2013
38	Apnarjeva Jama	*europaeus*	m1(1)	MIS 4	Slovenia	Malez and Turk 1990
39	Amalda Cave	*europaeus*	P4(1), m1(1)	MIS 2	Spain	Ripoll et al. 2010
40	Cova del Parpalló	*europaeus*	C(1), c(2), p2(1), p4(1), m1(1)	MIS 2	Spain	Ripoll et al. 2010
41	Cueva de Los Casares	*europaeus*	p4(1)	MIS 4, 3	Spain	Altuna 1973

Table 1. continued

N	Locality	Name of subspecies	Tooth (number)	Geological age	Country	Reference
42	Cueva del Boquete de Zafarraya	*europaeus*	P4(2)	MIS 3	Spain	Ripoll et al. 2010
43	Cueva del Rascaño	*europaeus*	p4(1)	MIS 2	Spain	Altuna 1981
44	Cueva Negra	*europaeus*	P2(1), p4(1), m1(1)	MIS 5, 3	Spain	Ripoll et al. 2010
45	Duranguesado region	*europaeus*	p2(1), p4(1)	MIS 5, 2	Spain	Ripoll et al. 2010
46	La Riera Cave	*europaeus*	P4(1)	MIS 2	Spain	Altuna 1986
47	Les Coves de Santa Maira	*europaeus*	C(1)	MIS 2	Spain	Ripoll et al. 2010
48	Los Moros I (Gabasa)	*europaeus*	P4(2)	MIS 4, 3	Spain	Ripoll et al. 2010
49	Obarreta	*europaeus*	m1(1)	MIS 5–2	Spain	Altuna 1983
50	Trinchera Galería	*europaeus*?	p2(2), p4(3), m1(3)	MIS 8–7	Spain	Ripoll et al. 2010
51	Grotte de Cotencher	*europaeus*	p2(1), m1(1)	MIS 4, 3	Switzerland	Adam 1959, Deák et al. 2019
52	Duoi U'Oi Cave	*antiquus*	p4(1)	MIS 5–3	Vietnam	Bacon et al. 2011

* minimum and maximum values of m1 measurements used according to Tedford et al. (2009)
** in this study, subspecies affiliation is indicated only in this table; locality names are indicated in text and Text-figs

parametric statistics to test the null hypothesis that there are no differences between the sexes in dental measurements or indices. For this purpose, the test of comparison of medians in samples of males and females was used. Preliminarily, it was found that the northern subspecies (*C. a. alpinus*, *C. a. hesperius*) differed significantly from the southern subspecies (all other recent subspecies) in some measurements. Therefore, the test was carried out separately for them in order to reduce the possible effect of geographical variability.

Variability in the extant dhole sample

There is geographic variability in modern *C. alpinus*, reflected in the description of 11 subspecies, but the validity of many of these is questionable (Durbin et al. 2004): *C. a. alpinus* (east of eastern Sayans Mountains, East Russia), *C. a. lepturus* (south of Yangze River, China), *C. a. dukhunensis* (south of the Ganges, India), *C. a. adustus* (North Myanmar and north-east India), *C. a. primaevus* (Himalayan Nepal, Sikkim and Bhutan), *C. a. laniger* (Kashmir and southern Tibet), *C. a. hesperius* (Tian Shan), *C. a. fumosus* (West Szechuan, China and Mongolia), *C. a. infuscus* (South Myanmar, Malaysia, Thailand, Laos, Cambodia and Vietnam), *C. a. sumatrensis* (Sumatra, Indonesia), and *C. a. javanicus* (Java, Indonesia).

A priori, our sample of 74 skulls was divided into groups belonging to the subspecies *C. a. alpinus* (12), *C. a. hesperius* (10), *C. a. laniger* (2), *C. a. primaevus* (10), *C. a. dukhunensis* (20), *C. a. adustus* (8), *C. a. infuscus*/*C. a. sumatrensis* (3), and *C. a. javanicus* (9), according to the taxonomic definition of the specimens in the collections and the geographical location of the material collection sites (Suppl. Tab. S1).

Multivariate analysis

The data processing method used has been described in detail previously (Puzachenko 2023). The main purpose of constructing a multivariate model of variability (hereafter referred to as a descriptive model) is to identify the main independent components of variability, in our case tooth size and proportions. In other words, the descriptive model reproduces the main "relationships" between different teeth and between the individual measurements of each tooth. By relationships we mean a greater or lesser consistency of variability. Orthogonal coordinates of a descriptive model were used as a generalized variables containing basic information about variation in size or "shape" of teeth.

First, we formally defined a "morphological system" as the logical intersection of a set of individuals (elements), a set of measurements (variables, which can assume different states of elements) and a set of metrics – the methods of measuring of disparity (similarities or dissimilarities) between elements. Second, we define "morphospace" as a multidimensional space that describes the relationships between elements in a Euclidean space of low dimensionality. To this end, we have used the method of non-metric multidimensional scaling (Davison 1983). The advantage of this method of "reducing the dimensionality of the original data" is that it allows us to use different metrics, not just covariance or correlation, like its well-known parametric analogue, principal components analysis. A second advantage is that it can partially describe non-linear relationships between elements, unlike many other dimensionality reduction methods. Depending on the metric used, two types of descriptive models are obtained: in the case of Euclidean distance, the model describes variability in size (SZM – model or morphospace) and the model describes variability in teeth proportions or "shape" (SHM – model or morphospace), in the case of rank Kendall's tau-b association (Kendall 1970). In the text, coordinates of SZM and SHM are denoted by the letters E (from Euclidean distance) and K (from Kendall's tau-b metric), respectively, with the addition of coordinate sequence number 1, 2, 3, …

For biological interpretation of descriptive models, Pearson correlation coefficients were calculated between them and each tooth measurement. In addition, multivariate linear regression models were constructed for each measurement using the coordinates as predictors.

We obtained and examined the following descriptive models: two models (SZM, SHM) for the whole sample, two
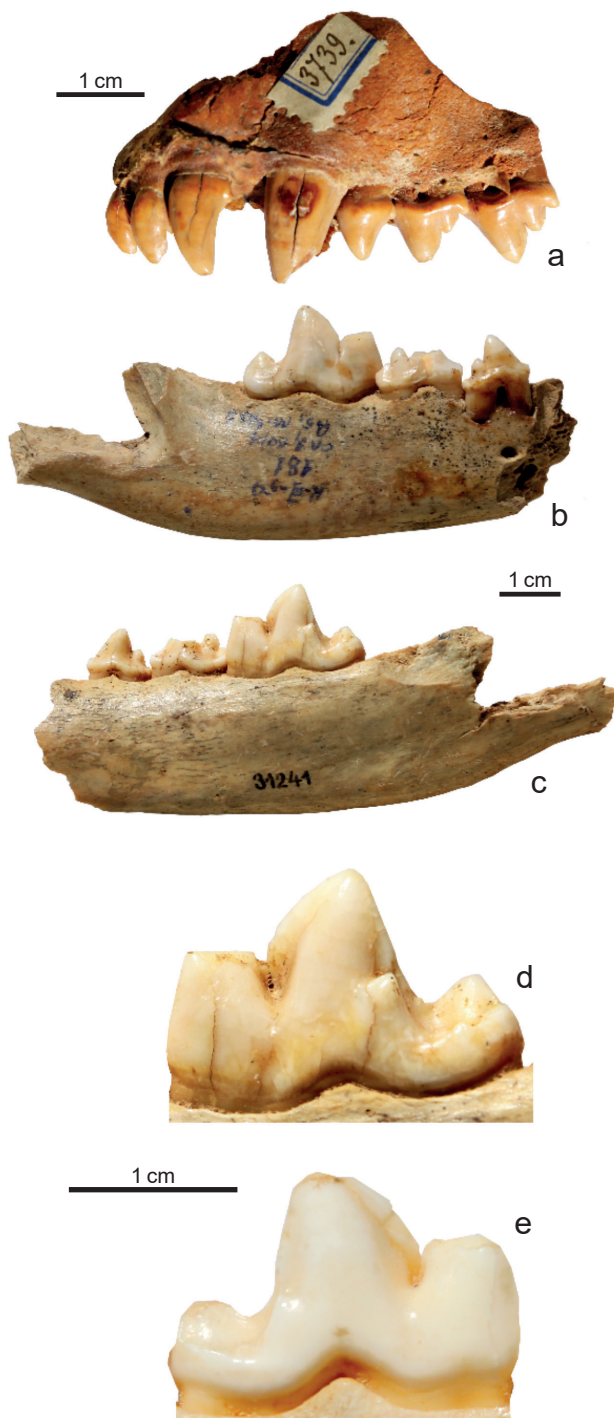
Text-fig. 2. *Cuon alpinus nischneudensis* (TSCHERSKY, 1879), Nizhneudinskaya Cave, left maxilla, ZIN O.3739, lectotype (a); *C. a. caucasicus* BARYSHNIKOV, 1978, Kudaro 3 Cave, right mandible, ZIN O.31241, holotype (b, c); buccal (a, b) and lingual (c) views. *Cuon a. caucasicus* BARYSHNIKOV, 1978, Kudaro 3 Cave, Caucasus, Late Pleistocene, right m1, ZIN O.31241, holotype (d); lingual view. *C. a. hesperius* (AFANASJEV et ZOLITAREV, 1935), Aksai, Tien-Shan, recent, left m1, ZIN O.15229, holotype (e); lingual view.

equal models each for the subspecies *C. a. alpinus* and *C. a. hesperius* and for all other subspecies. In the case of *C. a. alpinus* and *C. a. hesperius*, the full set of measurements was used, while for the other subspecies, measurements of

canines, paracone length and talonid length were excluded as these measurements were not taken.

The calculations required to obtain the descriptive models were performed using the NCSS 12 Statistical Software package (2018: ncss.com/software/ncss).

To examine the variability in individual measurements, including the lengths of p2 and p4, plots of sample medians with maximum and minimum values were made. The Mann-Whitney test for equal medians was used to compare the median values of tooth measurements in different subspecies. To account for the small sample sizes, Bonferroni-corrected p values for the probability of accepting the null hypothesis of equality of sample medians were given in the tables. The Mann-Whitney test was calculated using PAST v. 4.14. (Hammer et al. 2001).

Variability in the sampling of fossil dholes

For the fossil tooth samples, descriptive models were generated for individual teeth only. We added modern subspecies data to these models to assess similarities/ differences between fossil and modern dhole' teeth. We added the CL/CW, cW/cL, P4W/P4L and m1W/m1L indices to the measurements of canines and upper and lower carnassial teeth. This allowed us to restrict to a single type of two-coordinate descriptive model based on Euclidean distance matrix.

Sample medians were plotted and compared using the Mann-Whitney test for p2L and p4L.

Assessing the "quality" of the a priori taxonomic partitioning of the sample

Doubts have been raised about the validity of modern subspecies of dholes, as many have been described on the basis of small samples or highly variable characters such as coat colour. Fossil subspecies have been described on the basis of small samples and a limited list of characters. It is difficult to compare the relative contributions of geographic and temporal factors to variations in tooth shape or size, partly because of the scarcity of data.

To assess the validity of an a priori taxonomic classification based on tooth size variability, we independently partitioned a sample containing both fossil and modern material. Separate analyses were performed for each tooth. The null hypothesis of sample homogeneity was tested using various non-hierarchical and hierarchical cluster analysis methods (Rencher 2002). Note that it is impossible to provide a general, universal solution that would justify the choice of the "optimal" sample split. Textbooks usually recommend comparing the classification results obtained by different methods in order to assess the "stability" of the partitioning (Aldenderfer and Blashfield 1984).

We used 5 different partitioning methods. Three of them were non-hierarchical clustering methods: K-means (KM; Rencher 2002), medoid partition (PAM; Kaufman and Rousseeuw 2005), and Gaussian finite mixture model (GFM; Quiles et al. 2005). The next ones, UPGMA and McQuitty (weighted mean) methods (MQ), belonged to the hierarchical clustering methods (Charrad et al. 2014).

The "optimal number" of clusters for KM, UPGMA and MQ methods has been estimated in the R package NbClust
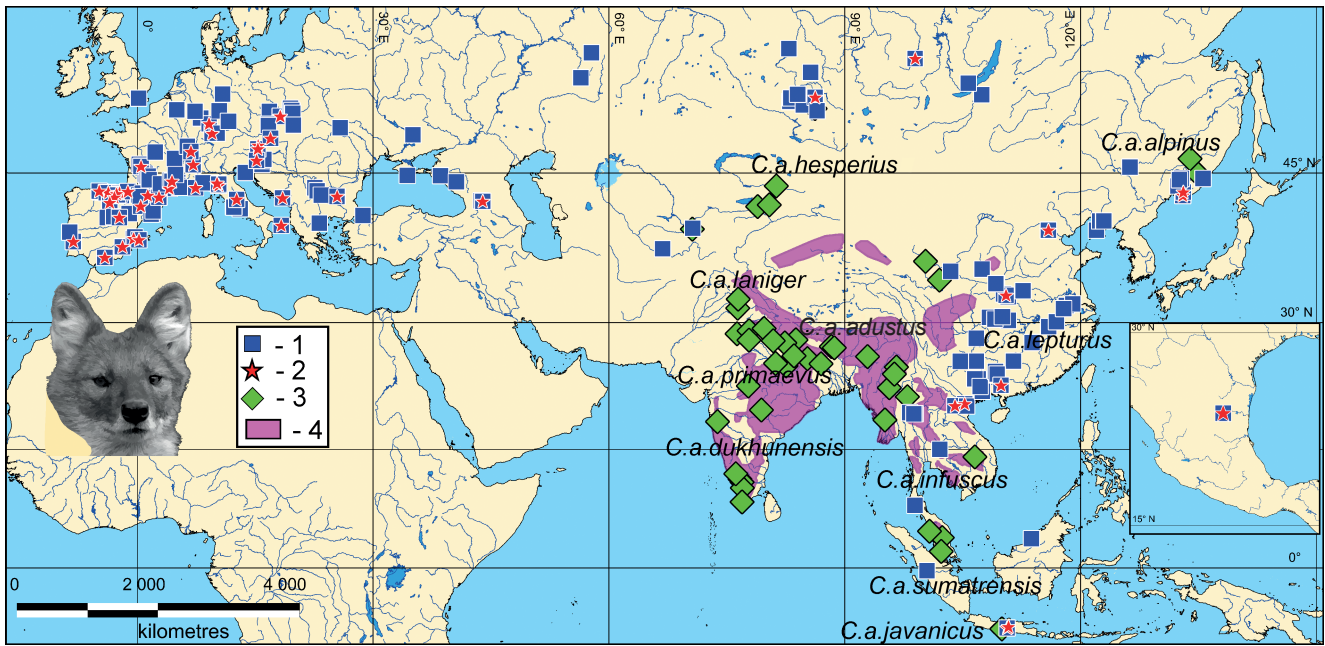
Text-fig. 3. Locations of Early – Late Pleistocene sites with *Cuon* sp. remains (1), sites from which material was used in this study (2), locations of extant *C. alpinus* samples used in this study (3), extant range of *C. alpinus* (4) according to Kamler at al. (2015); 11 putative extant subspecies of dholes are labelled.

(Charrad et al. 2014). The authors of the package use up to 30 tests (indices) to estimate this number. The decision is made according to the "majority rule" (MR), i.e., the maximum number of positive "tests" (for details see Charrad et al. 2014).

R package fpc (Hennig 2010, 2024) was used to find the optimal partitioning of the sample using the PAM method. In this case, the estimation of the optimal partitioning was based on the "average silhouette width" criterion. We applied GFM, implemented in the R mclust package (Scrucca et al. 2016), and the selection of the most relevant number of clusters in this case was based on the Bayesian information criterion (BAIC). The protocol of calculations and additional results are given in Supplementary Material.

Trends in time

We combined tooth size data with the geological age of the localities. In general, the geological ages of the localities with *Cuon* sp. remains considered here fall between the very late Early Pleistocene (~MIS 20) and early Holocene (MIS 1) (Tab. 1), i.e., ~800–0.1 ka BP. The age of the "modern" material from museums falls within the last 300 years.

Three geographical regions were identified in a more conventional way, for which time series were constructed separately for "Europe and the Caucasus" and "Northern Asia" that includes in our case the mountains of southern Siberia, the Russian Far East, northern China and the San Josecito Cave (Mexico). We include the raw data from the latter locality in the "North Asia" sample because they are very close to *C. alpinus* in their characteristics. The dating of this locality to the second half of MIS 3 (Cruz et al. 2023) suggests a migration from the Beringia region time not later than the MIS 4 stadial – the middle of the Late Pleistocene. The last region, "Southeast Asia", included the Indochina Peninsula, the Malay Archipelago and the territory of

southern China. Note that we have no palaeontological evidence that *Cuon* inhabited the "Indo-Himalayan" region (Jammu and Kashmir, India, Nepal, Bhutan, and Bangladesh).

The division of the material into geographical sub-samples is primarily due to the differences between the North Asian and Southern groups in modern dholes, as briefly described above. In addition, the variability of extinct European representatives of the species is of independent importance for understanding its evolution. The raw data are extremely unevenly distributed in time, which is typical of Pleistocene material. Most sites are dated to the Late Pleistocene. A number of sites have no instrumentally confirmed age or were dated over a wide range of dates. Finally, the data sets available for the various teeth are not equivalent in terms of volume and temporal coverage over the time interval examined.

Due to the limitations described above, we were only able to test the hypothesis of the presence/absence of more or less stable temporal changes in tooth size (trends) by presenting the material in graphical form.

Results

Sexual size dimorphism

According to the results of the median test, none of the tooth measurements showed sex-specific dimorphism (Tab. 2). However, the medians of the width/length ratios of the upper and lower carnassial teeth differed statistically significantly ($p < 0.05$) between males and females in the southern and northern subspecies samples. Indeed, as can be seen from the box plots in Text-fig. 4a–d, there is a general trend of variability in the proportions of both teeth: males have narrower teeth on average than females. However, the
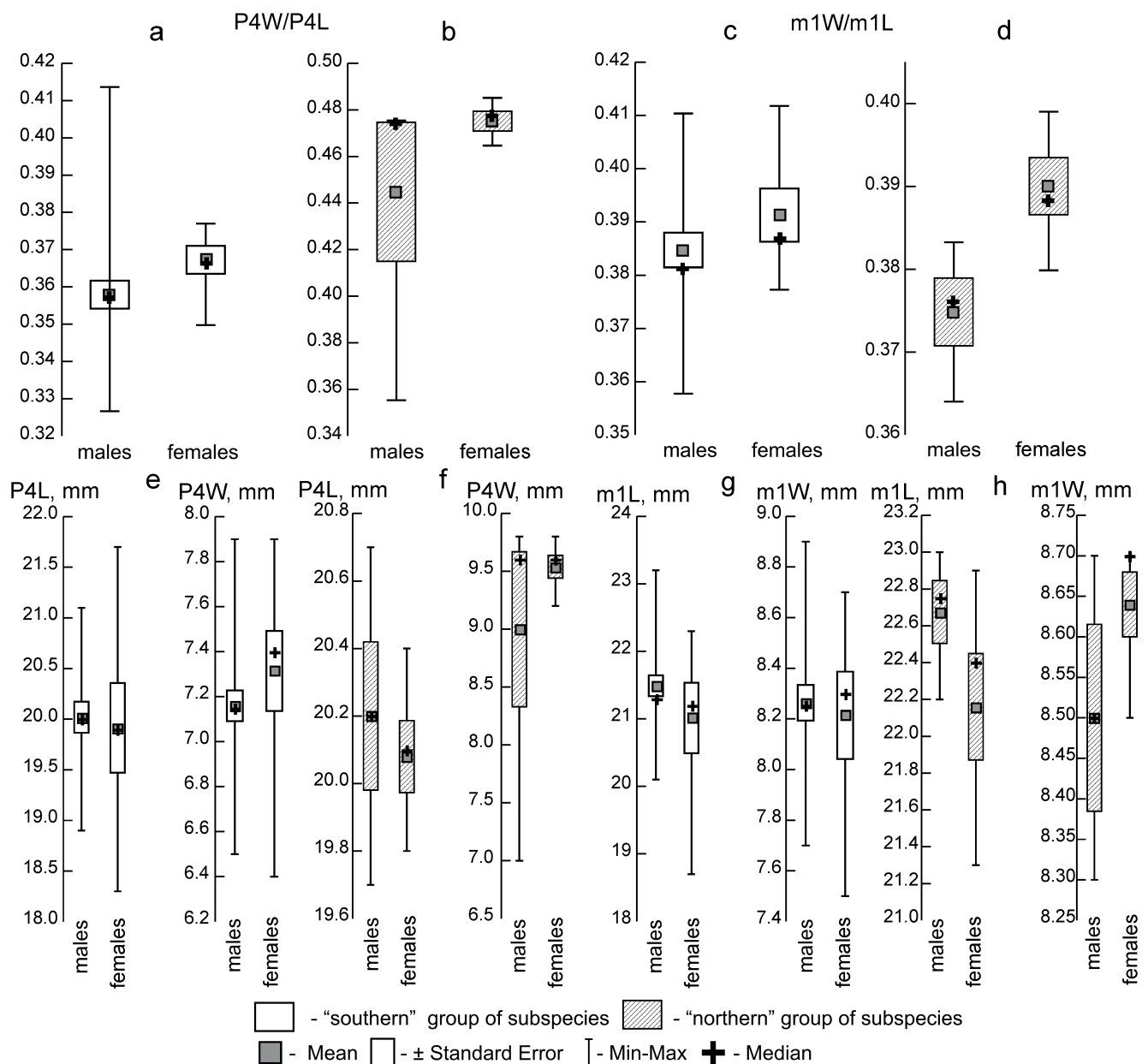
Text-fig. 4. Variations of measurements and indices of upper and lower carnassial teeth in southern (a, c, e, g) and northern (b, d, f, h) groups of subspecies of extant *C. alpinus.*

reasons for this weak SSD may not be the same for P4 and m1, and in southern or northern groups of subspecies (Text-fig. 4e–h). It is possible that females have P4 and m1 slightly wider on average compared to males.

The mean values of the indices in females and males do not differ significantly with widely overlapping their 95% confidence intervals. For example, in *C. a. alpinus* and *C. a. hesperius*, P4W/P4L was 0.475 (0.463–0.487) in females and 0.445 (0.349–0.539) in males, and m1W/m1L was 0.390 (0.381–0.399) and 0.375 (0.362–0.388), respectively.

Variability in the extant dhole

Two- or three-dimensional descriptive models were sufficient to reproduce the main patterns of variability in tooth size and shape in modern *C. alpinus* (Text-fig. 5a, b). The proportion of variance of original Euclidean distances or distances based on Kendall's tau-b association between morphosystem elements (individuals) reproduced by the

SZM and SHM models was 97.8 % and 97.3 %, respectively. Model coordinates, as independent predictors, reproduced 71 % to 97 % of the variance of the original measurements used to calculate distances between morphosystem elements. Variability in upper canine width and talonid length, which were not used in modelling because they were only available for *C. a. alpinus* and *C. a. hesperius* and one specimen of *C. a. javanicus*, are either not described by the models or show unordered random variability with respect to the coordinates. The variance of other measurements not used in the modelling (CL, cL, cW, P4Lp) is nevertheless reproduced by the models in the range of 33 % to 71 %.

The indicators of the first SZM coordinate were P4W, p2L and p4L, i.e., the measurements with the highest correlation (0.84, 0.85, 0.87) with the E1 coordinate (Suppl. Tab. S3). Indicators of the first SHM coordinate were the P4W/P4L (0.89) and p2L/m1L (0.92) indices. The indicator of the E2 coordinate was the width m1 (0.63). The length of the

345
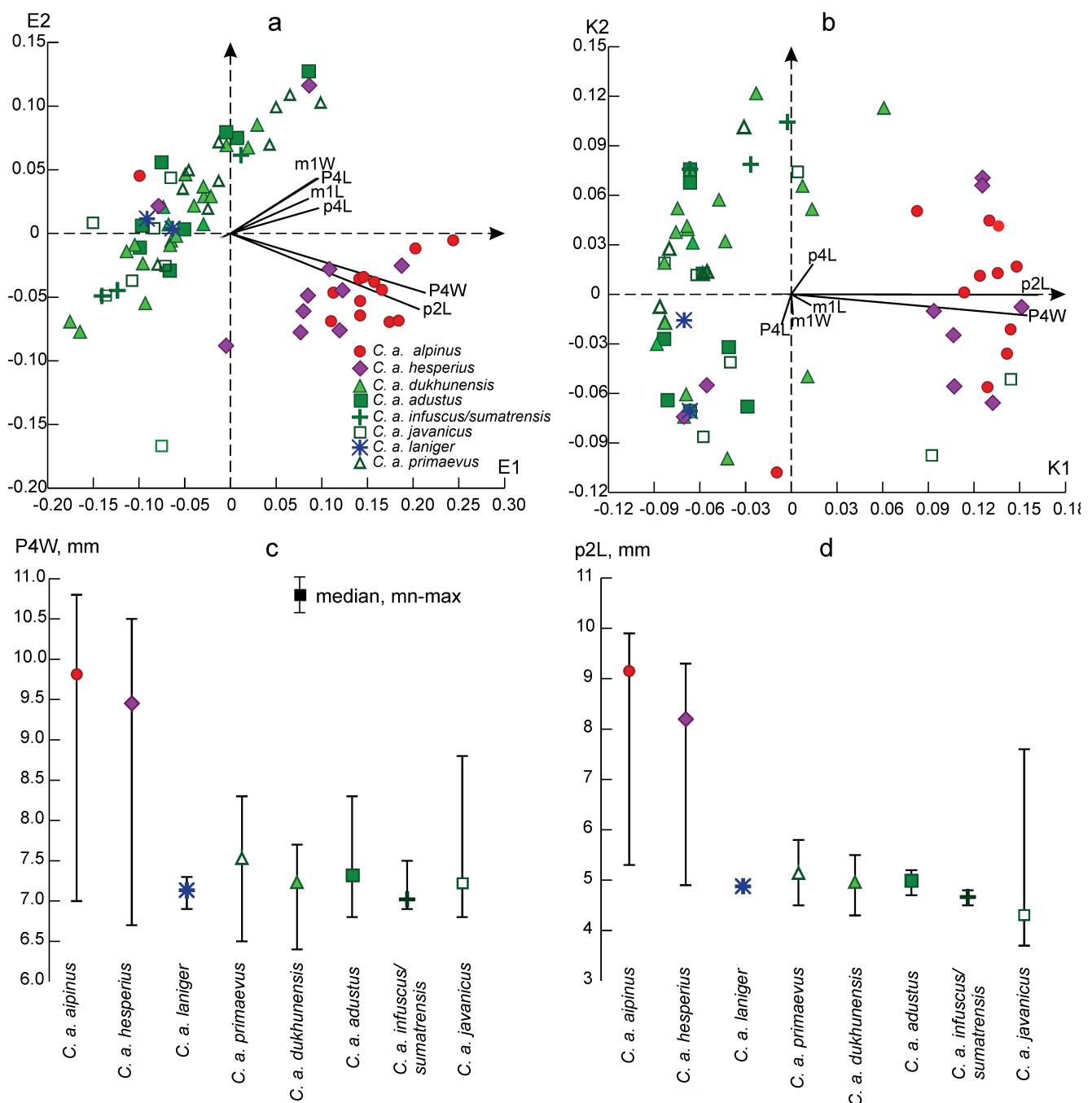
Text-fig. 5. Descriptive models of variability in tooth size (a) and shape (b) in extant subspecies of *C. alpinus*. **c, d:** variability in width P4 and length p2 – main measurements by which differentiation between northern and southern subspecies was observed.

paracone P4Lp and the measurements of the lower canines (cL, cW) correlated with the same coordinate. The indicator of the K2 coordinate in SHM was the ratio of the lengths of the fourth lower premolar and the lower first molar (p4L/m1L). Finally, the relative length of the paracone (P4Lp/P4L) showed the moderate negative correlation (–0.58) with the K3 coordinate.

In Text-fig. 5a, b it is clearly seen that the whole recent sample is divided into two groups of individuals; one group, with rare exceptions, includes *C. a. alpinus* and *C. a. hesperius*, and the second group includes representatives of southern subspecies. In general, the teeth of *C. a. alpinus* and *C. a. hesperius* are larger than those of the other dholes. Also, the groups differ not only in the absolute width of P4

and length of p2 (Text-fig. 5c, d), but also in the relative width and length of these teeth.
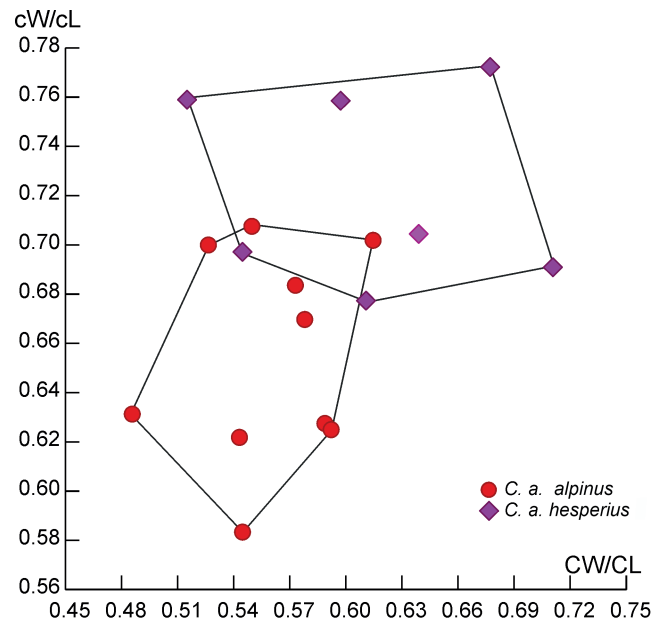
Table 3 (see also Suppl. Tab. S4) shows medians and min–max of tooth measurements in *C. a. alpinus*, *C. a. hesperius*, and the statistical significance of the differences between them and some subspecies from the southern group. From the data presented, it appears that, *C. a. alpinus* differs most from all subspecies (including *C. a. hesperius*), with *C. a. dukhunensis* and *C. a. javanicus* differing from it in the greatest number of measurements.

For the subspecies *C. a. alpinus* and *C. a. hesperius*, the individual descriptive models SZM and SHM had four and three coordinates respectively (Suppl. Tab. S5). The entire set of tooth measurements was used for their

Table 2. Median test (χ², p) for equality of medians of tooth measurements and indices in male and female sub-samples of *C. alpinus*

Tooth measurement and index	*C. alpinus* ssp. except *C. a. alpinus* and *C. a. hesperius*		*C. a. alpinus* and *C. a. hesperius*	
	χ2	p	χ2	p
CL	–	–	0.9	0.34
CW	–	–	0.03	0.85
CW/CL	–	–	0.09	0.76
P4L	0.01	0.93	0.09	0.76
P4W	1.45	0.23	0.9	0.34
P4W/P4L	5.2	0.03	1.1	0.29
cL	–	–	1.1	0.29
cW	–	–	1.1	0.29
cW/cL	–	–	1.1	0.29
p2L	0.29	0.59	2.72	0.1
p4L	0.29	0.59	0.09	0.76
m1L	0.01	0.9	2.72	0.1
m1W	0.008	0.93	0	1
m1W/m1L	0.29	0.59	5.8	0.02

Text-fig. 6. Scatterplot of CW/CL and cW/cL showing differences in shape of canine cross-section between *C. a. alpinus* and *C. a. hesperius*.

Table 3. Medians (Me) of tooth measurements in *C. a. alpinus*, *C. a. hesperius*, and statistical significance of differences between these subspecies and some southern subspecies, using Mann-Whitney test (Bonferroni corrected p).

	C. a. alpinus						*C. a. hesperius*					
	P4L	P4W	p2L	p4L	m1L	m1W	P4L	P4W	p2L	p4L	m1L	m1W
Me	20.4	9.8	9.2	13.5	22.7	8.7	20.5	9.5	8.5	12.6	21.8	8.5
Subspecies	Bonferroni corrected p											
C. a. primaevus	–	0.01	0.004	–	–	–	–	–	–	–	–	–
C. a. dukhunensis	–	0.001	<0.001	0.03	<0.001	0.02	–	0.02	0.004	–	–	–
C. a. adustus	–	0.03	0.009	–	–	–	–	–	–	–	–	–
C. a. javanicus	0.02	–	0.05	0.04	0.03	0.008	0.04	–	–	–	–	–

Table. 4. Mean (M), standard error (m) and Min–Max of tooth measurements and indices in *C. a. alpinus* and *C. a. hesperius* for which subspecies samples are statistically significantly different, according to Mann-Whitney test (Bonferroni corrected p presented).

Measurement	*C. a. alpinus*		N	*C. a. hesperius*		N	p
	M ± m	Min–Max		M ± m	Min–Max		
p2L	9.0 ± 0.35	5.3–9.9	12	7.6 ± 0.6	4.9–9.3	7	0.009
p4L	13.2 ± 0.27	10.7–14.5	12	12.5 ± 0.2	11.6–13.7	9	0.02
m1L	22.7 ± 0.16	21.7–23.7	12	21.8 ± 0.28	21.0–23.2	9	0.03
Index	M ± m	Min–Max	N	M ± m	Min–Max	N	p
cW/cL	0.66 ± 0.013	0.58–0.71	11	0.72 ± 0.015	0.68–0.77	7	0.05
p2L/m1L	0.40 ± 0.015	0.24–0.43	12	0.35 ± 0.027	0.23–0.40	7	0.01

construction. The SZM and SHM models reproduced 98.7 % and 91.8 % of the variance of the initial distances between individuals, respectively, indicating their high quality. On projections of both the SZM and SHM models onto their first two coordinates, the subspecies specimens occupied nearly overlapping or highly overlapping areas, reflecting their overall morphological similarity (Suppl. Fig. S1). Nevertheless, morphological differences between *C. a. alpinus* and *C. a. hesperius* can be detected at the level of "tendency" (Tab. 3). *C. a. alpinus* differs from *C. a. hesperius* in a number of quantitative characters, as shown in Table 4 (see also Suppl. Tab. S4). *C. a. alpinus* is characterized by

Table 5. Medians (Me) and Min–Max of tooth measurements in recent *C. alpinus* ssp., excluding *C. a. alpinus* and *C. a. hesperius*, with assessment of statistical significance of differences between them using Mann-Whitney test (Bonferroni corrected p)

Measurement	*C. a. laniger* Min. Max	*C. a. primaevus* Me Min–Max	*C. a. dukhunensis* Me Min–Max	*C. a. adustus* Me Min–Max	*C. a. infuscus/C. a. sumatrensis* Me Min–Max	*C. a. javanicus* Me Min–Max
P4L	19.6, 20.0	20.8 / 19.9–22.0	20 / 18.3–21.1	19.8 / 19.0–22.1	19.0 / 18.7–20.8	19.1 / 18.2–20.0
P4W	6.9, 7.3	7.5 / 6.5–8.3	7.2 / 6.4–7.7	7.3 / 6.8–8.3	7.0 / 6.9–7.5	7.2 / 6.8–8.8
p2L	4.8	5.1 / 4.5–5.8	4.9 / 4.3–5.5	5.0 / 4.7–5.2	4.5, 4.8	4.3 / 3.7–4.3, 7.6
p4L	11.4	12.7 / 12.1–13.5	12.3 / 11.0–13.4	12.5 / 11.4–13.2	12.0 / 11.8–13.4	11.5 / 10.4–12.2
m1L	20.8	22.2 / 20.7–23.5	21.1 / 18.7–23.2	21.2 / 20.2–23.2	20.1 / 19.8–22.0	21.2 / 20.1–22.2
m1W	8.3	8.5 / 7.8–8.9	8.2 / 7.5–8.9	8.5 / 8.0–9.1	7.7 / 7.7–8.6	8.1 / 7.7–8.2
Index	Min. Max	Me Min–Max	Me Min–Max	Me Min–Max	Me Min–Max	Me Min–Max
P4W/P4L	0.35, 0.37	0.37 / 0.33–0.38	0.36 / 0.34–0.39	0.37 / 0.34–0.38	0.37 / 0.36–0.37	0.38 / 0.34–0.48
p2L/m1L	0.23	0.24 / 0.20–0.25	0.23 / 0.21–0.26	0.23 / 0.22–0.25	0.23, 0.24	0.2 / 0.17–0.21, 0.38
p4L/m1L	0.55	0.57 / 0.55–0.61	0.59 / 0.54–0.62	0.57 / 0.54–0.63	0.61 / 0.59–0.61	0.54 / 0.49–0.57
m1W/m1L	0.4	0.38 / 0.37–0.40	0.39 / 0.36–0.41	0.4 / 0.38–0.41	0.389 / 0.38–0.39	0.38 / 0.36–0.39
N	2 or 1	10	20	8 or 7	3 or 2	7 or 5

| Mann-Whitney test. p	*C. a. primaevus*	*C. a. dukhunensis*	*C. a. adustus*	*C. a. javanicus*
C. a. primaevus		–	–	0.03; 0.03
C. a. dukhunensis	–		–	0.04; 0.03; 0.02
C. a. adustus	–	–		
C. a. javanicus	P4L; p4L	p2L; p2l/m1L; p4L/m1L	–	

larger lower premolars, especially p2, and m1. In addition, it has a smaller relative width of the lower canine than *C. a. hesperius*, due to its increased length (cL). The same feature was also expressed in the proportion of the upper canines, but with less contrast between subspecies (Text-fig. 6).

There were only two coordinates in the descriptive models for the group of southern subspecies (Suppl. Tab. S6). The SZM and SHM models reproduced 96.1 % and 87.7 % of the variance of the initial distances between individuals, respectively. The indicators for the coordinate E1 were P4L, m1L, m1W, E2 was P4W, K1 was p4L/m1L, and K2 was m1W.

As could be concluded from the modelling for all modern subspecies (Fig. 5a, b), the southern subspecies were virtually indistinguishable in their specific model spaces (Suppl. Fig. S2). The exception was *C. a. javanicus*, which differed in length P4 and p4 from *C. a. primaevus* and in p2L, p2L/m1L, p4L/m1L from *C. a. dukhunensis* (Tab. 5).

In general, *C. a. javanicus* has small teeth on average, except m1, compared to the two aforementioned subspecies with relatively large teeth.

Text-fig. 7 shows UPGMA trees illustrating the relative position of putative subspecies in the descriptive model spaces. Here we used the median values of the SZM and SHM coordinates for each subspecies as variables. Thus, the trees presented reflect information on both tooth size and proportion variability. For the full sample, including all subspecies, the above division into northern and southern subspecies groups is confirmed (Text-fig. 7a). On the tree constructed for the southern group only (Text-fig. 7b), a "southeastern" subgroup containing *C. javanicus* and *C. a. infuscus/C. a. sumatrensis* is distinguished. This subgroup is opposed to all other subspecies, which we have termed the Indo-Himalayan subgroup. In general, the trees shown correspond to the geographical distribution of the subspecies (Text-fig. 3).
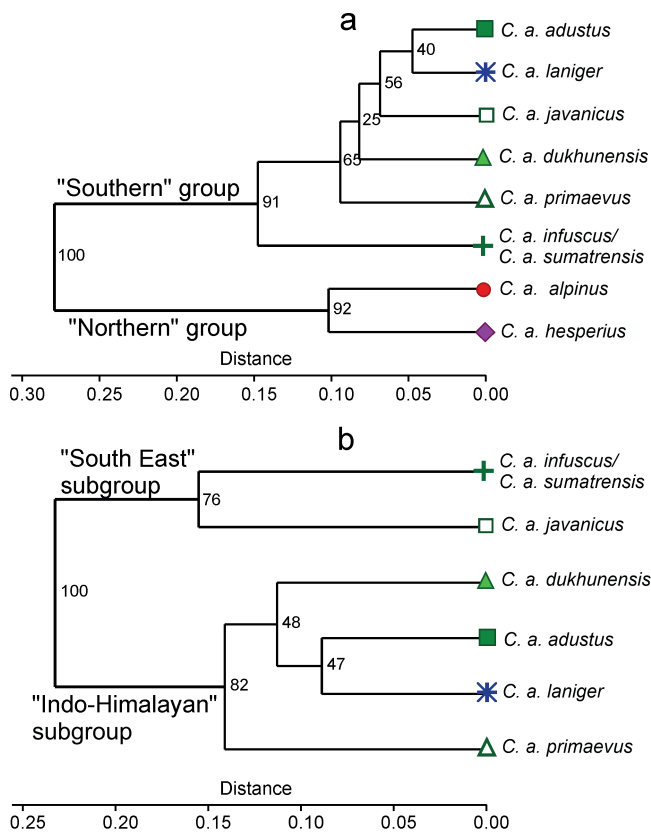
Text-fig. 7. UPGMA trees (Euclidian distance used) of dhole subspecies based on sample medians of coordinates of descriptive SZM and SHM models – a: all subspecies; b: southern subspecies group only. Numbers – bootstrap support for branching in percent (n = 100).

Comparison of fossils and extant dholes

In this section we use our own and literature data to assess dental variability in fossil dholes. Material from modern subspecies is also used for comparison with fossil material. We also used formal classification procedures to estimate a minimum objective number of morphological groups.

Upper and lower canines

The sample is divided into two groups based on the size and CW/CL of the upper canines (Text-fig. 8a). The first group includes modern subspecies with relatively large canines (*C. a. alpinus* and *C. a. hesperius*) and a specimen

of *C. a. javanicus* with small canines. The canines of the fossil dholes are significantly larger, wider and therefore more rounded in cross-section (Tab. 6). The fossil canines form the second morphological cluster. In addition to them, this cluster includes one representative each of *C. a. alpinus* and *C. a. hesperius*.

The partitioning of the upper canine sample into two clusters is stable, i.e., independent of the classification method used (Tab. 7).

The specimen from Bliznets Cave is characterized by its small size, but the most rounded cross-sectional shape.

The neighbor-joining tree in the Text-fig. 8c illustrates the relationships between subspecies and forms samples in the space of the descriptive model, and supports partitioning into two clusters.

The variability of the lower canine is less certain (Text-fig. 8b, Tab. 7). The canines of the fossil forms are slightly larger and more rounded in cross-section than those of the modern forms, but only at the level of tendency. In general, the variability between the fossil forms and the subspecies from the northern group (*C. a. alpinus* and *C. a. hesperius*) is close to continuous. The neighbor-joining tree in Text-fig. 8d also shows continuous variability of the lower canines. The specimen found in the Bliznets Cave has intermediate characteristics between *C. a. fossilis* and *C. a. caucasicus*.

Upper fourth premolar (P4)

In the descriptive model space, the sample of the fourth upper premolar is split into two morphological clusters (Text-fig. 9). This division is stable and independent of the formal classification method (Tab. 7). The differences between the clusters are determined by the tooth dimensions, but especially by its relative width (P4W/P4L).

The fossil samples are characterized by relatively wide premolars with a P4W/P4L index ranging from 0.45 to 0.53 (Tab. 8). Only two relatively small teeth belonging to *C. a. europaeus* fall into another cluster, which mainly comprises subspecies from the southern group of modern *C. alpinus*. In the latter, the range of P4W/P4L variation is 0.33–0.48, according to our data (Tab. 5).

The subspecies *C. a. alpinus* (completely) and *C. a. hesperius* (with the exception of three individuals) fell into the same group as the fossil forms. Their resemblance to Pleistocene dholes is due to the large size of the tooth, but primarily to its relative width. In the northern group

Table 6. Medians (Me) and Min–Max of upper and lower canine measurements and indexes in fossil *C. alpinus*

Measurement	*C. a. caucasicus*	*C. a. europaeus*	*C. a. fossilis*	Bliznetz Cave
	Me; Min–Max	Me; Min–Max	Me; Min–Max	
CL	11.0; 10.4–11.65	11.7; 10.97–11.94	–	10.3
CW	6.9; 6.4–7.15	7.5; 6.69–7.72	–	6.9
CW/CL	0.62; 0.56–0.66	0.64; 0.60–0.65	–	0.67
N	8	3	–	1
cL	10.4; 10.0–11.1	11.97; 10.3–13.0	11.0; 11.0–11.6	10.7
cW	6.57; 6.2–7.1	8.0; 6.6–8.78	7.3; 7.2–7.7	7
cW/cL	0.62; 0.59–0.69	0.65; 0.62–0.72	0.66; 0.65–0.66	0.65
N	6	8	3	1
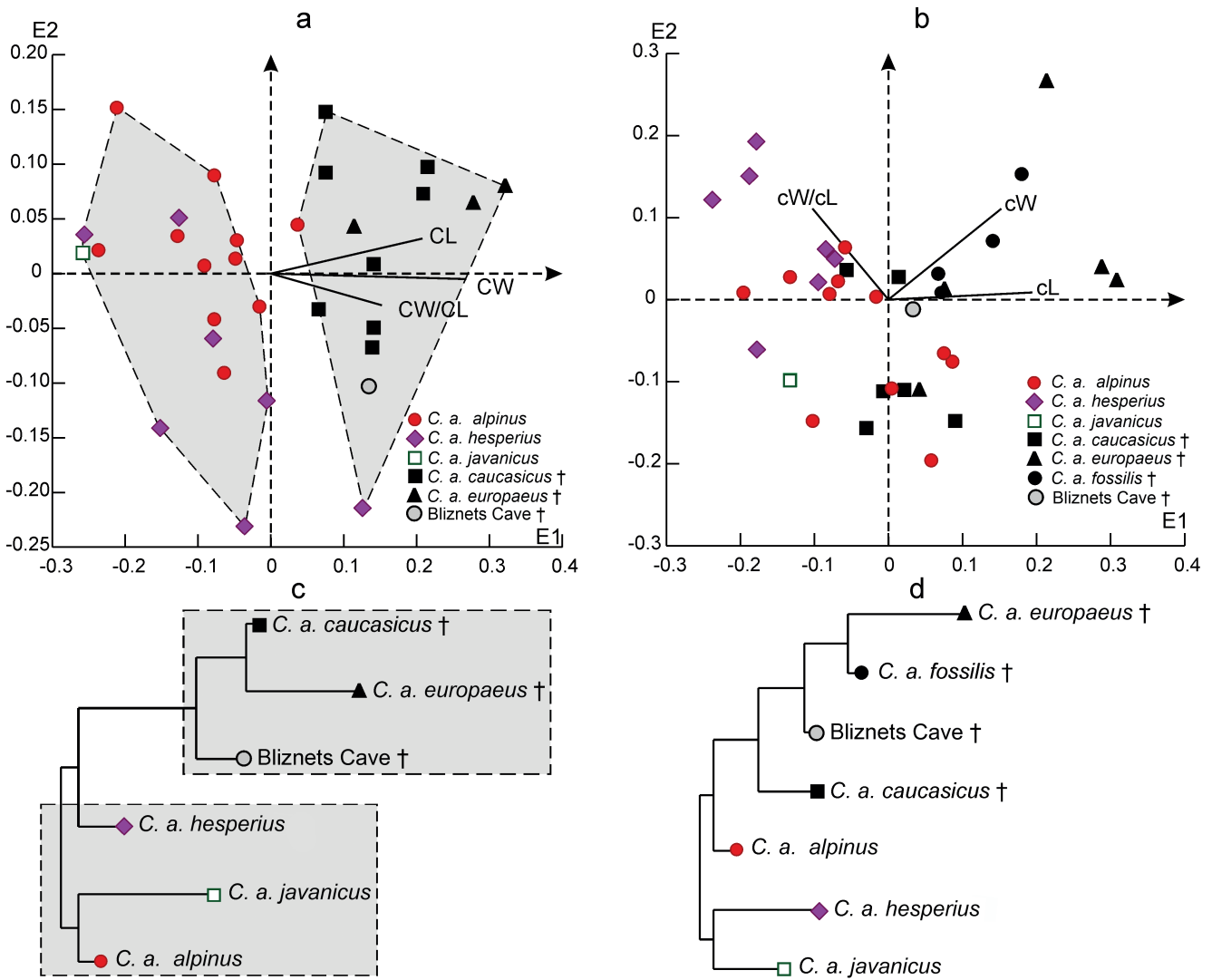
Text-fig. 8. Descriptive models of variability in upper (a) and lower (b) canines in fossil and present-day *C. alpinus*; convex hulls restrict specimens belonging to two formally distinct morphological clusters. c, d: neighbor-joining trees (Euclid distance) of fossil and extant *C. alpinus* subspecies and selected fossil samples based on medians of descriptive model coordinates for upper (c) and lower (d) canines.

of subspecies, the mean P4W/P4L values are 0.47 (*C. a. alpinus*) and 0.44 (*C. a. hesperius*), and the range of index variation is 0.34–0.51 (Suppl. Tab. S4).

The ranges of variability in length (19.7–21.5 mm) and width (6.7–10.8 mm) of P4 in *C. a. alpinus* and *C. a.*

hesperius only partially overlap with the corresponding ranges in fossil forms (19.4–24.4 mm and 9.6–14.6 mm, respectively). Thus, P4 in the northern group of subspecies is on average smaller than in Pleistocene *C. alpinus*, but in the ratio P4W to P4L, these subspecies are closer to the

Table 7. Number of clusters according to majority rule (MR) for different partition methods (KM. UPGMA, McQuitty), partitioning around medoids (PAM), Gaussian finite mixture model (GFM), sample number (N), and decision about putative number of morphological clusters.

Tooth	MR			PAM	GFM	N	Decision
	KM	UPGMA	McQuitty				
C	2	2	2	2	2	32	2 clusters are proposed
P4	2	2	2	2	2	98	2 clusters are proposed
c	3	2	2	3	3	37	continuous variability prevails
p2	2	2	2	2	2	89	2 clusters are proposed
p4	9	5	2	7	2	107	may be 2 clusters present; continuous variability prevails
m1	3	3	2	2	2; 3	134	may be 2 or 3 clusters present; a continuous variability prevails
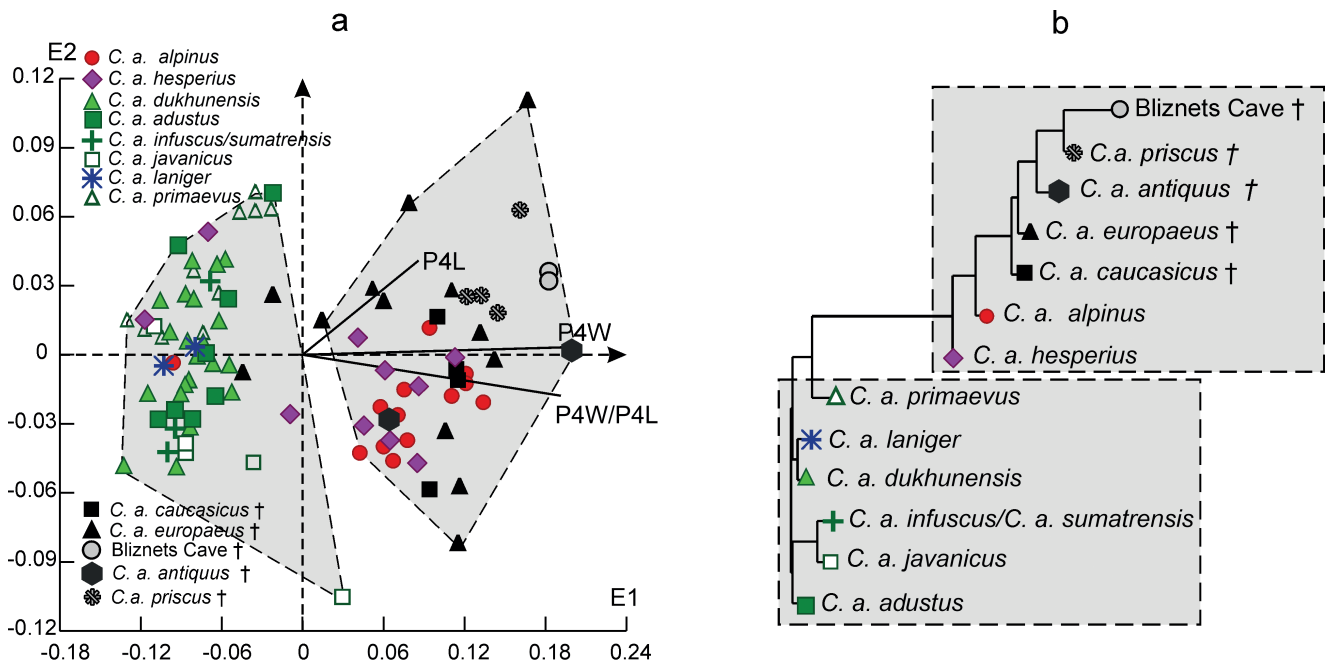
Text-fig. 9. Descriptive model of variability in upper forth premolar (a) and neighbor-joining tree (Euclid distance) of fossil and extant *C. alpinus* (b) based on medians of descriptive model; convex hulls restrict specimens belonging to two formally distinct morphological clusters.

Table 8. Medians (Me) and Min–Max of P4 measurements and indexes in fossil *C. alpinus*.

Measurement	*C. a. caucasicus* Me; Min–Max	*C. a. europaeus* Me; Min–Max	*C. a. priscus* Me; Min–Max	*C. a. javanicus* (*antiquus*)	Bliznets Cave
P4L	21.2; 19.8–21.7	21.5; 19.4–24.4	22.1; 22.0–23.2	20.3, 22.0	22.6, 22.7
P4W	13.0; 12.4–14.6	10.4; 9.65–11.7	11.0; 10.7–11.5	9.6, 12.0	11.8
P4lp	10.4; 10.0–10.5	14.9	–	–	14.5, 15.9
P4W/P4L	0.50; 0.48–0.51	0.50; 0.45–0.53	0.49; 0.486–0.50	0.47–0.54	0.52
N	4	13, 7, 1	4	2	2

Table 9. Medians (Me) and Min–Max of p2 and p4 length in fossil *Cuon* sp.

Measurement	*C. a. caucasicus* Me; Min–Max	*C. a. europaeus* Me; Min–Max	*C. a. fossilis* Me; Min–Max	*C. a. nizhneudensis*	*C. a. antiquus*	Bliznets Cave	Mocun Cave	Geographical Society Cave	San Josecito Cave
p2L	8.7, 9.8	9.5; 8.2–10.4	9.1; 8.9–9.9	9.4	–	9.6	9.28	–	8.9, 9.0
N	2	17	3	1	–	1	1	–	2
p4L	14.0; 13.75–14.6	14.55; 13.0–15.4	14.25; 13.7–14.8	14.7, 14.9	11.55	–	–	13.9	13.5, 13.8
N	6	22	4	2	1	–	–	1	2

extinct forms than to modern ones from the southern group. The position of the fossil dholes and *C. a. alpinus* and *C. a. hesperius* relative to the other modern subspecies is well illustrated by the neighbor-joining tree in Text-fig. 9b.

Within the P4 fossil sample, variability of P4 seems to be continuous (Text-fig. 9, Tab. 8), distinguishing it from the modern *C. alpinus* sample.

Lower second and fourth premolars (p2, p4)

The p2 sample was clearly divided into two formal clusters (Tab. 7), with a significant gap between them (Text-fig. 10a). One cluster consisted of modern subspecies from the southern group with an average tooth length of 4.3–5.1 mm (min–max: 3.7–5.8 mm) (Tab. 5). A single p2 (p2L = 7.6 mm) determined to belong to a specimen of the *C. a.*
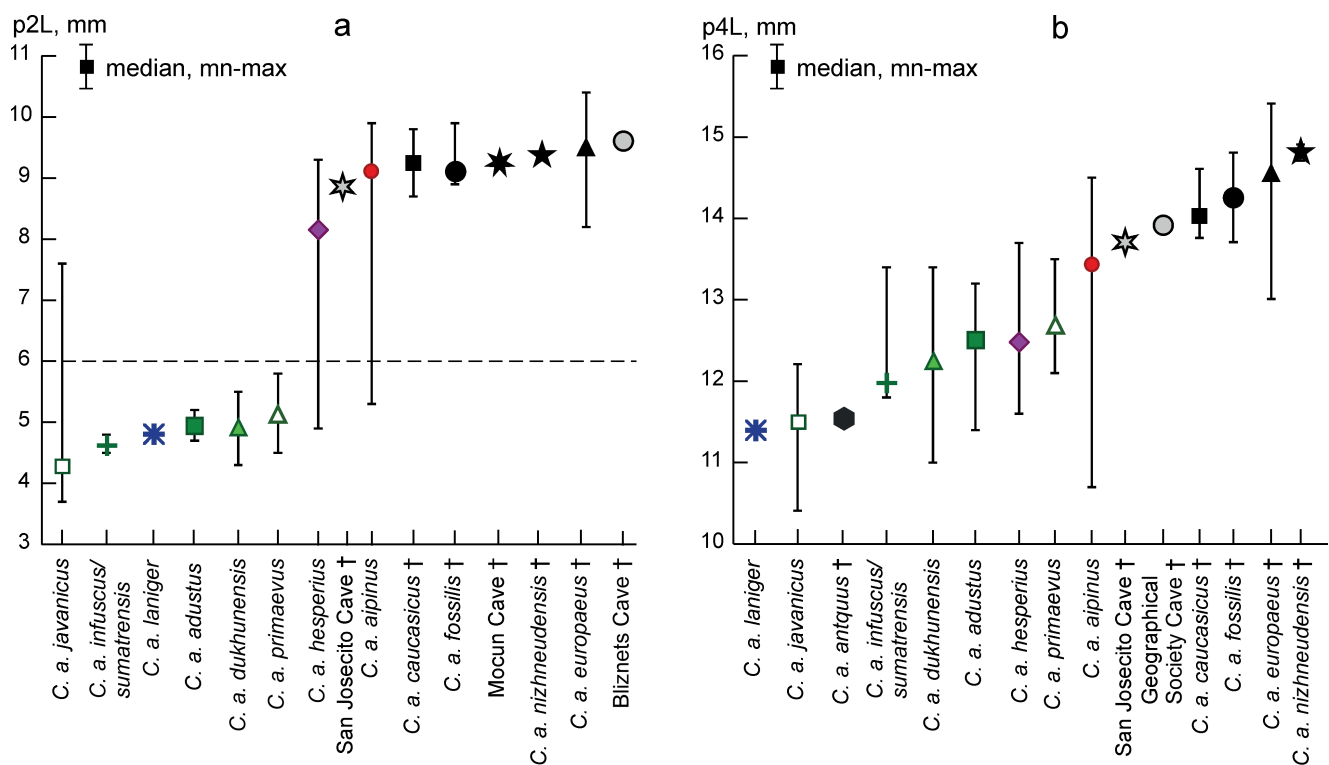
Text-fig. 10. Variations in second (a) and fourth (b) lower premolars in fossil and extant *C. alpinus*; dotted line drawn along boundary between two formally distinct morphological clusters.

javanicus extends well beyond the upper limit of the defined range (Text-fig. 10a).

The second morphological cluster includes the entire Pleistocene sample, and samples of modern *C. a. alpinus* and *C. a. hesperius*. Within the group of fossil forms, the widest range of variability in second premolar length (8.2–10.4 mm) was found in the sample of *C. a. europaeus* (Tab. 9). Among the fossil samples, the median tooth length was between 9 and 10 mm, and the mean value in *C. a. europaeus* was 9.5 ± 0.14 mm.

The mean p2 length in *C. a. hesperius* was 7.6 ± 0.6 mm, with a median of 8.2 mm and a range of 4.9 mm to 9.3 mm (Tab. 4). Similar parameters exist in *C. a. alpinus*: 8.98 ± 0.35 mm, 9.15 mm, 5.3–9.9 mm. The lower limit of variability ranges in the studied samples is determined by only two specimens with extremely short p2. If we exclude these specimens from the calculations, the ranges narrow to 6.0–9.3 mm and 9.0–9.9 mm for *C. a. hesperius* and *C. a. alpinus*, respectively. The length of p2 in *C. a. nizhneudensis*, specimens from the Mocun and Bliznets caves, and other fossil forms is within the range of variability of *C. a. europaeus*.

The data presented allow us to conclude that in fossil *C. alpinus*, the length of the second lower premolar varied within relatively narrow limits, from Europe to South East Asia, just as it varies today in most representatives of the subspecies from the southern group. The range of variability of p2 in *C. a. hesperius* and especially in *C. a. alpinus* overlaps significantly with the range of Pleistocene dholes. The length of p2 in specimens from the San Josecito Cave (Mexico) was closest to the median of *C. a. alpinus* (Text-fig. 10a). The last locality is the only one with *Cuon* remains in North America (Tedford et al. 2009), and was dated at 48–32 cal. ka BP (Cruz et al. 2023).

The variability of the fourth lower premolar does not allow us to distinguish fossil from modern *C. alpinus* in the general sample. Results of the formal classification depend on the method of sample division (Tab.7). This serves as an indirect indication of the continuous variability of p4 length. Nevertheless, Text-fig. 10b shows that, with the exception of *C. a. alpinus* and *C. a. antiquus*, this tooth was longer on average than in modern forms.

The range of variability of p4L in fossil forms (excluding *C. a. antiquus*) is 13.0–15.4 mm (Tab. 9), and in modern forms (excluding *C. a. alpinus*) it is 10.4–13.7 mm (Tabs 5, 6). The range of p4 length in *C. a. alpinus* is 10.7–14.5 mm, i.e., the p4 dimension in this subspecies is intermediate between modern and Pleistocene dholes. The p4 size of *C. alpinus* ssp. from the San Josechito Cave (Mexico) was between the median of *C. a. alpinus* and the value of specimen from Geographical Society Cave. Note also, the length of p4 in the *C. a. antiquus* specimen is within the interval of variability of *C. a. javanicus*.

In general, the entire range of variability in the length of this premolar in fossil forms falls within the range of variability for *C. a. europaeus*, as well as most of the range for *C. a. alpinus*. (Text-fig. 10b).

Lower first molar (m1)

The main component of variability m1 is related to its width, while the second component is related to the length and relative width of the tooth (Text-fig. 11a). In the space of the descriptive model, the regions of modern and fossil dholes overlap considerably. Results of the formal classification do not exclude the presence of 2 or 3 clusters, depending on the sampling partitioning method used (Tab. 7). This reflects the
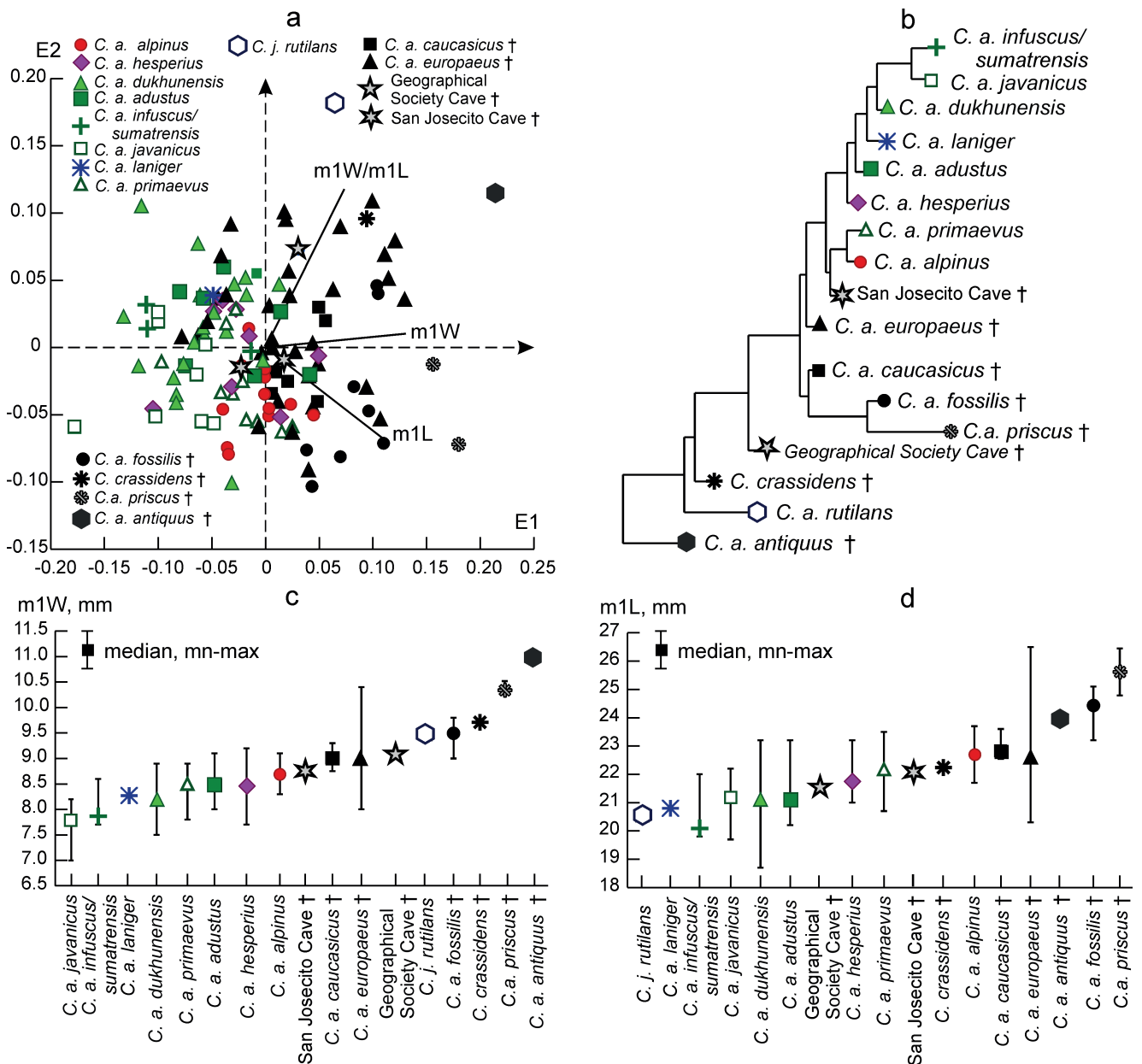
Text-fig. 11. Descriptive model of variability in lower first molar (a), neighbor-joining tree (Euclid distance) of fossil and extant *C. alpinus* (b) based on medians of coordinates of descriptive model. c, d: variations of m1W (c) and m1L (d) in fossil and extant *C. alpinus*.

fact that continuous variability dominates within the sample studied.

Indeed, both length and width of m1 form a continuous series of variability (Text-fig. 11c, d). Against this background, there is a general trend of decreasing molar size from Pleistocene forms to extant dholes. In fossil dholes, the width of m1 varies between 8.0–11.0 mm and the length between 20.3–26.5 mm (Tab. 10). The corresponding values of these intervals in modern *C. alpinus* are 7.8–9.2 mm and 18.7–23.7 mm, according to our data (Tabs 5, 6, Suppl. Tab. S4). Tooth proportions (m1W/m1L) do not change significantly: 0.38–0.42 in fossil taxa, 0.37–0.40 in modern taxa.
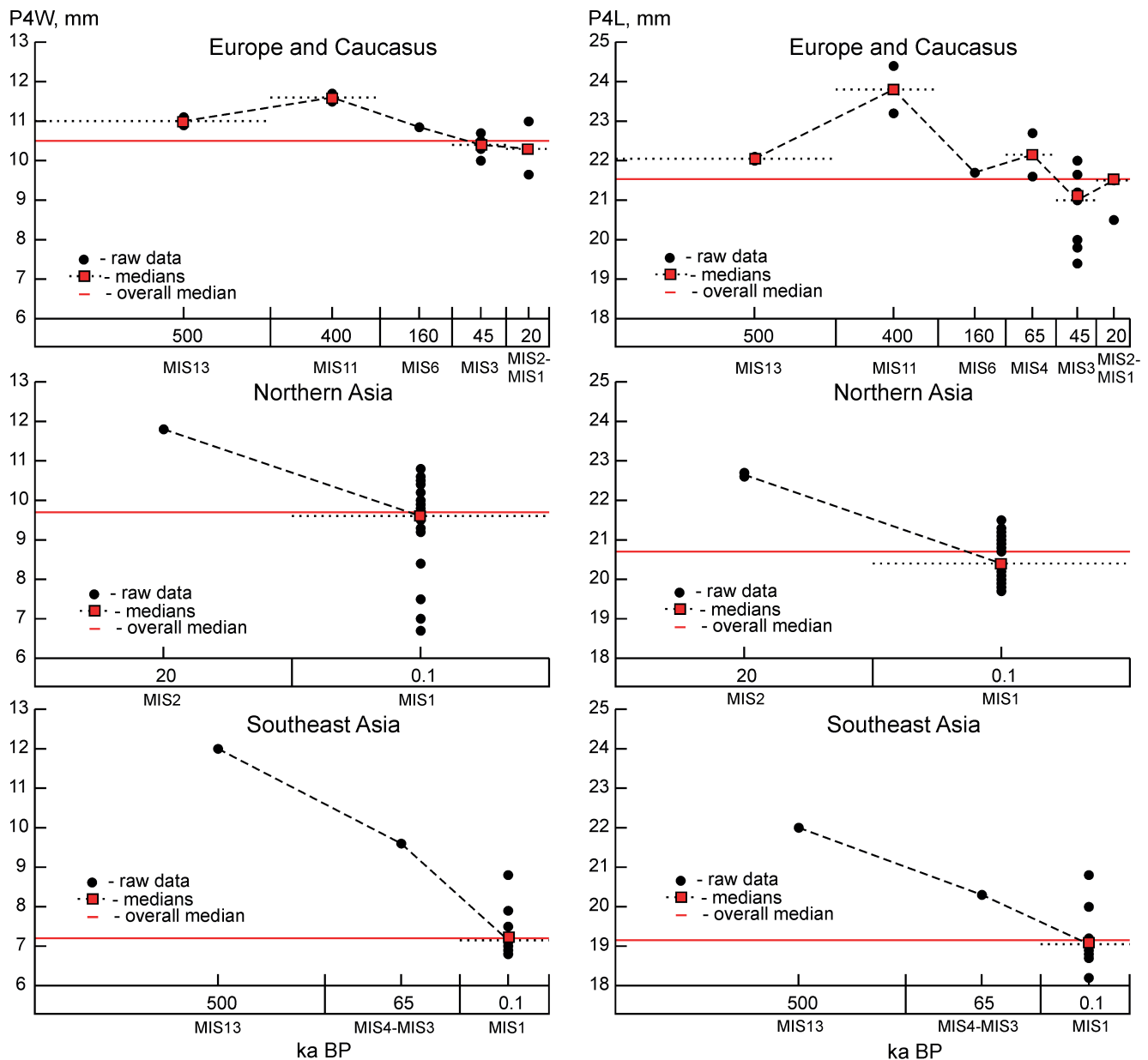
The neighbor-joining tree (Text-fig. 11b) reflects size and shape differentiation between modern and fossil dholes (Text-fig. 11b). Note the peculiar position on the tree of the *C. a. rutilans* (Yunnan, China; Colbert and Hooijer 1953)

specimen, which fell into the same group as the fossil *C. a. antiquus* and *Cuon crassidens* VON KOENIGSWALD, 1933 (= *C. alpinus* from Pandejan, Indonesia; see Tab. 1). R. Volmer (Volmer et al. 2019) revisited a mandible fragment from Pandejan site (holotype of *C. crassidens*) and showed that it shows a morphology typical for *C. alpinus*.
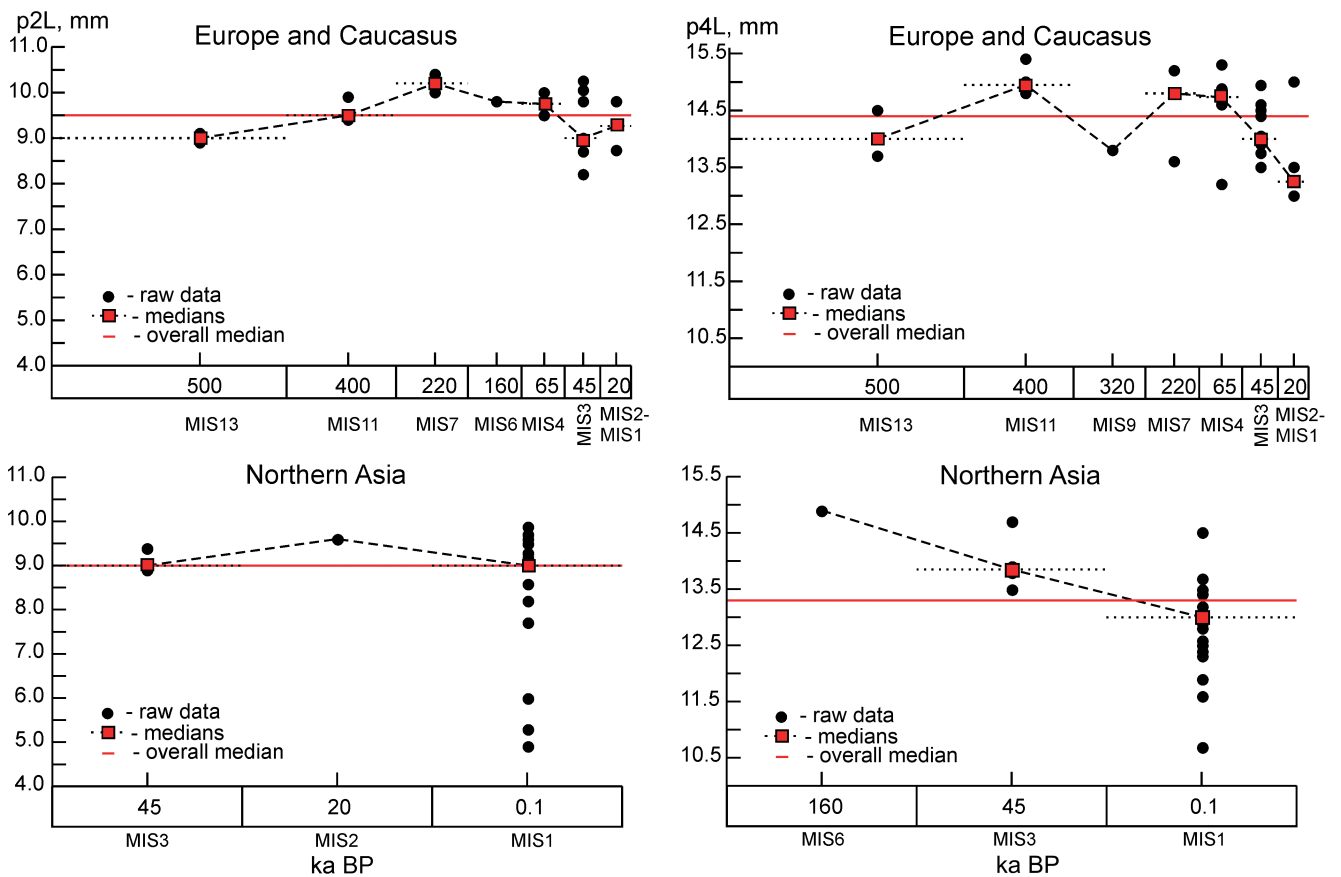
The association of this modern specimen with the fossil ones is a consequence of the large relative width of the tooth, which is 9.5 mm and a very modest length (20.6 mm). The relative width of the tooth is 0.46, bringing it closer to m1 of *C. a. antiquus* from Bailong Cave, which has the same relative width but much larger linear dimensions of the tooth (24 and 11 mm, respectively). The fossil m1 from the Far East of Russia (Geographical Society Cave) is included in this group due to the combination of the small length (21.6 mm) with relatively large width (9.1) of the tooth (m1W/ m1L = 0.42).

Table 10. Medians (Me) and Min–Max of m1 measurements and indexes in fossil *C. alpinus*.

Measurement	*C. a. caucasicus*	*C. a. europaeus*	*C. a. fossilis*	*C. a. priscus*	*C. a. antiquus*	Geographical Society Cave	San Josecito Cave
	Me	Me	Me				
	Min–Max	Min–Max	Min–Max				
m1L	22.8	22.6	24.5	26.29	24	21.6	22.0–22.6
	22.55–23.6	20.3–26.5	23.2–25.1				
m1W	9.0	9.0	9.5	10.4	11	9.1	8.5–8.9
	8.75–9.30	8.0–10.4	9.0–9.8				
m1tal	6.6	6.75	–	–	–	5.5	–
	6.4–6.9	5.9–7.8					
m1W/m1L	0.39	0.34	0.39	0.4	0.46	0.42	0.38–0.39
	0.38–0.41	0.37–0.44	0.37–0.42				
N	6	39, 36	11	1	1	1	2

Text-fig. 12. Time series of upper carnassials (P4) variations in different parts of *Cuon* sp. range, from Middle Pleistocene to Holocene.

Text-fig. 13. Time series of lower premolars p2 and p4 length variations in different parts of *Cuon* sp. range, from Middle Pleistocene to Holocene.

Representatives of the subspecies from the southeastern group, including *C. a. javanicus*, occupy the opposite position on the tree in relation to the group described above, approaching in size and shape the dholes from the Indo-Himalayan group of subspecies (Text-fig. 11b). Of all the dholes, this group has the slenderest lower carnassial teeth, with a relative width in the range of 0.36–0.39 (Tab. 5).

The subspecies *C. a. alpinus* and *C. a. hesperius* occupy an intermediate position on the tree, between the fossil forms and modern dholes from the southern subspecies group. *C. a. primaevus* is placed on the same branch with *C. a. alpinus*, because of its large m1 size (median tooth length in our sample was 22.2 mm, Tab. 5). The lower carnassials from the San Josecito Cave are on the same branch as *C. a. alpinus*.

Trends in time

Upper fourth premolar (P4)

In the western part of the range, on the territory of Europe, we can cautiously assume a trend towards a decrease in the size of this tooth in the Middle Pleistocene (Text-fig. 12). This trend ended in the middle of the Late Pleistocene. The length of the tooth decreased by about 12.5% and its width by 10.5% during the interval MIS 11 – MIS 3. For the region of Northern Asia, the data are insufficient to make an informed judgement about the trend. We can only note that the upper limit of tooth width and length in the Holocene sample is lower than the values of these measurements in the Late Pleistocene sample. A decrease in P4 size in the southeastern

part of the range probably also occurred from the Middle Pleistocene onwards. Although the data are insufficient to make an informed statement, it can be assumed that the size of this tooth was initially about the same as in the European part of the range. Eventually, the size of P4 in this region reached the minimum values for the species as a whole.

Lower second and fourth premolars (p2, p4)

The variability of p2 length did not show any temporal changes that could be classified as trends. Median tooth size changed little from the Middle Pleistocene until the species went extinct in the European part of the range. In the east, in the Northern Asia region, the situation was probably similar. Note only that the lower limit of tooth size in the Holocene regional sample is significantly lower than the median value of tooth length (Text-fig. 13).

The length of p4 in European dholes was relatively stable during the Middle Pleistocene and until the second half of the Late Pleistocene. Between MIS 3 and MIS 2, a decrease in the length of this tooth can be assumed (Text-fig. 13). In northern Asia, this trend may have been also pronounced in the Late Pleistocene. In any case, the medians for length of this tooth were approximately the same in both regions at the end of the Late Pleistocene, before the extinction of the species in Europe.

Lower first molar (m1)

The m1 size does not show directional change during the middle Late Pleistocene in dholes from Europe (Text-fig. 14). For the regions North Asia and Southeast Asia, we

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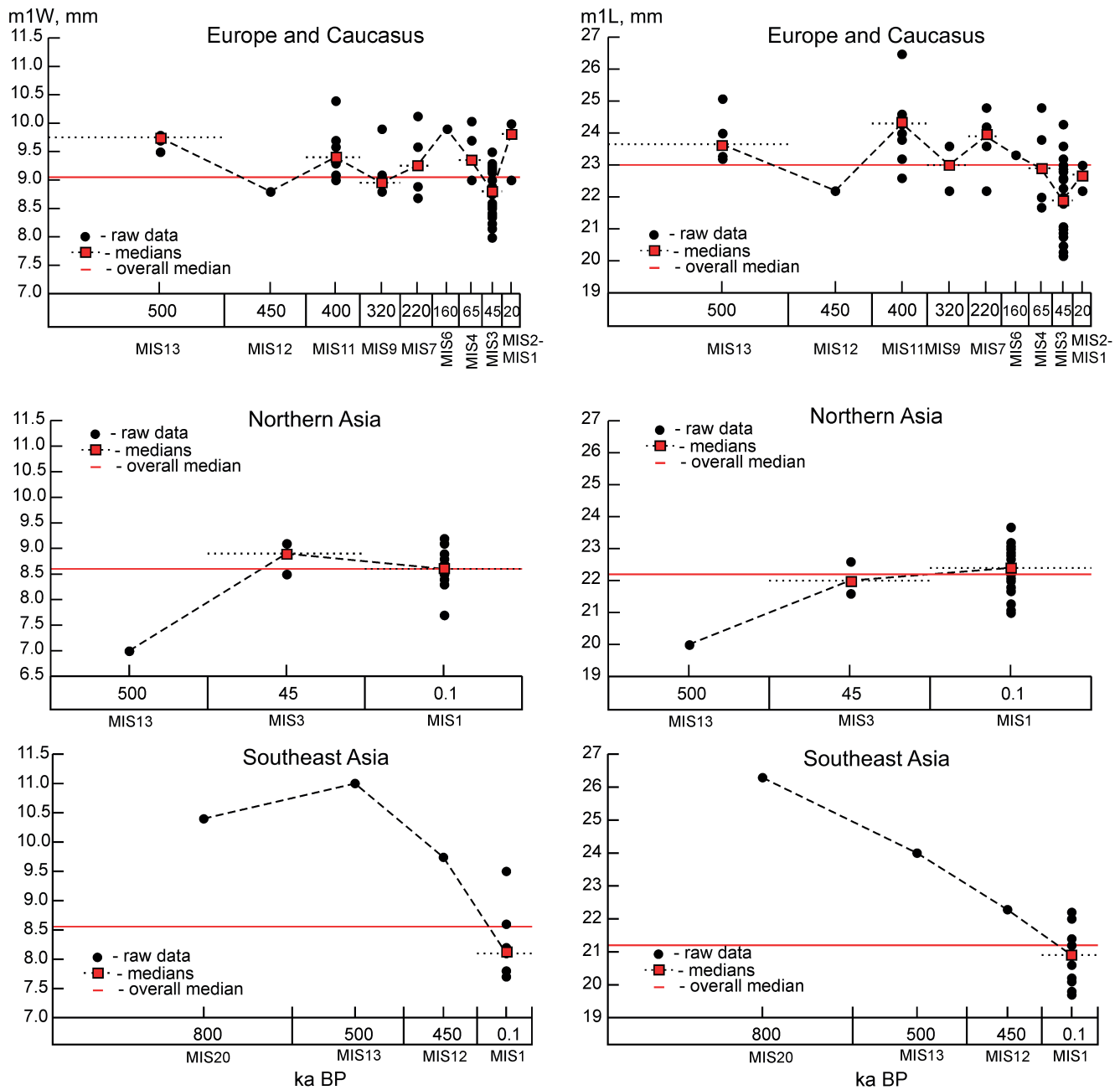
Text-fig. 14. Time series of lower first molar (m1) variations in different parts of *Cuon* sp. range, from Early Pleistocene to Holocene.

did not have sufficient data to make any statements. We do not exclude that in northern Asia, tooth size decreased slightly between MIS 3 – MIS 1. In the second region, there is more reason to believe that the size of the lower carnassial decreased throughout the interval, starting from the end of the Early Pleistocene (tooth length) or from the beginning of the Middle Pleistocene (tooth width).

Discussion

In this study we present material on the modern geographic size variability of teeth in dholes and the variability of fossil teeth from sites dating from the late Early to Late Pleistocene. We used our own data and previously published material (tooth measurements). We have not analyzed tooth morphology itself. Therefore, the morphotype variability

of *Cuon* fossils (Adam 1959, Bonifay 1971, Baryshnikov 1996, Petrucci et al. 2012, Marciszak et al. 2021) is not discussed. The problem of chronospecies, particularly in Europe (Brugal and Boudadi-Maligne 2011), has been left out of our discussions.

The hypothesis that there is no sexual size dimorphism (SSD) in teeth in this species was specifically tested, as considering or ignoring this form of variability may affect the interpretation of results from studies of spatial and temporal variability. In *C. alpinus*, "sexual dimorphism is not very distinct with no quantitative anatomical differences known" (Durbin et al. 2004). However, males tend to be slightly larger and heavier (Maisch et al. 2017). SSD not detected in postcranial skeletal elements (Ghezzo and Rook 2014). Sanchís et al. (2020) did not rule out SSD in animals from Indonesia and China, where males have "longer and wider teeth than females". However, the authors emphasized

the small sample size studied. We confirmed the possibility of SSD in extant dholes on carnassial size. However, the means of index values (P4W/P4L, m1W/m1L) in females and males were not significantly different, with their 95% confidence intervals strongly overlapping. Therefore, we cannot recommend the use of P4W/P4L or m1W/m1L indices for sex determination not only in extant, but even less so in fossil *C. alpinus*. The potential contribution of this form of variability to the overall variability in tooth size and proportions is not considered to be significant. The hypothesis that relatively small teeth (not only P4 and m1) in the fossil samples belong to females or the largest teeth to males does not appear to have sufficient support.

Geographical variability in the size and proportions of individual teeth in modern *C. alpinus* is clearly present. However, its correspondence with intraspecific systematics (Durbin et al. 2004) is not always confirmed. The analysis of tooth variability allowed us to identify two main geographical groups. The Northern group of taxa includes two subspecies of *C. a. alpinus* and *C. a. hesperius*. All other dholes form the Southern group, clearly contrasted by the sizes and proportions of the premolars P4, p2. Within the latter, animals with the smallest teeth from south-east Asia (Indonesia, southern Myanmar, Malaysia, Thailand, Laos, Cambodia and Vietnam), referred to as the South East subgroup, occupy some distinct position, based on the size of P4, p2 and p4. Formally, this is the range of the subspecies *C. a. infuscus*, *C. a. sumatrensis* and *C. a. javanicus* (Durbin et al. 2004). The remaining representatives of the species thus form the Indo-Himalayan subgroup, in which we have included the subspecies *C. a. adustus*, *C. a. laniger*, *C. a. dukhunensis* and *C. a. primaevus*. The position of *C. a. lepturus* (described from south of the Yangze River, China) in this scheme is not defined. We had no material on this subspecies.

It does not seem to us to be a coincidence that morphological differentiation at the considered levels of the geographic structure of the species manifests itself in the variability of the same teeth – the premolars. This circumstance points to the common basis of the evolutionary processes that led to the formation of modern geographic diversity within the species.

The subspecies *C. a. alpinus* and *C. a. hesperius* are close to each other with respect to the main components of variability (coordinates of the descriptive model) of tooth size. Nevertheless, we found a number of statistically significant differences between them in mean values of lengths p2, p4 and m1. A specific sign of subspecies differentiation was the cW/cL ratio, i.e., the shape of the canine cross-section, which was larger in *C. a. hesperius* (more rounded cross-sectional shape).

Tooth variability of Pleistocene and modern dholes was studied together. For this purpose, descriptive models of variability were constructed for each tooth separately. The upper canines of fossil animals were larger than those of present-day ones (our material was limited to *C. a. alpinus*, *C. a. hesperius* and *C. a. europaeus*, *C. a. caucasicus*), while their lower canines did not show such differences.

According to P4 size, all dholes were divided into two groups, one of which included fossil specimens and modern subspecies of the northern group with a wide premolar. In addition to the absolute width of the tooth, the variation in its relative size supports this differentiation. Thus, fossil forms throughout the *Cuon* range had relatively wide upper carnassial teeth. This archaic character is preserved in the subspecies *C. a. alpinus* and *C. a. hesperius*. In other modern members of the species, the fourth upper premolar is relatively narrow. In animals living in Europe and possibly northern Asia, the proportions of this tooth remained unchanged during the Middle to Late Pleistocene. At the same time, there was a process of gracialization of P4 in Southeast Asia, reflected in a reduction of P4W/P4L from about 0.54 (early Middle Pleistocene) to 0.38 and below (Holocene). This scheme should be confirmed on material that is more representative.

The length of the second lower premolar proved to be very conservative in the fossil record. Pleistocene animals had a large p2 (usually more than 8 mm). In contrast, in modern forms from the southern group of subspecies, this premolar is modest in size (usually less than 6 mm). It is noteworthy that in the subspecies of the northern group, the size of p2 is approximately the same as in the fossil forms. We can therefore hypothesize that the size of this premolar decreased in the southern part of the palaeorange in the Middle and Late Pleistocene. In the northern and northwestern parts of the range it remained the same size. This hypothesis also requires confirmation on palaeontological material, which we did not have in this study.

The length of the fourth lower premolar in fossil and extant *C. alpinus* is characterized by a continuous range of variability, with fossil forms (except *C. a. antiquus*) and *C. a. alpinus* having the largest p4 dimensions on average. In the small sample of *C. a. javanicus* and in specimens of *C. a. javanicus* and *C. a. laniger*, p4 had the smallest length. For the European part of the range, which has the most representative palaeodata, we found no trends in the variability of the length of this tooth. Some decrease in the size of p4 may have occurred at the end of the Late Pleistocene, but this needs to be confirmed on a broader evidence base. A similar hypothesis is possible for animals that inhabited the North Asia region. Due to the continuity of variability, the length of p4 does not allow us to divide the sample into morphological groups. But even in this case, we note that the similarity of *C. a. alpinus* (but not *C. a. hesperius*) with Pleistocene European dholes is striking, as is the small size of this premolar in animals from the southern group of subspecies.

The variability of the size of the lower carnassial tooth (m1) in *Cuon* sp. is related to its absolute and relative width. The most massive teeth, with wide crowns and high values of the m1W/m1L index were described in fossil dholes, especially in *C. a. antiquus* (Tab. 10). At the same time, against the background of a wide range of variability, we found no clear gaps between modern and fossil animals in either the width or length of this tooth, when considering the range of variability as a whole (Text-fig. 11). The subspecies *C. a. alpinus* and *C. a. hesperius*, as in a number of other cases, show archaic variants of variability, and accordingly occupy an intermediate position between Pleistocene and modern dholes, especially in terms of m1 width.

In the European region, m1 length and width show no directional changes in the Middle-Late Pleistocene (Text-fig.

14). Tooth dimensions oscillate around the sample median on this time interval. This statement does not exclude the existence of trends over shorter periods. Thus, in Europe, the length of m1 probably decreased between about MIS 7 and MIS 3 (MIS 2?) (Marciszak et al. 2021). However, the width of this tooth in our material does not show such a tendency.

For the Southeast Asia region, we hypothesized a progressive decrease in the dimensions of the lower carnassial in the Middle to Late Pleistocene, ranging from width and length values that may have exceeded those of early European dholes to the lowest values of measurements among the present forms (length m1). We consider this to be a possible evolutionary scenario that requires further testing. In this scenario, the robust lower carnassial is a primitive variant compared to the more gracile m1 in most modern dholes.

Tedford et al. (2009) found no significant differences between the characteristics of *Cuon* teeth from North America (San Josecito Cave) and those of *C. a. europaeus* from the European Late Pleistocene. According to our results, in terms of size, p2, p4 and m1 from the San Josecito Cave are closest to the teeth of modern *C. a. alpinus*. This seems logical, since it is very likely that the ancestors of *C. a. alpinus* were among the migrants to the New World in the Late Pleistocene (late Rancholabrean). It is possible that the animals migrated south along the Pacific coast, right across the area that is now the flooded shelf. This could explain the lack of other dhole remains in North America.

Conclusion

The analysis of tooth size variability in modern and fossil *Cuon* presented in this study revealed morphological differentiation between dholes inhabiting Pleistocene Europe (including the Caucasus), Siberia and the Far East, and dholes distributed in Southeast Asia. The differences between them seem to have increased progressively from the Middle Pleistocene onwards. While in northern Eurasia, the size of teeth may have been fairly stable until at least the Late Pleistocene, in Southeast Asia, a process took place that led to a decrease in the size of lower premolars and predatory teeth. This trend was most pronounced in the dholes that now inhabit the Sunda region. *Cuon* appear in this region as early as the early Middle Pleistocene (Volmer et al. 2019). Their evolution was influenced by periodic isolation on islands formed during Pleistocene interglacials.

We assume that the modern representatives of the northern group of subspecies (*C. a. alpinus* and *C. a. hesperius*) are the remnants (possibly already almost extinct; Makenov 2018) of a phyletic lineage or lineages distributed from the end of the Early Pleistocene in Eurasia from the Pacific Ocean to the Atlantic Ocean. At the west of their range, in Europe, they became extinct at the end of the Pleistocene.

South and Southeast Asia are inhabited by descendants of another lineage or lineages of dholes that have been indigenous to the region since about the early Middle Pleistocene, at least. Within this group, those living in the extreme south-east of Asia are morphologically distinct. Taking into account the peculiarities of the biology of the species, in particular their ability to migrate, it is possible

to assume that there has been periodic gene flow between northern and southern dholes living in Asia.

In conclusion, we wish to emphasize the productivity of comparative analyses of the variability of fossil forms and the variability of their direct descendants living in the present, where such a possibility exists. In particular, the scale of modern variability allows estimation of the scale of temporal variability in fossil forms. The modern spatial pattern of geographic variability can also be one of the sources of data for evolutionary hypotheses.

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