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CUON ALPINUS (PALLAS, 1811) FROM THE LATE PLEISTOCENE SITE OF INGARANO (FOGGIA, SOUTHERN ITALY) AND INSIGHTS ON THE EURASIAN MIDDLE TO LATE PLEISTOCENE RECORD.

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ABSTRACT: In this study, we report for the first time the presence of *Cuon alpinus* from the Late Pleistocene site of Ingarano (Foggia, southern Italy), represented by an right upper first molar. Considering the intricate and debated taxonomy of fossil dholes, our comparative analyses on dental samples (P^4, M^1, and M_1) of the extant and Middle to Late Pleistocene dholes from Europe, has been performed evidencing a relevant degree of morphological variability and a biometric uniformity of the considered teeth. Our results indicate the lack of clear morphological and biometric features for a reliable teeth-based classification of fossil dholes, questioning the validity of the fossil taxa currently proposed in the literature. Finally, to avoid the propagation of taxonomically questionable species, we suggest to refer all the Middle to Late Pleistocene material to *Cuon alpinus*.

Keywords: Canidae, carnivorans, dhole, biochronology, biometry, teeth.

1. INTRODUCTION

Cuon alpinus (Pallas, 1811), known as dhole, is a medium-sized social canid currently widespread in most of southeastern Asia including the western islands of Indonesia (Durbin et al., 2004; Wilson & Mittermeier, 2009; Castelló, 2018). Morphological and biometric data led Mivart (1890) to distinguish two extant species of *Cuon*, the northern dhole (*C. alpinus*) and the southern dhole (*C. javanicus*). On the contrary, Ellerman & Morrison-Scott (1966) reunited the diversity of the dhole under a single specific name, identifying 11 subspecies on the basis of their external features (e.g., differences in coat length, color pattern) (Castelló, 2018). Genetic analyses confirmed Ellerman and Morrison-Scott' hypothesis, finding no clear specific distinction, although such works only took into consideration populations from the southern part of the dhole distribution (e.g., Iyengar et al. 2005). Wilson & Mittermeier (2009) grouped all these subspecies under only three, *C. alpinus alpinus*, *C. alpinus hesperius*, *C. alpinus sumatrensis*. Therefore, there is a general consensus in considering the genus *Cuon* as monospecific, although the validity of the different subspecies is still debated.

The dhole is an active predator that lives in large packs, characterized by several dental features related to a hypercarnivorous diet (Van Valkenburg, 1991), such as the slicing premolars, the single-cusped talonid of the lower carnassials, the reduction or even the absence of the second upper molar and the lack of the lower third molar. Except for this latter character, peculiar of the genus *Cuon*, the hypercarnivorous dentition is shared with the extant genera *Lycaon* and *Speothos* (Thenius, 1954; Van Valkenburg, 1991) and the fossil *Xenocyon*.

Whereas today the species is confined to Asia, at the beginning of the Middle Pleistocene the dhole was widespread across Eurasia reaching western Europe (García García, 2003) and North America in the Late Pleistocene (Tedford et al., 2009). Such a wide geographical distribution is a common ecological trait of the Middle-Late Pleistocene canids as documented for *Canis mosbachensis* and *Canis lupus* (Sardella et. al., 2014; Bartolini Lucenti et al., 2017; 2020; Mecozzi et. al., 2017, 2020), both characterized by a large intraspecific variability and thus considered as polymorphic species. Fossil remains of dhole are exceptionally scarce and mainly represented by isolated teeth, fragmented cranial remains and few postcranial elements (Perez-Ripoll et al., 2010). Consequently, the morphological and biometric variability of these carnivorans throughout the Middle and Late Pleistocene is poorly known, fueling the debate on its origin and evolution (Brugal & Boudadi-Maligne, 2011, Petrucci et al., 2012; Ghezzo & Rook, 2014). Here, we offer a comparative study of selected teeth (P^4, M^1 and M_1) of extant and fossil dholes, including the well preserved right M^1 belonging to the first *Cuon alpinus* reported from the Late Pleistocene site of Ingarano.

Taxa		Extant distribution	Site	References	Age
C. alpinus alpinus	*	Central Russia, Western China, India, Bhutan and Bangladesh	-	Pallas, 1811	-
C. alpinus heperius	*	East Russia, China and Southeast Asia	-	Afanas'ev & Zolotarev, 1935	-
C. alpinus sumatrensis	*	Sumatra and Java	-	Hardwicke, 1821	-
Cuon europaeus	†	-	Caverne Mars (France)	Bourguignat 1875	Late Pleistocene
Cuon alpinus pyrenaicus	†	-	Malarnaud (France)	Filhol, 1888-1889	Late Pleistocene
Cuon bourreti	†	-	Malarnaud (France)	Harlé 1891	Late Pleistocene
Cuon alpinus fossilis	†	-	Certova dira (Czech Republic)	Nehring 1890-1918	Late Pleistocene
Cuon antiquus	†	-	Sichuan (China)	Matthew & Granger 1923	Middle Pleistocene
Cuon primaevus	†	-	Isturitz (France)	Bouchud, 1951	Late Pleistocene
Cuon priscus	†	-	Hundsheim (Germany)	Thenius 1954	Middle Pleistocene
Cuon alpinus caucasicus	†	-	Kudaro (Georgia)	Baryshnikov, 1978	Late Pleistocene

Tab. 1 - List of the fossil and extant (sub)species of *Cuon*. * indicates extant subspecies listed in Wilson & Mittermeier (2009). Fossil species are marked by † symbol.

1.1. Taxonomy of the European fossil dholes

In the last quarter of the XIX Century, in Europe several taxa have been ascribed to the genus *Cuon* (*C. alpinus fossilis*, *C. alpinus pyrenaicus*, *C. bourreti*, *C. europaeus*) (Tab. 1). Thenius (1954) erected the species *Cuon priscus* on the basis of the large-sized specimens from Hundsheim (Austria). Furthermore, the author introduced the subspecies *C. dubius stehlini* for the fossils from Rosières (France), suggesting similarities with the Chinese *C. dubius* described by Teilhard de Chardin (1940). Nowadays, the species "*C. dubius*" is commonly referred to the genus *Xenocyon* (Schütt, 1973; Tedford et al., 2009) or even the transitional *Sinicuon* (Wang et al., 2014). The form "*C.*" *stehlini* is now referred to *Lycaon/Xenocyon lycaonoides* (Rook, 1994; Martínez-Navarro & Rook, 2003, Sotnikova & Rook, 2010). Similarly, the species *Cuon rosi* from Cueva Victoria described by Pons-Moyá & Moyá-Solá (1978) is widely considered as *Lycaon/Xenocyon lycaonoides* (Madurell-Malapeira et al., 2013). The reason for this confusion between the Pleistocene remains of European dholes and those of genus *Lycaon/Xenocyon* lies in the similar development of several dental features. Adam (1959) attempted to reconstruct the affinities and taxonomy of European *Cuon*, suggesting the division of the European remains in three subspecies, all part of a single phyletic line: *C. a. priscus* - *C. a. fossilis* - *C. a. europaeus*. Bonifay (1971) considered valid three species for the Middle Pleistocene of Europe: *C. stehlini*, *C. priscus* and *C. alpinus* (the latter furtherly diversified into two subspecies, *C. alpinus fossilis* and *C. alpinus europaeus*). The subspecies *C. alpinus caucasicus* was erected by Baryshnikov (1978) on the basis of the Late Pleistocene fossil remains from various localities of the Transcaucasian region (Kudaro 1, Kudaro 3, Tsona cave). Recently, Brugal & Boudadi-Maligne (2011) revised the scheme proposed by Bonifay (1971) acknowledging three taxa for the Pleistocene fossil record of Europe: *C. priscus*, *C. a. fossilis* and *C. a. europaeus*. As mentioned above, the first occurrence of *C. priscus* has been reported from the early Middle Pleistocene site of Hundsheim (Austria) (Thenius,1954). Afterwards, this species has been documented until the Middle Pleistocene in some localities e.g., Lunel-Viel (France) (Bonifay, 1971), Caune de l'Arago (France) (Bonifay, 1971), Galeria Pesada (Portugal) (Trinkaus et al., 2003). During the late Middle Pleistocene, the first occurrence of another species of dhole, *C. alpinus*, has been reported from the late Middle Pleistocene site of Trinchera Galeria in Spain (Garcìa Garcìa & Arsuaga, 1997; Garcìa Garcìa, 2003). This taxon probably replaced *C. priscus* becoming part of the carnivoran guild for all the Late Pleistocene

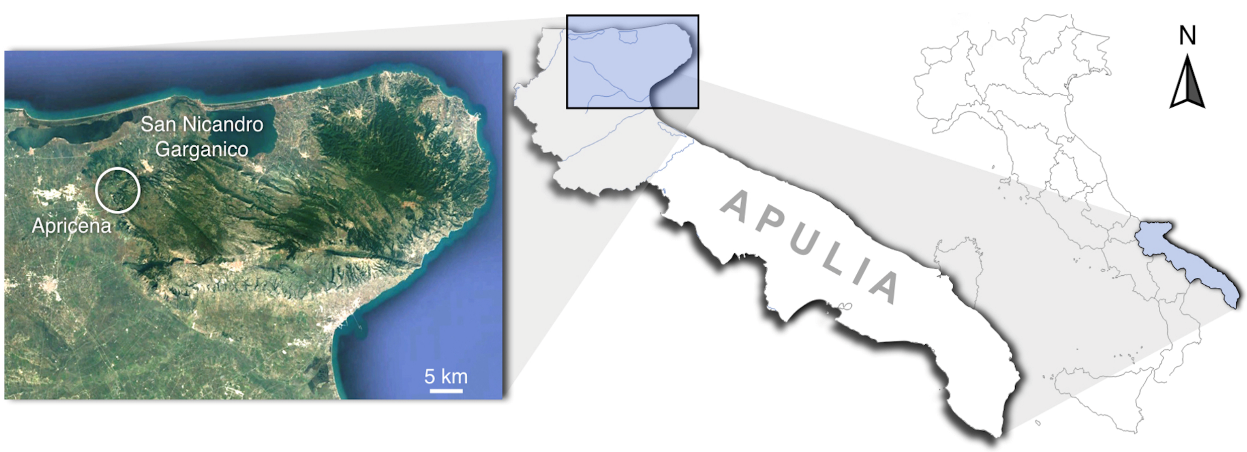

Fig. 1 - Geographic position of the Ingarano: a) map of Italy; b) zoom of the promontory of Gargano (image taken from GoogleEarth).

Sample	U_{ppm}	Th_{ppm}	$^{234}U/^{238}U$	$^{230}Th/^{234}U$	$^{226}Ra/^{238}U$	Age
ING-1	0.172 ± 0.002	< 0.005	1.015 ± 0.020	0.969 ± 0.018	n.d.	361.000 + 110-34
ING-2	2.768 ± 0.038	0.055 ± 0.005	1.122 ± 0.022	0,417 ± 0.010	n.d.	58.000 ± 2000
ING-3	2.487 ± 0.074	0.060 ± 0.006	n.d.	n.d.	0.604 ± 0.025	100 ± 7000
ING4	6.759 ± 0.170	0.175 ± 0.010	n.d.	n.d.	0.310 ± 0.010	40.000 ± 2000

Tab. 2 - Radiocarbon dating of speleothem and phosphathic material from the site of Ingarano (modified from Petronio et al., 1996).

until the Early Holocene, as reported from the Riparo Fredian site (Italy) (Cilli et al., 1998) and Les Coves de Santa Maira (Spain) (Pérez-Ripoll et al., 2010).

1.3. The site of Ingarano

The palaeontological site of Ingarano (Foggia, southern Italy) is located in the north-western area of the Gargano's promontory (Fig. 1). The deposit is a karstic filling succession within the Jurassic-Cretaceous limestone (Petronio et al., 1996; Petronio & Sardella, 1998; Bedetti & Pavia, 2007) dated with the $^{238}U/^{234}Th$ method (Tab. 2). A number of studies focused on the description of the rich vertebrate fauna of Ingarano site (levels B-E, Fig. 2) (Capasso Barbato et al., 1992; Petronio et al., 1996; Petronio & Sardella, 1998; Curcio et al., 2005; Bedetti & Pavia, 2007; Iurino, 2014; Iurino & Sardella, 2015; Iurino et al., 2015), including 41 species, listed below: Amphibians: *Rana* sp.; Reptiles: *Lacerta* sp.; Birds: *Circus aeroginosus*, *Aquila chrysaëtos*, *Falco cherrug*, *Falco columbarius*, *Alectoris graeca*, *Perdix perdix*, *Columba livia*, *Nyctea scandiaca*, *Pyrrhocorax graculus*, *Pyrrhocorax* sp., *Corvus corone*, *Corvus corax*; Mammals: *Erinaceus europaeus*, *Myotis blythi*, *Oryctolagus cuniculus*, *Lepus europaeus*, Arvicolidae indet., *Microtus* sp., *Microtus* ex gr. *arvalis/agrestis*, *Terricola savii*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela nivalis*, *Martes* sp., *Meles meles*, *Gulo gulo*, *Crocuta crocuta*, *Felis* sp., *Lynx lynx*, *Panthera pardus*, *Equus hydruntinus*, *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Rupicapra* sp., *Bos primigenius*. The faunal assemblage was deposited in a short time-span, chronologically referred to MIS 3 (Bedetti & Pavia, 2007). The talus, a deposit of unclear stratigraphical interpretation found near the sedimentary succession, is rich in vertebrate remains, including *Panthera spelaea*, *Hippopotamus amphibius*, *Coelodonta antiquitatis*, *Stephanorhinus hemitoechus* and *Palaeoloxodon antiquus*. No fossil remains of these taxa have been recovered from the levels B-E.

Up to now, the remains of medium-sized canid have been attributed to *Canis lupus* (Petronio et al., 1996; Petronio & Sardella, 1998; Bedetti & Pavia, 2007).

2. MATERIALS AND METHODS

The specimen INGND59 representes a right upper first molar and it is currently housed in the PaleoFactory laboratory, Department of Earth Sciences, at the Sapienza University of Rome.

Comparative fossil samples include: specimens of San Sidero, housed in the PaleoFactory laboratory, Department of Earth Sciences, Sapienza University of Rome; those of "Grotta" and "Tecchia di Equi", housed in the collection of the Geology and Paleontology section of the Natural History Museum of the University of Florence; and specimens of Wanxian housed in the Vertebrate Paleontology collections of the American Museum of Natural History (AMNH, New York, U.S.A.). The taxon from Wanxian was previously referred to *C. antiquus* by Matthew & Granger (1923) but currently is considered a junior synonym *C. alpinus*, see among others Castelló

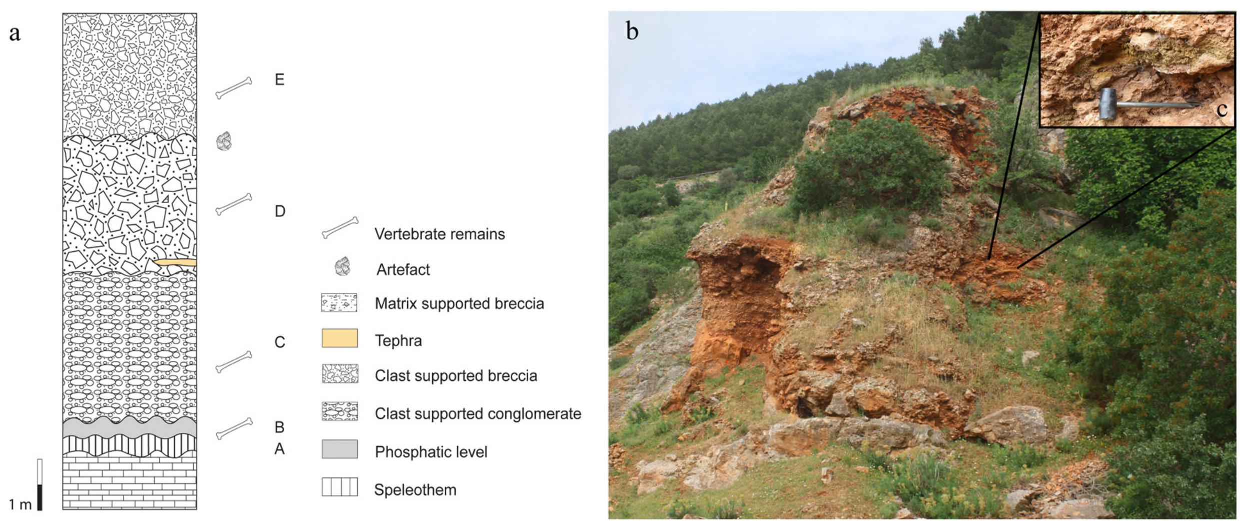

Fig. 2 - Fossiliferous site of Ingarano: a) schematic log of the stratigraphic succession; b) sedimentary succession.

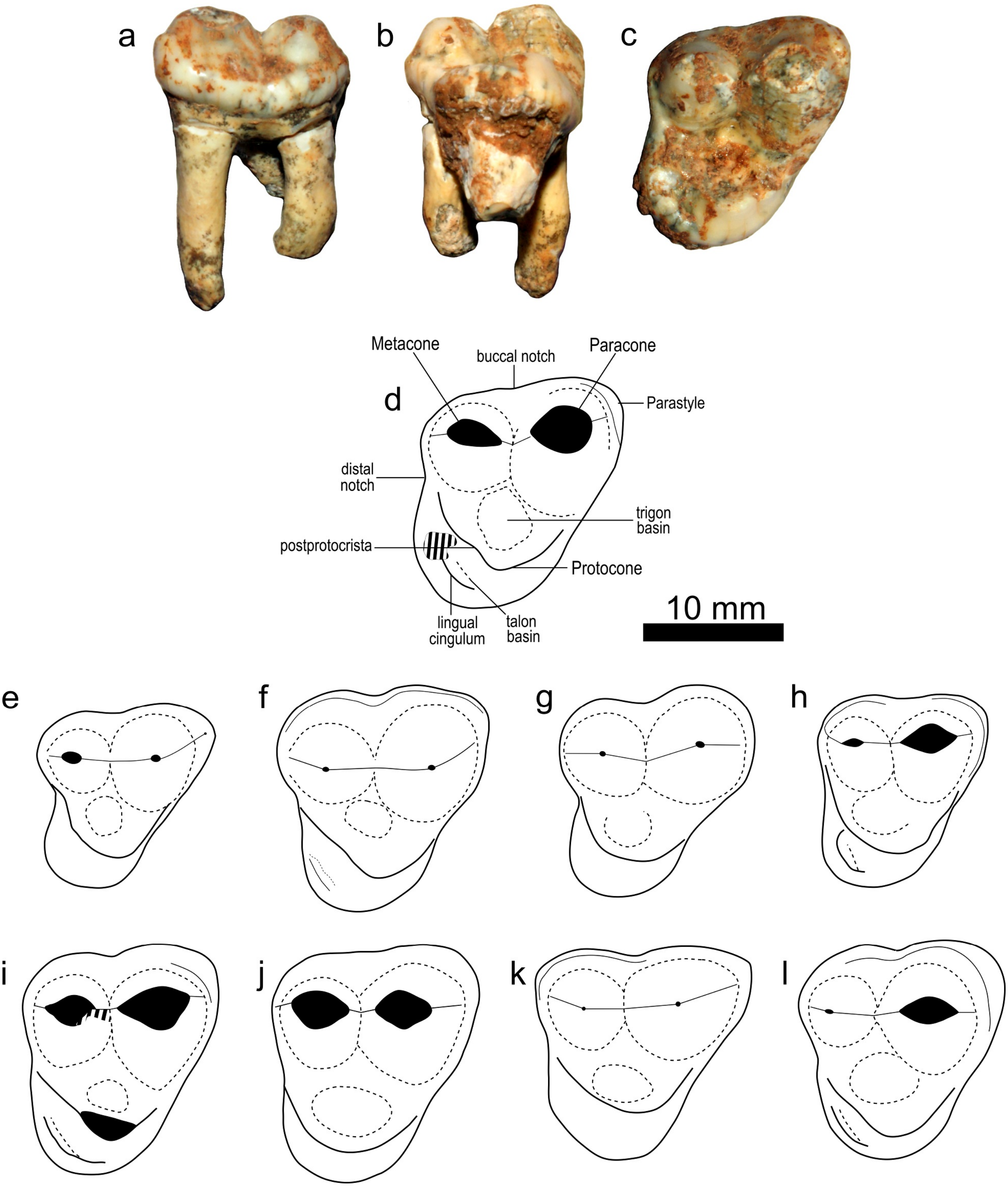

Fig. 3 - Variability of M[1] in extant and fossil *Cuon*. a–d) *Cuon alpinus* from Ingarano, INGND59, right M[1]; a) buccal view; b) lingual view; c) occlusal view; d) schematic outline of the occlusal morphology of INGND59. e–g) extant *Cuon alpinus*; e) AMNH 102083; f) IOZ 26747 (Tong et al., 2012); g) *Cuon alpinus hesperius* Afanasjev & Zolotarev, 1935, holotype, ZIN 23894, Zoological Institute of Russian Academy of Science. h–l) fossil *Cuon*. h) *Cuon alpinus*, AMNH 18391 (reversed), Wanxian (China); i) *Cuon alpinus*, AMNH 18727 (reversed), Wanxian (China); j) *Cuon alpinus europaeus* Bourguignat 1875, Obarreta (Portugal, from Perez-Ripoll et al., 2010); k) *Cuon priscus* Thenius, 1954, holotype from Hundsheim (Germany, from Thenius, 1954); l) *Cuon alpinus caucasicus* Baryshnikov, 1978, Kudaro (from Baryshnikov, 2012).

Species	Age	Number of specimens			p.values					
		P^4	M^1	M_1	P^4L	P^4GB	M^1L	M^1B	M_1L	M_1B
Cuon priscus	Middle Pleistocene	5	6	12						
Cuon alpinus	Middle Pleistocene	1	4	4	0.52	0.75	0.08	**0.00**	0.53	0.63
	Late Pleistocene	16	20	31	0.16	0.72	0.42	0.19	**0.00**	0.33
Extant *Cuon alpinus*		7	7	12	0.14	0.25	0.2	**0.00**	**0.00**	0.17

Tab. 3 - Table of p-values of linear model, *Cuon priscus* used as corner point.

(2018) (Tab. 1). Data on the extant *C. alpinus* were taken on the specimens of the Comparative Anatomy AMNH (New York, U.S.A.).

Following Driesch (1976), we measured the length (L) and breadth (B) of the P^4, M^1 and M_1. The measurements were taken to the nearest 0.1 mm with a digital caliper.

We used literature data on fossil dhole from the Middle to Late Pleistocene of Austria, Czech Republic, Slovakia, France, Germany, Greece, Italy, Spain, Hungary and Caucasian region (See supplementary material, Tab. S1). The specimens from Romain La Roche, Mosbach and Petralona have not been considered for biometric and morphological analyses as we exclude their attribution to the genus *Cuon* (see Discussion). Following Brugal & Boudadi-Maligne (2011), we consider the European fossil sample belonging to two taxa, *C. priscus* from the early to late Middle Pleistocene and *C. alpinus* from the late Middle to Late Pleistocene (Tab. S1).

The dataset was tested for normality distribution verification using Shapiro-Wilks test. As the dental variables resulted normally distributed, we performed a statistical parametric test. Differences in P^4L, M^1L, and M_1L of the Middle to Late Pleistocene specimens of Europe was evaluated using linear model with corner point parameterization testing the null hypothesis of no-differences between the mean of *C. priscus* and the other sample of Middle and Late Pleistocene *C. alpinus* and extant *C. alpinus* (p.value > 0.05). The statistical analysis was performed using the R software (R Core Team, 2019).

3. SYSTEMATIC PALAEONTOLOGY

Family Canidae Fischer, 1817
Genus *Cuon* Hodgson, 1838
Cuon alpinus (Pallas, 1811)

3.1. Description

INGND59 is an almost complete right M^1 missing part of the labial root (Fig. 3A-C). The crown is slightly worn and slightly wrapped by a crust formed by the clay matrix with calcite cementum. In occlusal view, the M^1 is buccolingually short. It possesses an enlarged paracone compared to the slightly shorter metacone. These cusps appear to be fused medially. In occlusal view, the buccal cingulum is not prominent and it is only marked at the level of the parastyle. The trigon basin is wide, round and deep, mesially girdled by a stout and large protocone. The post-protocrista distally shows a very reduced and barely visible metaconule. The talon basin is vestigial and a cingulum, although it is partially broken, lies lingually. The mesial cingulum is feeble. The embayment on the distal side of the tooth is rather reduced.

3.2. Morphological comparison

The fusion of the paracone and the metacone, as well as the development of the buccal cingulum of INGND59, resemble the condition observed in: *C. priscus* from Hundsheim (Thenius, 1954), *C. alpinus caucasicus* from Caucasus (Kudaro, Baryshnikov, 1996), *C. alpinus europaeus* from Spain (e.g., Obarreta, Peréz-Ripoll et al., 2010) and in those from Italian area of Melpignano and San Sidero (Petrucci et al., 2012; Iurino et al., 2013) (Fig. 3). The morphology of the lingual portion of the M^1 has a high degree of intraspecific variability (also at individual level, see Altuna, 1983). In occlusal view, the lingual portion of the INGND59 has a round and expanded outline similar to those of the specimens from Hundsheim (Thenius, 1954) (Fig. 3k), Wanxian ("Wan Hsien", Sichuan, China; Colbert & Hooijer, 1953) (Fig. 3h-i), Trinchera Galeria (García García, & Arsuaga, 1997), and different from that of other fossil and extant samples (e.g., Kudaro) (Fig. 3l) for their reduction of the distolingual lobe. A peculiar feature of the M^1 from Ingarano is the relative enlargement of the lingual portion compared to the buccal one. This morphology contrast with that observed in extant *Cuon* where generally the lingual side of the tooth is mesiodistally compressed (Fig. 3).

3.3. Biometric comparison

The results of the statistical analysis reveal slight differences in the dental traits (Fig. 4). In extant dhole, the range of the P^4L includes all the values of the fossil specimens, which are very similar to each other as the median of *C. pri*scus reaches the maximum value of the extant dhole. The length and breadth of the P^4 in *C. priscus* do not differ significantly from the other groups (p.values > 0.05) (Fig. 4a-b; Tab. 3). The Middle Pleistocene forms possess longer M^1 compared to the other groups, but its breadth is significantly lower than those of *C. priscus* and the Late Pleistocene *C. alpinus* (Fig. 4d). Similarly, the M^1B of *C. priscus* is larger compared to the Middle Pleistocene *C. alpinus* (Fig. 4c-d; Tab. 3). Whereas the M_1L of *C. priscus* statistically differs from those of the Late Pleistocene *C. alpinus* and the extant *C. alpinus*, no differences can be found in the breadth (Fig. e-f; Tab. 3).

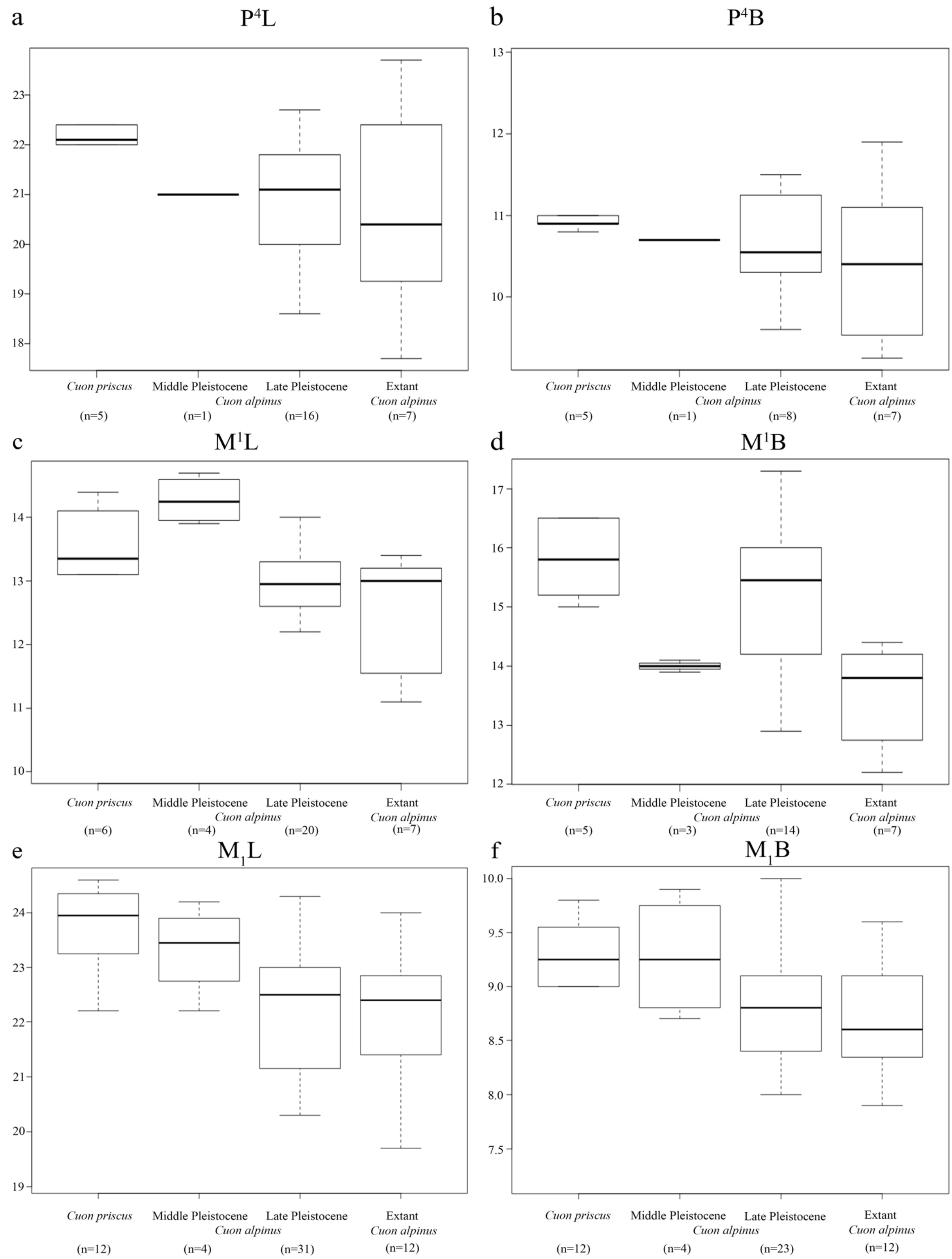

Fig. 4 - Boxplot of the length (a) and breadth (b) of P^4, the length (c) and breadth (d) of M^1 and the length (e) and breadth (f) of M_1 of Middle and Late Pleistocene *Cuon alpinus* and extant *Cuon alpinus*.

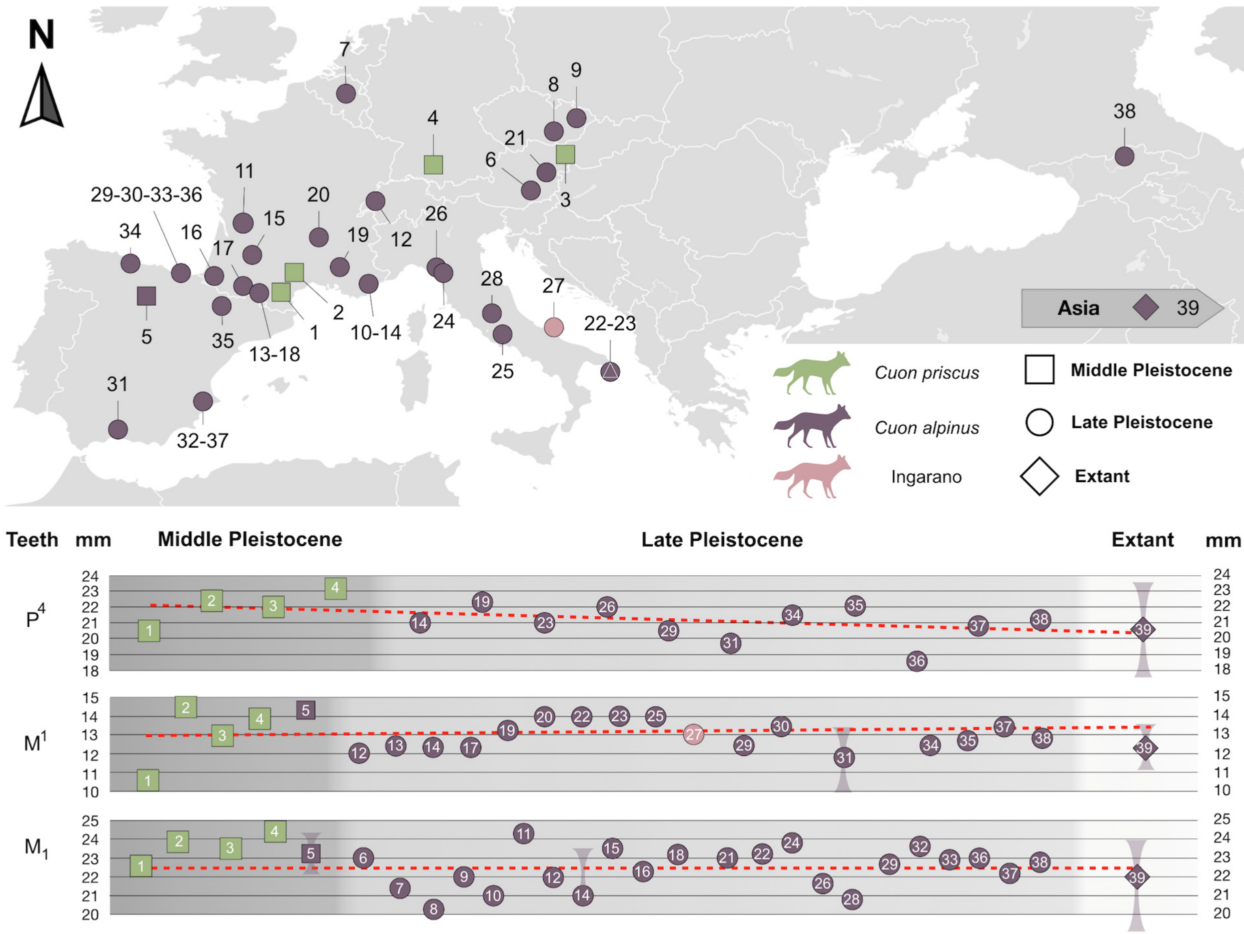

Fig. 5 - Length variation of the P^4, M^1 and M$_1$ of the European fossil Cuon from the Middle Pleistocene to the present days. Middle Pleistocene: 1) La Caune de l'Arago, 2) Lunel Viel, 3) Hundsheim, 4) Heppenloch; Late Pleistocene: 5) Trinchera Galeria; Late Pleistocene: 6) Repolust Hole, 7) Chokier, 8) Certova dira, 9) Sipka, 10) Ceverne Mars/Vence, 11) Fontechevade, 12) Grotte de Cotencher, 13) Grotte de la Carrière, 14) Grotte de l'Observatoire, 15) Grotta Vaufrey, 16) Isturitz, 17) La Niche, 18) Malarnaud, 19) Moula Guercy, 20) Verze, 21) Offenberger Hole, 22) Melpignano, 23) San Sidero, 24) Buca del Tasso, 25) Canale Mussolini, 26) Equi, 27) Ingarano, 28) Valserra, 29) Almada, 30) Bolinkoba, 31) Boquete de Zafarraya, 32) Cova Negra, 33) Duranguesado, 34) La Riera, 35) Moros de Gabasa, 36) Obarreta, 37) Parpallò, 38) Kudaro, 39) extant.

4. DISCUSSION

According to our results, the specimen INGND59 is morphologically and biometrically compatible with the M^1 of extant and fossil dhole, thus representing the first report of this carnivoran from the site of Ingarano. Despite the fact that the remains of *Cuon* are poorly documented and both geographically and chronologically dispersed, our morphological comparison has evidenced a quite large variability of the buccal and lingual profile of the M^1 among the considered samples, especially the cuspule-like postprotocrista distal to the metacone and both the buccal and distal notches (Fig. 3c-d). This variability would not appear to be taxon-related as the extant forms include almost all the range of features observed in the fossil samples, as exemplified by the three different M^1 morphotypes identified in the extant dhole specimens (Fig. 3e-g). Along with other variable dental features (e.g., the development of cuspulid-like lingual portion of the M$_1$ talonid), these subtle differences, might be the reason of the proliferation of the fossil species/subspecies/varieties of *Cuon* (Brugal & Boudadi-Maligne, 2011) (Tab. 1). The tooth from Ingarano falls in this range of morphologies although its lingual portion is among the widest of the considered sample. A certain degree of teeth variability among the Italian record of fossil *Cuon* has been reported by Petrucci et. al. (2012), where the authors highlighted how the shape and the occlusal surface of the M$_2$ change in all the Italian specimens. A similar variability of the M$_2$ in extant and fossil dhole has been reported also by Brugal & Boudadi-Maligne (2011). According to Mivart (1890) and Durbin et al. (2004) the M$_2$ variability documented in extant dhole would be linked to the latitudinal distribution, but for a more exhaustive explanation of such a teeth diversification a larger sample of fossil specimens is needed.

The Eurasian fossil record of the dhole is mainly represented by isolated or fragmentary cranio-dental elements, whereas postcranial bones and partially complete crania are exceptionally rare, which explains why the taxonomy of this carnivoran is principally based on teeth. Moreover, biometric data as the size of the lower carnassial, were considered as good parameters to discriminate the dhole from other Canidae (Ghezzo & Rook, 2014) or to distinguish between the fossil samples and to recognize different taxa (Brugal & Boudadi-Maligne, 2011). Nevertheless, up to now no statistical analyses were performed to support these hypotheses. The results of our study carried out on the P^4, M^1 and M_1, reveal that size differences among the extant and fossil samples are very small, with weak, if any, statistical significance (Fig. 4, Tab. 3). Differences can be found only in some variables without any consistent evidence of distinction between the known taxa. For instance, the M^1 length of the Middle Pleistocene *C. alpinus* reaches the highest values of the sample whereas the M_1 breadth is larger in *C. priscus* and in the Late Pleistocene *C. alpinus*. In general, the variability of the fossil groups is mostly included in that of the extant species, suggesting a biometric uniformity of the teeth size from the Middle Pleistocene to recent times. This contrasts with the hypothese put forward by Adam (1959), with three recognized forms (*C. alpinus priscus*, *C. alpinus fossilis*, *C. alpinus europaeus* in Adam 1959) based on the supposed trend of size decrease in the M_1 length. Such idea was confirmed by Brugal & Boudadi Maligne (2011). These authors separated the Middle Pleistocene apparently larger forms (*C. priscus*) from the Late Pleistocene ones (*C. alpinus*) on the basis of teeth size. The authors included among the Middle Pleistocene forms the samples from Mosbach, Petralona and Hundsheim, which are indeed characterized by larger teeth (Tab. S1). Nevertheless, it should be noted that the specimen of Mosbach was considered by Adam (1959) as *Cuon priscus*, but this material has not been described. Schütt (1974) ascribed the Mosbach specimen to *Xenocyon lycaonoides* for the retention of the M_3 in the hemimandible. Similarly, the left hemimandible from Petralona (KP No 205) was originally described by Kurtèn & Poulianos (1977) as belonging to *C. priscus*. The authors remark that the hemimandible is partially covered by a stalagmite crust, especially in the molar area, which prevents the acquisition of any biometric or morphological data of the M_2 and on the presence/absence of the M_3. Therefore, the classification was carried out without considering these characters. More recently, Baryshnikov & Tsoukala (2010) revised the fossil collection from Petralona stored at the Aristotle University of Thessaloniki, identifying three canid taxa: *Canis arnensis*, *Vulpes praeglacialis* and *Lycaon lycaonoides* (=*Xenocyon lycaonoides*). In the latter, the authors also included the remains previously classified as *Cuon priscus* by Kurtèn & Poulianos (1977) into *L. lycaonoides* (Baryshnikov & Tsoukala, 2010: 392). Another questionable attribution to *Cuon* is that of a large-sized specimen from Romain La Roche (CAN.1069) described by Argant (2010). The latter scholar reported the presence of the M_3 alveolus, yet there is a wide consensus among researchers in considering the absence of this tooth as one of the principal diagnostic characters to typify the genus *Cuon* from other canids (Schutt, 1973; Tedford et al., 2009). On such basis, the attribution of this specimen to *Cuon alpinus* is excluded and a more parsimonious attribution to *Canis lupus* could be suggested. According to this taxonomic clarification, we excluded the specimens from Mosbach, Petralona and Romain La Roche from our biometric analysis, evidencing the inconsistency of the time-related reduction of the teeth in European fossil dholes proposed by Adam (1959) and Brugal & Boudadì Malgine (2011). Indeed, size of the teeth seems to be uniform from the Middle Pleistocene to the present days (Figs. 4-5; Tab. S1), questioning the taxonomic reliability of the fossil specimens currently proposed in literature.

In sum, our results indicate the lack of clear morphological and biometric features for a reliable classification of the European fossil dholes, especially if based on teeth. Therefore, to avoid the proliferation of taxonomically questionable species, we suggest to consider all the Middle to Late Pleistocene material as *Cuon alpinus*.

5. CONCLUSION

The revision of the palaeontological collection from Ingarano allow us to identify for the first time the presence of *C. alpinus* in this Late Pleistocene site, enriching its carnivorans guild. This makes the Ingarano deposit one of the richest Late Pleistocene Italian sites in carnivorans, where also the occurrence of *C. lupus* is documented.

The results of this work show that some Pleistocene specimens that *Cuon* has been often confused with other hypercarnivorous taxa (e.g. *C.lupus* or *Xenocyon* spp.), thus confusing its taxonomic determination. Especially size was a feature historically used as the discrimination factor between different species/subspecies. Our analyses point out that no significant difference really exists between Middle and Late Pleistocene forms. This dimensional uniformity, at least in teeth size, contrasts with the evidence on other canids with a rather more conspicuous record (e.g., *C. mosbachensis* or *C. lupus*, among others Sansalone et al., 2015; Mecozzi et al., 2020) which experienced several shifts in size during glacial/interglacial phases (Mecozzi & Bartolini Lucenti, 2018). If this could be related to the bias of the record (i.e. its scarcity) or to the paleodietary and paleoecological aspects of these canids, are among the questions that still need to be answered. In the meantime, considering 1) the present knowledge of the fossil *Cuon*, 2) its scarce record in the Middle-Late Pleistocene of Europe, 3) its extant variability in morphology; our results favour the inclusion of the whole Middle-Late Pleistocene fossil record under the specific name of *Cuon alpinus*, rather than in two or more different (chrono) species. Despite this, we do not exclude that future studies based on new and more complete craniodental remains and better performing methodologies, may demonstrate the presence of additional fossil taxa.

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