Available online http://amq.aiqua.it
ISSN (print): 2279-7327, ISSN (online): 2279-7335

Alpine and Mediterranean Quaternary, 34 (1), 2021, 55-68 https://doi.org/10.26382/AMQ.2021.14

REVIEW OF *URSUS* MATERIAL FROM FONTANA RANUCCIO (MIDDLE PLEISTOCENE, CENTRAL ITALY): NEW INSIGHTS ON THE FIRST OCCURRENCE OF THE BROWN BEAR IN ITALY.

Jacopo Conti[1,2], Luca Bellucci[3,4], Dawid A. Iurino[2], Flavia Strani[2,4], Raffaele Sardella[2,4]

[1] Polo museale, Sapienza Università di Roma, Italy.
[2] Dipartimento di Scienze della Terra, PaleoFactory, Sapienza Università di Roma, Italy.
[3] Museo di Geologia e Paleontologia, Sistema Museale di Ateneo, Università degli Studi di Firenze, Italy.
[4] Istituto Italiano di Paleontologia Umana, Roma, Italy.

Corresponding author: J. Conti <jacopo.conti@uniroma1.it>

ABSTRACT: The Middle Pleistocene archaeo-palaeontological site of Fontana Ranuccio (Anagni, central Italy) yielded a rich faunal assemblage consisting of more than 20,000 fossil remains, including four human teeth and multiple bone and lithic tools. The *Ursus* specimens from Fontana Ranuccio were historically ascribed to *Ursus deningeri* and *Ursus arctos* although a formal study has never been carried out. In this work, we have described for the first time all the *Ursus* material from Fontana Ranuccio reassessing the taxonomical attributions and discuss the first occurrence of the brown bear in the Italian Peninsula. Biometrical and morphological analyses confirm the presence of *Ursus deningeri* but, due the scarcity of diagnostic features and/or their preservation, some isolated specimens have been ascribed to *Ursus* sp. The results of this work allow to reconsider the earliest occurrence of *U. arctos,* attested in the Italian Peninsula to the late Middle Pleistocene site of Bucine.

Keywords: *Ursus arctos*, *Ursus deningeri*, Galerian, biochronology, systematics, evolution, carnivores.

1. INTRODUCTION

In the Middle Pleistocene locality of Fontana Ranuccio (0.4 Ma; Pereira et al., 2018), *Ursus* fossils are represented by some isolated teeth and a third phalanx, found during the 1980s excavation campaigns led by researchers of the Istituto Italiano di Paleontologia Umana (hereinafter IsIPU). These remains were firstly assigned to *Ursus deningeri* by Bidditu et al. (1979) and Cassoli & Segre Naldini (1993) which described only three specimens without providing a detailed comparison. Few years later, Azzaroli (1983) reported the presence of the brown bear *Ursus arctos* in the "Ranuccio local fauna" without providing any description of the fossil remains, thus opening the issue on the possible co-occurrence of two bear species in the Fontana Ranuccio site. Successively, Palombo et al. (2002 and references therein) reported in their faunal list only the presence of *U. deningeri* at Fontana Ranuccio, but without performing any direct study of the fossil material. In later publications, some authors reported the first occurrence (FO) of *U. arctos* at Fontana Ranuccio without supporting this statement with any comparison or analysis (Capasso Barbato et al., 1990; Di Stefano et al., 1994; Sardella et al., 2006; Petronio et al., 2011). Finally, in a recent publication, Petronio et al. (2019) considered the bear remains from Fontana Ranuccio as *U. deningeri,* moreover indicating for this site the last occurrence (LO) of the species. As in the previous works, the attribution was probably made on the basis of literature data, since there is a lack of direct descriptions and analyses of the materials. As a consequence of these ambiguous attributions, the taxonomy of *Ursus* materials from Fontana Ranuccio has been doubtful. Therefore, on the basis of the above-mentioned literature as well as from a biochronological point of view, the FO of the brown bear or the LO of the Deninger bear in Italy, or even both, could potentially be documented at Fontana Ranuccio.

During the Pleistocene several fossil bear species are recorded in the Italian Peninsula, such as the Auvergne bear (*Ursus minimus,* Devèze de Chabrol & Bouillet, 1827), the Etruscan bear (*Ursus etruscus,* Cuvier, 1823), the Deninger bear (*Ursus deningeri,* von Reichenau, 1904), the cave bear (*Ursus spelaeus,* Rosenmüller, 1794) and the brown bear (*Ursus arctos,* Linnaeus, 1758) (Conti, 1954; Conti, 2019; Borselli et al., 1980; Bon et al., 1991; Mazza & Rustioni, 1994; Palombo et al., 2002; Petronio et al., 2007, 2020; Petrucci & Sardella, 2009).

The first occurrence of *U. deningeri* in the Italian Peninsula is recorded in the late Early Pleistocene sites

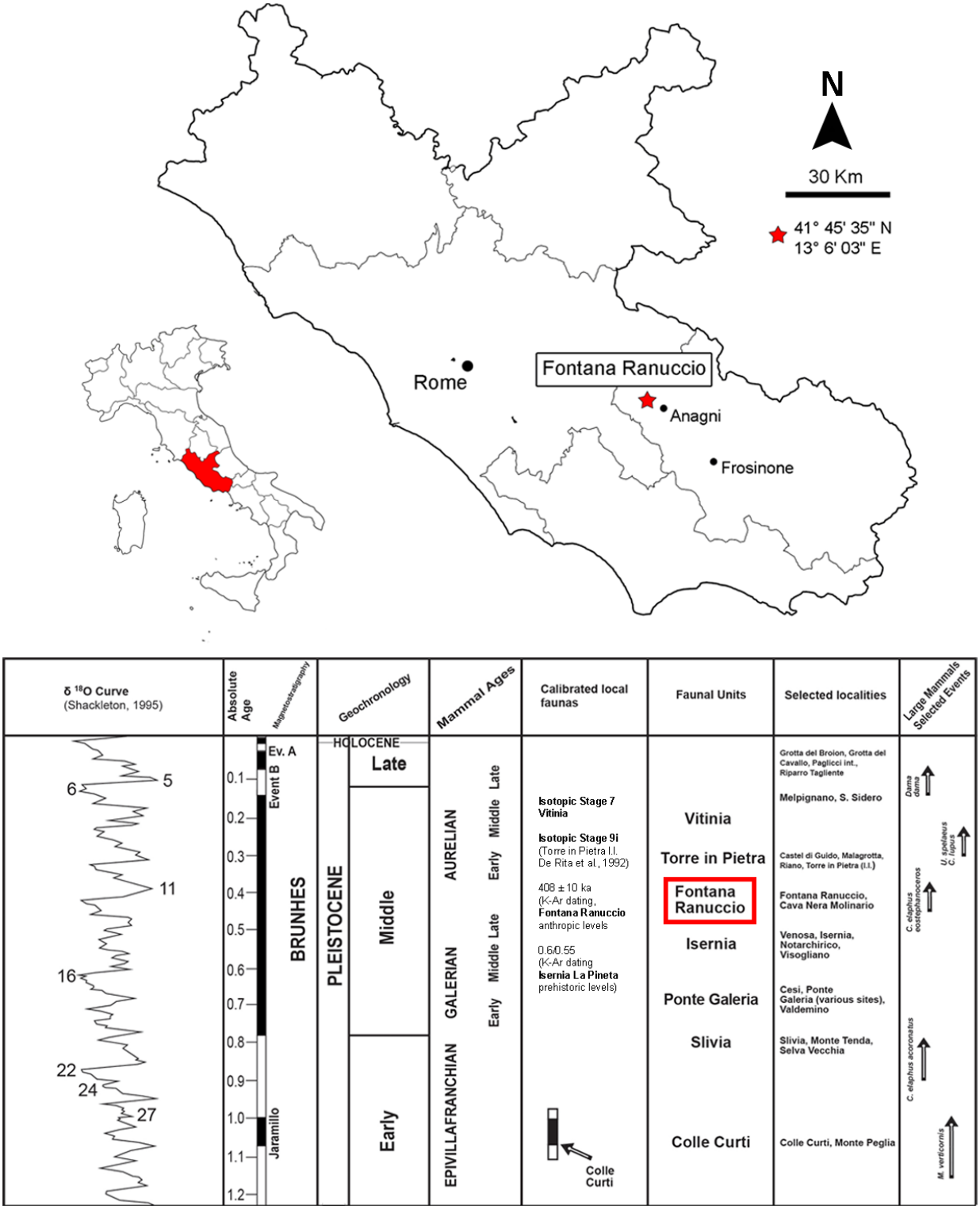

Fig. 1 - Geographical location of the Middle Pleistocene site of Fontana Ranuccio (modified by Strani et al., 2018a).

of Slivia (Ambrosetti et al., 1979; Palombo et al., 2002 and reference therein; Petronio et al., 2011, 2019). Other localities of the Early and Middle Pleistocene bearing *U. deningeri* remains are Bristie I° (Trentino Alto Adige; Lugli & Sala, 2000), Ponte Molle (Lazio; Petronio et al., 2011; Mecozzi et al., 2021), Selva Vecchia (Veneto; Bon et al., 1991), Isernia La Pineta (Molise; Peretto & Sala 2019), Visogliano (Friuli Venezia Giulia; Palombo et al., 2002 and reference therein) and Venosa (Palombo et al., 2002 and reference therein).

Inv. N°	Element	Side	Ontogenetic Stage	Lenght	Width	Species
FR 84 inv 56576	ph-3	Right	-	-	-	sp.
FR 89-1	p4	Right	Juvenile	13.6	8	sp.
FR 82-2 Res	i3	Left	-	9.9	10.3	sp.
FR 85-2 P3	i3	Right	-	9.8	10.1	sp.
FR Sd-2	I2	Right	-	10.7	8.5	sp.
FR 85-1 S1	c	Right	-	-	-	sp.
FR 84-1	m2	Left	-	-	-	sp.
FR 96-33	m1	Left	Prime adult (IV class)	-	10.8	sp.
FR sd-1	m2	Left	Juvenile (III class)	28.5	16.2	*deningeri*
FR 56575	m3	Right	Juvenile/prime adult (III/IV class)	26	18.4	*deningeri*
FR 06-411	M1	Right	Juvenile/prime adult (III/IV class)	25.2	18.4	*deningeri*
FR 56574	M1	Left	Prime adult (IV class)	27.6	18.3	*deningeri*

Tab. 1 - List of selected specimens used for morphological comparison. Asterisks indicate the material directly studied by the authors.

The oldest documented and figured specimen attributed to *Ursus arctos* in the Italian Peninsula comes from the late Middle Pleistocene site of Bucine (Upper Valdarno, Tuscany) (Masini et al., 1991; Ferretti, 1997; Gliozzi et al., 1997; Palombo et al., 2002). The material consists in a fragmented cranium with the presence of the upper fourth premolar and the first and second upper molars, now stored at the "Museo di Geologia e Paleontologia" at the Università di Firenze. The brown bear is also reported in Sicily from two late Middle Pleistocene/Late Pleistocene localities, Acquedolci and Contrada Camillà, both referred to the "*Elephas mnaidriensis* faunal complex" (Bonfiglio et al., 2001; Pavia, 2001; Marra, 2003). The material is abundant but fragmented, composed by three fragmentary hemimandibles, isolated teeth and fragmentary postcranial bones. Other fragmented bone elements (one indetermined tooth and a phalanx) come from the layer 18 Ripardo del Poggio (Salerno), dated approximately to MIS 6 (Boscato et al., 2009).

In this study, we present the first detailed description and comparative analysis of the bear specimens from Fontana Ranuccio in order to: (1) define their taxonomic status; (2) verify the possible co-occurrence of *U. arctos* and *U. deningeri* at the site; (3) define the biochronological aspects as the possible FO of *U. arctos* or the LO of *U. deningeri* in the Italian Peninsula.

2. GEOGRAPHICAL AND STRATIGRAPHICAL BACKGROUND

The archaeo-palaeontological site of Fontana Ranuccio (Fig. 1) is located in the Anagni Basin (Bidditu et al., 1979; Cassoli & Segre Naldini, 1993; Florindo et al., 2021 and references therein), about 90 km southeast of Rome, and it was discovered in 1976 during quarry activities for the exploitation of "pozzolana" (volcanic ash). Since then, researchers of the IsIPU have carried out different field activities, in particular under the direction of A. Segre (1978-2002), F. Parenti (2004-2018) and S. Grimaldi (2019 - present).

The fossiliferous layer has been recently dated to 0.4 Ma (Pereira et al., 2018). The vertebrate collection includes more than 20,000 specimens that are now stored in the IsIPU depository (Anagni, Frosinone). The large mammal assemblage have been attributed to 15 taxa (Biddittu et al., 1979; Cassoli & Segre Naldini, 1993; Strani et al., 2018a; Strani et al., 2018b; Strani et al., 2019): *Palaeoloxodon antiquus*, *Stephanorhinus* sp., *Equus* cf. *mosbachensis*, *Hippopotamus amphibius*, *Dama clactoniana*, *Cervus elaphus eostephanoceros*, *Praemegaceros* sp., *Bos primigenius*, *Sus scrofa ferus*, *Panthera* sp., *Crocuta crocuta*, *Canis mosbachensis*, cf. *Vulpes* sp., *Macaca sylvanus, Ursus arctos*, *Ursus deningeri* and *Ursus* sp. Small mammal remains are scanty and have been recently ascribed by Bona & Strani (2021) to *Microtus* (*Terricola*) sp., *Talpa* sp., *Elyomys* sp., *Lepus* sp., *Erinaceus* sp., Rodentia indet., cf. *Glis* sp. Finally, *Homo* remains have been reviewed by Rubini et al. (2014) and are associated to several (more than 800) lithic and bone tools (Segre, 1984). Since the pioneering work of Azzaroli (1983) this faunal assemblage is a reference for the Italian biochronological framework (Gliozzi et al., 1997; Petronio et al., 2011; Petronio et al., 2019 and references therein). Finally, Grimaldi et al. (2020) carried out a techno-functional study of the entire lithic assemblage identifying five groups of retouched tools i.e., cutting tools, pointed tools, scrapers, notches and denticulates.

3. MATERIALS AND METHODS

Ursus material from Fontana Ranuccio consists of 12 isolated remains (Fig. 2) now stored at the IsIPU laboratory in Anagni (Frosinone). This fossil material was mainly found in the 1980s field activities, in particular in the 1982, 1984, 1985 and 1989 years. Morphological analysis, descriptions and comparisons have been provided taking into account the from different researchers (Ballesio, 1983; Torres, 1988; Capasso Barbato et al., 1990; Argant, 1991; Mazza & Rustioni, 1994; Auguste, 1995; Rabeder, 1999; Quiles, 2003; Meloro, 2007; Wagner & Sabol, 2007; Wagner & Čermák, 2012). Morphological data have been compared with specimens of *U. etruscus*, *U. deningeri*, *U. spelaeus* and *U. arctos*

Species	Locality	Epoch	References	Repository
U. etruscus	Valdarno (Italy)	Early Pleistocene	Mazza & Rustioni 1994	Museum of geology and paleontology (Florence)
U. deningeri	Isernia La Pineta (Italy)	early Middle Pleistocene	Peretto & Sala 2019	National Palaeolithic Museum (Isernia)
U. deningeri	Hundsheim (Austria)	early Middle Pleistocene	Rabeder et al., 2010	Department of Palaeontology, University of Wien
U. deningeri	Koněprusy Caves (Czech Republic)	early Middle Pleistocene	Wagner & Čermák, 2012	National Museum (Prague)
U. deningeri	Kozi Grzbied (Poland)	Middle Pleistocene	Wagner & Čermák, 2012	Institute of Systematics and Evolution of Animals (Poland)
U. deningeri	Šandalja I (Croatia)	Middle Pleistocene	Wagner et al., 2017	Institute for Quaternary Palaeontology and Geology of the Croatian Academy of Sciences and Arts (Zagreb)
U. spelaeus	Caverna delle Fate (Italy)	Late Pleistocene	Conti 1954	Civic Museum G. Doria (Genova)
U. savini nordostensis ssp.	Cherskiy "Ovrag" (Siberia)	Late Pleistocene	Sher et al., 2011	Ice Age Museum (Moscow)
U. arctos	Deutsch-Altenburg (Austria)	Early Pleistocene	Rabeder et al., 2010	Department of Palaeontology, University of Wien
U. arctos	Bucine (Italy)	late Middle Pleistocene	Mazza 1998	Museum of geology and paleontology (Florence)
U. arctos	Vigna S. Carlo (Italy)	Late Pleistocene	unpublished data	MUST (Museo Universitario di Scienze della Terra) Sapienza, University of Rome
U. arctos	Winden (Austria)	Late Pleistocene	Rabeder et al., 2010	Department of Palaeontology, University of Wien
U. arctos	Kudaro 3 (Georgia)	Late Pleistocene	Baryshnikov 2010	Zoological Institute, Russian Academy of Sciences (Saint Petersburg)
U. arctos	Alps region (Italy)	Recent	unpublished data	MUSE Science Museum (Trento)
U. arctos	Banskà Bystrica (Slovakia)	Recent	unpublished data	Natural History Museum (Bratilsava)

Tab. 2 - List and Measures of *Ursus* material from the Fontana Ranuccio deposit (Measures in mm).

from selected European Pleistocene and Holocene localities (Tab. 1). The ontogenetic stage was inferred according the scheme proposed by Stiner (1998).

The measurements of mesiodistal length and buccolingual width have been taken with digital caliper to the nearest 0.1 mm on each fossil specimen (Tab. 2), with the exception of the teeth FR 85-1 S1, FR84-1 and the third phalanx (FR 84 inv 56576) due fragmentary preservation. Dentognathic morphology and measurements follow the terminology proposed by Rabeder (1999) and Torres (1988).

Despite the high biometric variability of the teeth in the Early and Middle Pleistocene bears, we performed standard bivariate plots of width vs. length of M1, p4, m2 and m3 in order to compare our samples with specimens from this time span in order to test possible biometrical patterns among the Fontana Ranuccio specimens and other Pleistocene ursid taxa (Torres, 1984; Capasso Barbato et al., 1990; Marra, 2003; Rabeder et al., 2010; Wagner et al., 2017 and personal measurements; Fig. 3).

4. SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Family Ursidae Fisher [De Waldheim], 1817
Genus *Ursus* Linnaeus, 1758
Ursus sp.

Referred material: I2 right (FR Sd-2), i3 right (FR 85-2 P3), i3 left (FR 82-2 Res), c right (FR 85-1 S1), p4 right (FR 89-1), m1 left (FR 96-33), m2 left (FR 84-1), ph -3 (FR 84 Inv 56576).

Incisors and fragmented material: the incisors, except FR Sd-2, are well preserved and show the typical *Ursus* morphology with a developed central cusp and the presence of two outlined lateral lobes; the distal one is less developed than the mesial one (Fig. 2 f-g-h). The lower canine (FR 85-1 S1), the second lower molar (FR 84-1) and the first lower molar (FR 96-33) are fragmented; therefore, it is not possible to acquire any linear measurement or identify any distinctive character to define a specific attribution (Fig. 2 i-l-m). However, it is possible to ascribe the specimen FR 96-33 to a prime adult individual (class VII). The third phalanx (FR 84 inv 56576, Fig. 2 n) shows a rather elongated morphology, although it is particularly worn. The proximal portion, which is articulated with the trochlea of the second phalanx, is semicircular and the dorsal and plantar swelling that characterize this anatomical portion of the bone element are poorly developed. The ungual portion is thin with a gentle dorsal curvature until the most distal portion, where it sharply curves. Due to high wear and the lack of any discriminant characters, we ascribe these remains to *Ursus* sp.

Lower fourth premolar: the lower fourth premolar (FR 89-1) has a very simple morphology, with narrow and elongated external profile. The protoconid is well developed and undivided, unlike the metaconid and the paraconid which are small and poorly developed. The presence of a tubercled area in the occlusal surface is not observed except for one small accessory cusp on

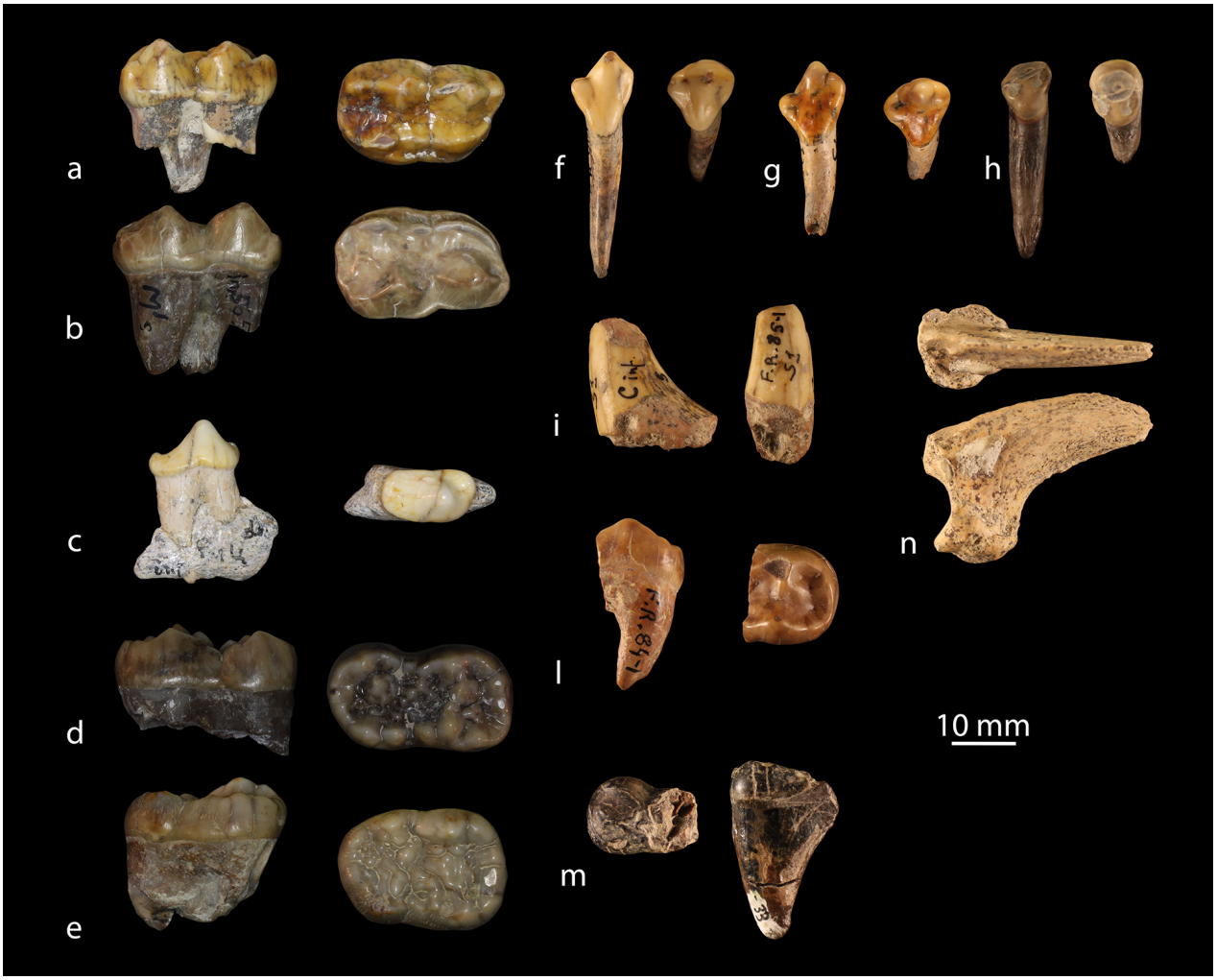

Fig. 2 - *Ursus* material from Fontana Ranuccio in occlusal and lateral views: a) M1 right (FR 06-411), b) FR M1 left (FR 56574), c) p4 right (FR 89-1), d) m2 left (FR sd-1), e) m3 right (FR 56575), f) i3 left (FR 82-2 Res), g) i3 right (FR 85-2 P3), h) I2 right (FR Sd-2), i) c right (FR 85-1 S1), l) m2 left (FR 84-1), m) m1 left (FR 96-33), n) III phalanx right (FR 84 inv 56576).

the lingual portion of the protoconid slope. All these features occur in the arctoid tooth morphology and can be found also in the Late Pleistocene and recent *Ursus arctos* (Reynolds, 1906; Torres, 1988; Capasso Barbato et al., 1990; Mazza & Rustioni, 1994; Quiles, 2003; Meloro, 2007; Rabeder et al., 2010). *U. deningeri* can display a higher morphological complexity of the occlusal surface characterized by many tubercles and by a much more elliptic external profile (Fig. 4 e-f-g-i), even if many remains such as the early Middle Pleistocene specimens from the site of Hundsheim (Austria, HH 305), C718 Cave (Czech Republic, Rv 20003) (Fig. 4 d-h), and some other specimens recorded from Sima de los Huesos (Spain, Middle Pleistocene, ca. 0.35 Ma), Caune de l'Arago, (France, Middle Pleistocene, ca. 0.50 Ma), Cal Guardiola (Spain, latest Early Pleistocene, ca. 1.2-0.86 Ma), display a p4 without any accessory cuspids and simpler morphology, remarking the high variability and the possible presence of ancestral characters displayed by *U. deningeri* (García et al., 1997, 2007; Quiles, 2003; Madurell-Malapeira et al., 2009; Rabeder et al., 2010; Wagner & Čermák, 2012; Arsuaga et al., 2014; Prat-Vericat et al., 2020).

This simpler morphology is related to the early Pleistocene Etruscan bear *U. etruscus,* characterized by the lack of accessory cusps or tubercled structures in the chewing surface of molariforms, and considered as ancestor of both lineages (Wagner & Sabol, 2007). The teeth of the Late Pleistocene cave bear (*Ursus* ex gr. *spelaeus*) show instead a higher complexity of the chewing surface (Fig. 4 k-l), contrary to what is observed in the Late Pleistocene and extant brown bears, which possess a simpler and secodont morphology of the occlusal surface through time (Fig. 4 m-n-o-p). These differences are probably related with the dietary habits of the two bear lineages, one omnivorous (*U. arctos*) and the other mostly herbivorous (*U. spelaeus*) (Terlato et al., 2018). Biometric analyses did not allow any specific discrimination regarding the Middle Pleistocene specimens (Fig. 3 b), while the dimensional range of *U.*

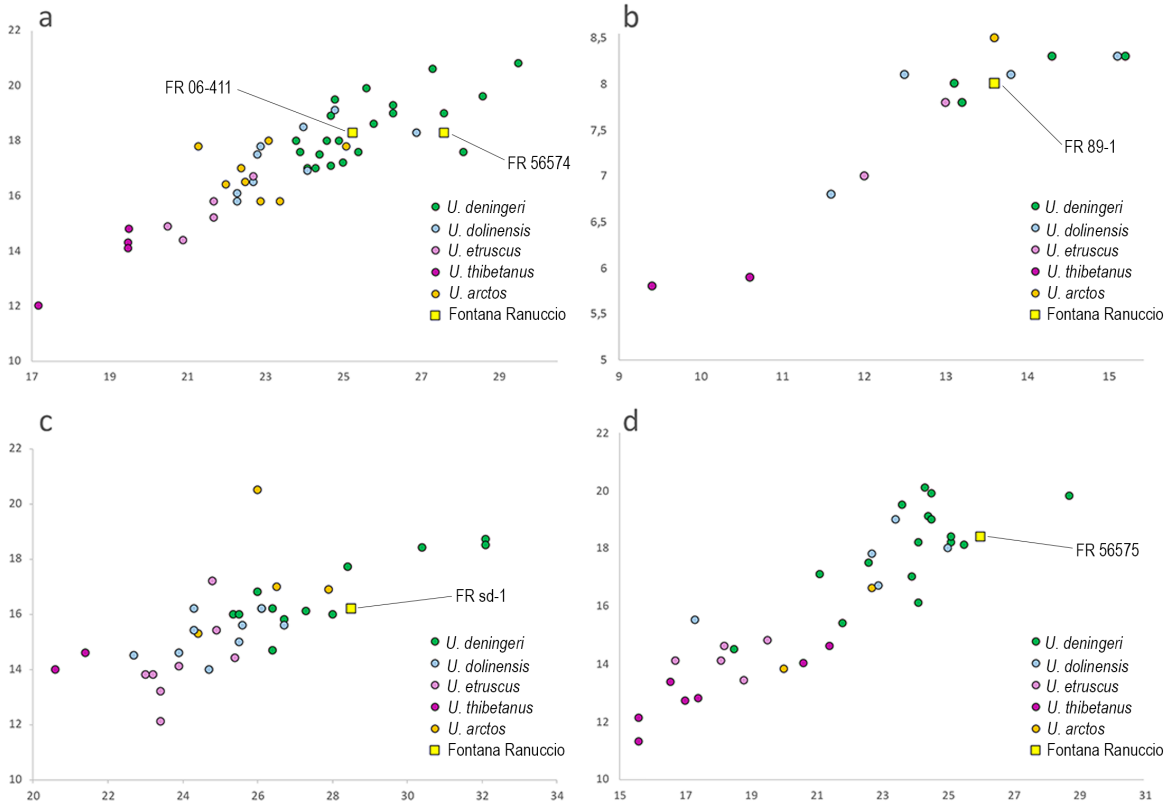

Fig. 3 - Comparison of the length and width scatter plots of various Early and Middle Pleistocene species of the genus *Ursus*. a) M1; b) p4; c) m2; d) m3.

deningeri and *U. arctos* strongly overlap (also due to the lack of sufficient data of the Early/Middle Pleistocene *Ursus arctos*). As mentioned above, a simple morphology, with the lack of accessory cusps in the lower p4 is a shared character between *Ursus arctos* and *Ursus deningeri*, specially during the late Early-Middle Pleistocene (Wagner et al., 2017). Despite the presence of *Ursus deningeri* in the deposit, the large variability of the morphology and biometric data do not allow a specific attribution of the isolated p4. To be more conservative we ascribe FR 98-1 to *Ursus* sp.

Ursus deningeri von Reichenau, 1904

Referred material: M1 left (FR 56574), M1 right (FR 06-411), m2 left (FR sd-1), m3 right (FR 56575).

Upper first molars: the specimen FR 56574 (Fig. 2 b) shows sub-quadrangular profile with a non-rectilinear protocone-hypocone line and the presence of some tubercled structures on the talon surface. The central constriction of the tooth is rather marked especially in the lingual portion and the main cusps are well developed. The biometric data show, as expected, an overlap between the deningeroid and arctoid specimens; despite this, we can observe that FR 56574 falls within the dimensional range mostly occupied by the Early-Middle Pleistocene *U. deningeri* (Fig. 3 a) and showing a rather large size of this tooth compared to the average dimension of *U. arctos*.

The specimen FR 06-411 (Fig. 2 a) has some different features from FR 56574. The metastyle and the parastyle are well developed, the metastyle more than the parastyle, and the talon shows a tubercled surface, more than FR 56574. On the other hand, the tooth has a quadrangular shape, the distal and proximal area show the same profile and the protocone-hypocone line appears quite straight. Biometric analyses indicate that the specimen is placed at the limit of the average dimensional range of *U. arctos*, falling within the variability of *U. deningeri* (Fig. 3 a). The occlusal surface of both teeth displays tubercles, a common speloid feature (Capasso Barbato et al., 1990; Quiles, 2003). According to Torres (1984) and Capasso Barbato et al. (1990) the straight protocone-hypocone line of FR 06-411 should be related to the arctoid lineage. The latter assumption stands up against the morphological comparison here proposed (Fig. 5), in fact specimens of *U. deningeri* from Hundsheim (Fig. 5 e-f) show the same straight protoipoconid line, more than brown bear, which instead presents a consistent variability for this character. Considered all these morphological and biometric features, we ascribe these specimens to *U. deningeri*.

Second lower molar: The specimen FR sd-1 (Fig. 2 d) is characterized by a high complexity of the occlusal

surface with the presence of numerous tubercled structures and accessory cusps, well representing the typical cave bear morphology (Fig. 6) consisting of a metaconid divided into three metastylids, typical of *U. deningeri* and *U.* ex gr. *spelaeus* (Capasso Barbato et al., 1990; Quiles, 2003; Torres, 1988). The biometric analysis still indicates a straight dimensional overlap between *U. deningeri* and *U. arctos*, which does not allow to distinguish the two species based on size. The specimen FR SD-1 falls perfectly in this overlap range (Fig. 3 c). Concerning the morphological features of the m2 from Fontana Ranuccio we ascribe this specimen to *U. deningeri*.

Lower third molar: The specimen FR 56575 shows a quadrangular outline with a rounded talonid. The occlusal surface is highly tubercled, typical of the speloid lineage (Capasso Barbato et al., 1990; Quiles, 2003; Torres, 1988) (Fig. 7). The tooth shows low worn structures and a well-developed entoconid and metaconid, the latter is composed by two distinct cusps. Biometric data also suggest the affinity of the specimen with the speloid group, fitting within the dimensional range of *U. deningeri* (Fig. 3 d). According to both morphological and biometric analyses, we ascribe this specimen to *U. deningeri*.

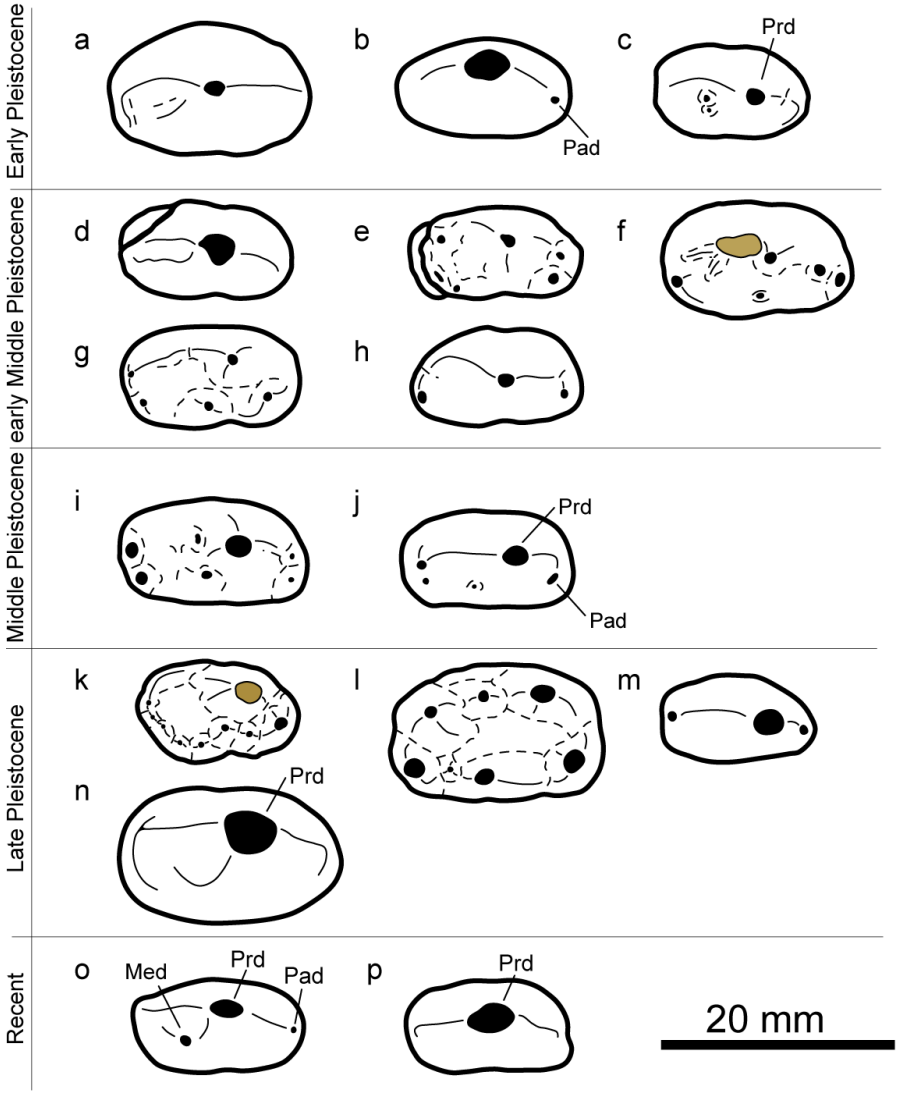

Fig. 4 - Comparison of the p4: a) *Ursus arctos* (left), DA-4B 18-36 (Deutsch-Altenburg, Early Pleistocene); b) *Ursus etruscus* (right, mirrored in the table), IGF 911 (Valdarno, Early Pleistocene); c) *Ursus etruscus* (left), IGF 4605 (Valdarno, Early Pleistocene); d) *Ursus deningeri* (left), HH 305 (Hundsheim, early Middle Pleistocene); e) *Ursus deningeri* (left), HH 306 (Hundsheim, early Middle Pleistocene); f) *Ursus deningeri* (left), Rv 20003 (Koněprusy Caves, early Middle Pleistocene); g) *Ursus deningeri* (left), Rv 20005 (Koněprusy Caves, early Midde Pleistocene); h) *Ursus deningeri* (left), n.c. (Isernia la Pineta, early Middle Pleistocene); i) *Ursus deningeri* (left), specimen H (Sandalja, Middle Pleistocene); j) FR 89-1 (right, mirrored in the table) (Fontana Ranuccio, Middle Pleistocene); k) *Ursus savini nordostensis* ssp. (left), IAM F-2365 (Ovrag, Late Pleistocene); l) *Ursus spelaeus* (left), P3021 (Caverna delle Fate, Late Pleistocene); m) *Ursus arctos* (left), ZIN 34595 (Kudaro 3, Late Pleistocene); n) *Ursus arctos* (left), V.1152 (Vigna S. Carlo, Late Pleistocene); o) *Ursus arctos* (left), 3399 (Alps, Recent); p) *Ursus arctos* (right, mirrored in the table), 3362 (Alps, Recent). Abbreviations: Med Metaconid, Prd Protoconid, Pad Paraconid.

5. DISCUSSION AND FINAL REMARKS

The presence of *U. deningeri* is confirmed at Fontana Ranuccio, as already proposed by Biddittu et al., (1979) and Cassoli & Segre Naldini, (1993). This species is widely distributed throughout Europe and quite well represented in Italy during the Middle Pleistocene (Fig. 8). *U. deningeri* was a medium-large sized bear generally deemed as the ancestor of *Ursus spelaeus s.l.* The transition between these two species occurred during the Middle - Late Pleistocene transition, so far these taxa are considered two chronospecies, phylogenetically closely related (Sardella et al., 2006, Valdiosera et al., 2007). From molecular studies a complex scenario emerges during the Late Pleistocene, with three different evolutionary lines: *U. spelaeus*, *U. ingressus* and *U. deningeri kudarensis* (Knapp et al., 2009). Late Pleistocene cave bear in particular retained the same character of the Middle Pleistocene Deninger bear, even if more marked,

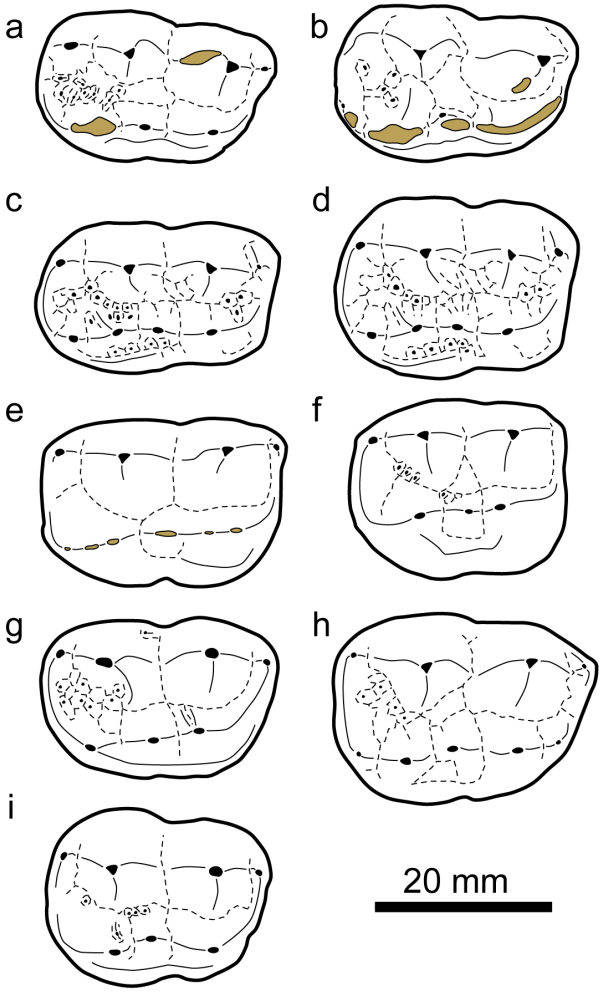

Fig. 5 - Comparison of the M1. a) FR 06-411 (right). b) FR 56574 (left, mirrored in the table). c) *U. deningeri* (left, mirrored in the table), HH/5/342 (Hundsheim, Middle Pleistocene) d) *U. deningeri* (left, mirrored in the table), HH/5/398, (Hundsheim, Middle Pleistocene). e) *U. arctos* (left, mirrored in the table), DA4B/18 (Deutsch-Altenburg, Early Pleistocene). f) *U. arctos* (right), DA4V/14 (Deutsch-Altenburg, Early Pleistocene). g) *U. arctos priscus* (right), W S.1 (Winden, Late Pleistocene). h) *U. arctos* (left, mirrored in the table), C. 4 (Banskà Bystrica, Recent). i) *U. arctos* (right), IGF 10961 (Bucine, late Middle Pleistocene). e-f-g-c) modified from Rabeder et al. (2010).

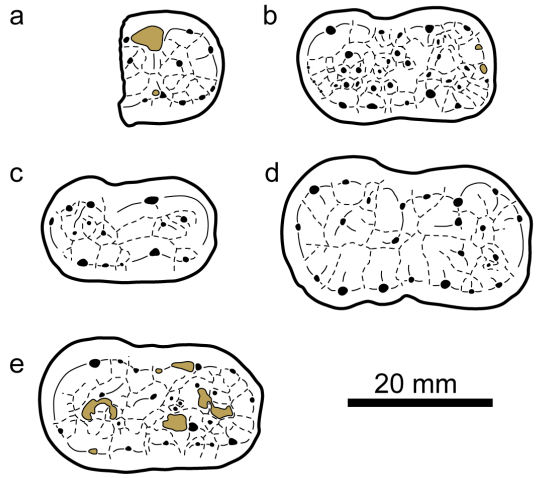

Fig. 6 - Comparison of the m2. a) FR 84-1 (left). b) FR sd-1 (left). c) *U. arctos* (right, mirrored in the table), 3364 (Alps, recent). d) *U. deningeri* (right, mirrored in the table), 1889/5/404 (Hundsheim, Middle Pleistocene). e) *U. deningeri* (left), MF/1346/37 (Kozi Grzbied, Middle Pleistocene), modified from Wagner et al. (2012).

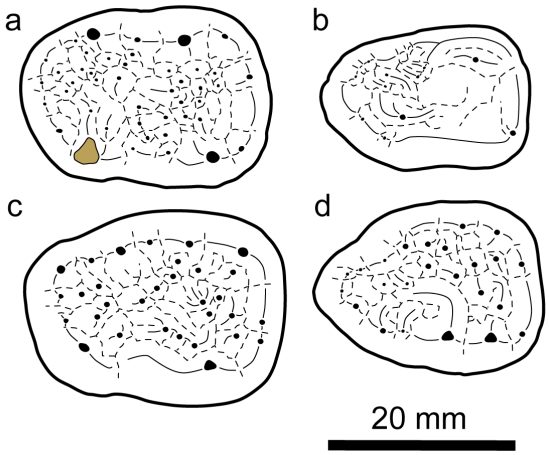

Fig. 7 - Comparison of the m3. a) FR 56575 (right). b) *U. arctos* (left, mirrored in the table), C.4, (Banská Bystrica, recent). c) *U. deningeri* (left, mirrored in the table), MF/1346/45 (Kozi Grzbiet, Middle Pleistocene). d) *U. deningeri* (left, mirrored in the table), Hund 382 (Hundsheim, Middle Pleistocene).

as the broad, domed, steep forehead, that result in a 'step' in the midsagittal plane (Santos et al., 2017).

During the Middle Pleistocene, *U. arctos* has been reported in some Italian localities: Bucine (Upper Valdarno, Tuscany; Mazza, 1998), Riparo del Poggio (Salerno; Boscato et al., 2009), Acquedolci and Contrada Camillà (Sicily; Bonfiglio et al., 2001; Marra, 2003; Pavia, 2001) (Fig. 8). The brown bear record from Riparo del Poggio is composed only by two elements (one indeterminate tooth and a phalanx), the deposit consists in a shelter which was part of a complex underground karst system, which was partially dismantled by sea erosion. The *Ursus arctos* material come from the lower level dated to the cold phase of MIS 6 (Boscato et al., 2009). The cranium from Bucine comes from one of many small fossiliferous deposits as Poggio Amaro, Le Capannelle, Pogi di Bucine, Capannole, Migliorini, Cava di Bucine, Cava Le Vigne, Cava del Rinoceronte, mostly situated along the Ambra creek, a left-hand tributary of the Arno river, and excavated since the 1940. No information is available on the exact locality where the cranium of *U. arctos* was recovered, but all the fossil remains are dated around the late Middle Pleistocene (referable to the Saalian cycle, from 340 ky to 120 ky ago; Mazza,

1998).

The bear remains from Sicily have been excavated in the last forty years, and have been found associated with *Cervus elaphus siciliae* and *Elephas mnaidriensis,* dated to the late Middle Pleistocene/Late Pleistocene (*E. mnaidriensis* Faunal Complex, from early MIS 6 to MIS 4 stages; Bonfiglio et al., 2001, 2003). The occurrence of the brown bear is also documented in some other sites of the north/eastern Italian Peninsula (see Bon et al., 1991), however this material needs further chronological and systematic analyses.

Since the uncertain dating of these deposits, it is possible to hypothesize that the Bucine specimen could be the F.O. of the brown bear in the Italian peninsula. A recent paleoenvironmental reconstruction based on dietary adaptations of ungulates from Fontana Ranuccio suggests that a mosaic of both closed and open landscapes characterized this locality around 0.4 Ma with a relative abundance of soft plant resources and probably affected by a marked seasonality (Strani et al., 2018a; Strani et al., 2019; Strani, 2020; Strani et al., 2021). A heterogeneous environment could have favored the coexistence of two different bear species in the area, which may have lived in sympatric conditions exploiting different trophic resources as largely documented in several Late Pleistocene localities of the Italian Peninsula (Capasso Barbato et al., 1990; Minieri et al., 1995; Palombo et al., 2002; Mazza et al., 2005).

Although palaeoecological considerations allow the presence of the two species, paleontological data do not show with any reliable evidence of the presence of *Ursus arctos*. The fossils from Fontana Ranuccio represent the LO of *Ursus deningeri* in Italy. New excavations are still ongoing carried on by IsIPU and new findings will better address many unsolved questions and shed new light on the distribution and evolution of bears in Europe.

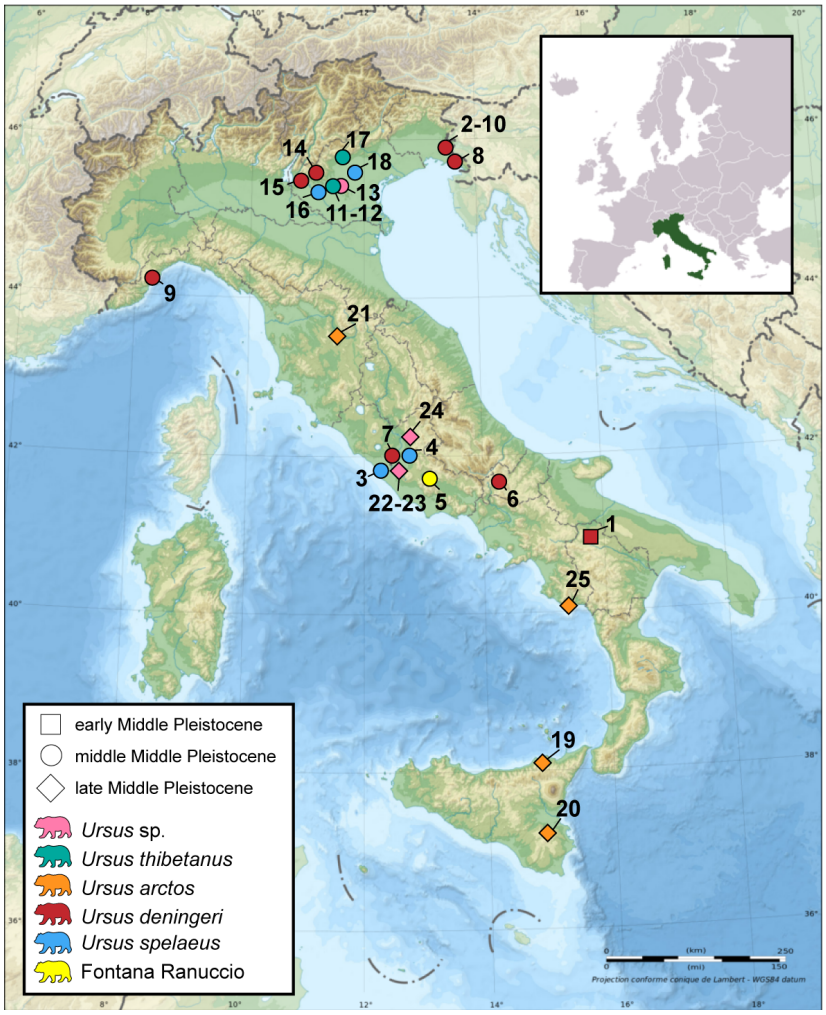

Fig. 8 - Distribution of the fossil bears during the Middle Pleistocene of the Italian Peninsula. 1) Venosa (van Heteren et al., 2019). 2) Bristie I (Lugli & Sala, 2000). 3) Cava Rinaldi (Petronio et al., 2019). 4) Cretone (Petronio et al., 2011). 5) Fontana Ranuccio (this work). 6) Isernia la Pineta (Peretto & Sala, 2019). 7) Ponte Molle (Petronio et al., 2011). 8) Slivia (Bon et al., 1991; Petronio et al., 2011). 9) Valdemino (Ghezzo et al., 2015). 10) Visogliano (Tozzi et al., 2000). 11) Cava Nord (Soave) (Rustioni & Mazza, 1993). 12) Cengelle 1 (Soave) (Rustioni & Mazza, 1993). 13) Castello (Soave) (Rustioni & Mazza, 1993). 14) Cerè (Ghezzo et al., 2013; Rossi & Santi, 2011). 15) Selva Vecchia (van Heteren et al., 2019). 16) Sorbano di Romagnano (Bon et al., 1991). 17) Fornace di Cornedo (Rustioni & Mazza, 1993). 18) Grotta di San Bernardino (Bon et al., 1991). 19) Acquedolci (Marra, 2003). 20) Contrada Camilla (Marra, 2003). 21) Bucine (Mazza, 1997; Petronio et al., 2019). 22) Castel di Guido (Caloi et al., 1998). 23) Prati Fiscali (Petronio et al., 2011). 24) Fara Sabina (Petronio et al., 2011). 25) Riparo del Poggio (Boscato et al., 2009).

ACKNOWLEDGEMENTS

We are very grateful to the Italian Institute of Human Paleontology for granting access to the material and for the continuous assistance during the analyses. We would like to express also gratitude to Martin Sabol (Comenius University, Bratislava), for advising and the inspiring discussion that made possible this work. We also thank the MuSe (Museo delle Scienze of Trento), the Parco Nazionale d'Abruzzo, Lazio e Molise, the Department of Geology and Paleontology of Comenious University (Bratislava, Slovakia), the Slovak Museum of Nature Protection and Speleology (Liptovský Mikuláš, Slovakia), the National History Museum (Wien, Austria), the Department of Paleontology of Wien University (Wien, Austria), for granting access to fossil and extant bear material used for morphological comparisons. We thank Chiara Delpino of Soprintendenza Archeologia Belle Arti e Paesaggio per le Province di Frosinone, Latina e Rieti (Ministero della Cultura) and the Italian Institute of Human Paleontology for granting access to

the palaeontological collections of Fontana Ranuccio.". We'd like to thank the two reviewers for providing useful comments that allowed us to improve our manuscript. JC acknowledges Sapienza, University of Rome for the funds provided by the call “Bando per il finanziamento di progetti di ricerca congiunti per la mobilità all’estero di studenti di dottorato del XXXI e XXXII ciclo n. 2682/2017”, that allowed the acquisition of part of the data present in this work.

REFERENCES

Ambrosetti P., Bartolomei G., De Giuli C., Ficcarelli G., Torre D. (1979) - La breccia ossifera di Slivia (Aurisina-Sistiana) nel Carso di Trieste. Bollettino della Società Paleontologica Italiana, 18(2), 207-220.

Argant A. (1991) - Carnivores quaternaires en Bourgogne. Doc. Lab. Géol. Lyon, 115, pp. 301.

Arsuaga J.L., Martínez I., Arnold L.J., Aranburu A., Gracia-Téllez A., Sharp W.D., Quam R.M., Falguères C., Pantoja-Pérez A., Bischoff J., Poza-Rey E., Parés J.M., Carretero M., Demuro M., Lorenzo C., Sala N., Martinón-Torres M., García N., Alcázar de Velasco A., Cuenca-Bescós G., Gómez-Olivencia A., Moreno D., Pablos A., Shen C., Rodríguez L., Ortega A.I., García R., Bonmatí A., Bermúdez de Castro J.M., Carbonell E. (2014) - Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. Science, 344(6190), 1358-1363.

Auguste P. (1995) - Cadres biostratigraphiques et paléoécologiques du peuplement humain dans la France septentrionale durant le pléistocène: apports de l’étude paléontologique des grands mammifères du gisement de Biache-Saint-Vaast (Pas-de-Calais). Doctoral Dissertation, Paris, Muséum National d’histoire Naturelle, pp. 1924.

Azzaroli A. (1983) - Quaternary mammals and the “End-Villafranchian” dispersal event - A turning point in the history of Eurasia. Palaeogeography, Palaeoclimatology, Palaeoecology, 44(1-2), 117-139.

Ballesio R. (1983) - Le gisement Pléistocène supérieur de la grotte de Jaurens à Nespouls (Corrèze)□: les Carnivores. Nouvelles Archives DuMuséum d’Histoire Naturelle de Lyon, 21, 9-43.

Baryshnikov G.F. (2010) - Late Pleistocene brown bear (Ursus arctos) from the Caucasus. Russian Journal of Theriology, 9(1), 9-17.

Biddittu I., Cassoli P.F., Radicati di Brozolo F., Segre A.G., Segre Naldini E., Villa I. (1979) - Anagni a K/Ar dated Lower Middle Pleistocene site, Central Italy: preliminary report. Quaternaria, 21, 53-71.

Bon M., Piccoli G., Sala B. (1991) - I giacimenti quaternari di vertebrati fossili nell’Italia Nord-Orientale. Mem. Se. Geol. Padova, 43, 185-231.

Bona F., Strani F. (2021) - New data on the Middle Pleistocene small mammal fauna from the *Homo* bearing site of Fontana Ranuccio (Anagni Basin, Central Italy). Alpine and Mediterranean Quaternary, 34 (1), 69-74.

Bonfiglio L., Mangano G., Marra A.C., Masini F. (2001) - A new Late Pleistocene vertebrate faunal complex from Sicily (S. Teodoro Cave, North-Eastern Sicily, Italy). Bollettino della Società Paleontologica Italiana, 2, 149-158.

Bonfiglio L., Di Maggio C., Marra A., Masini F., Petruso D. (2003) - Bio-chronology of Pleistocene vertebrate faunas of Sicily and correlation of vertebrate bearing deposits with marine deposits. Il Quaternario, 16(1), 107-114.

Borselli V., De Giuli C., Ficcarelli G., Mazzini M. (1980) - Casa Frata: una località fossilifera del Villafranchiano Superiore presso Terranuova Bracciolini (Arezzo) nel Valdarno Superiore. Bolletino della Società Paleontologica Italiana, 19(2), 245-258.

Boscato P., Boschian G., Caramia F., Gambassini P. (2009) - Il Riparo del Poggio a Marina di Camerota (Salerno): culture ambiente. Rivista di scienze preistoriche, 59(2009), 5-40.

Caloi L., Palombo M.R., Zarlenga F. (1998) - Late-Middle Pleistocene mammal faunas of Latium (central Italy): stratigraphy and environment. Quaternary International, 47, 77-86.

Capasso Barbato L., Minieri M.R., Petronio C., Vigna Taglianti A. (1990) - Strutture dentarie di Ursus arctos e di Ursus spelaeus della grotta di Monte Cucco (Sigillo, Perugia, Italia). Bollettino della Società Paleontologica Italiana, 29, 335-356.

Cassoli P.F., Segre Naldini E. (1993) - Le faune Villafranchiane: Costa san Giacomo e Fontana Acetosa. Dives Anagnia. L’Erma Di Bretscheider, Roma, 31-33.

Conti J. (2019) - Evolution of cranio-dental features and distribution of brown bear (Ursus arctos L., 1758) in Europe. Ph.D. Thesis. Sapienza University of Rome, pp. 177.

Conti S. (1954) - Morfologia comparata craniale ed encefalica degli orsi pleistocenici della Liguria. Memorie Del Museo Civico Di Storia Naturale “G. Doria” Genova, pp. 86.

Cuvier G. (1823) - Recherches sur les Ossemens Fossililes de quadrupédes. Paris, 5(1).

Devèze de Chabrol J.S., Bouillet J.B. (1827) - Essai géologique et minéralogique sur les environs d'Issoire, département du Puy-de-Dôme, et principalement sur la Montagne de Boulad, avec la description et les figures lithographiées des ossemens fossiles qui y ont été recueillis. Ursidae. Thibaud-Landriot, Clermont-Ferrand, pp. 140.

Di Stefano G., Petronio C., Sardella R. (1994) - Il significato biocronologico e paleoecologico di alcuni taxa di mammiferi del Plio-Pleistocene dell’Italia centrale. Studi Geologici Camerti, volume speciale 1994 “Biostratigrafia dell’Italia centrale”. Università degli Studi di Camerino, Camerino, 459-467.

Ferretti M. (1997) - *Mammuthus* cf. *primigenius* (Proboscidea, Mammalia), a new faunal element from the late Middle Pleistocene of Conca river (Cattolica, Romagna, Italy). Bollettino della Società Paleontologica Italiana, 36(3), 391-398.

Florindo F., Marra F., Angelucci D.E., Biddittu I., Bruni L., Florindo F., Gaeta M., Guillou H., Jicha B., Macrì P., Morigi C., Nomade S., Parenti F., Pereira A., Grimaldi S. (2021) - Environmental evolution, faunal and human occupation since 2

Ma in the Anagni basin, central Italy. Scientific reports, 11(1), 7056.

García N., Arsuaga J.L., Torres T.D. (1997) - The carnivore remains from the Sima de los Huesos Middle Pleistocene site (Sierra de Atapuerca, Spain). Journal of Human Evolution, 33(2-3), 155-174.

García N., Santos E., Arsuaga J.L., Carretero J.M. (2007) - Endocranial morphology of the *Ursus deningeri* von Reichenau 1904 from the Sima de los Huesos (Sierra de Atapuerca) Middle Pleistocene site. Journal of vertebrate paleontology, 27 (4), 1007-1017.

Ghezzo E., Berté D., Sala B. (2013) - The revalutation of Galerian Canidae, Felidae and Mustelidae of the Ceré Cave (Verona, Northeastern Italy). Quaternary International, 339-340, 76-89.

Ghezzo E., Boscaini A., Madurell-Malapeira J., Rook L. (2015) - *Lynx* remains from the Pleistocene of Valdemino cave (Savona, Northwestern Italy), and the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae). Rendiconti Lincei, 26(2), 87-95.

Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. Torre D. (1997) - Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Rivista Italiana di Paleontologia e Stratigrafia, 103(3), 369-388.

Grimaldi S., Santaniello F., Angelucci D.E., Bruni L., Parenti F. (2020) - A Techno-Functional Interpretation of the Lithic Assemblage from Fontana Ranuccio (Anagni, Central Italy): an Insight into a MIS 11 Human Behaviour. Journal of Paleolithic Archaeology, 3, 944–966.

Knapp M., Rohland N., Weinstock J., Baryshnikov G., Sher A., Nagel D., Rabeder G., Pinhasi R., Schmidt H.A., Hofreiter M. (2009) - First DNA sequences from Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Molecular ecology, 18(6), 1225-1238.

Linnaeus C. (1758) - Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. 1 (10th ed.). Laurentius Salvius, Stockholm. pp. 824.

Lugli C., Sala B. (2000) - La teriofauna del Pleistocene medio di Bristie I°(Carso Triestino). Atti del Museo Civico di Storia naturale di Trieste, 48, 35-58.

Madurell-Malapeira J., Alba D.M., Moyà-Solà S. (2009) - Carnivora from the late Early Pleistocene of Cal Guardiola (Terrassa, Vallès-Penedès Basin, Catalonia, Spain). Journal of Paleontology, 83(6), 969-974.

Marra A.C. (2003) - *Ursus arctos* from selected Pleistocene site of Eastern Sicily. Bollettino della Società Paleontologica Italiana, 42(1-2), 145-150.

Masini F., Sala B., Ambrosetti P., Azzaroli A., Ficcarelli G., Kotsakis T., Rook L., Torre D. (1991) - Mammalian faunas of selected villafranchian and galerian localities. In: INQUA SEQS, Subcommission for European Quaternary Stratigraphy, Cromer Symposium, Norwich., UK, 3-7 September 1990.

Mazza P. (1998) - Taphonomic analysis of late Middle Pleistocene mammal remains from Bucine. Bollettino della Società Paleontologica Italiana, 36, 381-390.

Mazza P., Rustioni M. (1994) - On the phylogeny of Eurasian bears. Palaeontographica, 230, 1-38.

Mazza P. (1997) - Taphonomic analysis of late Middle Pleistocene mammal remains from Bucine. Bollettino della Società Paleontologica Italiana, 36, 381-390.

Mazza P., Rustioni M., Agostini S., Rossi A. (2005) - An unexpected Late Pleistocene macaque remain from Grotta degli Orsi Volanti (Rapino, Chieti, central Italy). Geobios, 38(2), 211-217.

Mecozzi B., Iannucci A., Mancini M., Sardella R. (2021) - Redefining Ponte Molle (Rome, central Italy): an important locality for Middle Pleistocene mammal assemblages of Europe. Alpine and Mediterranean Quaternary, 34(1), 131-154
Doi: 10.26382/AMQ.2021.09

Meloro C. (2007) - La fauna quaternaria di Grotta Milano (Petina, Salerno). Atti I Convegno Regionale di Speleologia “Campania Speleologica” 1-3 giugno 2007 Oliveto Citra (SA), pp. 75-83.

Minieri M., Petronio C., Sardella R., Scarano M. (1995) - Le faune a mammiferi del Pleistocene superiore dell’Italia peninsulare. Quaderni Padusa, 1, 75-87.

Palombo M.R., Azanza B., Alberdi M.T. (2002) - Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach. Geologica Romana, 36, 335-368.

Pavia M. (2001) - The Middle Pleistocene fossil avifauna from the “*Elephas mnaidriensis* Faunal Complex” of Sicily (Italy): preliminary results. In 1° Congresso Internazionale: "La Terra Degli Elefanti", Roma 16-20 ottobre 2001, 497-501.

Peretto C., Sala B. (2019) - Isernia La Pineta (Isernia). Annali dell’Università di Ferrara. Sezione: Museologia scientifica e naturalistica, 15, 31-38.

Pereira A., Nomade S., Moncel M.H., Voinchet P., Bahain J.J., Biddittu I., Falguères C., Giaccio B., Manzi,G., Parenti F., Scardia G., Scao V., Sottili G., Vietti A. (2018) - Integrated geochronology of Acheulian sites from the southern Latium (central Italy): Insights on human-environment interaction and the technological innovations during the MIS 11-MIS 10 period. Quaternary Science Reviews, 187, 112-129.
Doi: 10.1016/j.quascirev.2018.03.021

Petronio C., Di Canzio E., Salari L. (2007) - The Late Pleistocene and Holocene Mammals in Italy: new biochronological and paleoenvironmental data. Palaeontographica, Abt. A, 279, 147-157.

Petronio C., Bellucci,L., Martinetto E., Pandolfi L., Salari L. (2011) - Biochronology and palaeoenvironmental changes from the Middle Pliocene to the Late Pleistocene in Central Italy. Geodiversitas, 33(3), 485-517.

Petronio C., Di Stefano G., Kotsakis T., Salari L., Marra F., Jicha B.R. (2019) - Biochronological framework

for the late Galerian and early-middle Aurelian Mammal Ages of peninsular Italy. Geobios, 53, 35-50.

Petronio C., Angelone C., Atzori P., Famiani F., Kotsakis T., Salari L. (2020) - Review and new data of the fossil remains from Monte Peglia (late Early Pleistocene, Central Italy). Rivista Italiana di Paleontologia e Stratigrafia, 126 (3), 791-819.

Petrucci M., Sardella R. (2009) - *Ursus etruscus* Cuvier, 1823 from the Early Pleistocene of Monte Argentario (Southern Tuscany, Central Italy). Bollettino della Società Paleontologica Italiana, 48(2), 89-94.

Prat-Vericat M., Rufí I., Llenas M., Madurell-Malapeira J. (2020) - Middle Pleistocene Ursus deningeri from Grotte de la Carrière (Réseau Lachambre, Têt Valley, Eastern Pyrenees). Journal of Iberian Geology, 46(2), 163-175.

Quiles J. (2003) - Les Ursidae du Pléistocène moyen et supérieur en Midi méditerranéen: apports paléontologiques, biochronologiques et archéozoologiques. Doctoral Dissertation, Paris, Muséum National d'histoire Naturelle, pp. 1307.

Rabeder G. (1999) - Die Evolution des Höhlenbärengebisses. Verlag Der Österr. Akad. Der Wiss., 11, 1-102.

Rabeder G., Pacher M., Withalm G. (2010) - Early Pleistocene bear remains from Deutsch-Altenburg (Lower Austria). Mitteilungen Der Kommission Für Quartärforschung Der Österreichischen Akademie Der Wissenschaften, 17, 1-135.

von Reichenau W. (1904) - Beiträge zur näheren Kenntniss der Carnivoren aus den Sanden von Mauer and Mosbach. Abhandlungen der Grossherzolich Hessischen geologischen Landesanstalt zu Darmstadt. 4(2), 14.

Reynolds S.H. (1906) - Monograph of British Mammalia of the Pleistocene period. The Bears. London Palaeontographical Society, 2, 1-35.

Rosenmüller J. (1794) - Quaedam de Ossibus Fossilibus Animalis cuiusdam, Historiam eius et Cognitionem accurationrem illustrantia. Thesis, Leipzig, pp. 34.

Rossi M., Santi G. (2011). *Ursus deningeri-spelaeus* group from Cerè Cave (Veneto, North Italy) in the new evolutionary frame of the cave bear. Part one: skulls and mandibles. Annalen des Naturhistorischen Museums in Wien. Serie A für Mineralogie und Petrographie, Geologie und Paläontologie, Anthropologie und Prähistorie. Naturhistorischen Museum, Wien, 567-590.

Rubini M., Cerroni V., Festa G., Sardella R., Zaio P. (2014) - A revision of hominin fossil teeth from Fontana Ranuccio (Middle Pleistocene, Anagni, Frosinone, Italy). Journal of Human Evolution, 77, 204-216.
Doi: 10.1016/j.jhevol.2014.09.002

Rustioni M., Mazza P. (1993) - The Tibetan-like bear from Grotta di Reale, Porto Azzurro (Isle of Elba, Italy). Il Quaternario, 6(1), 35-38.

Santos E., Gómez-Olivencia A., Arlegi M., Arsuaga J.L. (2017) - Cranial morphological differences within *U. deningeri - U. spelaeus* lineage: A double traditional and geometric morphometrics approach. Quaternary International. 433, 347-362.

Sardella R., Palombo M.R., Petronio C., Bedetti C., Pavia M. (2006) - The early Middle Pleistocene large mammal faunas of Italy: an overview. Quaternary International, 149(1), 104-109.

Segre A.G. (1984) - Considerazioni sulla cronostratigrafia del Pleistocene laziale. Atti Della XXIV Riunione Scientifica Dell'Istituto Italiano Di Preistoria e Protostoria, Istituto Italiano Di Preistoria e Protostoria, Firenze, 149-154.

Sher A. V., Weinstock J., Baryshnikov G. F., Davydov S. P., Boeskorov G. G., Zazhigin V. S., Nikolskiy P. A. (2011). The first record of "spelaeoid" bears in Arctic Siberia. Quaternary Science Reviews, 30(17 -18), 2238-2249.

Stiner M.C. (1998) - Mortality analysis of Pleistocene bears and its paleoanthropological relevance. Journal of Human Evolution, 34(3), 303-326.

Strani F. (2020) - Impact of Early and Middle Pleistocene major climatic events on the palaeoecology of Southern European ungulates. Historical Biology, in press.
Doi: 10.1080/08912963.2020.1782898

Strani F., DeMiguel D., Bona F., Sardella R., Biddittu I., Bruni L., De Castro A., Guadagnoli F., Bellucci L. (2018a) - Ungulate dietary adaptations and palaeoecology of the Middle Pleistocene site of Fontana Ranuccio (Anagni, Central Italy). Palaeogeography, Palaeoclimatology, Palaeoecology, 496, 238-247.
Doi: 10.1016/j.palaeo.2018.01.041

Strani F., Profico A., Manzi G., Pushkina D., Raia P., Sardella R., DeMiguel D. (2018b) - MicroWeaR: a new R package for dental microwear analysis. Ecology and Evolution, 8, 7022-7030.

Strani F., Pushkina D., Bocherens H., Bellucci L., Sardella R., DeMiguel D. (2019) - Dietary Adaptations of Early and Middle Pleistocene Equids From the Anagni Basin (Frosinone, Central Italy). Frontiers In Ecology And Evolution, 7, 176.

Strani F., Bellucci L., Iannucci A., Iurino D.A., Mecozzi B., Sardella R. (2021) - Palaeoenvironments of the MIS 15 site of Cava di Breccia - Casal Selce 2 (central Italian Peninsula) and niche occupation of fossil ungulates during Middle Pleistocene interglacials. Historical Biology, in press.
Doi: 10.1080/08912963.2021.1935920

Terlato G., Bocherens H., Romandini M., Nannini N., Hobson K.A., Peresani M. (2018) - Chronological and Isotopic data support a revision for the timing of cave bear extinction in Mediterranean Europe. Historical Biology, 31(4), 474-484.

Torres P. (1984) - Ursidos del pleistoceno-holoceno de la Península Ibérica. Doctoral Dissertation, E.T.S.I. Minas (UPM) pp. 653.

Torres P. (1988) - Osos (Mammalia, Carnivora, Ursidae) del Pleistoceno Ibérico (*U. deningeri* Von Reichenau, *U. spelaeus* Rosenmüller-Heinroth, *U. arctos* Linneo). Boletín Geológico y Minero, 99, 4-940.

Tozzi C., Falgueres C., Mallegni F., Masini F., Negrino F. (2000) - Les industries du Paléolithique inférieur de Visogliano, Trieste, Italie, dans leur contexte stratigraphique, biostratigraphique et géochronolo-

gique. Les prémiers habitants de l'Europe, Tautavel 10-15 avril 2000, Resumen de communications, pp. 104.

Valdiosera C.E., García N., Anderung C., Dalén L., Crégut-Bonnoure E., Kahlke R.D., Stiller M., Brandström M., Thomas M.G., Arsuaga J.L., Götherström A., Barnes I. (2007) - Staying out in the cold, glacial refugia and mitochondrial DNA phylogeography. Molecular Ecology, 16, 5140-5148.

van Heteren A.H., Arlegi M., Santos E., Arsuaga J.L., Gómez-Olivencia A. (2019) - Cranial and mandibular morphology of Middle Pleistocene cave bears (*Ursus deningeri*): implications for diet and evolution. Historical Biology, 31(4), 485-499.

Wagner J., Sabol M. (2007) - Remarks on Biharian bears (Ursidae: Ursus) from the territory of Slovakia. Scripta Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, 35, 159-164.

Wagner J., Čermák S. (2012) - Revision of the early Middle Pleistocene bears (Ursidae, Mammalia) of Central Europe, with special respect to possible co -occurrence of spelaeoid and arctoid lineages. Bulletin of Geosciences, 87(3), 461-496.

Wagner J., Jiangzuo Q., Lenardić J.M., Liu J. (2017) - Taxonomic revision of bears from the locality Šandalja I (Croatia) and its biostratigraphic consequences. Fossil Imprint (Formerly Acta Musei Nationalis Pragae, Series B-Historia Naturalis), 73(3-4), 533-544.

Ms. received: November 17, 2020 *Revised: March 23, 2021*
Accepted: June 3, 2021 *Available online: July 8, 2021*