Earth Science Department

Sapienza Università di Roma

Ph.D. Thesis

Evolution of cranio-dental features and distribution of brown bear (*Ursus arctos* L., 1758) in Europe.

Conti Jacopo

XXXI Cicle

Supervisor: *Prof. Raffaele Sardella*
Co-Advisor: Dawid Adam Iurino
Ph.D. Coordinator: *Prof. Giovanni B. Andreozzi*

Table of contents

1 Introduction.....5
1.1 Open questions and aims of the thesis.....6
2 The evolution of the Ursidae family.....7
3 Recognise the brown bear in the fossil record.....16
3.1 The cranium.....17
3.2 The mandible.....19
3.3 The dentition.....21
3.3.1 Incisors and canines.....22
3.3.2 Premolars.....24
3.3.3 Molars.....26
4 Methods.....32
4.1 The database.....32
4.2 Morphometrical analysis.....34
4.3 Morphometric geometry.....36
4.4 2D Morphometric geometry.....38
4.5 3D Morphometric geometry.....41
4.6 From real to virtual.....42
4.6.1 Axial tomography.....43
4.6.2 The photogrammetry.....46
4.6.3 Tac or photogrammetry?.....50
5 Paleogeography of the brown bear.....52
5.1 Late Pliocene (Early and Middle Villafranchian).....52
5.2 Early Pleistocene (Late Villafranchian).....53
5.3 Early Middle Pleistocene and Middle Pleistocene.....55
5.4 Late Middle Pleistocene.....56
5.5 Late Pleistocene (Early Glacial - Periglacial).....57
5.6 From the Late Maximum Glacial to the rising of the temperatures.....59
5.7 The Holocene.....62
5.8 Final remarks.....65
6 The brown bear in Italy.....68
6.1 A look at the present.....68
6.1.1 The teeth.....69
6.1.2 Final remarks.....74
6.1.3 The cranium.....75
6.1.4 Final remarks.....79
7 Fossil brown bear in Southern-Central Italy.....81
7.1 Grotta del Cervo.....81

    - 7.1.1 The site 81
    - 7.1.2 Material 82
    - 7.1.3 Description 83
    - 7.1.4 Final remarks 86
  - 7.2 Grotta degli Orsi Volanti 87
    - 7.2.1 The site 87
    - 7.2.2 Material 87
    - 7.2.3 Description 88
    - 7.2.4 Final Remarks....90
  - 7.3 Vigna S. Carlo (Monteverde)....91
    - 7.3.1 The site 91
    - 7.3.2 Material 91
    - 7.3.3 Description 92
    - 7.3.4 Final remarks 94
  - 7.4 Ingarano 94
    - 7.4.1 The site 94
    - 7.4.2 Material 96
    - 7.4.3 Description 98
    - 7.4.4 Final Remarks....104
  - 7.5 Grotta della Lupa 105
    - 7.5.1 The site 105
    - 7.5.2 Material 106
    - 7.5.3 Description 107
    - 7.5.4 Final Remarks....111
  - 7.6 Gran Carro 111
    - 7.6.1 The site 111
    - 7.6.2 Material 112
    - 7.6.3 Description 113
    - 7.6.4 Final Remarks....118
  - 7.7 Discussion....120
- 8 The first occurrence of brown bear in Italy 121
    - 8.1.1 Material and methods 121
    - 8.1.2 Comparison and description....123
    - 8.1.3 Final remarks 128
- 9 The brown bear brains 130
  - 9.1 The brain....131
    - 9.1.1 Material 133
    - 9.1.2 Description 134

9.1.3 Final Remarks......135
10 General Discussion......137
11 Conclusions......139
12 References......141
13 Supplementary material......151
14 Acknowledgement......174

1 Introduction

The extant brown bear (*Ursus arctos,* Linnaeus 1958) is the most common and widely distributed members of the family Ursidae, which occupies different environments of the Palearctic region, including deciduous and coniferous forests, grasslands and alpine tundra (Servheen et al., 1999; Zedrosser et al., 2001; McLellan et al., 2008; Colangelo et al., 2012). Consequently, to its wide distribution, the brown bear shows a high variability in body mass, comprised between 150-280 cm and a body weight ranging from 130-300 kg for males and 80-250 kg for females (in Europe). In addition to the intraspecific variability, the remarkable differences in body proportions between males and females indicate also a marked sexual dimorphism in this species (Ohdachi et al., 1992; Colangelo et al., 2012) Such plasticity has fuelled debates among specialists during the last decades, especially concerning taxonomic aspects, with several different subspecies proposed (Erdbrink, 1953; Akhremenko and Sedalishchev, 2008; Colangelo et al., 2012; Benazzo et al., 2017). The evolutionary history of the brown bear based on the fossil evidences is a tricky issue, mostly because of the geographical and chronological variability (Sommer and Benecke, 2005) and the scarcity of the fossil remains from the late Early Pleistocene, when the first occurrence in Europe is proposed by (Rabeder et al., 2010). The oldest occurrence of *U. arctos* in Italy was documented from only four Middle Pleistocene localities, Bucine (Tuscany), Contrada Camillà and Acquedolci (Sicily) and Fontana Ranuccio (Latium) (Ferretti, 1997; Gliozzi et al., 1997; Mazza, 1997; Palombo et al., 2002; Marra, 2003).

During the Late Pleistocene, the fossil evidences of brown bear are reported in several different localities (Smirnov and Golovachov, 1998; Sommer and Benecke, 2005; Valdiosera et al., 2007) suggesting an almost homogenous distribution of this large carnivore on the whole European continent. Frequently associated with the more common and better documented cave bear (*Ursus* ex gr. *spelaeus*), whose remains are often abundant and, in some cases, difficult to distinguish from those of the *U. arctos*, especially the early Late Pleistocene material (Torres, 1988; Capasso Barbato et al., 1990).

Both the genetic and fossil evidence, indicate a sharp demographic decline in European brown bear populations, occurred during the Last Glacial Maximum when their distribution was restricted to at least four different glacial refugia: the Iberian Peninsula, the Italian Peninsula, the Balkans and the Carpathians (including north-western Moldova). This fragmentation seems to be driven prevalently by climate and environmental changes through a decrease in resource availability (Davison et al., 2011). According to Albrecht et al., (2017) the brown bear decline is also reported throughout the Holocene (last 11.700 years) when the climate conditions were more stable and temperate and the human communities established competitive relationships with bears, as suggested by many archaeological and historical evidences (Sommer and Benecke, 2005). In Italy two living subspecies of brown bear are reported: *U. arctos arctos*, distributed in the central-eastern Alps and related to the eastern Europe populations, and *U. arctos marsicanus* (Altobello 1921) restricted to the central Apennines (Benazzo et al., 2017) with origins and affinities still debated among specialists. The latter subspecies shows a peculiar skull morphology with a marked frontal step, similar to those observed in *U.* ex gr. *spelaeus*. Genetic studies also show a peculiarity in this population, suggesting that the Apennine bear diverged between 2 and 3 kya form other European and Italian populations with a complete isolation since ~1,500 y ago (Colangelo et al., 2012; Benazzo et al., 2017). According to this scenario, the origin of the Apennine bear is very recent, and this agrees with the total lack of any osteological evidence of “Marsicanmorphotypes” during the Late Pleistocene and the whole Holocene, making this subspecies completely unknown in the archaeozoological record. On the other hand, also the holocenic remains of *U. arcto*s from the Apennine area are quite scarce, hardly available and with very few published data, mostly attributable to dated grey literature. As a consequence, in the central Appenine the presence of brown bear remains is currently documented for only few archaeological sites (Silvestri, 2017). Thus, the study of new ursid materials from the Italian Peninsula is of crucial interest to understand the evolution of *U. arctos* during the Holocene, especially in such a relevant area for the origin and conservation of one of the most peculiar ursid of Europe.

1.1 Open questions and aims of the thesis

The introduction raise some issues and open questions that are still unsolved today and tha may be summarized in points:

A) Lack of international scientific documentation regarding the material of *Ursus arctos* in the Italian territory.
B) Lack of reliable data on the first evidence of brown bear in Italy.
C) Lack of fossil evidence and of a clear evolutionary-adaptive model of the subspecies *Ursus arctos marsicanus* (Altobello 1921), currently living in the central Appennines.
D) There is no exhaustive description of the diagnostic characters of *Ursus arctos* during the Middle and Late Pleistocene compared with the material of the speloid lineage.

The aim of this work is to aswere those open questions, addressing them one by one, and then analysing the results in the overall context.

This text can be divided in two parts: one that includes descriptions and methods and a second with the report of the analysis and the results.

The first part will be developed by defining the general evolution of the genus *Ursus*, to understand in more detail the current knowledge and doubts about the evolutionary path of this mammal; specific attention will be given to the main topic of the work: the brown bear.

The work will evolve highlighting the main characteristics that distinguish the various bear species. Much of this part has been elaborated taking as reference point the milestones works about the different morphologies among Ursids and personal experience.

Therefore, in order to facilitate reading, I decided to include in the chapter "Methods" the techniques used for the entire work, which led to the subsequent results. The choice of this division was made to allow the reader not to dwell constantly on the "how" but to have a general and clear framework of "what" and avoid unnecessary repetitions in case of use of the same analysis for different topics.

The second part of the work will focus on the distribution of the genus *Ursus* over time and its dispersal in relation with the Quaternary climate changes and faunal turnovers; thereafter, various morphometric and morphological analyses will be presented, carried out on the various cranial and dental anatomical portions of recent, fossil and sub-fossil specimens. The aim is to highlight and analyze specific features that divide the different species and subspecies in the variability of the genus and to integrate them into a paleobiogeographic framework.

Finally, a focus on the central-southern region of Italy (the current area of *U. arctos marsicanus*) will be presented, analyzing in detail all the findings from Pleistocene and Holocene deposits in the area. In the work will also be discussed the topics regarding the first evidence of *U. arctos* in Italy and a specific study of bear encephalic endocasts.

Each chapter ends with a specific discussion of the analyses treated, which will be presented again together in the general discussions.

2 The evolution of the Ursidae family

The evolution of the bear, as well as the phylogeny that regulates the relationships between the extant species, presents many shortcomings, rising many debates over time. Researchers agree on a few assumptions: i) the juggler bear (*Melursus ursinus* Shaw, 1791) appears to have become detached from the other species at an early stage of the evolutionary history of the family, ii) there is a close relationship between the American black bear (*Ursus americanus* Pallas, 1780) and the Asian black bear (*Ursus thibetanus* Cuvier, 1823) and also between the brown bear (*U. arctos*) and the polar bear (*Ursus maritimus* Phipps, 1774) (Yu et al., 2007).

The Ursidae family probably appears in the late Oligocene with the genus *Cephalogale* from which the 5 main subfamilies evolve: 1) Hemicyoninae, 2) Agriotheriinae, 3) Tremarctinae, 4) Ursidae e 5) Ailuropodinae (Hendey, 1972; McLellan and Reiner, 1994).

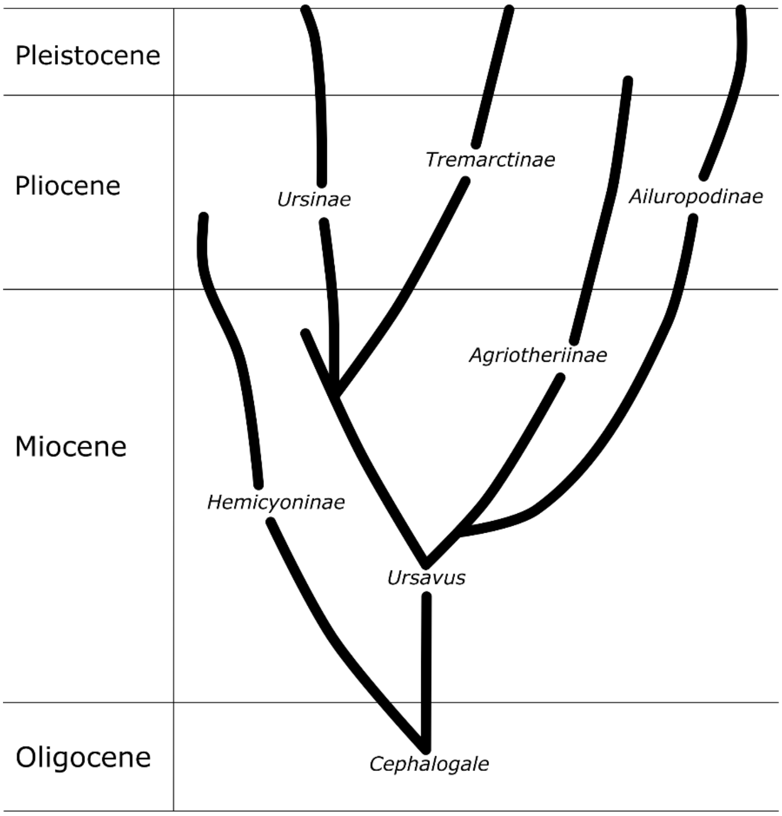


Figure 1: ***Phylogeny of Ursidae subfamilies. Modified from Mc Lellan 1994.***

Excluding the group of hemicyonids (intermediate between bears and canids) the remaining groups descend from a common ancestor: the genus *Ursavus* (Erdbrink, 1953; Kurtén, 1966; Mitchell and Tedford, 1973; Thenius, 1979).

The first representative of this genus is *Ursavus elmensis*; a small animal, with the size of a fox terrier and rather primitive, which lived during the first part of the Miocene (10ky) (Crusafont and Kurtén, 1976). From it, two bigger and more massive species belonging to the same genus descend and spread in Eurasia: *Ursavus primaevus* (Gaillard, 1899) (ancestor of the subfamily of Agrotheriinae) and *Ursavus brevirhinus* (Hofmann, 1887) (ancestor of the subfamily of Ursinae) (Crusafont and Kurtén, 1976; Baryshnikov, 2007a).

The short-faced bear *Agriotherium* (Ursidae, Carnivora) was one of the most successful and widespread taxon among the Ursidae family, with different species reported in Europe (Gervais, 1859; Viret, 1939; Stach, 1957; Morales, 1984; Argant, 1996; Montoya et al., 2001), Asia (Lydekker, 1878; Zdansky, 1924; Frick, 1926; Pilgrim, 1932; Howell, 1987; Qiu et al., 1991; Ogino et al., 2011), Africa (Hendey, 1980) and North America (Dalquest, 1986; Miller and Carranza-Castañeda, 1996; Samuels et al., 2009) from the Late Miocene to the beginning of Pleistocene. Today, the presence of this giant terrestrial carnivore in Europe was reported only in few sites as Venta del Moro and Alcoy-Mina (Late Miocene, Spain), Sables de Montpellier and Vialette (Late Pliocene, France) and Węże (Pliocene, Poland) with few craniodental remains and in Collepardo (Pliocene, Italy) (Bellucci et al., 2018.).

Dispite the systematic position *Agriotherium* is still debated, this genus is classified in Ursideae by most researchers, as the genus *Indarctos* with whom shared similar geographic distribution during the Late Miocene.

According to Matheus, (1995; 2003) and Sorkin, (2006), *Agriotherium* was not an active predator, though its diet includes a large amount of animal material, which probably was obtained by scavenging, especially on large vertebrate carcasses (Baryshnikov, 2007a). The rest of its diet included plant material composed mostly of coarse foliage obtained by unselective grazing (Mattson, 1998). Croitor and Brugal, (2010) expressed some doubts that *Agriotherium* could be an effective specialized scavenger since its premolars were quite small and weak, apparently not suitable for hard bone material crushing. Other authors (Kurtén, 1966; Oldfield et al., 2012) support the hypothesis that short-faced bears were omnivorous, capable of active predation on relatively large terrestrial pray and able to consume vertebrate carcasses and plant material.

The extinction of this genus in Europe was synchronous with Azzaroli's Elephant-*Equus* event ca. 2.5 Ma (Argant, 1996).

The other genus of the sub-family Agrotheriinae is *Indarctos*. Petter and Thomas, (1986) mention two species in Europe and Asia: *Indarctos atticus* (Weithofer, 1888) e *Indarctos arctoides* (Deperet, 1895). The former is divided into 3 subspecies and its range expands mainly in Asia and south-eastern Europe (Thenius, 1956). The sub-species *I. atticus atticus* (Dames 1883) is present in the deposits of Hungary (Baltavar), of Greece (Pikermi, Samos, even if Nagel and Koufos, (2009) described in their work, new material named *I. atticus*, without any subspecific name), of Turkey (Küçkücekmecc) and of Iran (Maragheh); the subspecies *I. atticus largelii* (Zdansky, 1924) is common in the deposits of the Shansi district (China) and, at the end, the subspecies *I. atticus punjabiensis* (Lydekker, 1884) described only from the Himalayan mountain range, in Siwaliks. Despite these studies, *Indarctos atticus* subspecies represent probably only different geographical records without distinct and statistically verifiable morphological differences, for this reason maybe have to be reconsidered the subspecific name, as made by Nagel and Koufos (2009).

Also the species *Indarctos arctoides* is distribuited mainly in Central Europe with two subspecies described: *I. arctoides vireti* (Villalta & Crusafont, 1943) found only in the deposit of Vallés-Pénédès, Spain (Casanovas-Vilar et al., 2016) and *I. arctoides arctoides* (Deperet, 1895) in Western Alemannia (Germany) and Pfaffstätten (Austria).

Numerous fossils remain (almost 1960) attributed to the species *I. arctoides* (without any subspecies reference) came from the Batallones-3 site (Late Miocene) in the fossiliferous locality of Cerro de los Batallones (Madrid, Spain). The material from this site seems to represent the most complete finding of the species if not of the whole genus (Abella et al., 2013).

Genus *Indarctos* is also recorded in Central Asia, in the Kalmakpay deposit, Kazakhstan (Late Turolian-Late Miocene) (Sotnikova et al., 1997).

The evolution of the other bears lineage (the Ursinae subfamily), from *Ursavus brevinius*, is quite well documented in Europe during the last 5 million (Thenius, 1959; Crusafont and Kurtén, 1976).

Ficcarelli reports as the first species belonging to the genus *Ursus*, *U. ruscinensis* found, as its name succeeds, in the Ruscinian deposits.

The type-specimen came from the locality of Perpignan (France) and described for the first time from (Deperet, 1890).

Ficcarelli, (1979) in his work suggests that *Ursus ruscinensis* represent an archaic from of the genus, which will give origin to *Ursus minimus* (Devèze & Bouillet, 1827) during the Early Villafranchian in Europe and then to *U. etruscus* during the Middle-Late Villafranchian in the Eurasian territory.

This assumption is justified by the author because some dental characters of *U. minimus* seem to be more evolved compared to some findings of *Ursus etruscus* (Cuvier, 1823) (Fig 2 A - B).

Nevertheless, he points out that many doubts about this evolutionary vision of the genus *Ursus* still remain, specially for the missing fossil material during the Late Pliocene (Early Villafranchian) and he does not completely reject a more linear view of the evolution of the bear like *U. ruscinensis - U. minimus - U. etruscus* (Fig 2 C – D).

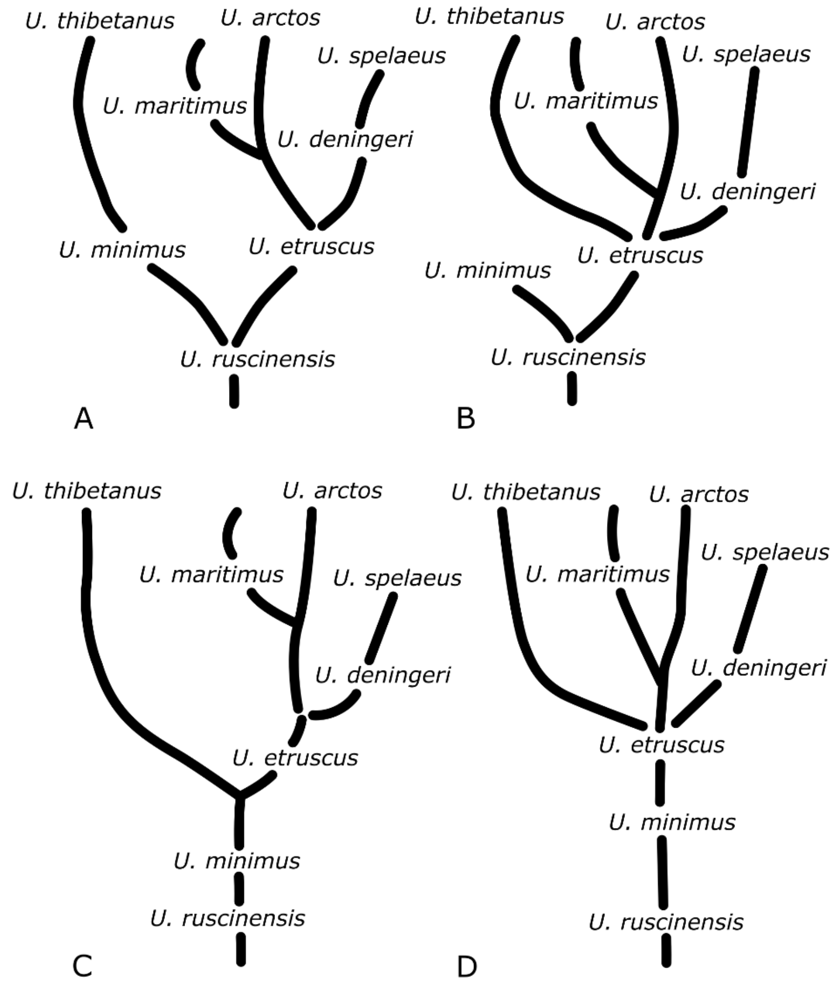


Figure 2: ***Different evolution models of genus Ursus.*** *Modified from Ficarelli 1979*

However, many authors consider *U. minimus* as a direct descendant of *Ursavus brevinius,* assuming *U. ruscinensis* as a synonymous of *U. minimus*.

U. minimus was a small animal, with arboreal adaptations and archaic characters from which, during the whole Pleistocene, will develop all the current evolutionary lineage: the American and Asiatic forms (*U. americanus* and *U. thibetanus*), Asian forms (*Helarctos malayanus* Raffles, 1825) and arctoid and speloid forms in Europe and Asia (McLellan and Reiner, 1994).

The typical skull of this species has a rather elongated profile with the neurocranium more developed than the muzzle. The mandible is short and massive with the ramus that forms an angle of almost 90° with the body. The dentition is complete and shows all the premolars, even if the teeth are often small with a relatively large occlusal surface (Mazza and Rustioni, 1994; Quiles, 2003). Remains of *U. minimus* are described both in Europe than in Asia during the all Pliocene (from MN14 to MN16).

The italian most significative remains come from the Early Villafranchian deposits of Triversa, Gaville Arondelli, and Ponzano (Baryshnikov and Zakharov, 2013).

As for many of the Pleistocene bears, the taxonomic attribution of the findings related to this species also appears to be controversial and with different filetic opinions on single specimen.

Many authors describe the findings of this minute form with various species of the genus *Ursus* depending mostly on the continental position and the age of the deposits: *Ursus boeckhi* Schlosser, 1899; (Early Pliocene, Europe), *U. minimus s.str.* (Late Pliocene, Europe), *Ursus (Protarctos) yinanensis* Lì, 1993 (Late Pliocene, China) and *Ursus abstrusus* Bjork, 1970 (Early Pliocene, North America) (Lì, 1993; Tedford and Harington, 2003; Wagner, 2010).

Baryshnikov, (2007b) suggests instead that these should be used as subspecies for the species *U. minimus* to indicate its strong intraspecific variability. The problem instead is simplified according to Morlo and Kundrát, (2001) for which all the bear finds of this period in Europe should be assigned to the species *U. minimus*.

The difficulty of a certain taxonomic name is derived also from the great similarity of characters of *U. minimus* with respect to *Ursus thibetanus* (Asian black bear) especially with regard to dental morphology. This similarity has often led to the determination of bear Pliocene material to *U. ex. gr. Minimus-thibetanus* (Sotnikova, 2008; Wagner, 2010).

A crucial step in the evolution the genus *Ursus* is undoubtedly the Etruscan bear (*Ursus etruscus*). Remains of this species are found in abundance in both Europe and Asia, from the Late Pliocene to Early Pleistocene, sign of an excellent adaptability. *Ursus etruscus* is a pivotal species because is widely accepted as the common ancestor for both the brown bear (*Ursus arctos*) and the cave bears (*Ursus deningeri* and *U.* ex gr. *spelaeus*) (Kurtén, 1976; Argant, 2001; Rabeder et al., 2010). On the contrary (Mazza and Rustioni, 1994) regard the asiatic black bear group (*Ursus minimus-thibetanus*) as ancestral to the other bear groups replacing *U. etruscus* at the end of Early Pleistocene, suggesting that the latter is only distributed in lower latitudinal region and represent an extinct lineage of the evolution genus *Ursus* (Pacher, 2007).

Despite the phylogenetic position, this animal was characterized by a medium-large size with an elongated snout and the presence of all the anterior premolars (P1-P3), all features linked to a more carnivorous diet, rich in fish (Medin et al., 2017).

The skull has a lateral profile with a slight convexity interrupted at the level of the nasal and a rather slender sagittal crest.

Remains of this species have been found in the sites of Olivola (the most ancient, during the Upper VIllafranchian), Monte Argentario, Pietrafitta, Pirro and Coste San Giacomo in Italy (La Rosa et al., 1992; Petrucci and Sardella, 2009; Bellucci et al., 2012); Mygdonia Basin, Tsiotra Vryssi in Greece (Koufos et al., 2017); Trlica Fauna in Montenegro (Vislobokova and Agadjanian, 2015); North Sea I and Tegelen in Netherland (Post et al., 2001), Ahl al Oughlam in Morocco; Punta Lucero, Orce, La Puebla de Valverde in Spain (Kurtén and Pairó, 1977); Saint Vallier, Sénèze in France (Viret, 1954; Argant, 2004); Kuruksay in Tadjikistan (Sotnikova, 1989) Nihewan Basin in China (Qiu and Qiu, 1995).

If the specific attributes of the material coming from Colle Curti in Italy and Venta Micena in Spain are considered valid, the species seems to survive until the passage Villafranchian- Early-Galerian when it will give away to the two evolutive lineage of the genus *Ursus* that characterized all the Middle Pleistocene and expecially the Late Pleistocene, the arctoid lineage (*U. arctos* and their subspecies) and the speloid one (*U. deningeri*, *U.* ex gr. *spelaeus* and their subspecies) (Baryshnikov, 2008).

As will be further explored in the next chapter, during the Early Pleistocene and the early phases of the Middle Pleistocene, the two lineages show often unclear diagnostic characters, making difficult to clearly assign to a sure taxonomical position of the oldest material.

What is clear, however, is that the genus *Ursus* begins to change; the size increases, reaching impressive dimensions and shows more and more peculiar adaptations (especially in dentition) related to an omnivorous diet until to become totally herbivorous with *U.* ex gr. *spelaeus* (Terlato et al., 2018).

The oldest remains of *U. deningeri* have been in Spain from the Cal Guardiola deposit (Late Early Pleistocene, (Madurell-Malapeira et al., 2009) in Slovakia from Honce (Wagner and Sabol, 2007) dated to the Early/Late Biharian transition. The attributions of *Ursus rodei* (Musil, 2001), *Ursus dolinensis* (Garcia and Arsuaga, 2001) (see below) and *Ursus savini* (Andrews, 1922) remain uncertain. The latter has been described in the Middle Galerian deposits of England (type locality: Bacon Forest Bed) considered by some authors as ancestor of *U. deningeri* (McLellan and Reiner, 1994). Other paleontologists don't agree this vision and suggest that *U. savini* should be considered a synonymous of *U. deningeri* (Mazza and Rustioni, 1994; Grandal-d'Anglade and Vidal Romaní, 1997; Baryshnikov, G. and Boeskorov, G., 1998; Baryshnikov and Foronova, 2001; García and Arsuaga, 2001); on the other hand, according to Wagner, (2010), this form is only a local endemic race related to the deninger-speloid clade.

Remains of *U. deningeri* in late Early Pleistocene deposits are quite rare (Wagner, 2010). Material has been described from Germany in Dorn-Dürkheim 3 (Franzen, 1999), Würzburg-Schalksberg (Mäuser, 1987) and Georgia in Akhalkalaki (Baryshnikov, 2007a).

This species was characterized by a medium-large size with a characteristic swelling on the frontal portion of the skull without a real step (like in *U.* ex gr. *spelaeus)*. The skeleton was robust and rather massive.

At the beginning of the Middle Pleistocene (Late Biharian) the findings are more common and have a fairly homogeneous distribution especially in the central-eastern portion of the European territory.

Localities with *U. deningeri* from this period include among others, deposits from Czech Republic (cave C718, Koněprusy caves, Chlum I and IV) (Wagner, 2004; 2005); Poland (Kozi Grzbiet); (Wiszniowska, 1989) and Hungary (Kövesvárad) (Jánossy, 1963).

In Italy, findings of *U. deningeri* come from the Slivia (Friuli Venezia Giulia) (Ambrosetti et al., 1979), Monte Peglia (Umbria) (Freudenthal et al., 1976), Viatelle (Veneto) (Bartolomei et al., 1977) and Isernia La Pineta (Basilicata) (Peretto et al., 2015).

During all the Middle Pleistocene (Early Toringian, Late Galerian and Aurelian) fossil remains of *U. deningeri* are described in most of the Western and Central Europe deposits. The key material of this species come from: Hunsheim, Deutsch-Altenburg (Austria); Erpfingen 4, Mauer (Germany), La Romieu, Château (France), Cueva Mayor (Spain); Tarkő (Hungary); Westbury (Great Britain) and Petralona (Greece) (Wagner, 2010).

During the late Middle Plestocene *U. deningeri* expires, replaced by its descendant *U.* ex gr. *spelaeus* in a rather gradual way to make difficult to differentiate the first forms of the former from the ancestral forms of the latter (Sardella et al., 2006).

The real cave bears, *U.* ex gr. *spelaeus* (so called for the huge remains founds in cave, "spēlēum" means cave in latin), lives in Europe until the end of the Late Pleistocene, sharing the European territory with both the brown bear and the hominids (*Homo sapiens* and *Homo neandertalensis*).

U. ex gr. *spelaeus* shows very specific characteristics that suggest an herbivorous adaptation, justify by the body size increasing and the presence of large molars, with a wide and complex occlusal surface (Torres, 1984; Capasso Barbato et al., 1992).

I don't want to dwell too much on this species in this chapter because there are so many literature and studies concerning all the biological and taxonomical aspects of *Ursus ex gr. spelaeus.* I will mention some of these papers later, in some specific case during the following chapter.

The last species that I need to introduce is the principal topic of my work: the brown bear.

I tried to go as much as deeper in the question related to its evolution, distribution and the samples that are described under this specific name or that can be synonymized under the species *U. arctos*.

As already mentioned, the origin of *Ursus arctos* and its spread in Europe, is still a controversial topic and there are many doubts on the taxonomic position on fossil material specially during the Galerian.

From Middle Pleistocene, specimens with undoubtful arctoid characters, have been found over the years in the localities of BiSnik (Marciszak et al., 2011), Pinilla de Valle (Alferez et al., 1985), Hunas (Hilpert, 2002), and in Taubach, in Ehringsdorfand and Vence (Argant, 1996) during the Last Interglacial (Pacher, 2007). However, in agreement with (Pacher, 2007; Rabeder et al., 2010), are recognized forms very close to *U. arctos* already in the Early Pleistocene in the Deutsch-Altenburg deposit. The presence of early Pleistocene brown bear is also supported also by paleontological data (Kurtén, 1977; Rabeder et al., 2010) and molecular data (Loreille et al., 2001; Bon et al., 2008), that sets the split between speloid and arctoid lineage at 1.2 – 17 million years ago. Although other author suggests an earlier divergent time at 2.8 million years ago (Krause et al., 2008).

The presence of bear material with characters very close to the arctoid lineage during the Early Pleistocene is also evidenced by the findings from Untermasfeld described by Musil, (2001) and named as a new species *U. rodei*. According to Olive, (2006) and Rabeder and Withalm, (2006) *U. rodei* is however a young form of *U. arctos*, while for Argant, (2010) and Baryshnikov, (2007a) this represents one of the oldest fossil materials related to *U. deningeri*.

Another key finding of the Early Pleistocene concerns the material of Atapuerca - Trinchera Dolina 4 (TD4) described by García and Arsuaga, (2001) and Valdiosera et al., (2007) under the name of *Ursus dolinensis*. The material is composed by a jaw, two fragments of maxilla, some unguals and phalanges, which shows some some typical speloid features but also other the typical characters of *U. arctos*, suggesting “that it represents an early arctoid bear". Finding of this species also come from the Arda River (Castell'Arquato, Piacenza, Northern Italy) (Bona and Sala, 2016).

During the early Middle Pleistocene another noteworthy form is described by Soergel, (1926) under the name *Ursus suessenbornensis* from Süßenborn, Germany; for a long time, this material has been recognize as the first forms of cave bear and often considered as a subspecies of *U. deningeri* (Soergel, 1926; Kurtén, 1969; Baryshnikov, 2007a). Mazza and Rustioni, (1994) first and Rabeder et al., (2010) later, agree that the findings of Süßenborn should be attributed to *U. arctos*, even if the latter recognizes in the deposit also the material of *U. deningeri*.

In the Middle Pleistocene (Middle Galerian) the findings are still scarce; brown bear material can be recognized in the deposits of La Romieu, France (Prat and Thibault, 1976; Torres Pérez-Hidalgo, 1992); Vergranne, France (Chagneau and Prat, 1983); Arago, France (Moigne et al., 2006); Chateau, Br. 4, France (Moigne et al., 2009); Hundsheim, Austria (Withalm, 2001); Cueva Mayor, Spain (Rabeder et al., 2010). In Italy the brown bear appears for the first time during the Late Galerian at Fontana Ranuccio (Azzaroli et al., 1988) and is recorded during the Early Aurelian in Bucine, Acquedolci and Contrada Camillà (Mazza, 1997; Marra, 2003) even if the morphological and chronological data are still uncertainties.

During the Late Pleistocene the presence of *Ursus arctos* is much better documented even if, compared with *Ursus ex gr. spelaeus*, are very few (Museum and Univesity deposits are literally full whit fossil remains of cave bear). It is spread throughout Europe (see chapter 4) and up to North Africa (Erdbrink, 1953).

Pacher, (2007) in its exhaustive review of the evolutionary history of brown bear highlights how, during the Late Pleistocene, this form is often assigned to the names of *Ursus prearctos* (Boule, 1919)*, U. arctos* or *Ursus priscus* (Goldfuss, 1818) and synonyms.

Freudenberg, (1914) studing the specimen from Taubach, grouped all the bears from the Last Interglacial as *U. priscus*, but, on the basis of size differences, recognized some distinct forms, which he called *U. arctos* var. *priscus.*

Boule, (1919) was the first that separates the smaller and stratigraphical older specimens as *U. prearctos*, considering it as ancestor of both modern brown bears and the large *U. priscus*, considerning the last one an extinct lineage of the genus. This vision was reintroduced also by Torres Pérez-Hidalgo, (1992).

Rode, (1935) emphasized the identity of *U. priscus* with *U. arctos* and classified the fossil remains from Taubach as *U. taubachensis,* while Thenius, (1956) grouped all the Late Pleistocene brown bear as *U. arctos priscus*, following the the vision of Boule, considerning them it as an extinct lineage of the arctoid clade. Kurtén, (1957)considered the large Late Pleistocene bears as a distinct subspecies *U. arctos priscus* and was the first that highlighted the dwarfing trend started at the end of the Last Cold Stage that lead to modern European brown bear.

Another important trend concerning the brown bear characters has been presented by Musil, (1964), which emphasized some clear differences in the dentition of modern European brown bears, and the brown bears of the loess area, which he classified as *U. arctos priscus*. (Pacher, 2007).

Other sample of brown bear from Late Pleistocene can be found in Zoolithen Cave and Weimar-Ehringsdorf in Germany (Goldfuss, 1823; Pacher, 2007; Rabeder et al., 2010), Grays Thurrock in England (Rabeder et al., 2010), Maspino, Ingarano, Monte Cucco and Monteverde in Italy (Koby, 1944; Capasso Barbato et al., 1990; Petronio and Sardella, 1998b), Grotte de Malarnaud in France Vyvieranie Cave and Važec Cave in Slovakia (Sabol, 2001), Murygino in Russia (Baryshnikov and Boeskorov, 2004), Winden in Austria (Thenius, 1956).

Marciszak et al., (2015), in his excellent work, compared the cranial morphology of Late Pleistocene brown bears, subdividing them in three chronosubspecies. The oldest, *U. arctos kamiensis* (*Ursus kamiensis* sensu Vereshchagin, 1959) characterized by great robustness and large size (Baryshnikov and Boeskorov, 2004) and distributed only in Asia; *U. arctos priscus*, a subspecies also characterized by large dimensions without reaching those of *U. arctos kamiensis*, mainly dispersed in almost all Europe during the Late-Middle Pleistocene and Late Pleistocene.

The last brown bears from post-glacial and Holocene, are all described with the subspecies *U. arctos arctos* Linnaeus, 1758 (Sabol, 2001).

U. arctos arctos differ from *U. arctos priscus* due to the smaller size of the body, lack of some premolars (P1-P3) and a leaner structure of the skeleton (Sabol, 2001).

Despite the morphological differences between those subspecies, the names *Ursus arctos priscus* or *Ursus priscus* are to be considered nomina delenda according to Patcher (2007). I agree with this opinion but, in my statistical analysis I kept the term *"U. arctos priscus"*, to compare their features with the sample of the other fossil brown bears.

It is worth pointing out that many studies have however confirmed that *U. arctos*, given its extreme mobility (Baryshnikov, 2007a), evolved and differentiated through the Late Pleistocene without major genetic barriers; therefore, the taxonomic morphological features described by some authors, do not characterize significant phylogenetic units (Marciszak et al., 2015).

Concerning the phylogenetic tree presented by various authors on the genus *Ursus* and the family Ursidae, I can not express myself with a personal hypothesis because I did not have the opportunity to personally observe much of the *Ursus* material. So, I decided to resume the various evolutionary hypotheses proposed over time by different authors (mentioned above) at different scales of detail (Fig 3 and 4).

However, I agree with Ficarelli 1979 and Erdbrink 1945 when they note that the evolution of the genus *Ursus* is one of the most controversial and less clear regarding the great mammals of the Quaternary and to date it is impossible to discard one or the other evolutionary hypothesis with certainty.

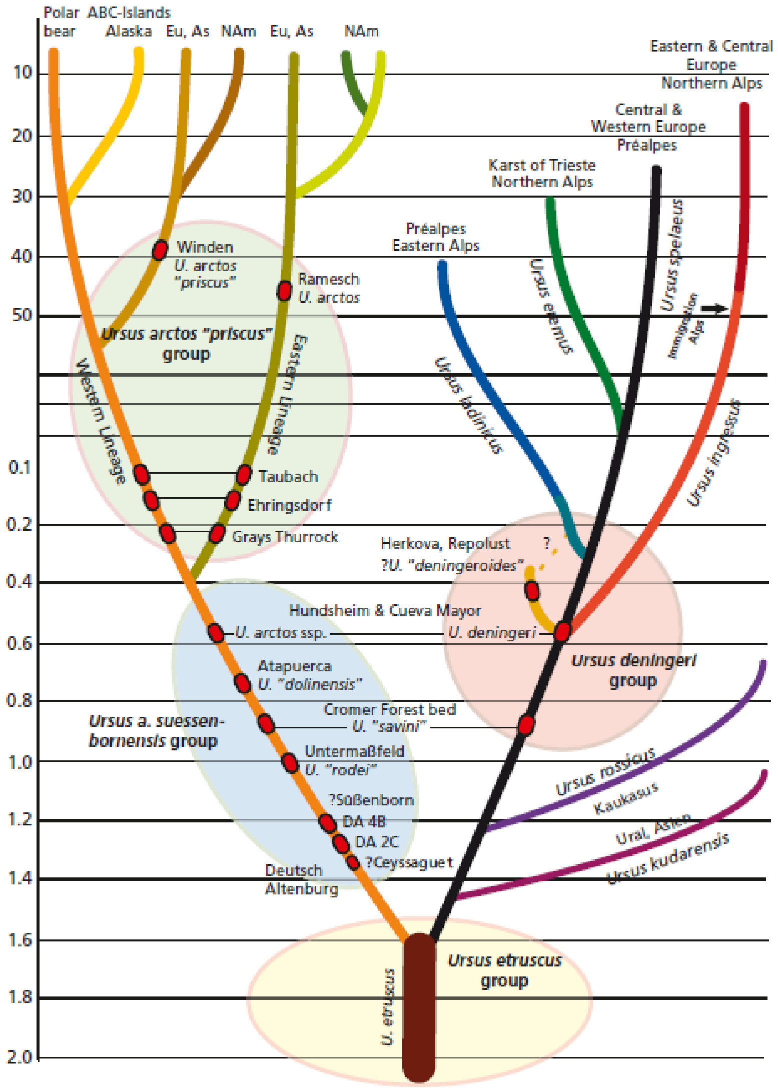


Figure 3: ***Evolution scheme proposed by Rabeder 2010***

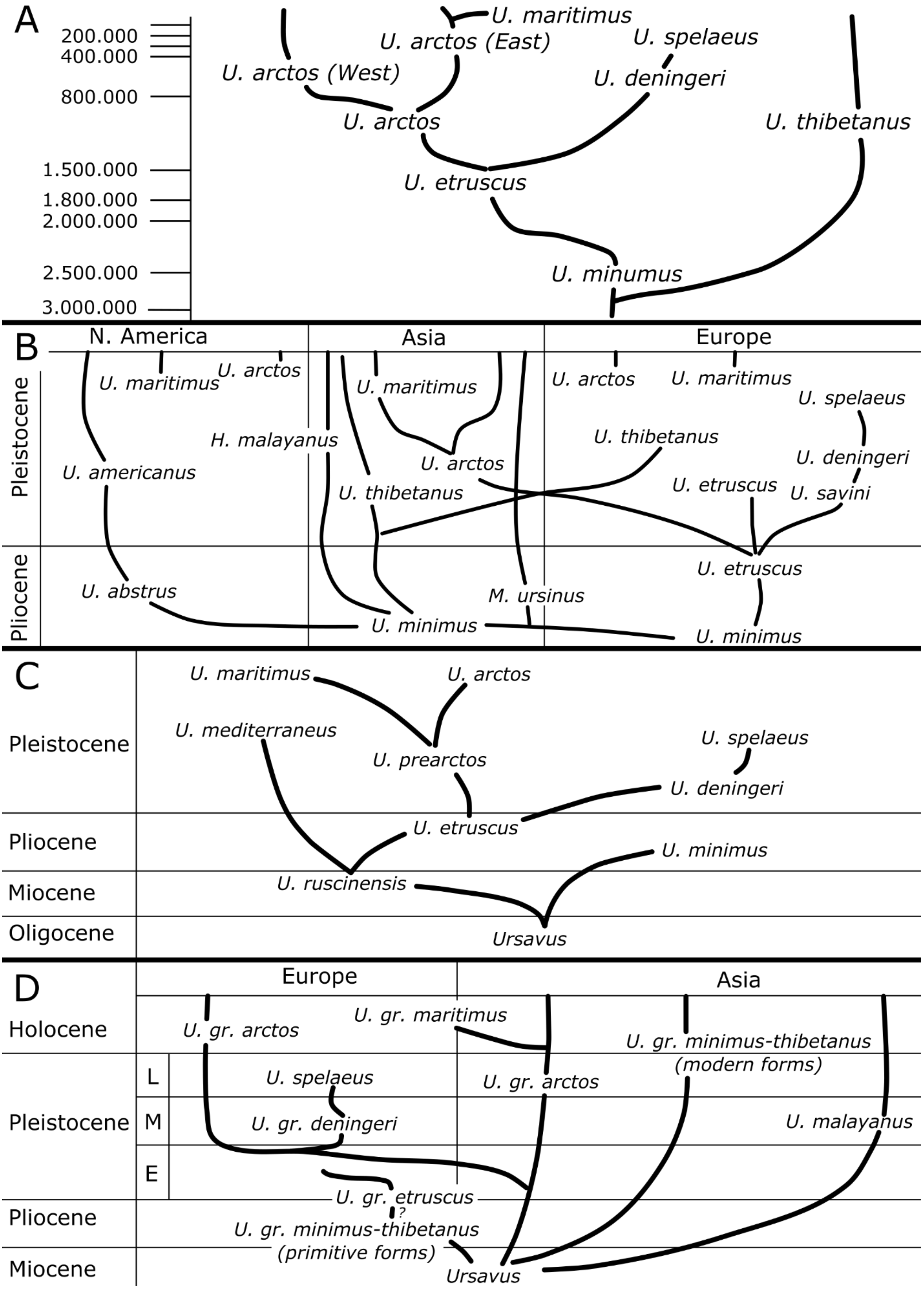


Figure 4: ***Different possible evolution scheme of the genus Ursus.*** *A) Modified from Argan 2001. B) Modified from MC Lellan 1994. C) Modified from Torres 1992. D) Modified from Mazza & Rustioni 1994.*

3 Recognise the brown bear in the fossil record

Large mammals display a variety of adaptations to survive and thrive in different biomes which are reflected in their anatomy, representing a source of important information about the ecological settings of their environment and evolutionary history.

The cranial and teeth morphology is one of the first anatomical districts which undergoes major changes during climate alteration, and mostly reflects new adaptations to different ecosystems and ecological condition. For example, the cranial bones often preserve traces of muscle attachments in the form of ridges, crests, and other superficial features that are the basis for the reconstruction of the musculature structure in fossil animals. Skull bones also preserve clues about the neural organs (the brain and nervous system) and the sensory organs (frontal sinuses).

As part of the food ingestion system, cranium, mandibles and teeth are also very informative regarding their diet and the way they procure the food for themselves (Anyonge and Baker 2006; Arribas and Palmqvist 1999; Biknevicius et al. 1996; Binder and Van Valkenburgh 2000; Christiansen and Adolfssen 2005; Van Heteren et al., 2016).

Furthermore, most of the taxa descriptions are based on cranial bones due to their highly conservative characters which contain, in some cases, many information about sex, age and diseases.

Moreover, the analysis of the material from a specified geographic area and distributed over time, can give a lot of information about the morphological changes in a specific taxon and describe with precision its evolutionary history.

Many authors, in the past, tried to clarify the distinctive morphological features of the various species of the genus *Ursus* during the Plestiocene and between the extant populations indicating one or another character to distinguish a species from another (Erdbrink, 1953; Thenius, 1959; Torres, 1984; Capasso Barbato et al., 1990; Mazza and Rustioni, 1994; Rabeder, 1999; Quiles, 2003; Wagner and Čermák, 2012).

In this chapter I will present a summary, dividing the various anatomical regions of the skull and analyzing them individually both from a morphological and functional point of view (when possible), indicating some peculiar characteristics of the various species of the genus *Ursus*: *Ursus deningeri* von Reichenau 1906, *U.* ex gr. *spelaeus* Rosenmüller 1794, *Ursus arctos* Linnaeus 1758.

First, I have to underline once again the great morphological variability that characterizes this animal both in the living (*Ursus arctos*, Linnaeus 1758) and in the fossil. In fact, since the 1800s for the various modern populations, were assigned more than 200 specific names to indicate an extreme differentiation of habits, dimensions and body characters (Erdbrink, 1953).

This variability is accentuated in the fossil record, which is represented by specimens showing an extreme morphological differentiation (considering that only skeletal features can be observed) that has reached over time an incredibly high number of *nomen dubium* or cases of synonymy.

Moreover, as already mentioned above, the "speleoid" characters are extremely recognizable in a vast and rich sample of large individuals. However, this safety is not guaranteed for individuals of small size and non-advanced ontogenetic stage. This variability often led to erroneous taxonomic attributions of some findings, based on non-apomorphic characters. In fact, some authors, considering more or less diagnostic some characters, that led the attribution of different names to the same specimen.

This problem reaches its peak in the Middle Pleistocene and in the early Late Pleistocene, where the less derived forms of the line of the cave bears tend to be confused with those of the arctoid lineage, presenting very similar dental and cranial characters therefore difficult to distinguish (Rabeder, 1999).

Another discriminating factor concerns the scarcity of brown bear specimens compared to those referable to the cave bear yet argumented by Fabiani 1927.

Infact, in the European cave, is very easy to find a huge quantity of specimens attributable to *Ursus* ex gr. *spelaeus*, associated with few material (often isolated and fragmented) described as *Ursus arctos* (due the different taphonomic condition of the cave and the open-air land). Last but not least, the issue of the taxonomic attribution is related to the huge variability between the different ontogenetic stage of the specimens and the sexual dimorphism showed in the genus (Torres 1988). For those reasons it is crucial to not underestimate those characters during the statistical analysis and the taxonomical attribution.

3.1 The cranium

The vertebrate cranium serves the all-important function of protecting the brain, and the principal sensorial organ located in the head (sight, olfaction and hearing).

Obviously, protection is not the only function of the cranium, but it plays an extremely important role in the modes and type of feeding. In fact, many of the cranial morphologies that are reunited among vertebrates reflect strictly the ecological habits of the various species (especially in the type of dentition and the presence or absence of deep furrows for the allocation of powerful muscles). Moreover, the morphology of the skull presents the main characters of sexual dimorphism.

The bear skull has generally an antero-posteriorly elongated shape (Fig. 5). The zygomatic arch is generally very large, to allocate the mighty masseter muscles to provide a great bite strength, associated also with a specialization in consuming fibrous vegetable (Mattson, 1998; Christiansen, 2008).

Throught the time, various Ursids species show different shape of the frontal bone but generally, the supraorbital ridge is pronounced with a good development of the orbital apophysis.

Bears are characterized by an excellent hearing and an extremely developed sense of smell; this is reflected in a very large nasal cavity with very complex turbinates.

The sagittal crest is often quite developed, specially in relation to other large carnivorous vertebrates; generally, in large individuals it can be quite impressive, even if it is variable and depends very much on the ontogenetic stage of the individual and the allometry (Torres, 1984).

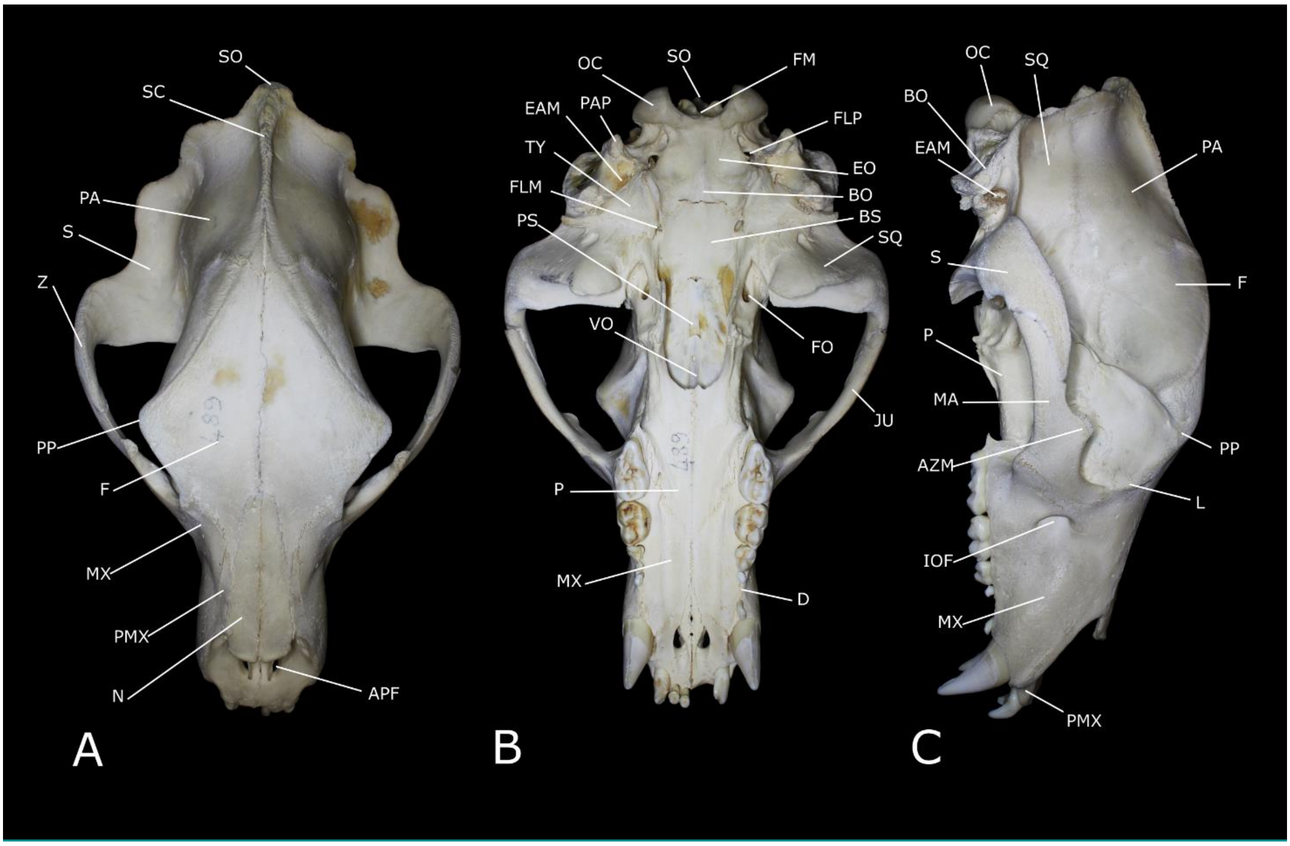


Figure 5: ***Cranium of a Marsican bear (U. arctos marsicanus). A) Dorsal view – APF)*** *Anterior palatine foramen.* ***F)*** *Frontal bone.* ***MX)*** *Maxilla.* ***N)*** *Nasal.* ***PA)*** *Parietal.* ***PMX)*** *Pre-maxilla.* ***PP)*** *Post-orbital Process.* ***S)*** *Squamosal.* ***SC)*** *Saggittal Crest.* ***SO)*** *Supra-occipital crest.* ***Z)*** *Zygomati arch.* ***B) Ventral view – BO)*** *Basi-occipital.* ***BS)*** *Basi-sphenoid.* ***D)*** *Diastema.* ***EAM)*** *External auditory meatus.* ***EO)*** *Ex-occipital.* ***FLM)*** *Foramen lacerum medium.* ***FLP)*** *Foramen Ipoglossus* ***FM)*** *Foramen magnum.* ***FO)*** *Foramen ovale.* ***J)*** *Jugal.* ***MX)*** *Maxilla.* ***OC)*** *Occipital condyle.* ***P)*** *Palatine.* ***PAP)*** *Par-occipital process.* ***PS)*** *Presphenoid.* ***SO)*** *Supra-occipital crest* ***SQ)*** *Squamosal.* ***TY)*** *Tympanic.* ***VO)*** *Vomer.* ***C) Lateral view - AZM)*** *Zygomatic apophysis of the malar.* ***BO)*** *Basi-occipital.* ***EAM)*** *External Auditory meatus.* ***F)*** *Frontal.* ***IOF)*** *Infra-orbital foramen.* ***L)*** *Lacrimal.* ***MA)*** *Malar.* ***MX)*** *Maxilla.* ***OC)*** *Occipital condyle.* ***P)*** *Palatine.* ***PA)*** *Parietal.* ***PMX)*** *Pre-maxilla.* ***PP)*** *Post-orbital Process.* ***S-SQ)*** *Squamosal.*

The cave bear (*U.* ex gr. *spelaeus*) shows a huge body size, with robust and globular bone structures and, to lighten the weight of the skull, it presents a very good pneumatization of the internal portions (Torres, 1984). In lateral view, in the skull of *U.* ex gr. *spelaeus* the neurocranial portion shows a convexity shape and, in the frontal portion, is moderately or abruptly interrupted in the orbital region with a relative thickening of the orbital apophysis (Quiles, 2003) (Fig 6).

This character is also generally found in *U. deningeri* but less pronounced. In *U. arctos*, on the other hand, the frontal portion presents a more sub-rectilinear profile up to almost convex structures and generally never shows the strong stop, except in some specific cases, as in the males of the subspecies *U. arctos marsicanus* and in larger grizzly individuals (*Ursus arctos horribilis* Ord 1815).

In a facial view, the upper contour of the frontal in *U. arctos* is regularly convex, while in the speloid lineage, it presents a strong thickening of the tuber frontalis and of the orbital apophyses. The internal contours of the orbits are sub-linear in the cave bears, while more oblique in the arctoid forms.

The zygomatic arches are clearly more developed in the proximal portion of the skull in *U. deningeri* and *U.* ex gr. *seplaeus* rather than in *U. arctos*. In *Ursus arctos marsicanus* this character is accentuated and the whole shape of the skull turns out to be much more like a square than a quadrangular, with the very wide zygomatic arches in relation to a reduced total length (Colangelo et al., 2012).

In an upper view, the facial portion of the cranium is shorter than the neurocranial portion in *U. arctos*; while in *U.* ex gr. *spelaeus* it is relatively more elongated; the muzzle of the latter presents an enlargement to the level of the canines and a thickening in the lower portion of the nasal cavities (Quiles, 2003).
The narrowing of the neurocranium is more pronounced in *U.* ex gr. *spelaeus* than in *U. arctos* with the width of the front greater than the maximum width of the neurocranium. in brown bear fossils, the difference is balanced and generally reversed.

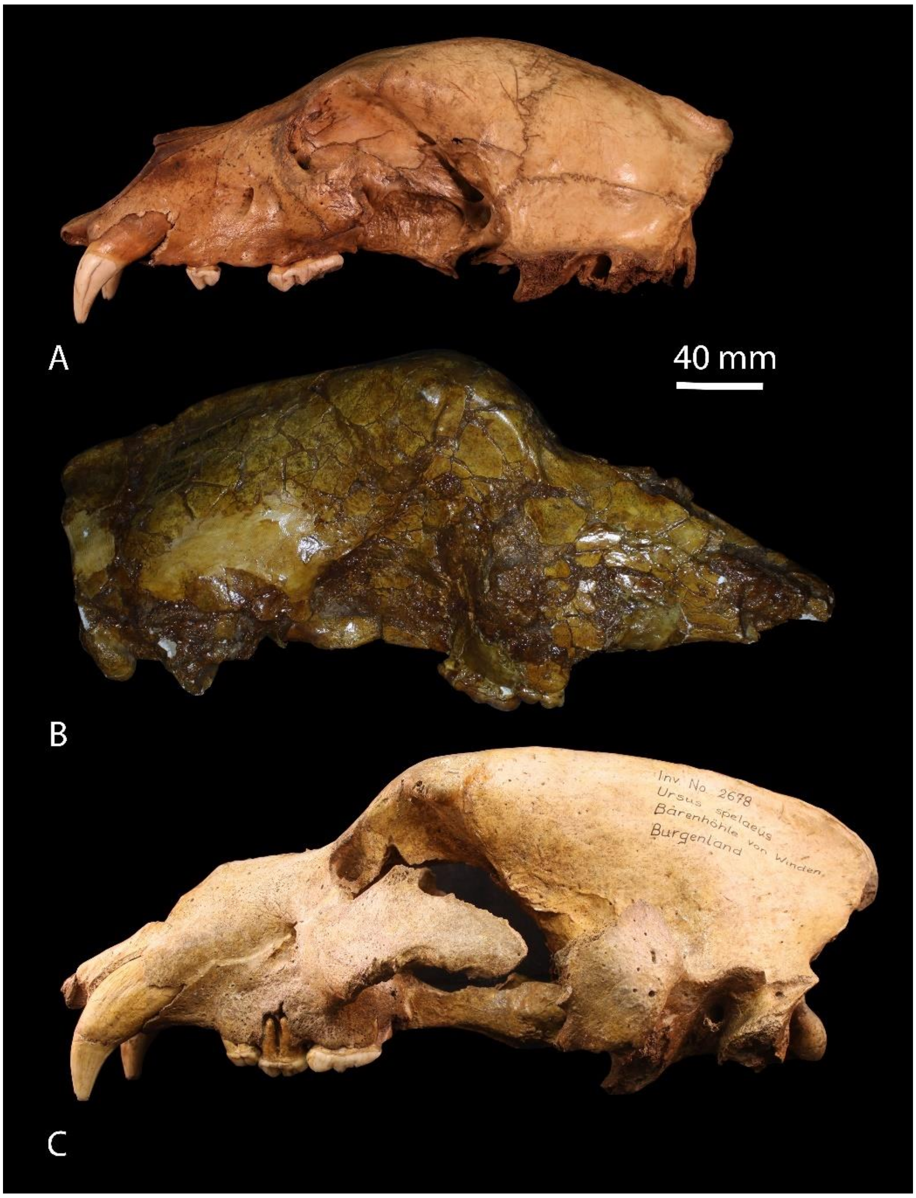


Figure 6*: *Comparison between cranium of various Pleistocene bears. A) Ursus arctos, *2842/1 - Laufenberg, Late Pleistocene.* ***B) Ursus deningeri,*** *Hund II - Hundsheim, Middle Pleistocene.* ***C) Ursus spelaeus,*** *2678 – Winden, Late Pleistocene.*

3.2 The mandible

As the location of initial food ingestion and mechanical processing, the morphology of the lower jaw (together with the upper jaw) is pivotal to understand the feeding habits of mammalss. For carnivorans, the cranium and the mandible are also involved in the all-important function of killing prey, and it is this function that often defines the overall mandible shape.
The lower jaw is made up of two hemimandibles which are formed by two main branches, the vercal branch (or ramus) which is inserted in the zygomatic area with the coronoid process, and the horizontal branch (or

body) where the teeth are housed (Fig. 7). In the distal portion of the hemimandibles there is both the angular process and the articular condyle, a cylindrical bone obliquely oriented, that allows the articulation with the skull.

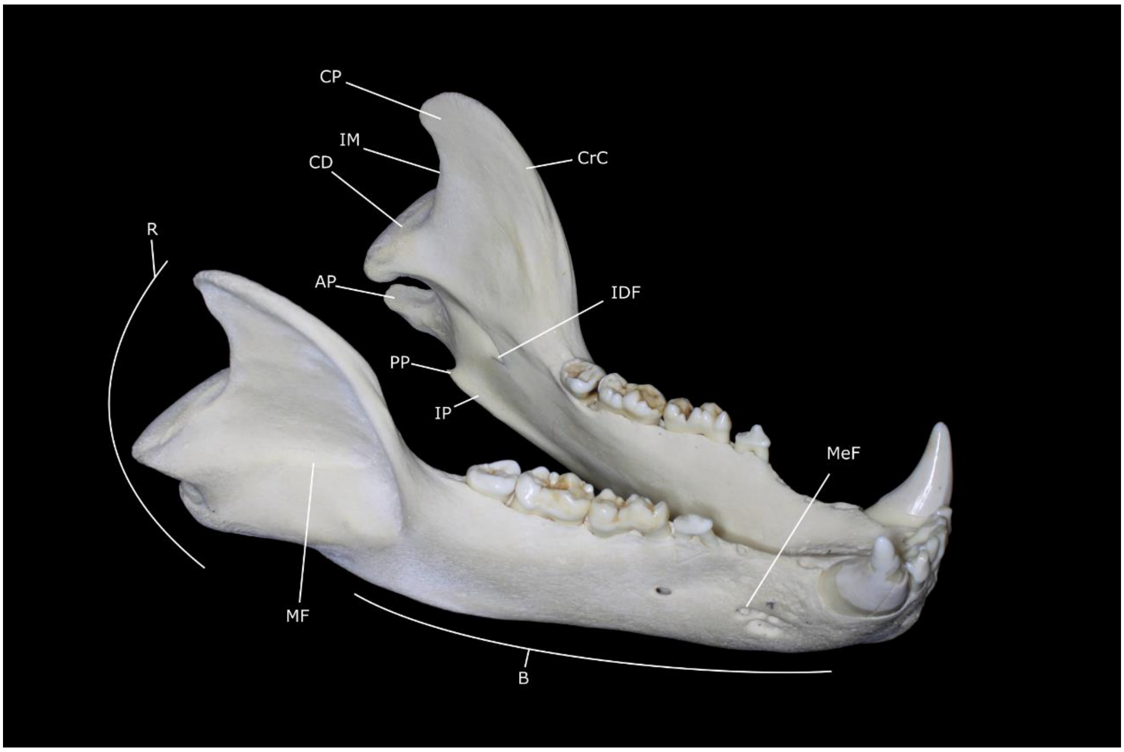


Figure 7: ***Mandible of a marsican bear (U. arctos marsicanus). AP)*** *Angolar process.* ***B)*** *Body of the mandible.* ***CC)*** *Condiloid crest.* ***CD)*** *Condyle.* ***CP)*** *Coronoid process.* ***CrC)*** *Coronoid crests.* ***IDF)*** *Inferior dental foramen.* ***IM)*** *Incisura mandibulae.* ***IP)*** *Insertion of the Pterygoid muscle.* ***MeF)*** *Mental foramen.* ***MF)*** *Messeteric fossae.* ***PP)*** *Pterigoid process.* ***R)*** *Ramus of the mandible.*

In *U.* ex gr. *spelaeus* the horizontal branch of the hemimandible is extremely massive and shows a slightly convex ventral profile in its medial portion. In the arctoid line, this is straighter and generally more gracile (Torres, 1988; Argant, 1991; Mazza and Rustioni, 1994; Quiles, 2003) (Fig. 8). In *Ursus arctos marsicanus* this character is similar to *U. arctos* fossil even if the gracility of the horizontal body in the portion under the canine region is more pronounced and is characterized by a relatively long diastema.

Together with the coronoid process, the horizontal branch forms an angle that changes in the various species, it is straighter in *U.* ex gr. *spelaeus,* while it is gradually widening in the arctoid forms.

In *U.* ex gr. *spelaeus,* the condyle and the angular process are located higher than the base of the mandible. This portion, on the other hand, is clearly lowered in *U. arctos* and slightly less in *U. deningeri* (Prat and Thibault, 1976; Ballesio, 1983).

In a posterior view, the distal condyle is massive in *U.* ex gr. *spelaeus* with the lingual portion much more robust of the buccal one, showing a sub-trianglular shape. This form is very similar in *U. deningeri* although with a less accentuated development. In *U. arctos* the condyle is narrower and more pointed in the lingual portion, forming an almost perfect cylinder (Torres, 1984).

Still in posterior view the base of the posterior portion of the horizontal branch is much more curved in *U.* ex gr. *spelaeus* rather than in all the other species taken into consideration.

The pterygoid muscle surface is more extensive longitudinally in *U.* ex gr. *spelaeus* than in *U. deningeri*. This surface appears instead reduced in *U. arctos* and is characterized by a small distal prominence on the lower edge of the branch.

This character is linked to a different freedom of movement of the jaw showed by the various species and related to different eating habits. In fact, reduced pterygoid muscle and elongated condyle (*U. arctos*) characterize animals with less strictly vegetarian diet, as opposed to the cave bears which possess elongated pterygoid muscle and massive condyle.

Rabeder et al., (2010) underlines, however, how often many of these characters are mixed and lower jaws belonging to the speloid lineage may have arctoid morphologies, probably linked to size and allometric factors. For this reason, the ramus results to have a limited validity in the taxonomic attribution.

Figure 8: ***Comparison between mandible of various Pleistocene bears. A) Ursus arctos**, 14360 - Haraska, Nizke Tatry, Late Pleistocene. **B) Ursus deningeri**, Hund II - Hundsheim, Middle Pleistocene. **C) Ursus spelaeus,** P 3022 - Cava delle Fate, Late Pleistocene.*

3.3 The dentition

The concept of dental adaptation is very important. In 1956, Spanish vertebrate paleontologists Miguel Crusafont-Pairo and Jaime Truyols-Santonja (Crusafont and Truyols, 1985) published an insightful study of carnivoran functional morphology in which they categorized carnivorans into hypercarnivores and hypocarnivores based on their dental morphology. A *hypercarnivore* is an animal that has elongated the shearing blade of the carnassial teeth at the expense of the grinding part of the dentition (usually molars).

In contrast, a *hypocarnivore* is an animal that has shortened the shearing blade of the carnassial teeth and enlarged the grinding part of the dentition behind the carnassial. The bear is one of the best examples of a hypocarnivore diet, which in some cases will be transformed in a complete herbivores diet (such in the Giant Panda, *Ailuropuda melanoleica*, David 1869) in which the shearing part of the carnassial teeth is radically reduced, and the grinding parts of the molars are extremely broadened.

This feature is also reflected on fossil bears because the great ecological difference between the speloid and the arctoid lineage is mainly recorded on the dental structure.

In fact, first in *U. deningeri* before and then in *U.* ex gr. *spelaeus* the general morphology of the molar and premolar teeth becomes more complex, with the presence of numerous accessory cusps, tubercles and developed girdles. Even about the general dimensions of the teeth, gradual changes over time are appreciated. From relatively small structures (as can be found in *U. etruscus*) during the Early Pleistocene, we found very large and wide teeth as in those of *U.* ex gr. *spelaeus* during the late Late Pleistocene, with a rather developed occlusal surface.

The passage from a simpler morphology to a more complex one has been widely studied by Prof. Rabeder (Rabeder, 1999) on findings attributed to *U.* ex gr. *spelaeus* and coming from various deposits of different ages. This study showed that even within the variability of this species there are trends that describe a gradual change in time, especially in molariform teeth.

The dentition formula of the genus *Ursus* is generally the same. The most archaic form is represented by *U. minimus* and *U. etruscus*:

$\mathrm{I}\,\frac{1\,2\,3}{1\,2\,3}\,\mathrm{C}\,\frac{1}{1}\,\mathrm{PM}\,\frac{1\,2\,3\,4}{1\,2\,3\,4}\,\mathrm{M}\,\frac{1\,2}{1\,2\,3}$ *U. minimus*, *U. etruscus* dental formula

During the Middle and Late Pleistocene, with the introduction of even more omnivorous forms, the dental formula is changed, but still remains some variability, especially on the presence or absence of some upper and lower premolars (with the exception of the fourth premolar).

Generally, most of the *U.* ex gr. *spelaeus* show a loss of the first and the third premolars and often shows a dentition like:

$\mathrm{I}\,\frac{1\,2\,3}{1\,2\,3}\,\mathrm{C}\,\frac{1}{1}\,\mathrm{PM}\,\frac{4}{4}\,\mathrm{M}\,\frac{1\,2}{1\,2\,3}$ *U.* ex gr. *spelaeus* dentition formula

About *U. arctos*, the presence of the first and third premolars is often documented and, as previously described, distinguishes the subspecies "*U. arctos priscus*" (with the only presence of the first premolar) from the Holocenic *U. arctos arctos*, even if this character is not always confirmed. A question mark, however, is represented by *U. deningeri*, in fact their dentition is quite variable while has been found and described some specimens with presence of the first premolar. For this reason, for taxonomical purposes, the dental formula is only useful to a limited degree (Rabeder et al., 2010).

$\mathrm{I}\,\frac{1\,2\,3}{1\,2\,3}\,\mathrm{C}\,\frac{1}{1}\,\mathrm{PM}\,\frac{1\,(3)\,4}{1\,(3)\,4}\,\mathrm{M}\,\frac{1\,2}{1\,2\,3}$ *U. arctos*, and *U. deningeri* dentition formula

3.3.1 Incisors and canines

The incisors in general are small, with a flat cutting edge placed in front of the jaw and of the mandible. On close examination, there is usually one main cusp on the incisors and two smaller cusps flanking either side (Fig. 9) showing different character between the bear species.

The canines are the fanglike teeth that deliver the killing bites, and carnivorans display their canines for maximum effect in a threatening posture. All bears have prominent canine with a slightly concave crown. It has an elliptical section developed anteroposterior with a convex profile in the lateral portion. The canine is the most powerful tooth and is located at the height of the suture between the the premaxillary and maxillary bones in the upper and lower jaw. In ursids, the size of canine teeth tends to be a very high dimorphic character (Torres, 1984).

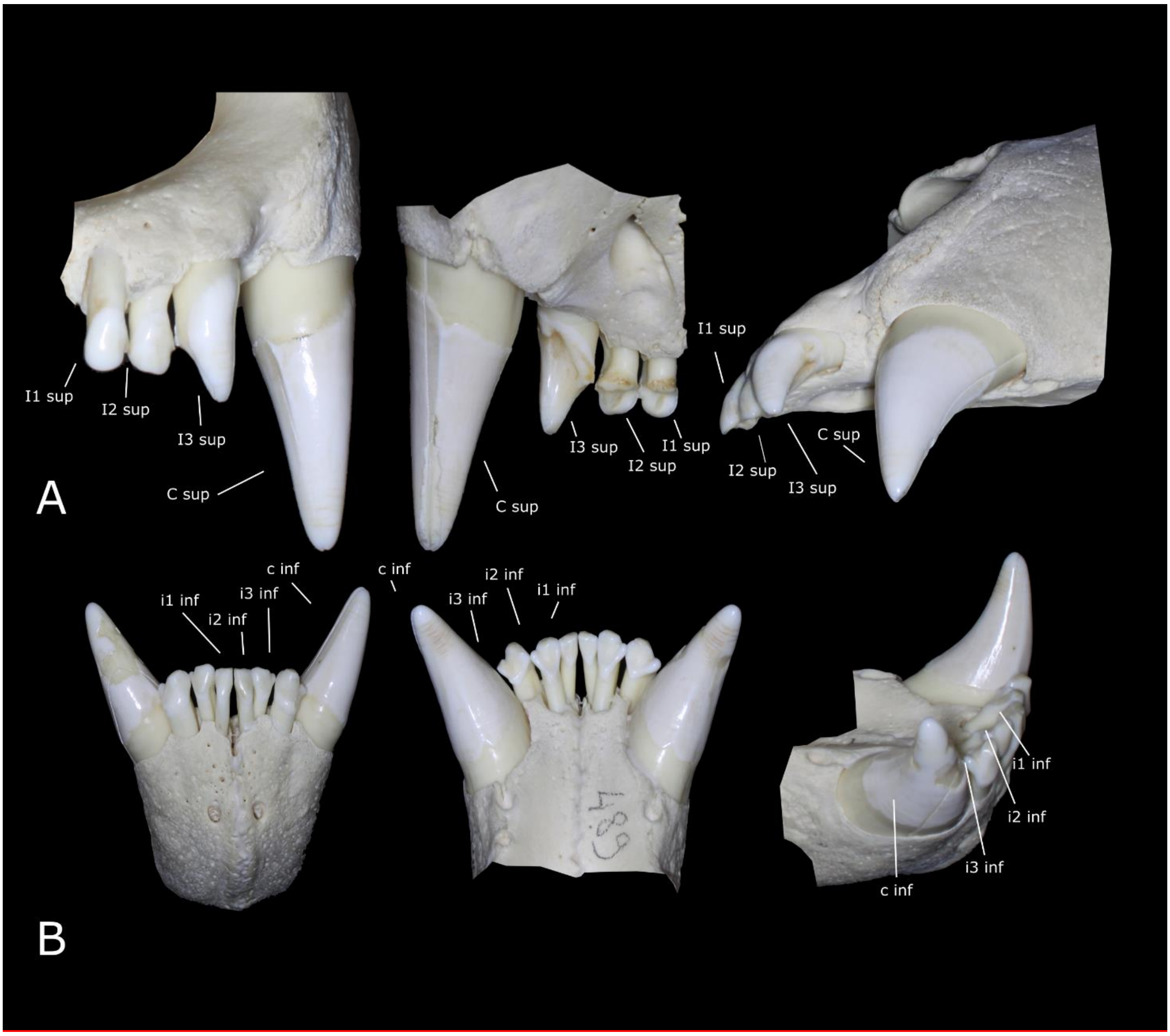


Figure 9: ***Focus of the Upper (A) and Lower (B) Incsisors and Caninse.*** *Frontal, dorsal and lateral view (Ursus arctos marsicanus).*

3.3.1.1 *First and second upper incisor*

The general morphology of the first and second upper incisors is extremely similar showing two lateral lobes marked by a superior furrow in the lingual portion of the tooth. This condition often makes it extremely difficult to distinguish between them (Torres, 1988; Rabeder, 1999). The greatest difference between the various species can be appreciated from the features of the lateral surface of the tooth, where the distal lobe is poorly developed in *U. deningeri* and *U.* ex gr. *spelaeus* and instead is much better marked in *U. arctos* (Capasso Barbato et al., 1990).

3.3.1.2 *Third upper incisor*

Unlike the other two upper incisors, the third one it is quite recognizable in the fossil record showing a different appearance, with a more arched shape with a noticeable groove in the lingual portion of the tooth. The differences between *U. arctos* and *U.* ex gr. *spelaeus* on the morphology of this tooth are quite evident (Argant, 1991). In arctoid forms there is generally a higher crown, sharper, less curved forward, with a narrower base. On the contrary, in the speloid forms the third upper incisor has a lower crown, more bulbous in the internal portion, generally is characterized by a bent forward of the upper part of the teeth to form almost a hook. Also, the base, in the cave bears, is generally wider (Capasso Barbato et al., 1990; Argant, 1991).

The occlusal surface in *U. arctos* has a rather deep groove that clearly defines the edges of the central and mesial lobe. On the contrary, in the cave bears, this furrow is much less pronounced, making the central and mesial lobe less defined (Torres, 1988; Capasso Barbato et al., 1990; Rabeder et al., 2010). The size also tends to grow in the evolution of the cave bear while it remains constant in *U. arctos*.

3.3.1.3 *First and second lower incisor*

The same difficulty in distinguishing the first two upper incisors is also found in the lower dentition. In fact, these are small-sized teeth with a slight groove which, in the mesial portion, form a small cusp. The latter is generally more developed in the lineage of the cave bear rather than in the arctoid forms (Torres, 1988).

3.3.1.4 *Third lower incisors*

The third lower incisor is much more robust than the other two. It presents a significant morphology with a groove that runs through the tooth from the distal to the mesial portion, defining a main and a lateral cusp that develops in height and outwards. In *U. arctos* the central cusp is often less developed than in the cave bears. Another distinctive feature is the size of the crown, generally larger and wider in *U.* ex gr. *spelaeus* than in *U. arctos*.

3.3.1.5 *The canines*

As in incisors it is often difficult to distinguish the various species from single canines as it is also very difficult to distinguish a superior canine from a lower canine (Prof. Rabeder, pers Comm.). Nevertheless, if the specimen is consisting of both the mandible and the skull it is possible to observe that the upper canine is always greater than the lower one and, from the aboral view, the upper canines are straighter whereas the lower ones are more S-shaped.

Both are characterized by a long root (about three times the size of the crown) that deeply creeps into the maxilla and mandible.

Generally, in the brown bears, the canine has a more gracile root than in cave bears, whose mesio-distal part is slightly rounded, while the crown is well developed with a rather pointed tip (Torres, 1988; Quiles, 2003). The swelling is more pronounced in *U. deningeri,* but the general morphology is however very similar to the arctoid. The greatest difference can be seen in *U.* ex gr. *spelaeus* where the root is extremely large, and the mesio-distal swelling reaches the highest dimensions (Torres, 1988; Argant, 1996; Quiles, 2003).

3.3.2 Premolars

The premolars are the teeth between the canines and the molars. In the genus *Ursus*, as described in the dentition section, the presence or absence of the first three premolars both upper and lower is a character with high variability between the various species (disappearing in *U.* ex gr. *spelaeus)*. The morphology of these premolars is extremely simplified, with a unique and rounded cusp, often reduced in size. The only noteworthy premolars are the lower fourth and the upper fourth (the carnassial) that shows very different shape in the various species, especially in relation to the diet, reaching a maximum size and complexity in the Late Pleistocene cave bears (Fig. 10).

As for all molariforms, also in the premolars there may be some accessory cusps (which take the name of the main cusp associated with the "style" ending, Eg. Parastyle), and furrows that delimit the oblique portions of the main ridges.

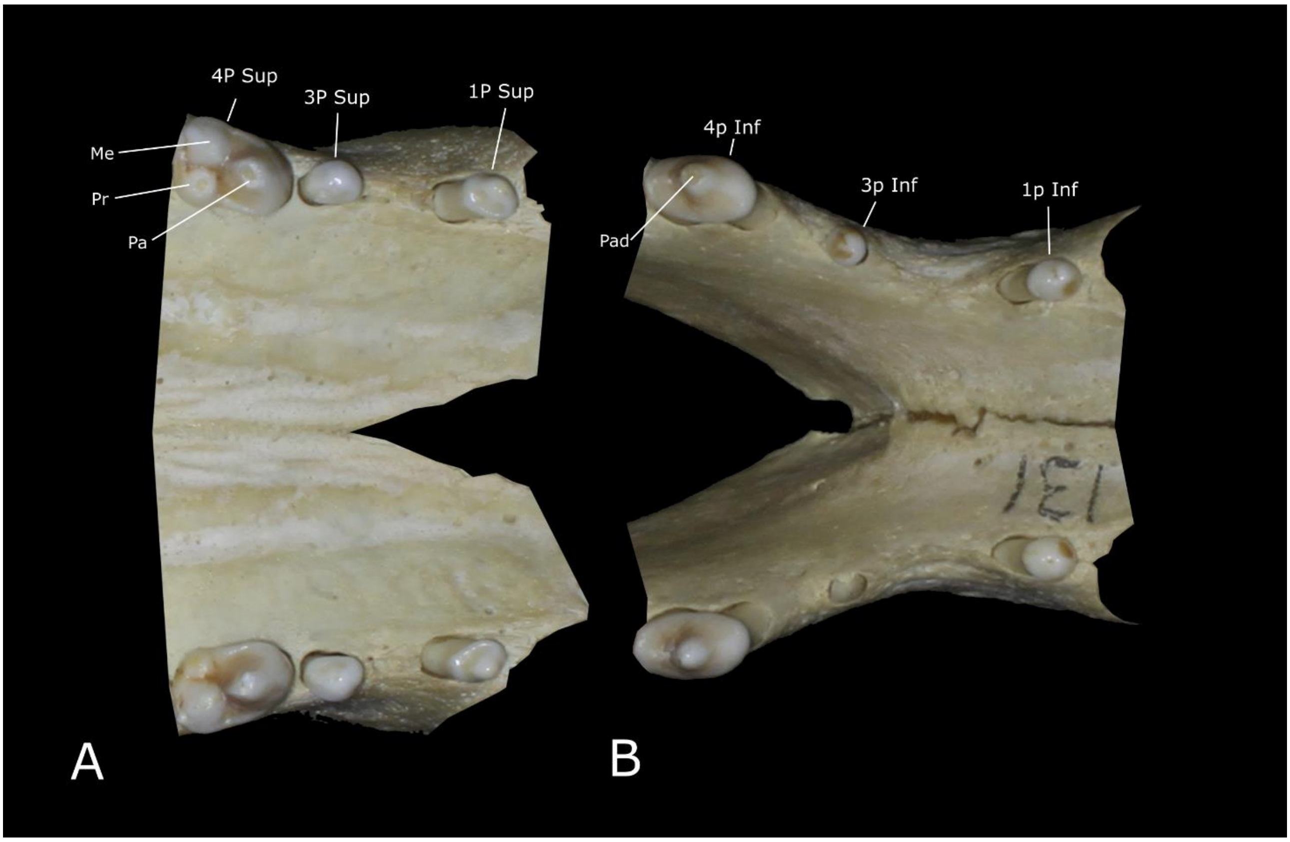


Figure 10: ***Focus on the Upper (A) and Lower (B) premolars (Ursus arctos marsicanus)***. ***Pr)*** *Protocone.* ***Pa)*** *Paracone.* ***Me)*** *Metacone.* ***Pad)*** *Paraconid.*

3.3.2.1 *Fourth upper premolar*

The fourth upper premolar is a tooth formed by three main cusps, the Paracone and the Metacone in the labial portion of the maxilla, and the Protocone in the lingual portion. The shape remains to an isosceles triangle with the Paracone as the highest cusp and the Protocone in a more or less advanced position in the anterior portion of the tooth. In the labial portion there is often a cingulum that develops mainly under the crest that unites Paracone and Metacone (Fig. 10).

In *U.* ex gr. *spelaeus* the ridge that joins the two main cusps becomes increasingly less marked by decreasing of the profile of the cupids. In the Early Pleistocene in species such as *U. etruscus* the tooth is simple, with three distinct cusps. This morphology is also often found in *U. arctos*, even if the Protocone is more advanced by moving in the central position in the tooth (Argant, 1991). In *U. deningeri* the morphology does not differ much from the arctoid ones, the Protocone becomes more and more prominent and begin to appear various tubercles on the central portion of the occlusal surface. In *U.* ex gr. *spelaeus* the Protocone increases in volume and begins to split, also there is the maximum complexity of the occlusal surface with the presence of tubercles and accessory cusps (Torres, 1984; Mazza and Rustioni, 1994; Quiles, 2003) (Fig. 11).

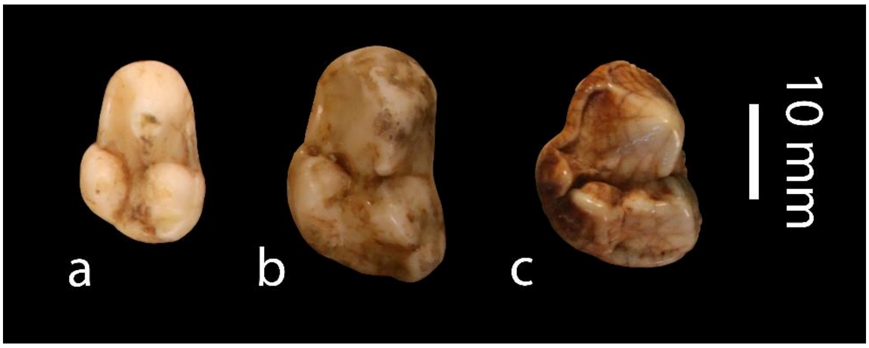


Figure 11*: Comparison of the left M1: **a) U. arctos,** 2847-2 – Laufenberghohle, Late Pleistocene **b) U. deningeri,** 1889-5-406 - Hundsheim, Middle Pleistocene **c) U. spelaeus,** Brojon - Comparison collection, Late Pleistocene.*

3.3.2.2 *Fourth lower premolar*

The fourth lower premolar is very interesting tooth, that shows a good variability between the different species and establish a high value evolutive trend (Torres, 1984). This tooth is extremely simple, basically composed by only one cups, the protoconid, with an elliptic shape (Fig. 10).

As already pointed out by Reynolds, (1906), the fourth inferior premolar is a discriminating element for the species *Ursus arctos* and *U.* ex gr. *spelaeus* (Reynolds, 1906; Torres, 1984; Mazza and Rustioni, 1994; Meloro, 2007).

In fact, the tooth in *U. arctos* is narrow, with the Protoconid as the only main cusp and an anteroposterior development; on the contrary, in *U.* ex gr. *spelaeus* , this lower fourth premolar presents a more circular or even rectangular shape, with the presence of numerous accessory cusps, up to rise a shape that show a flat occlusal surface, such as a Talonid, made up of numerous tubercles.

Although it is extremely easy to distinguish the cave bear lineage from the arctoid ones during the Late Pleistocene due the increasing size and complexity of the occlusal surface morphology in cave bear, the characters of the fourth premolar in *U. deningeri* and *U. arctos* tend not to differentiate much during the Middle Pleistocene. In fact, the variability is extremely high in *U. deningeri* presenting both relatively circular teeth, with a wide Protoconid, the presence of accessory cusps, and also relatively narrow structures without the presence of any purely speloid character (Wagner and Sabol, 2007; Wagner and Čermák, 2012).

Figure 12: ***Comparison of the lower p4: a) U. arctos*** *(left), C.4 - Banskà Bystrica, Recent.* ***b) U. deningeri*** *(right), Hund II - Hundsheim, Middle Pleistocene**. c) U. spelaeus** (right), MJ-ZT U93 - Zapadne Tatry mts., Late Pleistocene.*

3.3.3 Molars

In the genus *Ursus*, the molars are formed by some main cusps and other smaller accessory ones, located in different position of the chewing surface (Fig 13). As the incisors, canines and premolars, the molars consist of two sets: the deciduous (or milk) molars and permanent molars.

However, it is easy to see that species generally adapted to a carnivorous diet, shows narrower and generally simpler molars, with well-differentiated cusps and not very complex occlusal morphologies unlike the omnivorous. The increasing in size, and the presence of cusps and accessory ridges are peculiar in the genus *Ursus* and, most accentuated in the cave bear lineage.

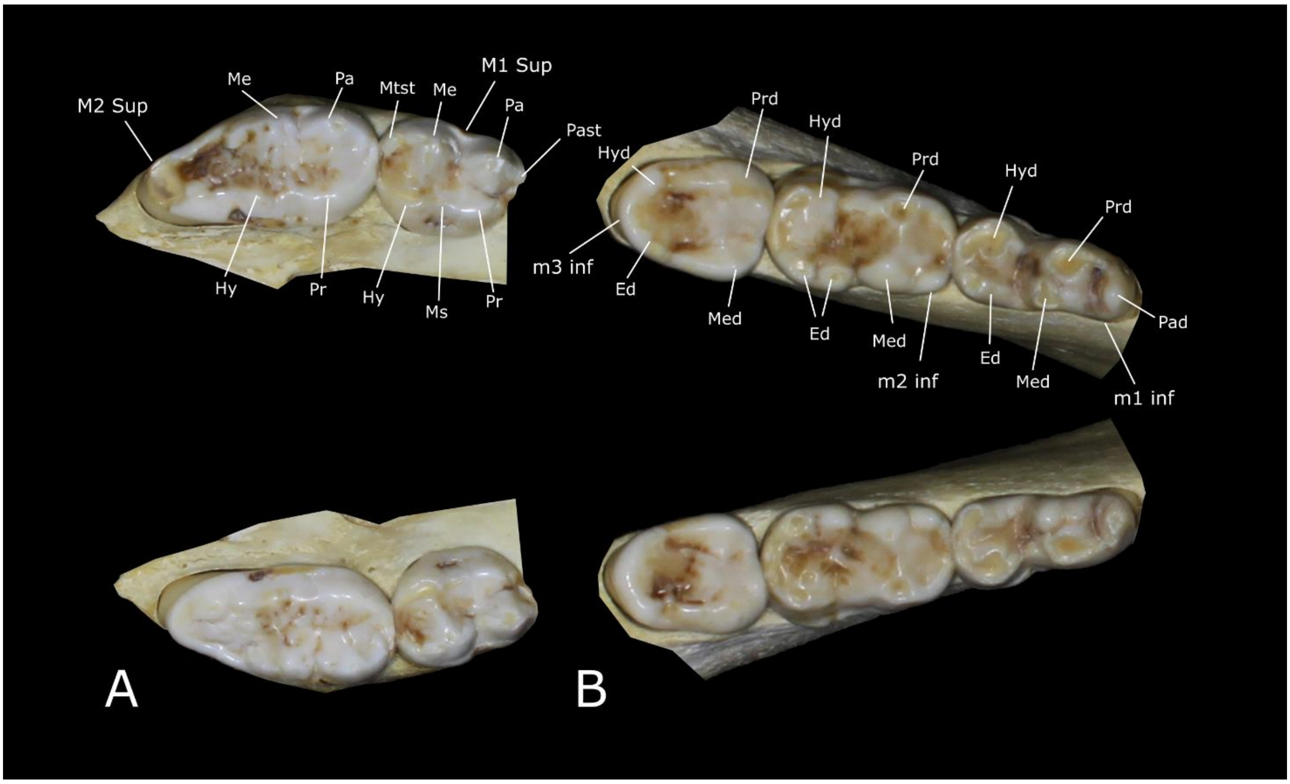


Figure 13: ***Focus on the Upper (A) and Lower (B) molars (Ursus arctos marsicanus): Pr)*** *Protocone.* ***Pa)*** *Paracone.* ***Me)*** *Metacone.* ***Ms)*** *Mesocone.* ***Hy)*** *Hypocone.* ***Past)*** *Parastyle.* ***Mtst)*** *Metastyle.* ***Pad)*** *Paraconid.* ***Prd)*** *Protoconid.* ***Med)*** *Mesoconid.* ***Ed)*** *Entoconid.* ***Hyd)*** *Hypoconid.*

3.3.3.1 *First upper molar*

The first upper molar is a rather characteristic tooth, from the upper view presents a trapezoidal contour, with a marked outer edge. The occlusal surface is formed by four main cusps (Paracone, Protocone, Metacone and Hypocone) divided by two transverse grooves that divide the tooth into four main portions. Often there is the presence of a less developed cusp (the Mesocone) between the Hypocone and the Protocone. Generally, the labial girdle is rather developed, while on the buccal side there may be the presence of accessory cusps in the posterior and anterior portion of the tooth associated with the Paracone and the Metacone.

Generally, the first upper molar in *U.* ex gr. *spelaeus* differs from *U. arctos* due to the less pointed cusps, a wider occlusal surface and the presence of the best developed styles, even if the latter are often found also in the arctoid forms and characterized by a larger Parastyle than the Metastyle (Quiles, 2003; Wagner and Čermák, 2012). Another feature that distinguishes the two forms of the Late Pleistocene is the crest that unifies Para and Hyopocone. In the cave bears, this ridge appears to be curved in the anterior portion of the tooth while, in the brown bear tends to have a more rectilinear course and parallel to the ridge that joins the Meta- and the Protocone (Ballesio, 1983; Auguste, 1995).

In *U.* ex gr. *spelaeus* the talon is wider and often characterized by a developed tubercled surface, as the basal cingulum, which appears more complex than in the brown bear (Capasso Barbato et al., 1990; Argant, 1991). The first upper molar in *U. deningeri*, shows some characters typical for speloid lineage like the talon developed with the presence of tubercles, the presence a of a Metastyle larger than Parastlyle (oppositely than in *U. arctos*) and the crowns somewhat more opened in Late Biharian *U. deningeri* than in recent *U. arctos*. On the contrary, the central constriction is relative width, a more typical character of the arctoid forms and opposite to the trend of the speloid lineage (Wagner and Čermák, 2012) (Fig. 14).

Figure 14: ***Comparison of the upper M1: a) U. arctos*** *(left), GrCa-U3 - Gran Carro, Holocene.* ***b) U. deningeri*** *(left), Hund 1889-5-406 - Hundsheim, Middle Pleistocene.* ***c) U. spelaeus*** *(left), Brojon - Comparison collection, Late Pleistocene.*

3.3.3.2 *First lower molar*

The first lower molar is the tooth that keeps most of all the carnivorous features. In fact, together with the upper fourth premolar constitutes the carnassials, the typical teeth of carnivors that has the function of cutting the meat. Morphologically it is an elongated tooth, with the frontal portion (trigonid) much narrower than the posteror portion (talonid), divided by a rather evident central narrowing. It has five main cusps: Paraconid, Protoconid, Metaconid, Hypoconid and Entoconid. During the evolution of the genus *Ursus*, adaptation to a more or less omnivorous and herbivorous diet had evident consequences in the morphology of the first lower molar, such as increased length, height of the crown and enlargement of the talonide. All these characters tend to increase the chewing surface, which predisposes to a diet rich in vegetables.

Rabeder, (1999) define various morphotypes of the Entoconid describing an archaic one (*U. etruscus* and *U. arctos*), one intermediate (*U. deningeri*), and a last strictly speloid in which the surface of these cusp increases the shredding potential of the tooth. In fact, the Entoconid in *U. arctos* is often divided into two unequal cusps (with the distal one more voluminous than the other) by a shallow groove (Ballesio, 1983).

In *U. deningeri* instead, the Entoconid increases in size and is divided into three parts, generating the same number of cusps more or less clearly identifiable in which the size decreases from posterior to anterior one (Koby, 1944). In *U.* ex gr. *spelaeus* this cusp has a bicuspidated morphology (in addition to the presence of accessory cusps) and the dimensions of the main cupids are often of the same size of the other (unlike in *U. arctos*) (Capasso Barbato et al., 1990).

In *U.* ex gr. *spelaeus* the occlusal surface is rather convex due to an increase in the size of the Metaconid while the indentation of the lingual border between Trigonid and Talonid is markedly more pronounced in *U. arctos* than in *U. spelaeus* (Altuna, 1973).

In the anterior portion of the tooth, the Paraconid is clearly more developed in *U.* ex gr. *spelaeus* than in *U. arctos*, in which it is often confused with the trigonide crests. The Talon is generally much wider in speloid forms (Mazza and Rustioni, 1994) and often is characterized by a strong tubercled surface. Also the lateral cingulum results more developed in the cave bears than in the brown bear (Capasso Barbato et al., 1990).

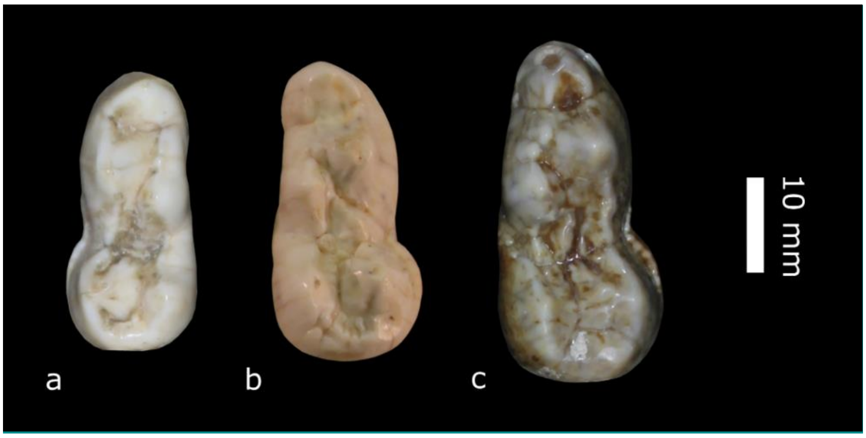


Figure 15: ***Comparison of the lower m1: a) U. arctos*** *(left), C.4 - Banskà Bystrica, Recent.* ***b) U. deningeri*** *(right), Hund 371 - Hundsheim, Middle Pleistocene.* ***c) U. spelaeus*** *(right), MJ-ZT U93 - Zapadne Tatry mts., Late Pleistocene.*

3.3.3.3 *Second upper molar*

The second upper molar is the tooth that shows the most robust morphology (if the canine is excluded) of all the dentition of the genus *Ursus* (Torres, 1984). It has a rather elongated shape and there is generally a slight torsion along the longitudinal axis which increase in the speloid forms (Capasso Barbato et al., 1990). The cusps often have very similar dimensions between them and are generally divided by more or less deep furrows. The talon is generally less large than the max width of the anterior portion of the tooth. As highlighted by Quiles, (2003) the morphology of the second upper molar is extremely variable between the various species and only general characters can be delineated for the various evolutionary lines.

In general, the structure of the tooth in *U. arctos* is rather derivate in comparison with the speloid lineage, with an upraised portion in the anterior part of the tooth, constituted principally by a pointed and not divided Paracone and Metacone. On the contrary, the talon is rather flattened with the sporadic presence of some tubercles. In *U. deningeri* the morphology of this tooth was defined by Argant, (1991) as a "shoe sole" with the main cusps wider and less pointed than in the arctoid lineage and a stronger tuberculated surface in the internal portion of the tooth. Instead, in *U.* ex gr. *spelaeus* a more "tennis racket" morphology is showed (Clot, 1980; Torres, 1984; Argant, 1991) with a reduction of the occlusal surface of the talon (the handle of the racket). Moreover, the chewing portion has a strong tubercolated surface with the presence of numerous granules and small furrows. Also, the distal portion of the tooth is morphologically different compared to the one typical of the arctoid lineage. It has a tripartite subdivision of the main cusps that are much sturdier and developed in width, giving the tooth a bunodont appearance.

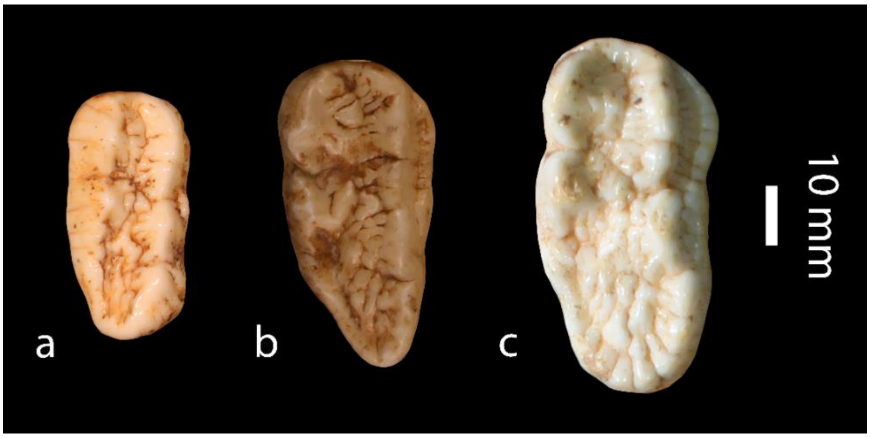


Figure 16: ***Comparison of the upper M2: a) U. arctos*** *(left), 717b - Ingarano, Late Pleistocene.* ***b) U. deningeri*** *(left), Hund 1889-5-406 - Hundsheim, Middle Pleistocene.* ***c) U. spelaeus*** *(left)***,** *Z 982 - Medvedia jaskyna, Late Pleistocene.*

3.3.3.4 *Second lower molar*

The second lower molar is the tooth which has a more hypocarnivorous morphology in comparison with the other carnivorans (i.e. dogs). It shows a rectangular shape, characterized by a more or less developed lateral narrowing. Also in this case, the tooth is divided into two portions, the anterior (Trigonid) and a posterior (Talonid) slightly narrowed by a constriction. On the surface are located the main cusps, that are generally four: Metaconid and Protoconid in the trigonid and the Hypoconid and the Entoconid in the Talonid; sometimes, the largest cusp of the cusplet ridge at the mesial crown margin, can be distinguished as a Paraconid. In the anterior portion of the tooth there is a characteristic crest that joins the two main anterior cusps and divides the trigonide into two slight depressions. Between these depressions the distal one is deeper than the internal one. This morphology gives the tooth a general bracing that goes back to the forward portion. The second lower molar It is the widest tooth of the lower dentition and often presents an undeveloped cingulum on the labial portion (Torres, 1984).

The comparison of the width of the trigonid with that one of the Talonid generally plays as a specific taxonomic distinction for this tooth (Fig. 17). According to Prat and Thibault (1976) and Argant (1991), the front portion is generally larger than the posterior one in *U. arctos* while it is equal or even lower in *U. deningeri*. From the direct observation of fossil and recent material I can affirm that this character is not confirmed, having often observed in *U. arctos* a slightly more developed Talonid of the Trigonid. On the contrary this trend is clear in the cave bear from Late Pleistocene where the proximal portion is wider than the distal one.

The ornament and the complexity of the occlusal surface can be quite clearly distinguishing in the two evolutionary lineages; the second lower molar in *U. arctos* doesn't show often a strong toberclulation of the occlusal surface, that is generally occupied by the lateral profile of the main cusps. *U. deningeri* has a rather high complex surface with the presence of accessory cusps but, this character, is extremely emphasized in *U.* ex gr. *spelaeus*, where the chewing surface often becomes very large with the presence of accessory cusps and "ridge".

The constriction of the tooth is more accentuated in *U.* ex gr. *spelaeus* which has an 8-shape, while *U. arctos* it seems much more a rectangle (Mazza and Rustioni 1994). Generally, we can discriminate also the species of the Middle Pleistocene by the Protoconid, which often is divided into two parts in *U. deningeri* while only one cusp is showed in *U. arctos*.

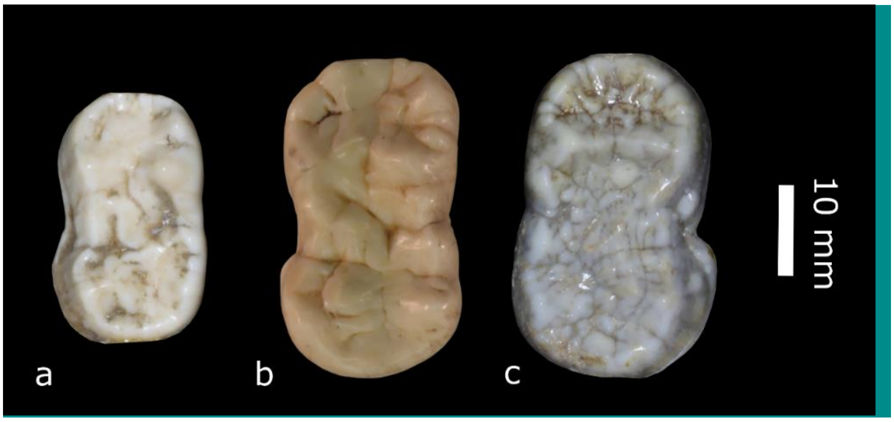


Figure 17: ***Comparison of the lower m2: a) U. arctos*** *(left), C.4 - Banskà Bystrica, Recent.* ***b) U. deningeri*** *(left), Hund 373 - Hundsheim, Middle Pleistocene.* ***c) U. spelaeus*** *(left), MJ-ZT U93 Zapadne Tatry mts., Late Pleistocene.*

3.3.3.5 *Third lower molar*

The third lower molar is the shortest tooth of the entire series of molariforms, it shows often a morphology from circular to subtriangular, with the presence of numerous tubercles and a rather flat occlusal surface.

The main cusps are often very low and are very easily confused between the ridges and the furrows of the chewing surface. It is the last tooth to emerge in the permanent dentition and, in younger individuals can be often found not erupted.

Generally, due to the poor development of the cusps, the complexity of the occlusal surface and the size of the tooth are the most diagnostic features for the lower third molar (Fig 18). In fact, between *U. etruscus* up to *U.* ex gr. *spelaeus* there is an increasing of the tooth size with an extremely variable crown morphology within each species. Characteristic is undoubtedly the presence of numerous ridges and furrows in the tooth of *U.* ex gr. *spelaeus* that is opposed to a much simpler tooth that can be observed in recent and specimens of *U. arctos.*

Figure 18: ***Comparison of the lower m3: a) U. arctos*** *(left), C.4 - Banskà Bystrica, Recent.* ***b) U. deningeri*** *(left), Hund 381 - Hundsheim, Middle Pleistocene.* ***c) U. spelaeus*** *(left), MJ-ZT U93 Zapadne Tatry mts., Late Pleistocene.*

4 Methods

For the good achievement of the goals proposed in my research, it was necessary first of all to census and catalog most of the the material of brown bear from the Italian peninsula and Europe.

Due the impossibility of observing all the material in person, many of the data collected comes from the literature, which consists of a large number of works, both general (only faunal lists) and more specific, with precise descriptions and taxonomic analysis of the findings.

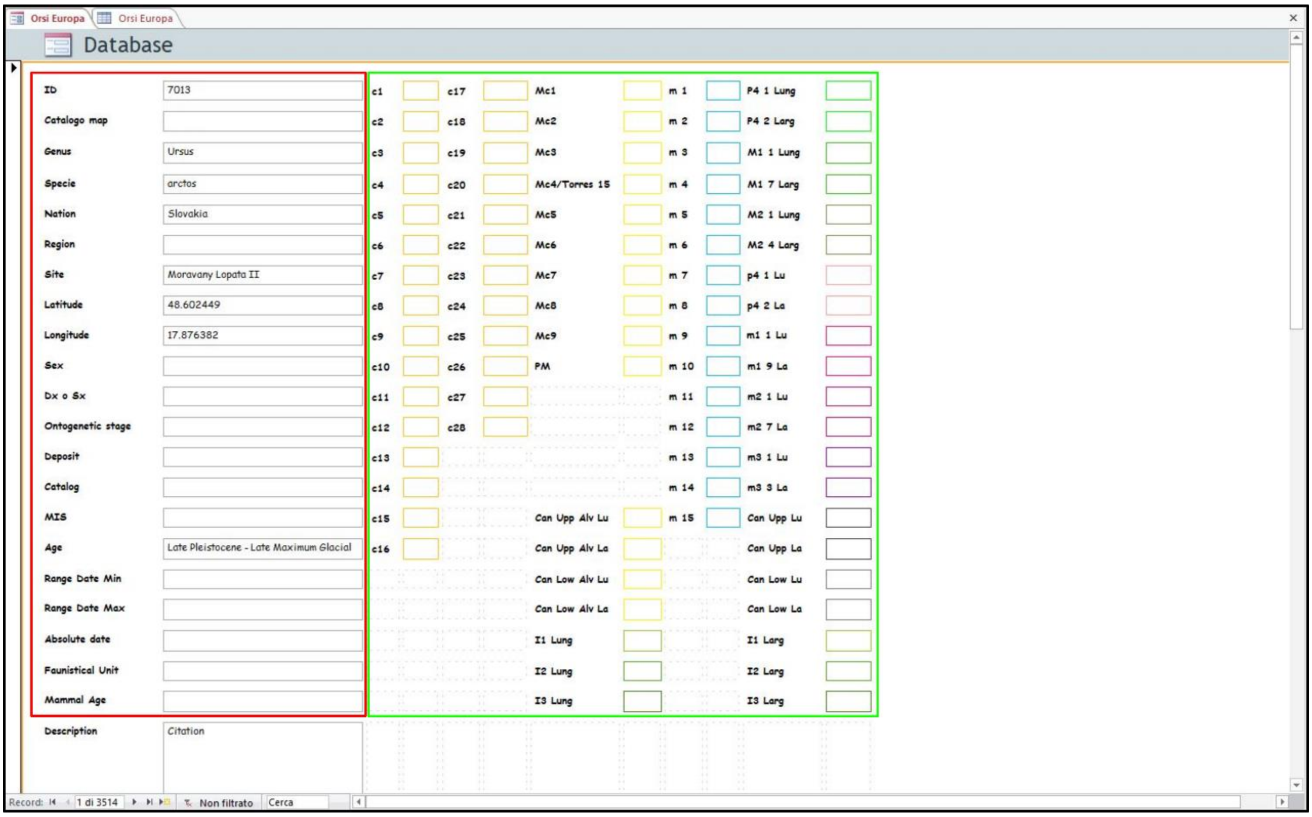
Mainly, my work has focused on the brown bear findings and all those sepecimen that have been associated, in the past, with the arctoid lineage. Despite the mainly attention to this species, I decided to collect as much data as possible also on the fossil evidence of other species, to compare not only the different morphology but also the ecological and the dispersal dynamics between the various bear forms.

As already mentioned, the evolutionary history of the brown bear is rather discussed. It can be traced back to the first phases of the Lower Pleistocene (Rabeder 2010) and then develops throughout the Middle and Late Pleistocene up to the present day, with peculiar forms and different adaptations between the different species. To better outline the dynamics of dispersion and evolution of this mammal, I thought to analyze all the possible material in reference to the whole Quaternary.

4.1 The database

Microsoft Access was used to create the database. This software allows to create a relational database in which various elements are inserted in rows. Every one of this is linked to a certain number of characteristics (columns), in which you can enter data relating to the selected element.

The choice to use this software is due to the possibility to use masks that have a simple and immediate interface, with which you can browse the various elements (Fig 14).



ID	7013
Catalogo map	
Genus	Ursus
Specie	arctos
Nation	Slovakia
Region	
Site	Moravany Lopata II
Latitude	48.602449
Longitude	17.876382
Sex	
Dx o Sx	
Ontogenetic stage	
Deposit	
Catalog	
MIS	
Age	Late Pleistocene - Late Maximum Glacial
Range Date Min	
Range Date Max	
Absolute date	
Faunistical Unit	
Mammal Age	
Description	Citation

Figure 19: ***Mask of the database.*** *The red square, descriptive informations; the green square, quantitative informations.*

Each element has precise characteristics that are the same for all of the specimen and are divided into two categories: numerical and descriptive.

The numerical columns represent all the measurements that can be made on a complete specimen, with skull, mandible and all the dental elements; for faunal list or fragmented specimen the boxes are still present, but they are not filled in.

The descriptive categories, on the other hand, reflect all those items necessary to define the object about its various general aspects (such as age, site or species).

The construction of a functioning database is the basis of the success of the various analyses, allowing easily to group under a single set all those finds that are included in a certain category. At the same time, it allows to create numerical tables only of some interested the anatomical portions, such as a specific tooth or some specific measurements of the jaw.

To do this, it was necessary to create a unique card for each element. To allow the acquisition of all the information related to each type of finding, whether it be skull, mandible or a simply report of faunal lists of a deposit.

Leaving aside the numerical columns, for which reference should be made to the next paragraph, it is considered necessary to underline some of the criteria used to insert the information into the descriptive columns.

Regardig the column “species”, I kept the original names reported on tags, and the most recent taxonomic attribution for the element that I didn’t analyse directly.

The "site" column contains the name of the location where the deposit is located and, when possible, the name of the excavation; however, on some occasions, for smaller area not included in the register, the closest adjacent larger location is chosen as the reference point.

In the "Reference" column, the papers from which the information relating to the various cataloged finds was taken are reported. If only the faunal record is listed, the information relating to the reference article is recorded in capital letters and in parentheses the works cited within.

It should be noticed, however, that part of this database (especially for the most recent material) was obtained from the work of Prof. Benecke and derived from the project (Holocene history of the European Vertebrate Fauna, http://datenportal.ianus-fdz.de/pages/collectionView.jsp?dipId=1650048#collectionOverview for which, some of the references of the most recent sites, do not maintain this criterion of style.

In order to establish a rule regarding the age of the various elements, it was necessary to create different columns (Age, Mammal Age Fauna Unit, Precise Dating, Mis, Max and Min Dating Range).

In fact, in various papers, the dating can be indicated by absolute age, biochronology on micromammals or macromammals, fauna units, lithic and climatic oscillations related to the analysis of oxygen isotopes.

Therefore, given the difficulty of relation between the ages of the various finds, I have chosen a general wording for the column " Age " which is characterized by a wide subdivision of the chronological scale: Early-Middle-Late Pleistocene, Holocene and Recent (wich correspond to all the specimens after the end of Roman culture).

The column "Catalog" represents the index name of the find (when present) and it is closely linked to the reference structure in which this fossil element is deposited (column "Deposit").

To describe the ontogenetic stage of the fossils analyzed, I considered the structure of the skull (when possible), and used the method proposed by Stiner in 1998 that analyzes the dental wear. So, I divided the specimen into four ontogenetic stages (Juvenile, Young adult, Adult and Old adult) (Fig. 19) divided themselves into various classes (even if it was developed only for in situ teeth and it can be used for isolated teeth only with the caution).

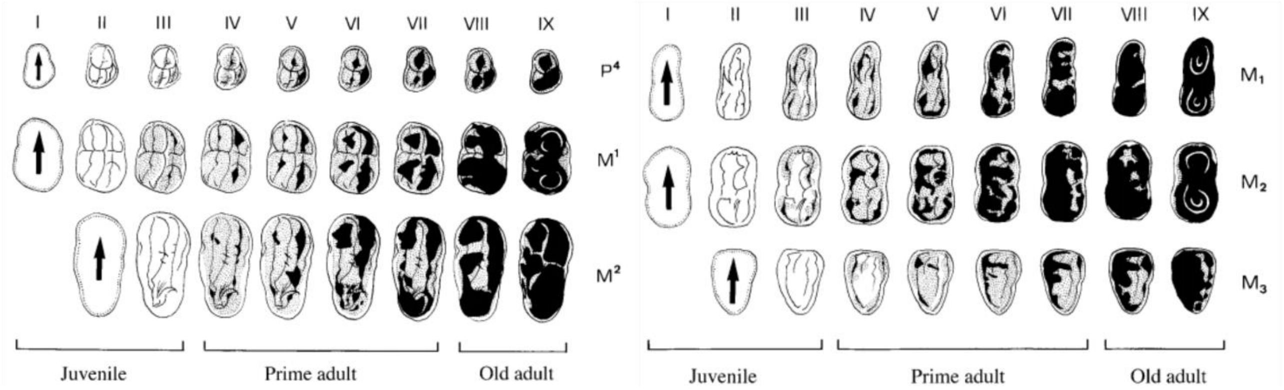


Figure 20: ***Tooth eruption wear stages for lower and upper cheek teeth proposed by Stiner 1998.***

The sex of the various elements, when possible to identify it, is indicated with M if male and F if female. The presence of parentheses indicates that the characters are more inclined towards one or the other genre, but the data is uncertain.

The "description" box contains all the additional information on the object, such as the anatomical part found or some of the distinctive features of the specimen, which cannot be categorized (e.g. if fragmented).

Finally, columns relating to the longitude and latitude of the various sites have been added. This allows not only to have geographical information of the findings but also to export this data to create maps in georeferencing software.

In fact, thanks to the possibility to select only a part of the database (e.g. referred to a certain category such: species, age, region or country), it is possible to create distribution map. This process is indispensable for the study of the paleogeography of various species and the ecological relationships that characterized them.

The acquisition of the coordinates of the sites (when not present in the papers) was obtained using google maps (https://www.google.com/maps). This online service allows the visualization and search of maps relating to almost the totality of the earth's surface and extrapolate the LAT and LONG coordinates.

With this procedure, I was able to record almost all the coordinates of the various sites surveyed in the database. The missing data refer to sites with generic names and locality not specified in the reference papers, or to places that no longer exists.

QGIS software was used to create the maps. This allows, through shapefiles, to display the several coordinates of the sites placed in a white map of the world. The software also recognizes the various columns of the database, reporting them on the map in the form of indexes that could be categorized with the various colors and symbols to allow greater clarity (See Cap 5).

For the statistical analysis of the collected data and the graphic visualization of the results, the excel software of the Office 2016 package was used.

4.2 Morphometrical analysis

For the collection of the morphometric data of the skull the scheme proposed by Marciszack et al, (2015) has been taken as reference. This scheme consists of twenty-eight linear measurements on the skull and nine taken on the jaw.

To collect data coming from older papers or referred to other schemes, the configuration of these measures has been converted; therefore, all measures respect the scheme shown in the Fig. 21.

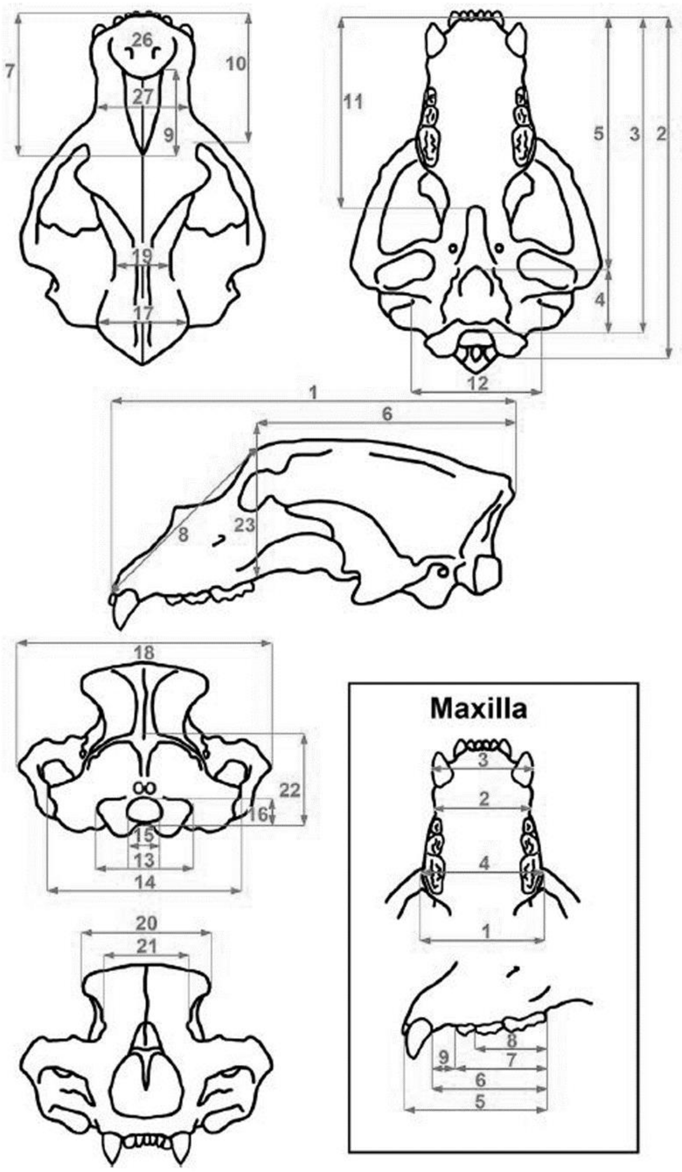


Figure 21: ***Scheme of the measurements taken on the skull.*** *Modified from Marciszack et. al., 2015.*

For the measurements of the mandible I used the scheme proposed by Torres, (1988) for which, on each finding, fifteen linear measurements are recorded (Fig. 22).

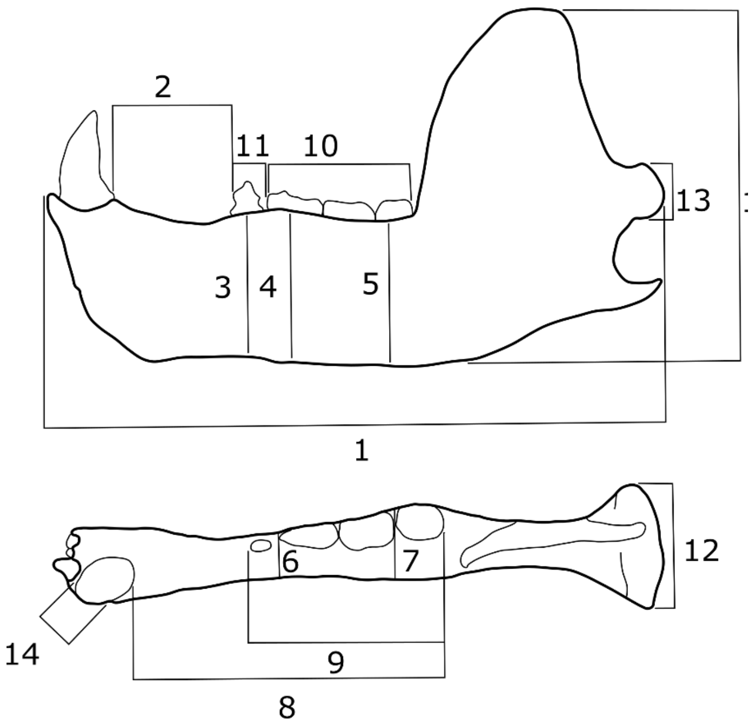


Figure 22: ***Scheme of the measurements taken on the emimandible.*** *Modified from Torres 1984*

Only the maximum length and the maximum width were collected on the dental elements; regarding the canine, the measurement on the tooth was taken at the base of the crown; if absent, I took the width and the length of the alveolus and referred to two distinct columns of the database.
Upper case is referred to upper dentition (e.g. M2 for upper second molar) and lower case for lower dentition (e.g. m2 for lower second molar).

4.3 Morphometric geometry

Morphometry has traditionally used a quantitative approach, based on linear measurements, angles and indices. Although this is a useful and, in many cases, indispensable methodology, it still has an intrinsic limitation, derived from the exclusion of some useful diagnostic information, represented by the geometric relationships between the different morphologies of the object examined.
More precisely, values of length, width and depth do not allow to describe a shape by themselves. For this reason, many authors have attempted to increase the number of data with further measurements, possibly made in the same direction as others already acquired (e.g. Torres, in his doctoral thesis, managed to take up to 14 different measurements on a single tooth), leading to a redundancy of the data. Finally, it should be stressed that the distance between two points is inevitably related to its size, wich is, in the case of superior organisms, related to their ontogenetic stage.
The qualitative approach has always been the other side of the medal, constituting an extremely used and effective method to determine the peculiar characteristics of the various specimens; unfortunately, this does not allow the use of objective and replicable ratios, and is often subject to a high subjectivity.
The synthesis of the two approaches was possible thanks to a group of researchers including F. Bookstein and J. Rohlf who, at the beginning of the 1980s, developed a new methodology called "Geometric Morphometry" (Bookstein, 1991). This, with the development of new and increasingly powerful computer and calculation tools, allows a quantitative analysis of the forms, rather than analyzing the individual linear measurements or numerical indices.

Slice, (2005) define the morphometric geometry as “the suite of methods for the acquisition, processing, and analysis of shape variables that retain all of the geometric information relevant to the original structures”.

It is important to underline that in the word “shape” has a distinct meaning from the word “form”, which are translated in the same way into Italian, French and Spanish (forma, modeler and formar). The word “shape” indicates only the appearance without counting the size of the object under examination, the word “form” inserts, within its definition, also the dimensions of the object.

In order to compare the various shapes, it is necessary to reduce these forms to a set of points (two-dimensional or three-dimensional) called landmarks. These points are taken on the object and are recorded in an abstract, multidimensional and non-Euclidean morphospace (Kendall's space) (Bookstein, 1991). These points are represented by spatial coordinates, quantitatively comparable with their counterparts belonging to another configuration.

To make a correct comparison between the various configurations, a correspondence between them is necessary, both on the positioning of the landmarks and on their number. The choice of the location of the various points is extremely important and must respect as much as possible the homologous structures of the object.

Because not all the skull portions have the same "weight" and represent more or less variable characters, the landmarks taken can be traced back to three categories, decreasing by degree of homology (Bookstein, 1991; Rabeder and Withalm, 2006):

1 Type 1) landmarks occur where tissues or bones meet (anatomical landmarks, biologically homologus)

2 Type 2) landmarks are defined by a local property such as maximal curvature (geometric landmarks, spatially homologus)

3 Type 3) A landmark having at least one deficient coordinate, for instance, either end of a longest diameter, or the bottom of a concavity.

When it is not possible to recognize precise anatomical points, but it is still needed to describe the shape of a curve, it is possible to use Semilandmarks, which form a separate configuration and describe a shape in relation to the main landmarks.

Once all the landmarks configurations have been created, the comparison is made by superimposing the various homologous landmarks and calculated the spatial difference between those points.

To do this, however, it is necessary first to cancel the effects of position, scale and orientation of configurations, through a process called Procruste Overlay or Generalized Procruste Analysis (GPA). Subsequently, the configurations are rotated to minimize the sum of the average squared deviations between the corresponding points, and finally they are scaled to the same size, surrounding a common point, called centroid size.

After that procedure, the new spatial coordinates, or Procruste coordinates, are comparable and can be used in multivariate statistical analysis (Fig. 23).

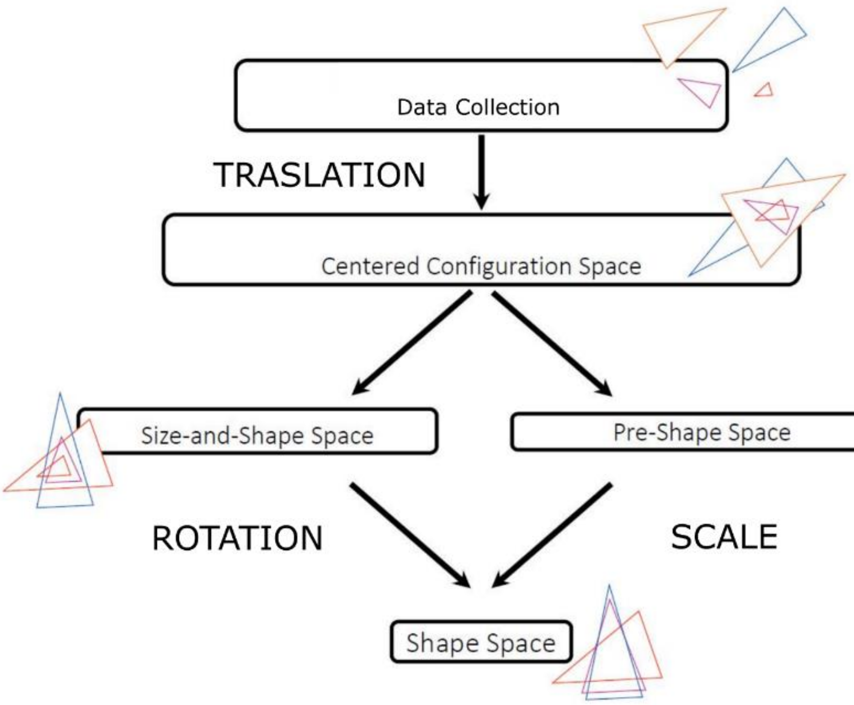


Figure 23: ***Scheme of the procruste analysis.*** *(thanks to the Dott. Fabio Divincenzo).*

Regarding the application of this methodology on recent specimens of the genus *Ursus*, some Italian authors have already proposed different 2D configurations both on the mandible and on the skull. From those analysis they outlined some very distinct morphologies in the various modern populations of the European continent (Loy et al., 2008; Colangelo et al., 2012; Meloro et al., 2017).

As mentioned above, geometric morphometry is applicable to both two-dimensional images and three-dimensional objects. The main difference is that in the latter case it is also possible to take into account the depth of the object, and the proportions do not undergo a deformation depending on the method of image acquisition; however, it should be noted that, in the case of teeth or surfaces that extend on a two-dimensional plane, the analysis of 2D configurations are as effective as three-dimensional ones.

4.4 2D Morphometric geometry

To carry out the two-dimensional analysis I used occlusal standard photographs of the molariform teeth. The photos were taken with an 18.1-megapixel digital single-lens reflex camera (DSLR) Canon EOS 1200D.

The acquired photos were then scaled to the same size using the tps Deg software (ver 232) and, using the same software, I created the landmarks configurations. For each tooth a configuration was created with a specific number of points (different from each other) in order to fully analyze both the occlusal profile of the tooth and the position of the main cusps:

- third lower molar (m3) – 50 landmarks; starting point on the mesial margin (No cusps)
- second lower molar (m2) – 60 landmarks; starting point on the mesial margin. Protoconid, Entoconid (posterior cusp), Metaconid, Hypoconid (posterior cusp).
- first lower molar (m1) – 60 landmarks; starting point on the distal margin. Paraconid, Protoconid, Hypoconid, Entoconid (posterior cusp); Metaconid (posterior cusp).
- fourth lower premolar (p4) – 40 landmarks; starting point on the distal margin. Protoconid
- second upper molar (M2) – 120 landmarks; starting point on the mesial margin; 80 landmarks on the ridges of the cusps; starting point on the center of the talon. (No cusps).

- first upper molar (M1) – 120 landmarks; starting point on the mesial margin. Paracone, Metacone, Hypocone, Mesocone, Protocone.
- fourth lower premolar (P4) – 50 landmarks, starting point on the mesial margin. Paracone, Protocone, Metacone.

For the lower dentition only right elements were analyzed, while for the upper portion, the left ones were selected. In order to not lose information in case one of these elements was missing, I made a mirroring of the dental element to allow the inclusion of it in the statistical analysis (Fig. 24).

For the Generalized analysis of Procruste and the acquisition of covariance, the morphoJ software (Ver 1.06) was used. Also, by the same software, has been created the matrix of the spatial points, that was then ordered through the analysis of the main components (PCA). This last step was made through the statistic software PAST3 (ver 1.0.0).

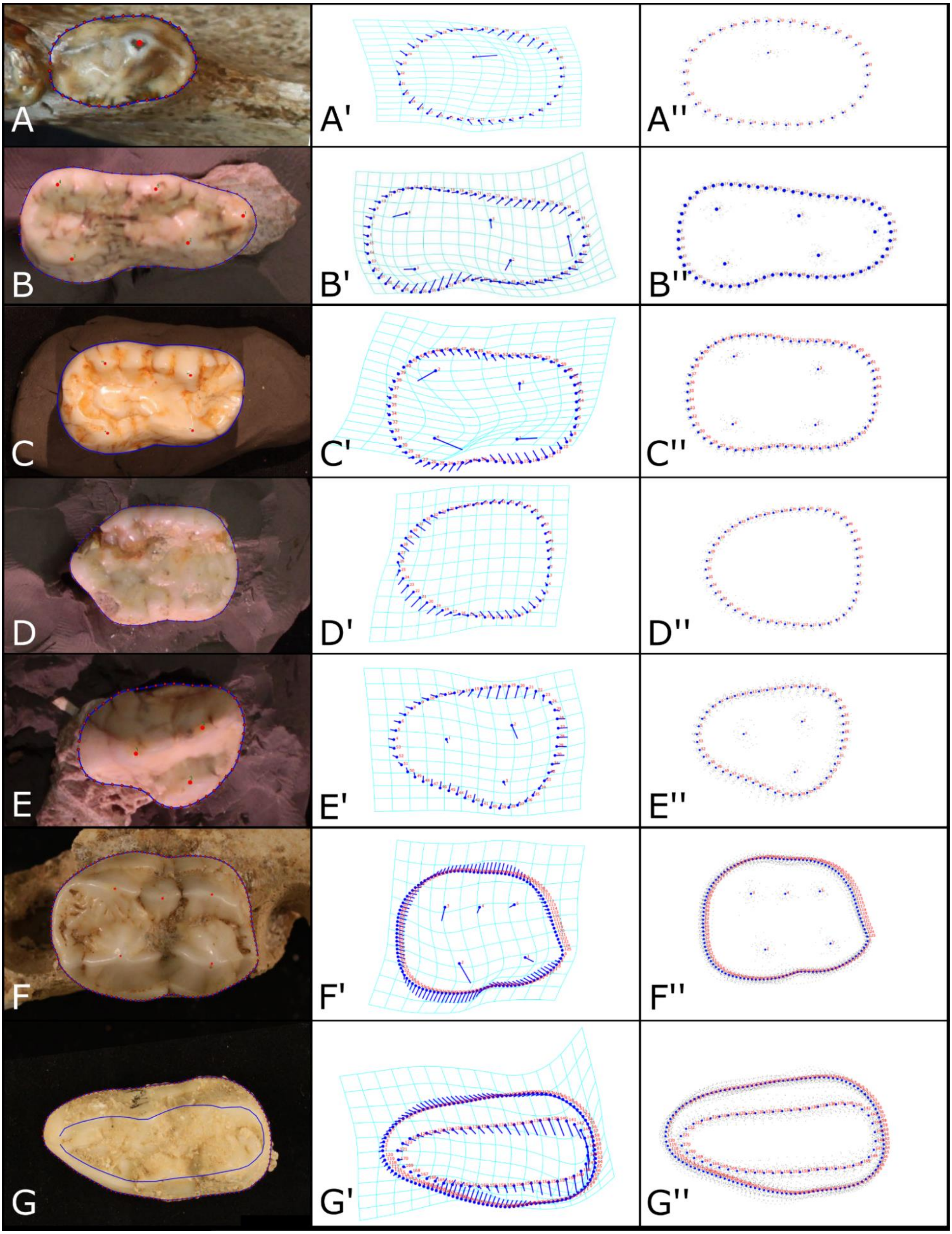


Figure 24: ***Morphometric geometry analysis of the molariform: A)*** *lower p4 lendmarks configuration.* ***B)*** *lower m1 lendmarks configuration.* ***C)*** *lower m2 lendmarks configuration.* ***D)*** *lower m3 lendmarks configuration.* ***E)*** *upper P4 lendmarks configuration.* ***F)*** *upper M1 lendmarks configuration.* ***G)*** *upper M2 lendmarks configuration.* ***The Letters with one apex correspond to the PCA with the deformation greed; the letter with two apexes correspond to the procrust analysis.***

4.5 3D Morphometric geometry

For the production of the three-dimensional models, I used both photogrammetry and tomographic scans (see below). Once obtained, I created a configuration of landmarks that is representative of the general morphology of the skull and that represents as accurately as possible the general shape. The final configuration has 54 points, 42 of which are even (i.e. symmetrical on the right and left sides) and 12 odds, which has been acquired through the use of the Amira software (ver 5.4.5, www.visageimaging.com) Fig. 25 and Table 1.

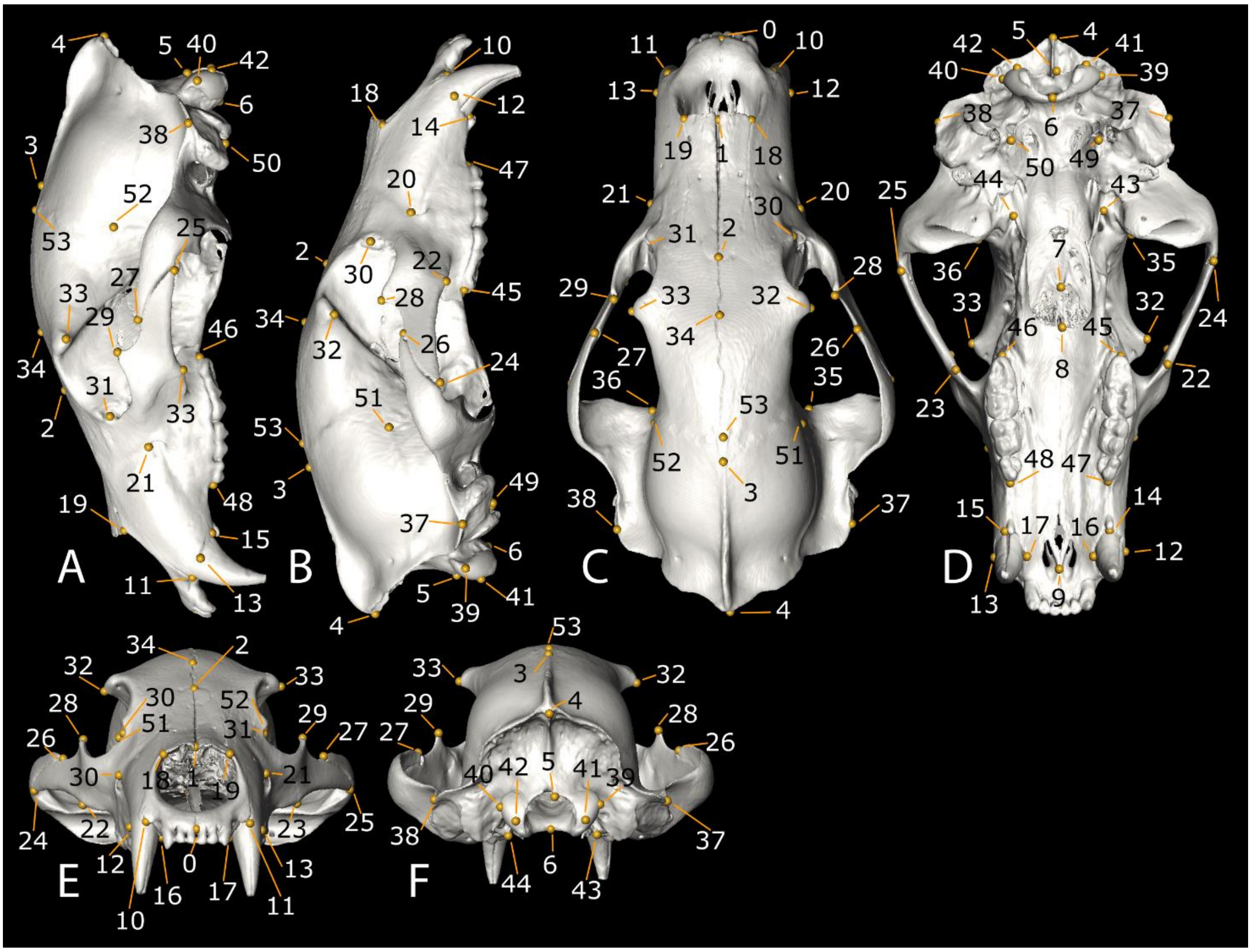


Figure 25: ***Scheme of the landmarks taken on the 3d models of the cranium.*** *Complete list in the Table 1.*

Table 1: ***3D Landmarks list***

N°	Description	Side	N°	Description	Side
0	Alveolar margin between the central incisive (Prosthion)	Mesial	**27**	Dorsal point of the malar-squamosal suture	Left
1	Upper edge of nasal cavity	Mesial	**28**	Upper margin of the Zygomatic apophysis of the malar	Right
2	Upper portion of naso-frontal suture (Nasion)	Mesial	**29**	Upper margin of the Zygomatic apophysis of the malar	Left
3	Initial point of the Sagittal Crest	Mesial	**30**	Upper portion of the lacrimal crest	Right
4	Most distal point of the cranium (Ophistocranion)	Mesial	**31**	Upper portion of the lacrimal crest	Left
5	Posterior portion of the Foramen Magnum (Opistion)	Mesial	**32**	External margine of the Post-Orbital Process	Right
6	Anterior portion of the Foramen Magnum (Basion)	Mesial	**33**	External margine of the Post-Orbital Process	Left
7	Distal margin of the Presphenoid	Mesial	**34**	Beginning of the frontal inflession	Mesial
8	Distal portion of the Palatine bone	Mesial	**35**	Most internal portion of the upper crest of the squamosal articulation	Right

9	Mesial point of the incisive foramen	Mesial	**36**	Most internal portion of the upper crest of the squamosal articulation	Left
10	Distal crest of the canine alveolus	Right	**37**	external portion occipital crest in proximity of the Squamosal-Parietal suture	Right
11	Distal crest of the canine alveolus	Left	**38**	external portion occipital crest in proximity of the Squamosal-Parietal suture	Left
12	External crest of the canine alveolus	Right	**39**	Most lateral portion of the Occipital Condyle	Right
13	External crest of the canine alveolus	Left	**40**	Most lateral portion of the Occipital Condyle	Left
14	Internal crest of the canine alveolus	Right	**41**	Most prossimal portion of the Occipital Condyle	Right
15	Internal crest of the canine alveolus	Left	**42**	Most prossimal portion of the Occipital Condyle	Left
16	Proximal crest of the canine alveolus	Right	**43**	Proximal portion of the foramen Ovale crest	Right
17	Proximal crest of the canine alveolus	Left	**44**	Proximal portion of the foramen Ovale crest	Left
18	Crest of the nasal cavity in proximity of the suture between the maxillar bone and the nasal bone	Right	**45**	Distal portion of the Upper 2nd molar alveolus	Right
19	Crest of the nasal cavity in proximity of the suture between the maxillar bone and the nasal bone	Left	**46**	Distal portion of the Upper 2nd molar alveolus	Left
20	Upper portion of the infra-orbital foramen	Right	**47**	Mesial portion of the Upper 4th premolar alveolus	Right
21	Upper portion of the infra-orbital foramen	Left	**48**	Mesial portion of the Upper 4th premolar alveolus	Left
22	Ventral margin of the malar, in proximity of the malar-maxillar suture	Right	**49**	Proximal portion of the basi-occipital Process	Right
23	Ventral margin of the malar, in proximity of the malar-maxillar suture	Left	**50**	Proximal portion of the basi-occipital Process	Left
24	Ventral point of the malar-squamosal suture	Right	**51**	Congiunction of the Parietal-Squamosal suture and the Parietal-Frontal suture	Right
25	Ventral point of the malar-squamosal suture	Left	**52**	Congiunction of the Parietal-Squamosal suture and the Parietal-Frontal suture	Left
26	Dorsal point of the malar-squamosal suture	Right	**53**	Upper portion of the Parietal-Frontal suture, in proximity of the Saggittal Crest	Mesial

As already mentioned above, the number and the position of each landmarks of the same fossil element must be equal. This assumption does not allow the use of findings that are not complete or with fractures that have occurred on one or more anatomical points considered in the configuration.

In order to overcome this problem, in the case of fragmented findings it is possible to effectively estimate missing data using standard statistical analysis techniques (Arbour and Brown, 2014).

This system exploits the overlapping of Procruste analysis (carried out by means of the 'fixLMtps' function, 'Morpho' package of the R software) aligning the configurations of the incomplete samples with those of the complete one, estimating the positioning of the missing landmarks through the application of the TPS (Thin Plate Spline) algorithm; the result is to be considered more reliable when there is a high number of complete configurations in the sample.

The configurations were finally analyzed with the free statistical software R, through the use of the packages “Arothron” and “Morpho”. These allowed the production of the GPA and the graphs representing the distribution of the general shape of the skulls according to first and the second principal components.

4.6 From real to virtual

Today, technology has made great progress and continues to develop, especially in the field of digital and virtual. In fact, even in the world of paleontology, computer graphics and multimedia analysis have become standard tools for achieving scientific goals (Mallison and Wings, 2014; Petti et al., 2018).

One of these tools is represented by the digitization and virtual reproduction of objects, obtained through software and hardware more and more within everyone's grasp. Today the most used techniques to obtain a three-dimensional model of an object are three. The first is the Computed Tomography that allows, through an x-ray scan, the faithful reproduction of both the internal and the external portion of an object.

The second is the laser scanner, its acquisition relies on the triangulation built by a structured light beam intercepting the surface of the specimen, being detected by a sensor put at a known distance from the source (Aiello et al., 1998; Friess et al., 2002).

The last is the photogrammetry, is based on the assemblage of one or more series of images of the object in its different views (Baltsavias, 1999). The images are usually photos taken by an operator and commonly grouped in different chunks, one for each norm.

Among the three techniques, the most expensive and time-consuming is certainly the Tac, since it requires, among other things, also authorized medical personnel for its operation.

In spite of this, the model obtained, in addition to being perfectly scaled and oriented in space, allows the visualization of internal portions. This let us to acquire a greater number of information in comparison with the other two methodologies.

Even the laser scanner allows the digitization of an object returning a model scaled and oriented in space, and for its use is not necessary to specialized personnel, however, the cost of the machine is quite high and, as already mentioned, reproduces only the external portion of the object without giving any information of the inner parts.

Photogrammetry, like laser scanners, allows the digitization only of the external portions of the object but, unlike the first two techniques, it is extremely economical. In fact, to acquire 3D models it takes only a camera and a dedicated software. With this technique, it is not possible to analyze the internal portion of the object but, using photogrammetry, it is possible to digitalize extremely large surfaces or objects that would be impossible to reproduce virtually through the other two methods, as for example happens on palaeo-archaeological sites (Conti et al., 2017b).

Regardless of the techniques used, the possibility of having a three-dimensional model of a specimen, has many advantages. First of all, it is possible to analyze the fossil several times, even if located in depositories of different cities. Secondly, the production of virtual databases allows both the preservation of the specimens, and the possibility to rapidly share information between various researcher. Last but not least, the possibility of creating virtual museums and thus facilitate the dissemination of the findings with the general public.

In this thesis I used only material digitized by Computed Tomography and Photogrammetry.

4.6.1 Axial tomography

CT, or CAT scans, was developed independently by a British engineer named Sir Godfrey Hounsfield and Dr. Alan Cormack and consists in special X-ray tests that produce cross-sectional images of an object placed on a special machine using X-rays and a computer.

The machine uses a planar radioactive beam that crosses, with a series of single two-dimensional sections, the entire volume of the object anlyzed.

This beam is collected by a receiving sensor (opposite to the source), and reproposed as a two-dimensional image using a dedicated processor (Iurino et al., 2013). The volumetric units (voxels) acquired can be represented by the resolution of the beam (in pixels) and by the depth of the beam thickness (mm).

Using the information obtained, it is possible to assign to each volumetric unit a code proportional to the absorption capacity of the X-ray unit. Each voxel is then coloured with a shade of grey according to the density of the object.

The reference scale ranges from 1000 Hounsfield units for air, to 0 for water, to 3095 for thicker materials (Iurino et al., 2013). At this point, to obtain an image in three dimensions, is it possible to overlap consecutive plates and process them all together using specific software. At the same time, is it possible to study the information of each individual slices (Iurino and Sardella, 2015).

By setting the absorption values within a certain range of values it is possible to obtain the image only of those pixels that have a specific density and, therefore, to obtain three-dimensional reconstructions only of certain tissues or structures, excluding other morphological or disturbing components (Bruner and Manzi, 2006).

Since the last thirty years this technology has evolved with more and more effective systems, increasing both the resolution of the images and the timing of the execution, so much to become a tool of analysis widely used in modern evolutionary biology and also in vertebrate paleontology. (Bruner and Manzi, 2006).

The use of CT scans is extremely suitable for the study of very fragile specimens or fossils incorporated in thick matrices of sediment; in fact, such conditions often make difficult the measurements and sometimes even the morphological analysis, which can only be carried out through invasive interventions that would lead to a high risk of damage to the find.

The tomographic scan allows to evercome these problems by returning a three-dimensional model of both the external surface of the fossil and its internal characteristics, giving the operator the opportunity to observe the object at 360 ° and to determine the presence of structural abnormalities or pathologies (Iurino and Sardella, 2015).

The usefulness of tomographic scanning and the use of virtual restoration techniques is evident even when the material is disjointed or is made by scattered fragments. In fact, by scanning and digitizing all the elements involved, it is possible to "reconstruct" the artefact by uniting the various portions digitally or to keep the various elements "suspended" in an anatomical position, within a digital environment.

This process is extremely advantageous for morphological comparisons, making immediate and clear the anatomical position of each element, as in the specific case represented by the analysis of a the juvenile rhinoceros skull from the site of Melpignano FIG 26 (Conti et al., 2017a).

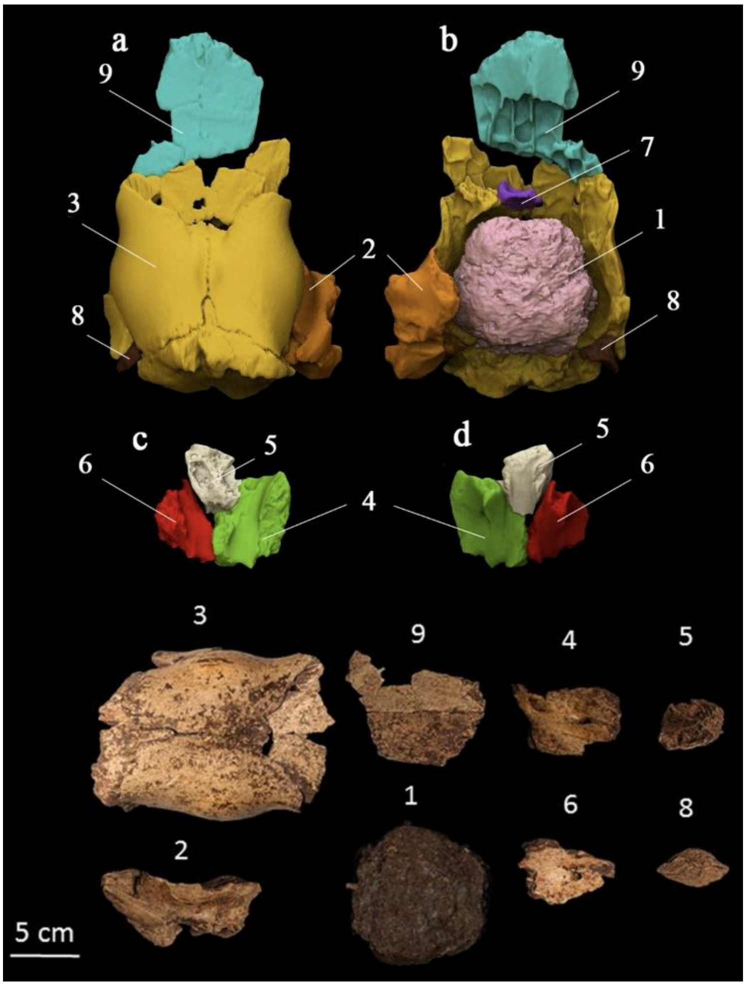


Figure 26: ***Example of a virtual restored neurocranium of a juvenile Rhinocerontidae specimen. Dorsal view of:* *1)*** *natural endocast;* ***2)*** *right temporal bone;* ***3)*** *Neurocranium;* ***4 – 5 – 6)*** *Sphenoid bone;* ***7)*** *Fragment of neurocranium;* ***8)*** *Fragments of left temporal bone****.*** ***a – c)*** *Dorsal view;* ***b – d)*** *Ventral view.*

Finally, the possibility of analysing an artefact using tomographic scanning is extremely useful in many other activities not directly linked to scientific use.

As an example, the illegal trade of fossils has always been a threat to the scientific relevance of specimens recovered from the black market. Most of the specimens are often devoid of any information about the provenance or taxonomic attribution and, most of the time, the specimens are clearly made-up to hide the reconstructed portions, with the risk of losing the information about the truly preserved elements.

In these cases, the tomographical analysis risults a needed tool to recover important data from traded fossils, that could still be useful to improve our knowledge of the life in the past.

This process allows to discriminate and virtually separate the fossilized portion from the reconstructed one, avoiding an invasive procedure that could damage the specimen as in the case of the Elasmosaridae cranium from Serrapetrona Museum (Fig 27) (Conti et al., 2016).

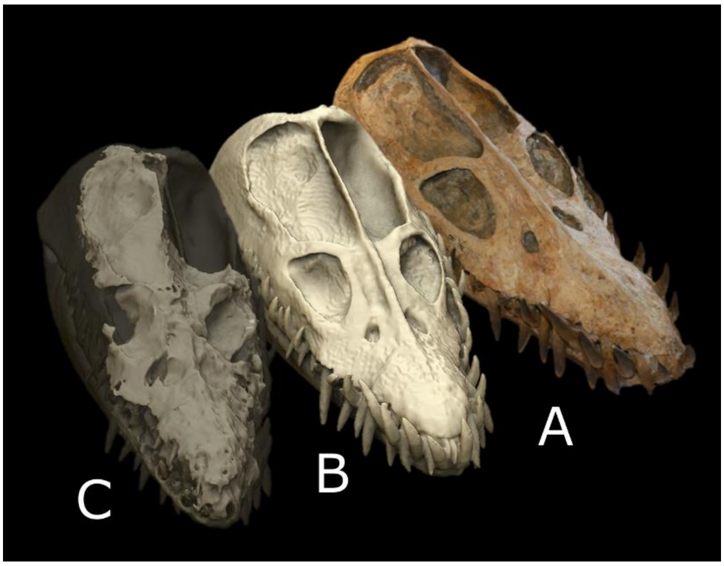


Figure 27: ***Validating analysis on the Elasmosaridae cranium from Serrapetrona Museum (Marche, Italy).*** ***A)*** *Photograph of the skull;* ***B)*** *Digitalized model of the skull by TAC;* ***C)*** *Evidence of the true remaining bone portion inside the specimen.*

4.6.2 The photogrammetry

Photogrammetry is the derivation of 3D information on points, lines and areas on objects or terrain from photographic image sequences.

This technique allows to recreate three-dimensional models of individual objects, scenes or even entire portions of geographical areas returned with the real-life texture. Objects are created with the real proportion, allowing to collect information about linear measurements, areas and volumes.

The process involves taking a series of photographs of an object from different angles to computationally generate a 3D model by comparing features across the photographs.

Photogrammetry depends strictly on the quality of the images; regardless of the power of the computer or the software used, if the photos are not taken properly (which does not always mean beautiful photos) it will not be possible to achieve a good result.

The actual process of creating a 3D model from photographs starts with the program using, e.g., the SIFT algorithm (Lowe, 1999) to find specific points on each image (Mallison and Wings, 2014).

Then, the images are processed to compare these points and get their overlap; then, the coordinates of the points are displayed by the software that reproduces a cloud of colored dots which is called "sparse cloud".

Since alignment does not require the use of all available points in high resolution images, usually only a small percentage of points are used to keep the calculation times tolerable.

Then, using all the other points of the various photos, another cloud is produced, with many more points than the previous one, which is called "dense cloud". This cloud can be produced at various levels of detail (low, medium, high and highest) from which derives the final mesh, whose quality obviously depends on the resolution chosen for the dense cloud.

To produce the texture, the color information of the points obtained from the dense cloud are processed, providing the final model (Fig. 28).

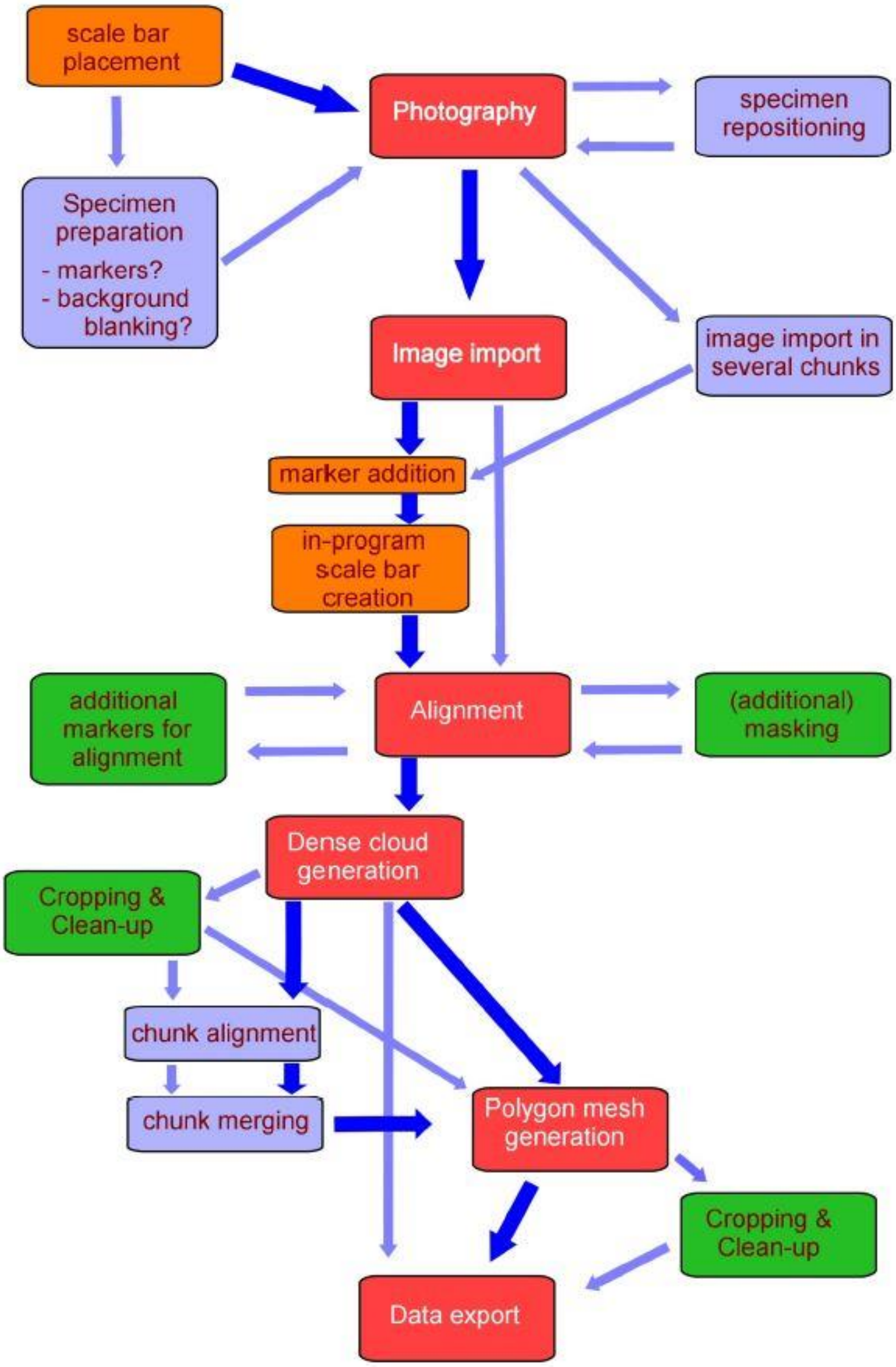


Figure 28: ***Standard workflow to digitalize an object with photogrammetry.*** *Modified from Mallison 2014.*

Today there are many software of photogrammetry, personally I used Agisoft photoscan (www.agisoft.com) that I found extremely user friendly; for a more specific comparison between the various existing programs I refer to the excellent work of Green et al., (2014).

To make a 3D model of an object it is not necessary to have a high-performance camera, but, as already mentioned, the better the photos, the more precise the model.

For my work, I used a 15-megapixel digital single-lens reflex camera (DSLR) Canon EOS 500D. The camera mounts an 18.0 Megapixel CMOS (APS-C) image sensor, it is equipped with a Canon EF lens and it possess a Canon’s DIGIC 4 image processor. To process the data, I used a PC with Intel(R) Core i5-6600 as processor, 16,00 GB RAM and Windows 10 as operating system.

In order to get the best shots, I also used a standard tripod for stabilizing the camera, mobile LED lights and a lens ring of LEDs to always achieve the optimal shooting light and, when possible, a remote control to minimize the vibrations of the camera.

The reference focal for a medium size skull is between F6 and F11 (I usually impose it on F9) but obviously it depends considerably by its size. The focal length affects how much of the object is focused and, consequently, also the lighting necessary for an optimal shot (the higher the focal length, the less the object will be illuminated in the photo).

To adjust the brightness of the photo, it is necessary to set the exposure time; the higher the exposure time, the brighter the photo, at the same time, it will be necessary to pay more attention to the vibrations of the camera; in this regard, to get a good tripod and a remote control for shooting at a distance are extremely efficient to not make shaded photos.

The setting of the ISO depends exclusively on the size of the object. Generally, the ISO should be kept as low as possible. To digitalize the material, I have always used ISO to 100 but, for larger objects such as buildings, statues or caves it is possible to increase a little this parameter to better adjust the brightness of the shot.

Photogrammetry uses the same principle as the human eye to perceive depth, so to produce a three-dimensional surface only 3 photos are needed. Obviously to recreate the entire surface it is necessary that all the portion of the object are impressed at least in one photo, and each photo have to be overlapped with another, both horizontally and vertically.

To reproduce an optimal model of a bear skull, 3 sets of about 16 shots in 3 different view are needed: one horizontal to the specimen, one at 30° and the last at 60°. The sixteen shots for each point of view are taken by rotating the specimen (or rotating around it) at an angle of about 15° for each shot. Moreover, it is always good to take two zenithal photos of the object (one per side) to obtain also all the information of the dorsal part of the object. The total therefore always oscillates around 55 photos per model.

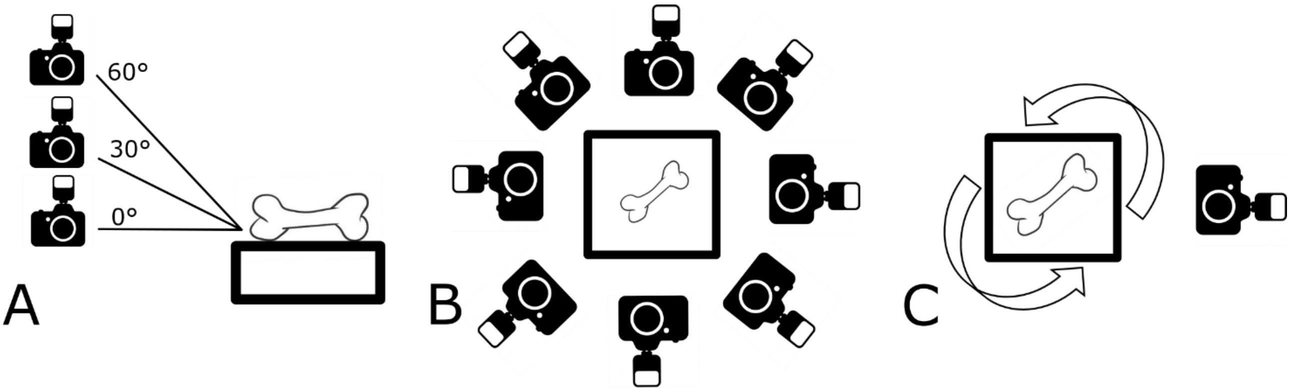


Figure 29: ***Camera positioning for the photogrammetry. A)*** *Different angle of the different set.* ***B)*** *"Walk-around" method.* ***C)*** *"Turn table" method.*

To make a three-dimensional model is it possible to use two methods; turn the object while keeping the camera stationary or turn the camera while keeping the object stationary; Agisoft Photoscan allows both these techniques which are called: a) Turn table and b) Walk-around (Mallison and Wings, 2014).

With both methods it is possible to create a model of the same quality but, depending on the technique chosen, the parameters and the method of the photo acquisition changes. During my work I had the need to develop both techniques, since each one adapts efficiently to a given type of specimen and to various lighting situations.

a) Turn table (Fig 29 C)

In this mode the photos inevitably need a homogeneous background for the photograph; this condition can be obtained by using a photographic lightbox or green screen. The object, to be digitized, must be positioned in the center of camera lens, to gain the perfect focus of every portion of the subject.

The model must be placed on a stable pedestal with recognizable goods stitches, often made by a plasticine marker or coloured dots.

The support surface is extremely important; indeed, it is necessary to be able to rotate the object without changing its position (even a small inclination can mean having to start taking pictures again from the beginning).

Given the possibility of monitoring the light and focus, the use of this mode allows to produce a very precise and detailed texture and an extremely detailed model. On the other hand, the align step (see fig 27) result much more difficult than the other technique, and it is always necessary to adjust the photos to eliminate the black background.

b) Mobile Camera (Fig 29 B)

This mode is useful for large fossils that do not fit into a lightbox. The object remains on a table or pedestal and the camera rotates around. In this method, the position must never be altered. It is also recommended not to change the surrounding "landscape" (such as moving furniture or turning lights on or off) because software records and uses every object that comes into the frame of the shot, to align the photos.

In this regard, the main purpose of shuting photos in this method is to set the focus on the object and, at the same time be able to take in the shot also what is in the background (a closet, a desk, chairs or a wall with paintings) making it appear blurred.

In this way, the "blurred background" will help the alignment of the photos to have a proper representation of the object.

This mode is extremely faster, because the object can remain still and the photos adjusting is not required. On the other hand, it requires much more physical space since the camera with the trestle has to rotate around the fossil. Moreover, without a controlled brightness area, there are often texture problems to the object rendering. To solve the problem, it is possible to take pictures in a completely dark room, lighting the specimen using only a ring of LEDs on the camera. This allows the lighting of the object with constant parameters, and the result level will be the same of that achieved th rough the use of a lightbox.

Once the model has been created, it will have spatial coordinates and dimensions relative to the virtual space generated by the software. It is therefore necessary to scale it to the original dimensions. To do this it is first necessary to take a linear measurement on the real object, possibly between two easily recognizable anatomical points and report them on the virtual model (Fig. 30 A). Since the relational distances between the various points of the model are consistent with the distances between the points of the original model, the entire model will be automatically scaled.

The last step to obtain a complete skull model (both with the upper and the lower portion) is the most delicate and time-consuming. First, it is necessary to make two chunks of photos, one of the Upper portions and one of the Lower portions by rotating the specimen, in order to obtain the three-dimensional model of both in upper and lower view.

The two models must necessarily have a portion of overlap with each other. On both models it is necessary to insert three landmarks on homogeneous points. Subsequently, relative coordinates must be inserted (the same for each point) to orient the object in the same way in both models (Fig 30 B). Once oriented, the models must be cut at the height of the overlapping portion and joined by using a software command that allows the overlap of the two models to obtain a complete one (FIG 30 C).

Figure 30: ***3D model building of the 2847-1 cranium from Laufenberghohle (Wien).*** ***A)*** *Scaling the object.* ***B)*** *Select and erasing of the upper and lower portion of the model.* ***C)*** *Final and complete 3D model with texture.*

This last step is of crucial importance to analyze and study complete skulls or structures with a diagnostic upper and lower portion.

4.6.3 Tac or photogrammetry?

As already mentioned above, the Tomographic Scan returns a virtual model extremely faithful to the original; on the contrary, with the photogrammetry, due the dependence to the quality of the photos and the goodness of the triangulation software, it is possible to produce a bad model without the same shape of the specimen.

In order to ensure uniformity in the proposed statistical analyses, it was therefore necessary, first of all, to analyse how far the three-dimensional model obtained by photogrammetry deviated from the model obtained by TAC and, if this difference could significantly affect the quality of the statistical analyses carried out.

Thanks to a collaboration between the Department of Animal and Human Biology, the Department of Earth Science of Sapienza, University of Rome, and the work carried out together with some colleagues from University of Bologna, it was possible to create a three-dimensional model of the Neanderthal skull, called "Saccopastore 1", both by tomographic scanning and photogrammetry. The surface of the two models has been compared using geometric morphometry through the software R; (the results are currently being published, (Buzi et al., 2018).

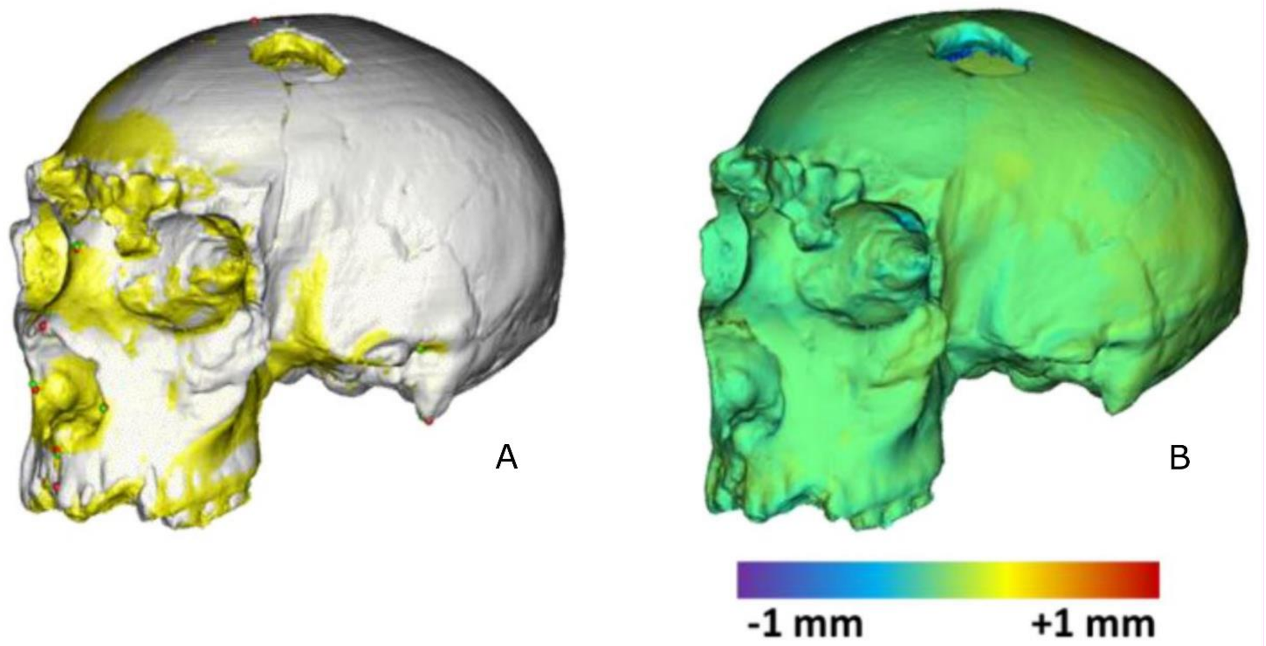


Figure 31: ***A)*** *the overlapped models of SCP1* ***(white: CT-scan); yellow: photogrammetry),*** *aligned after GPA.* ***B)*** *Mesh distance performed between the two 3D models. Modified by Buzi et al., 2018.*

The resulting analysis shows that the distance between the two meshes and the landmarks is low, indicating a full overlap of the two 3D models. The only areas that are not perfectly aligned are those portions that are difficult to photograph and illuminate during the photogrammetry shuting session.

From this work it is clear that the use of photogrammetry allows the production of extremely accurate three-dimensional models, with differences from the original that do not reach the unit of the millimeter.

Given the small extent of the error, we agreed that the use of photogrammetry is suitable for the production of consistent three-dimensional models for geometric morphometry analysis. Therefore, the bear skulls obtained during my work by CT and photogrammetry were both included in the database for morphological analysis.

5 Paleogeography of the brown bear

The current distribution of the brown bear is the result of a long evolutionary history, beginning in the Early Pleistocene and passes through all of the various climate and faunal changes that characterize the entire Quaternary.

In order to fully understand this matter, it was necessary to census as many findings as possuible related to the genus *Ursus* from European deposits, and then show it as distribution maps, divided by different time laps (Late Pliocene, Early Pleistocene, early Middle Pleistocene, Late Pleistocene, Late Maximum Glacial and Holocene) in order to correlate the faunistical and climate data.

5.1 Late Pliocene (Early and Middle Villafranchian)

During the entire Quaternary period, a great number of climate change leds, during the last millions of years, to a change in the faunal assemblages, and the subsequent modification in the morphological structure of vertebrate species (both micro and macro). These phases are called "dispersal event", introduced by (Repenning, 1980).

The first dispersal event concerns the transition from the Ruscinian faunas (the so called Pliocene Golden Age (Agustí and Antón, 2002) to the Villafranchian faunas, which occurred about 3.2 My ago, when temperatures drop dramatically due to the glaciation event, which led to a strong latitudinal climatic gradient.

During this period the species adapted to the warm climates of rainforest are replaced by associations more suitable for climates with cold winters and dry summers. This happened not only in herbivorous associations, but also in the carnivorian guild.

Infact, despite most of the carnivores of “modern” appearance that emerged during the Early Pliocene still persists, new species appeared, like: *Vulpes alopecoides, Nyctereutes megamastoides* (evolved from *N. donnezani*), and new forms of felids (Agustí and Antón, 2002).

After that, another important global climate change occurred, which led to another faunistical changing, in the period between 2.6 and 1.8 My, called *Elephas-equus* dispersal event (Azzaroli, 1983).

At that time the average annual temperatures continue to drop. The whole planet (specifically, the Northern Hemisphere) entered in a new era of periodic extensive glaciations with alternations of cold- and warm-temperate phases in cycles of 41,000 years (unlike the Pliocene oscillations).

The lowering of temperatures leads to the replacement of European forests with tundralike vegetation over large areas of northern and central Europe. The early stages of aridification and partial landscape opening were reflected by the large mammal faunas, that roamed over all western Palaearctic regions (Middle VIllafranchian fanuas) (Kahlke et al., 2011).

During this period the faunas begin to change, although not as drastically as during the previous faunal transition.

Infact, smaller-sized browsing and grazing ruminants were first accompanied, and then replaced, by herds of larger-sized grazers (Khalke 2011); like the immigration of the first elephant and especially the replacement of the genus *Hipparion* by the modern monodactyl horse (genus *Equus*) (Azzaroli, 1983).

Among the carnivores there is not a big change in the faunistic structure, even if, this period, represents a crucial moment for the genus *Ursus*. In fact, the strictly carnivorous species *U. minimus* begins to be replaced by a more omnivorous form (even if still strongly linked to meat consumption) represented by the species *U. etruscus* mainly distributed in southern Europe (see Chapter 3).

5.2 Early Pleistocene (Late Villafranchian)

Another decisive period in the history of the Quaternary faunas is called "the wolf event", represented by the Late Villafranchian faunal assosiation. This turn-over is characterized by a new climate change that occurs during the interval from 1.8 My to 1.2 My in which, the global temperatures, continue to fall gradually (still governed by the 41 ka periodicity effect), albeit with a lower intensity and with some milder and wetter peaks.

These steady climatic alternations led to the increasing of specialization of the faunal elements (Kahlke et al., 2011) and to a drastic change in the carnivors guilds, especially in dogs and hyenas. In fact, the name Wolf event indicates the entry of the modern dog (represented by *Canis etruscus*) into Europe, which ended the Pliocenic dominance established by the raccoon dogs and foxes (Azzaroli, 1983; Agustí and Antón, 2002).

During all these climatic phases and faunal turnover, the genus *Ursus* does not seem to show great morphological or philetic changes and, despite the scarce presence of fossil data, it is represented by only two species for almost a million years: *U. minimus - thibetanus* before and *U. etruscus* after.

As shown in figure 32, although there is a change in the arrangement of the canids and carnivores, the distribution of the bear remains rather unchanged and, for the entire last phase of the Early Pleistocene a single species is described in the European deposits: *U. etruscus*.

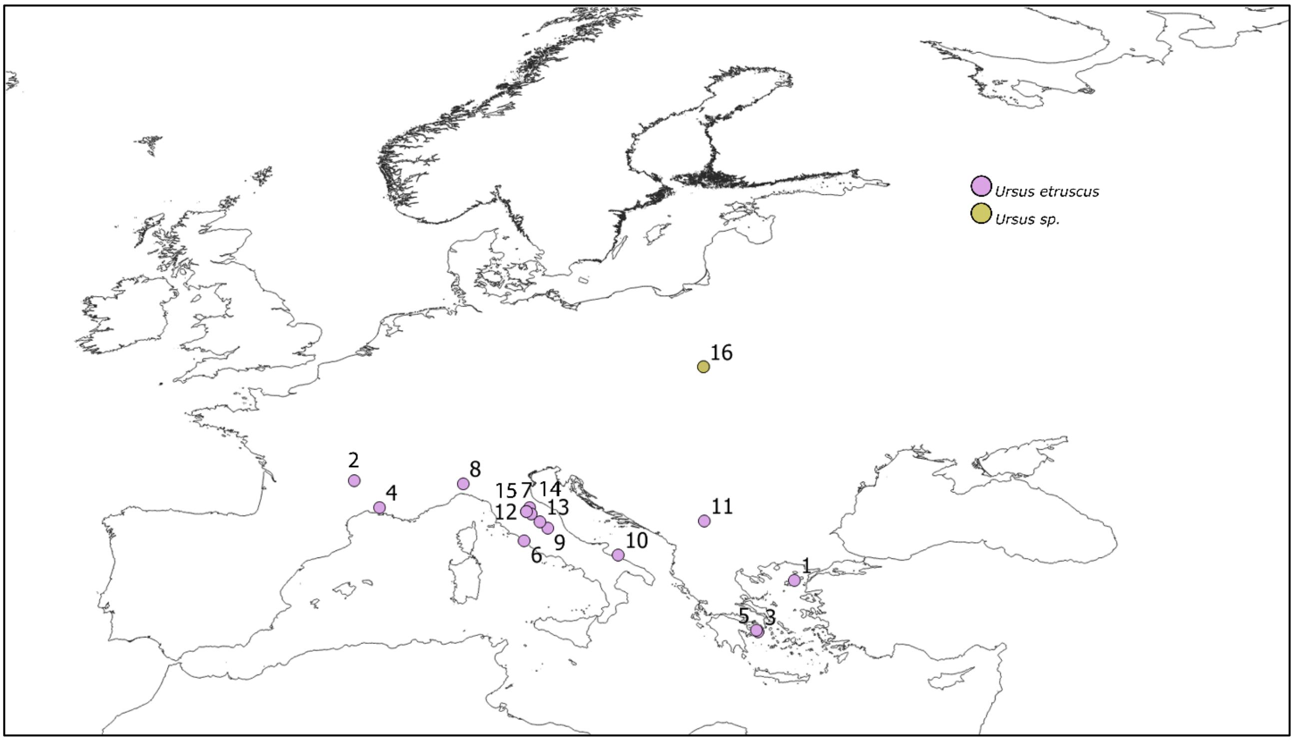


Figure 32: ***Distribution of the Ursidae during the end of Late Villafranchian.*** *(Deposit list in the Supplementary Information, Table 10).*

Most of its distribution, however, is relegated almost exclusively in the Mediterranean area. The most significant specimens have been found in Italy, especially in Tuscany and Apulia (Olivola, Pietrafitta and Pirro Nord), in France with the deposits of Blassac La Girondie and La Sartanette, Porch d'entrée, and in Greece in Apollonia and Makinia.

As already mentioned in chapter 2 the passage from *U. etruscus* to the forms of Ursid of the Pleistocene is highly debated. Mazza and Rustioni, (1994), according to Zapfe, (1948), consider *U. etruscus* as an extinct line and that the *U. arctos* lineage originates from some forms of the Asian *minimus-thibetanus* group. On the contrary, much of the scientific community consider it as the common ancestor of both the arctoid and spleloid line (See Cap.2).

During my work I had the opportunity to quickly observe only material from the Valdarno area and therefore I do not have the necessary data to reach conclusions supported by scientific observations.

Nevertheless, analyzing the distribution, I agree with the first hypothesis, since it seems that *Ursus etruscus* is gradually moving towards lower latitudes (maintaining a wide longitudinal distribution) at the end of the Villafranchian, maybe in order to look for that condition of milder climate and forest that characterized the Middle Villafranchian.

As has been mentioned several times during this thesis, the evolutionary history of the brown bear is recent (Pleistocene). Its origin must be "searched" at the end of the Early Pleistocene when the climate was characterised by a more or less uniform alternation of global temperatures. This led, for the first time, to a clear-cut faunistic specializations, dividing the large mammal world into assemblages of various forested habitats and those of open landscapes (Kahlke et al., 2011).

In fact, global temperatures begin to fluctuate, and specialised areas with ecosystems ranging from wet temperate to hot arid are formed throughout Europe, giving rise to an increasingly diverse faunistical variety called Epivillafranchian biochrone (Kahlke et al., 2011; Bellucci et al., 2015).

This climatic condition is set in the time interval from 1.2 ky to 0.9 ky and it is a moment of transition in which not only the climate is subjected to a drastic warming during certain phases, but also begins to change the regime of cyclicality that changed from 41 ky, to 100 ky (Kahlke et al., 2011).

In this diversified context, the history of the modern bear begins, and the first form with arctoid characters are described in European deposits. Alongside the brown bear, also the spread of the speloid lineage with the first forms of *U. deningeri* began. *U. etruscus* is still present but only with few deposits, and disappear during the passage Epivillafranchian-Galerian, which also marked the beginning of the Middle Pleistocene.

In the Epivillafranchian deposits, paleontologists found diversified forms, such as *U. dolinensis*, *U. rodei* (which deserves to be reviewed, since its taxonomic condition is still dubious), (Baryshnikov, G. and Boeskorov, G., 1998; Olive, 2006; Rabeder and Withalm, 2006; Moigne et al., 2009; Wagner, 2010) and *U deningeri* in central Europe Fig. 33.

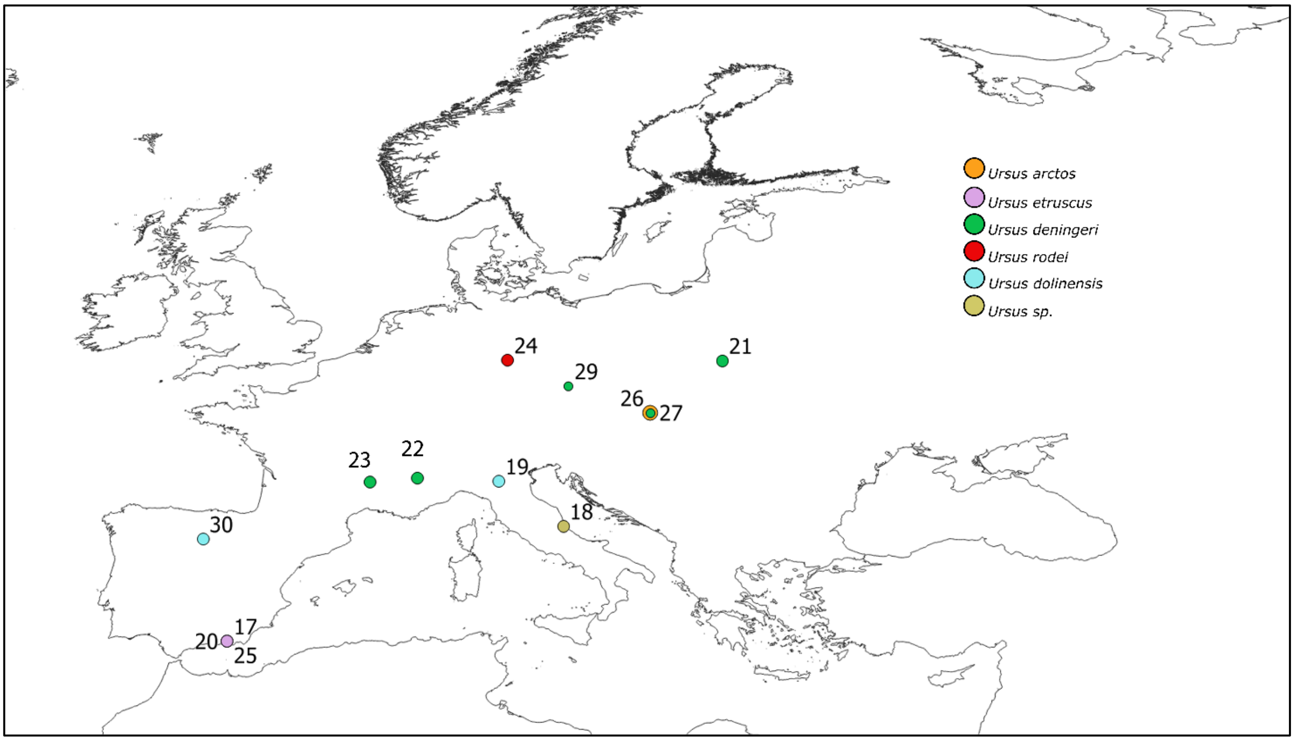


Figure 33: ***Distribution of the Ursidae during the Epivillafranchian – Galerian****. (Deposit list in the Supplementary Information, Table 10).*

During the end of the Early Pleistocene the sites with finds related to the genus *Ursus* are very limited, and many of these forms are represent by fossils with ambiguous characters and subjected to constant taxonomic changes by scientists.

Among these, a noteworthy site is certainly Deutsch-Altenburg, where the first presence of the brown bear in Europe is reported. As previously discussed, although this material has been studied in depth by Rabeder et al., (2010) the whole scientific community does not totally agree with them, keeping a question mark on the first presence of *U. arctos* in Europe.

5.3 Early Middle Pleistocene and Middle Pleistocene

During the early phases of the Middle Pleistocene, global temperatures suffers a drastic decline, followed by a series of glacial pulsations; in this scenario, the ice caps start to grow, whit the subsequent covering of much of the northern hemisphere.

The vegetation also starts to change; in continental areas an environment of steppes and coniferous forests becomes established, while a more thermophilic vegetation persists only in the Mediterranean regions.

This period is also characterized by a lot of eustatic oscillation following the glacial-interglacial dynamics. The sea level drops about 150 m. in some regions, creating natural bridges between the various continents, facilitating numerous migratory flows.

A peculiar effect of the lowering of the sea level during the cold phases, and its the subsequent reinvigoration during the warmer periods, characterized the typical faunas of the Mediterranean. In fact, thanks to the development of ephemeral tongues of land, the continental faunas immigrated inside the islands remaining blocked. This isolation produced a series of typical endemic island faunas that are now found in Mediterranean deposits (Corsica, Sardinia, Sicily, Malta, Crete and Cyprus).

Despite the endemic faunas, most of the large mammals that had appeared at the end of the Early Pleistocene persisted, characterized by: *Elephas antiquus, Stephanorhinus hemitoechus, S. kirchbergensis, Bison schoetensacki, Sus scrofa, Crocuta crocuta, and Macaca sylvana*. However, other genera from the Early

Pleistocene disappeared, such as the large sabertoothed cats of the genus *Megantereon* (Agustí and Antón, 2002).

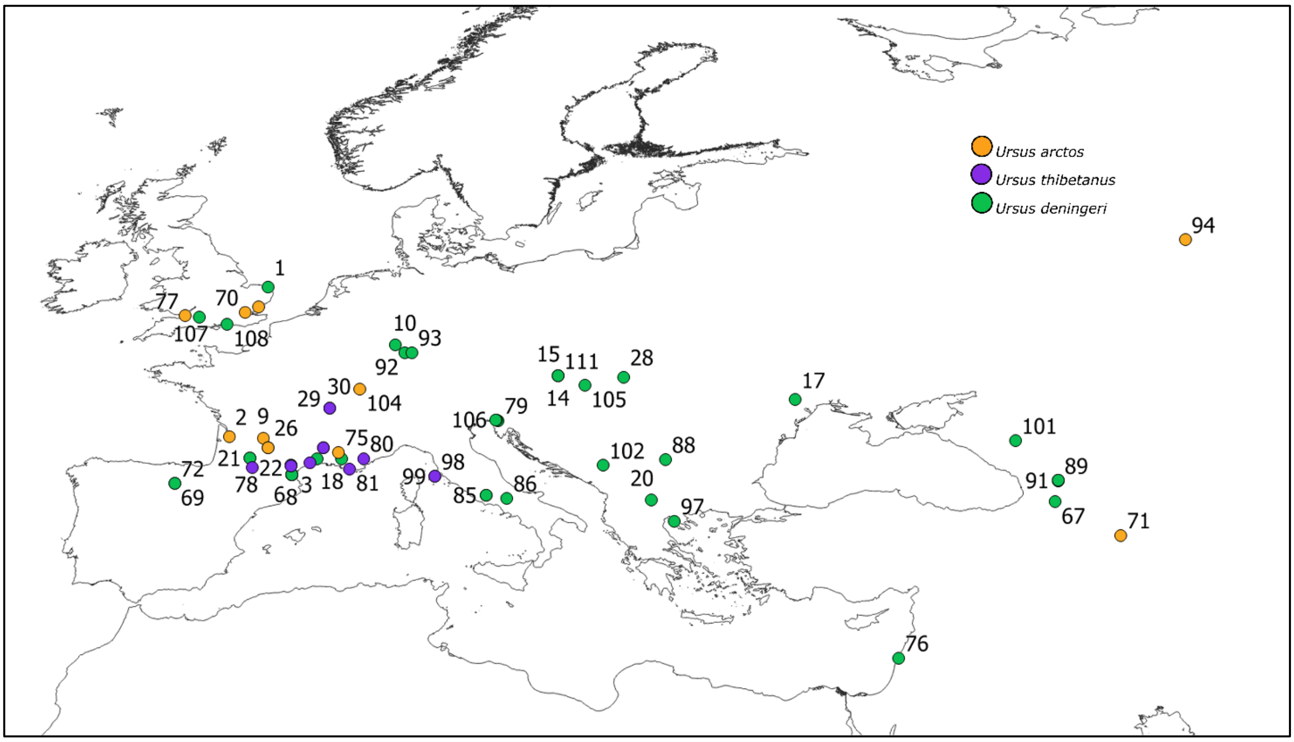


Figure 34: ***Distribution of the Ursidae during the Early Middle Pleistocene – Middle Pleistocene.*** *(Deposit list in the Supplementary Information Table 11).*

The most represented species are still *U. arctos* and *U. deningeri*, flanked by Asian black bear (*U. thibetanus*) that reappears in Europe for a short time (Mazza and Rustioni, 1994).

The first two species are often described in the various deposits togheter, giving the impression that the two different ecological habits (herbivorous and omnivorous) starts to emerge during the first portion of the Middle Pleistocene.

5.4 Late Middle Pleistocene

Starting from the isotopic stage 11 (late Middle Pleistocene), temperatures begin to rise, entering the so-called "last interglacial period", which will culminate with the increase of maximum optimum climate during the Eemian (isotopic stage 5e, at the beginning of the Late Pleistocene)At the middle latitudes, the summer temperatures were about 2°C higher than today, and the global sea level was about 4 to 6 m higher. In northern Europe, the glaciers were also less developed than today, and the vegetation consisted mainly of a broad-leaved/mixed forest dominated by oaks.

A new Mammal age begins, the Aurelian, during which the taxa which constitute the nucleus of the present faunas, appear. Those changes involved species adapted to a forest, open spaces and intermediate environments. The mammal communities became more and more similar to the modern ones, with the decrease of species of great size and the increase of those of medium or small size. This period culminates with the exotic Eemian faunas, testified by the presence of hippopotamuses, lions and monkeys in the European deposits.

We have very little information about the genus *Ursus*; the main cause is the lack of deposits with sure datings, the scarce presence of specimens and the taphonomic condition of the deposits (Fig 35).

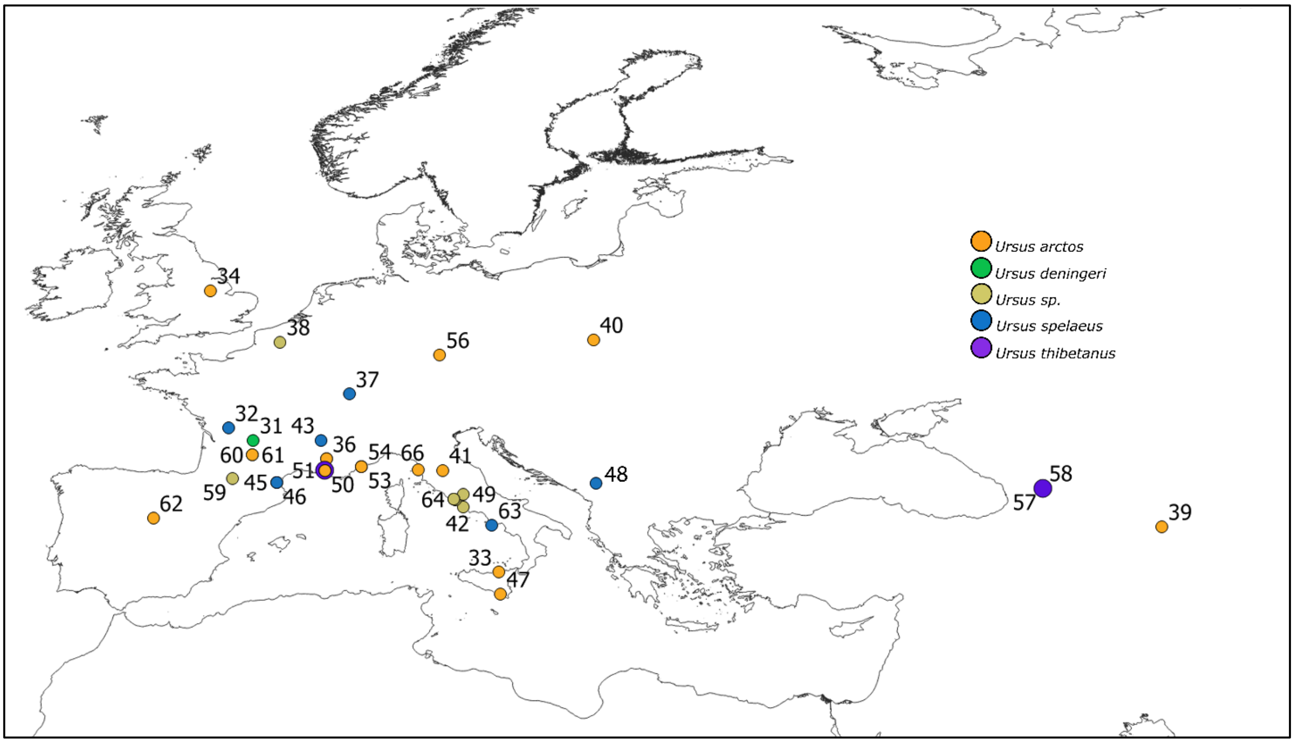


Figure 35: ***Distribution of the Ursidae during the Late Middle Pleistocene.*** *(Deposit list in the Supplementary Information Table 11).*

Despite this, the general distribution is still homogeneous, with remains in Spain, France, Germany, England and Italy. During this period, however, two important changes take place: the first is the gradual disappearance of the Asian black bear (*Ursus thibetanus*) whose remains only in two sites relicts far apart from each other (Grotta des Cedrès in France and Kudaro 3 in Southern Ossetia). The other important element is the beginning of the presence of *U.* ex gr. *spelaeus*.

In fact, the end of the Middle Pleistocene, is the moment in which the purely speleoid characters manifest themselves in *U. deningeri,* which gradually evolved in the real cave bear. At the same time, the material of *U. arctos* is still represented by few specimens in comparison with the speloid lineage but still evenly distributed throughout becomes fewer and fewer in European deposits.

Despite this, fossils of both lines continue to be found often within the same deposits (e.g. Caves du Lazaret CIII in France and Hundsheim in Wienn) showing once again an increasingly clear distinction of ecological niches and a sharing of the territory by the two species.

5.5 Late Pleistocene (Early Glacial - Periglacial)

Immediately after the climatic optimum represented by the Eemian, the climate conditions changed rapidly, and a sharp cooling started a new glacial phase 115,000 years ago. Between 115,000 and 75,000 years ago, several fluctuations occurred as a succession of stadial (cold) and interstadial (temperate) minor pulses in the context of this glacial phase (Early Glacial).

In fact, the marine isotopic profiles show two very marked climatic deterioration: the first at the passage from the OI substage 5e and the second at the end of the OI stage 5. The terrestrial data show a significant decrease in the sea level on the coasts of Norway already in the final phase of the Eemian (Middle-Late Pleistocene passage), suggesting that the glacial masses began to increase in volume even before the end of the last interglacial era.

The further development of the glacial coulters is evidenced by an eustatic lowering of the sea level of about 60m at the passage from the top of the OIS 5e to that of the OIS 5d Fig. 36.

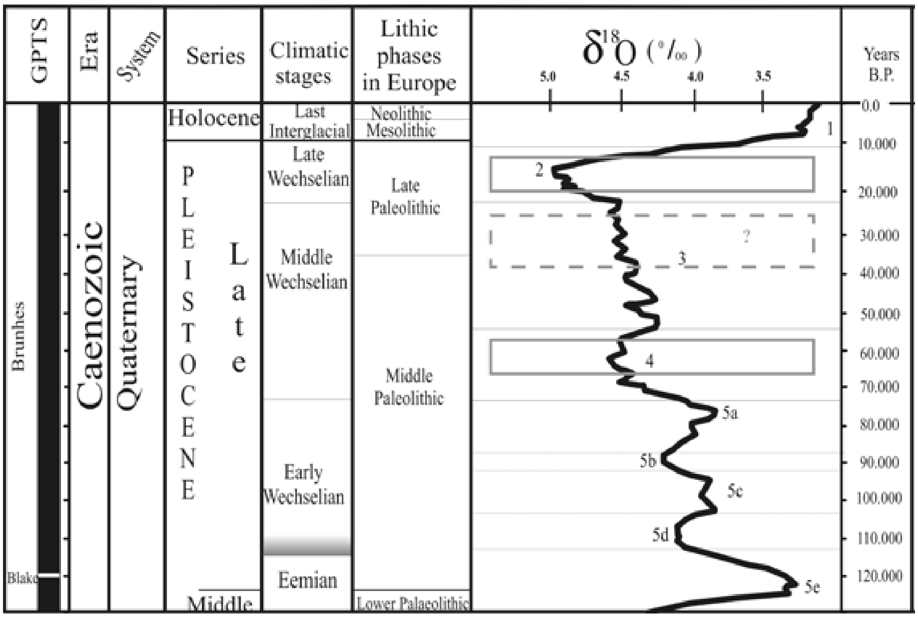


Figure 36: ***Correlation between the Climate stages and the oscillation of the Ossigen Isotopes.***

Subsequently, temperatures decrease further from isotopic stage 4, to the isotopic stage OIS2, reaching the true glacial maximum. Terrestrial data show that in this period the temperatures of Northern Europe should not exceed 10 ° C.

The data (based mainly on pollen sequences) show that in this cold period, there is the existence of different interstadial episodes of short duration, with relatively milder climates, in which the dry steppe vegetation is replaced by the dwarf shrub tundra.

During this climatic phase, the typical faunas of the Eemian, such as the Hippopotamus, the elephant and the rhinoceros, began to disappear, while horses and deer continued to characterise much of the European territory. Important is the appearance of the woolly rhinoceros, *Coelodonta antiquitatis* which, together with the presence of *Mammuthus primigenius*, testifies to the establishment of steppe environments and the rigidity of temperatures.

This mixture of steppe and tundra elements also highlighted by small mammals, as reflected by the coexistence of marmots, susliks, and jirds with lemmings. Among the carnivores, most of the Middle Pleistocene species survived into the Late Pleistocene, although represented by larger and more robust "cave" variants that are often described as separate species or subspecies (e.g. *Crocuta Crocuta spelaea* and *Phantera spelaea*) (Agustí and Antón, 2002).

Also in bears it is registered a considerable increase in size, especially in the cave bear that reaches the largest size during the glacial maximum).

The brown bear also shows an increase in size. But, as already widely described in chapter 2, unlike the cave bear, these trend tend to decrease rather than increase, showing first larger archaic forms (*"U. arctos kamiensis"* Vereshchagin, 1959) and then less robust forms (*"U. arctos priscus"* Goldfuss, 1818) (Marciszak et al., 2015).

With regard to the bear distribution, it can be observed that it remains constant in Central Europe, even if, during the coldest phases, their presence at higher latitudes decreases leaving only a testimony in the deposit of Brown Bank (Denmark) (probably due the taphonomy condition of the deposits).

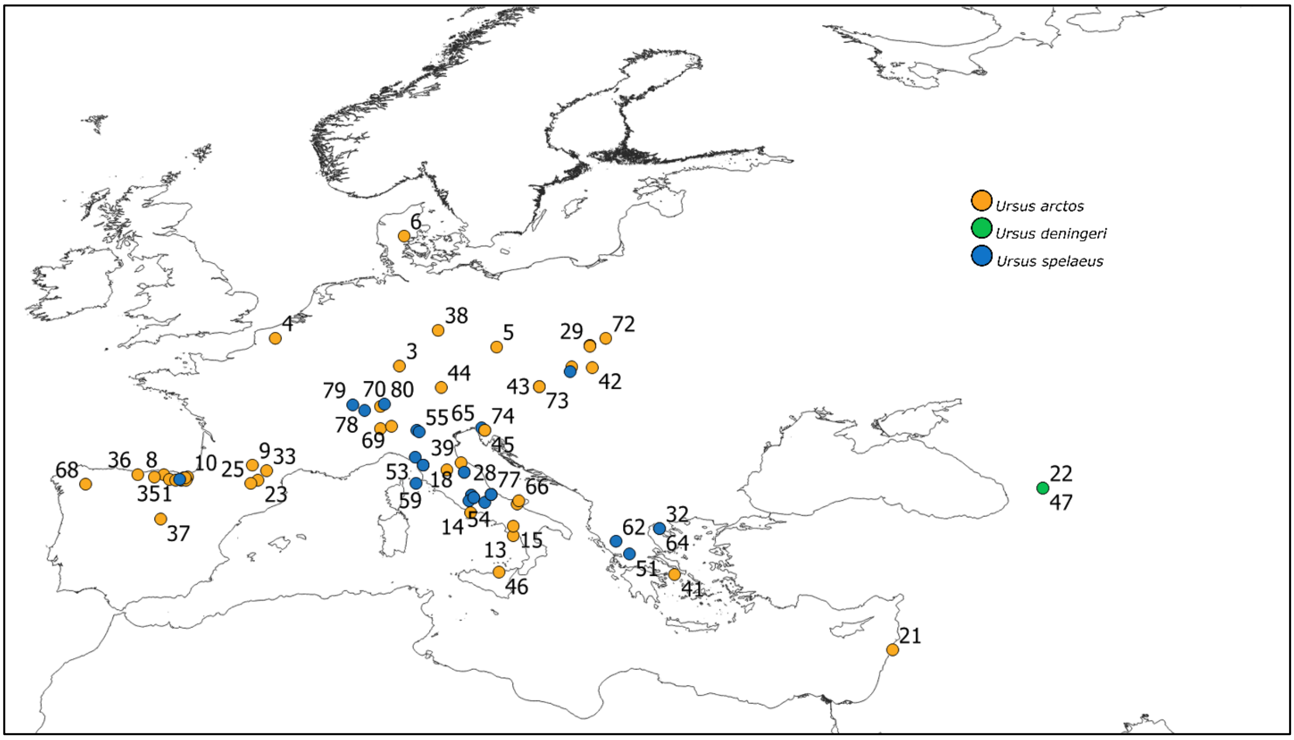


Figure 37: ***Distribution of the Ursidae during the Late Pleistocene and Periglacial (Ia).*** *(Deposit list in the Supplementary Information Table 12).*

In general, the findings of *U. arctos* increase (also thanks to the greater quantity of deposits of this period) as showed by the Fig 37. It is good to underline that this map presents most of the bone elements of brown bear (focus of this thesis) while it does not record all the material referable to *U.* ex gr. *spelaeus* that is extremely more abundant.

Barhisnikov, (2002, 2012) described *Ursus deningeri* only in Caucasus during the Late Pleistocene, found in different deposits with different age. those specimens are referred to the lineage *U. deningeri prekudarensis-U. deningeri-U. d. kudarensis*. Brown bear remains have been also described by the same author from the area and attributed to *Ursus arctos binagadensis* (point 22).

As mentioned before in regard to "*U. arctos priscus*", the use of subspecies for fossil material has to be avoided. For this reason, the names *U. arctos* and *U. deningeri* (or *U.* ex gr. *spelaeus*) are more suitable for those specimens.

Otherbrown bear specimens are found in numerous deposits in Spain, Germany, France, Italy, Greece and in many karst areas in Eastern Europe. Despite the abundance of sites, the specimens related to *U. arctos* are often very few in comparison to those related to *U.* ex gr. *spelaeus* and, most of the cases, are represented only by post cranial remains or fragmented portions of skulls and mandibles; such a condition is related to the taphonomy of the deposits and the different ecology of the two species. Infact, brown bears use to live more on open air sites where the fossilization conditions are worst than in caves, place where cave bears use to live and die.

5.6 From the Late Maximum Glacial to the rising of the temperatures

The Pleistocene glacial phase culminates in the OIS 2 isotope stage (23 000-18 000 years ago (Kukla et al., 2002) and is the coldest moment of the entireLate Pleistocene. It is called LMG (Late Maximum Glacial).

At this time, much of Northern Europe was covered with ice, and the global vegetation is reduced even more, establishing, throughout the European territory, a steppe biome dominated by Artemisia, Gramineae, and Chenopodiaceae.

Most of the European Pleistocene fauna is relegated to various areas of southern Europe (such as Spain, Italy and Greece) which constituted real glacial shelters (Bennett et al., 1991; Taberlet and Bouvet, 1994; Hewitt, 1996), while faunas adapted to more rigid climates such as mammoths and woolly rhinos continued to dominate the central European territories.

Despite the possibility of moving to more temperate areas, the lack of vegetation and the increasingly massive presence of arid and almost desert environments (Martini et al., 2014) in the European territory, has meant that the last Late Pleistocene was a period of many "Last Occurrence", including *Homo neandertalensis*.

One of the most important extinction is undoubtedly the one of of *U.* ex gr. *spelaeus* , which desappeared in the Alps and adjacent areas around c. 24 000 years BP, approximately coincident with the start of GS-3 (Pacher and Stuart, 2009).

In Italy the last evidence was dated to 22,760 ± 130,14 yr BP obtained by radiocarbon-dating analysis on the Chiostraccio Cave (Siena, Tuscany, central Italy) specimens.

The causes were initially attributed to the reduction of the genetic flow (Hewitt, 1996; Taberlet et al., 1998; Randi, 2003; Rowe et al., 2004), by surviving in small, restricted and separate populations (Musil, 1980; Hofreiter et al., 2002; Valdiosera et al., 2007) (bottleneck effect).

This hypothesis was then refuted by the work of Hofreiter et al., (2002), which observed that the mtDNA diversity in cave bears was similar to the diversity observed in current brown bear mtDNA gene pools. So, without the evidence of a genetic impoverishment in final cave bear populations, decreasing resource availability during the beginning of MIS 2.

Although the discussion on glacial shelters is still extremely representative for Europe during the glacial maximum, some studies have shown that not all tempearate fauns and floras disappear at the highest latitude during this time of maximum cooling (Sommer and Nadachowski, 2006; Magri, 2008).

Among these faunas, there is also the brown bear which, despite undergoing a drastic thinning of its areal, survived both in mainland southern Europe, but is still uniformly distributed throughout Eurasia, as demonstrated by findings in England (Paviland Cave), Austria (Willendorf II, Grubgraben), France (Duruthy, Harzabaletako Karbia, Oilascoa, Le Rond du Barry), Slovakia (Moravany Lopata II) and Moldova (Ciuntu) (Fig 38) (Valdiosera et al., 2007; Davison et al., 2011). The scarcity of the fossil remains could be linked to different taphonomic conditions in comparison of other periods, and therefore the distribution of the species could be wider than those showed in the pictures.

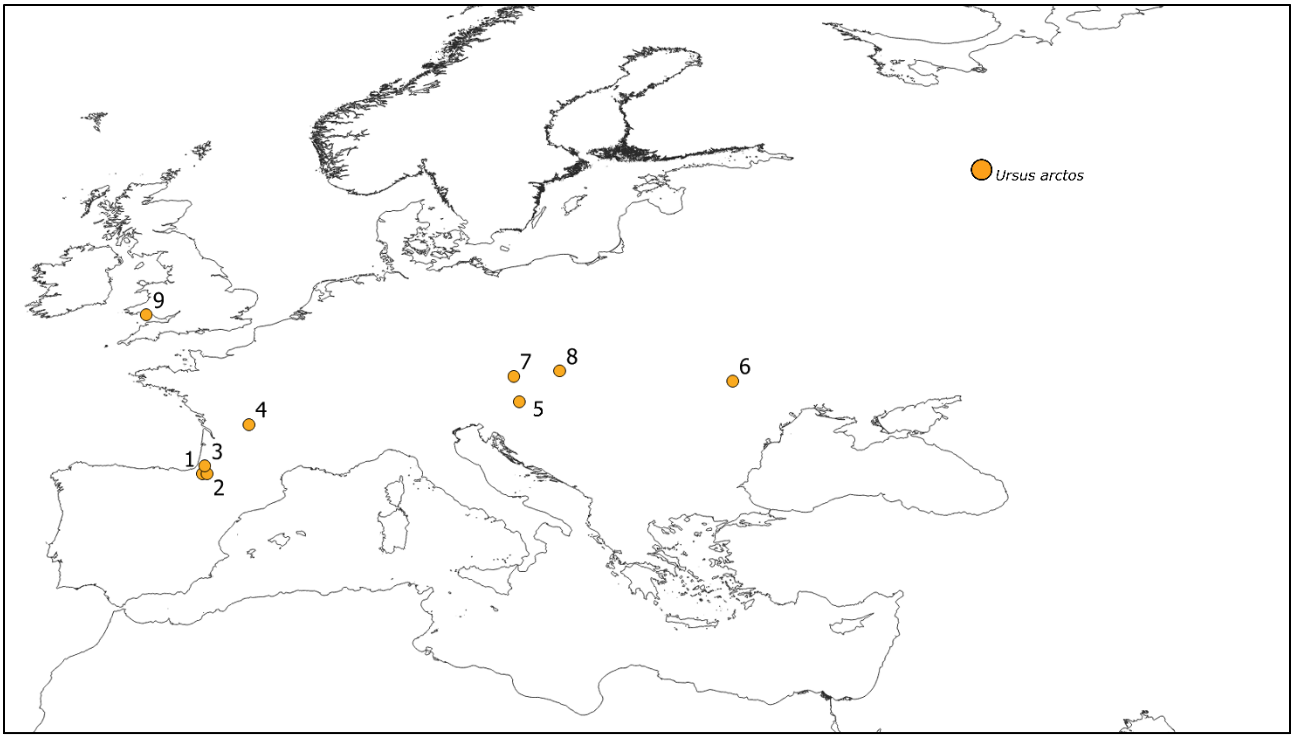


Figure 38: ***Distribution of the Ursidae during the Late Maximum glacial.*** *(Deposit list in the Supplementary Information Table 13).*

At the end of the last glacial period, 14,000 years ago, the ice sheets started to retreat once again, and a new interglacial phase started. In Eurasia, the steppe-tundra, the original habitat occupied by many of the Ice Age animals, split and became decimated (Agustí and Antón, 2002).

This climate recovery leads to the extinction of numerous species adapted to cold climates (such as mammoths and woolly rhinos) that survive until the end of Dryas III (8,300 ky ca) leaving a large part of European territory to species adapted to a temperate climate or forest.

In this moment, also the brown bear begins to be extremely more diffused, definitively colonizing also the highest latitudes, and representing, after the extinction of the cave bear, the only species of the genus in Europe (without obviously counting the presence of *U. maritimus* in the arctic cap) Fig 39.

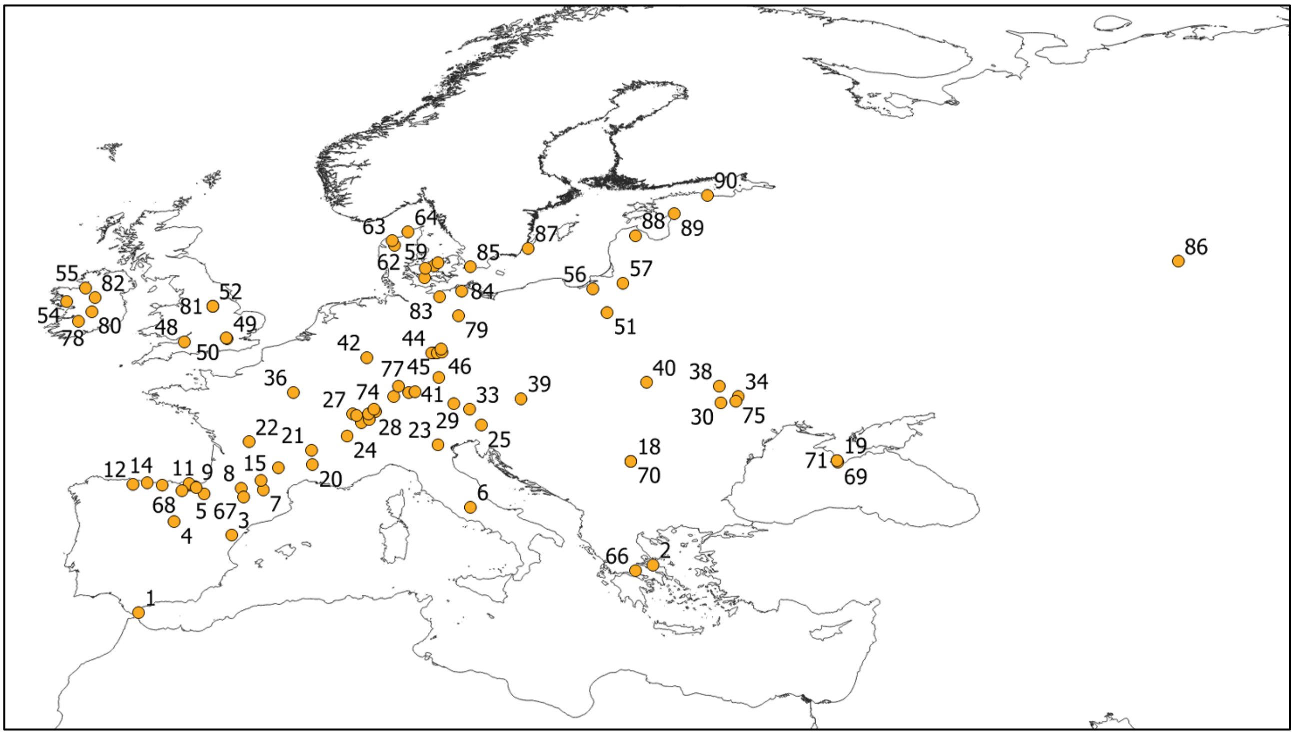


Figure 39: ***Distribution of the Ursidae during the Late Glacial and Pre-Boreal.*** *(Deposit list in the Supplementary Information Table 14).*

In fact, from the beginning of the Holocene, the brown bear begins to be much more present in the deposits of all Europe, expanding its area to the east, touching the southern coasts of Spain on the Strait of Gibraltar (Devil's Tower, Bate 1928), to the north with the populations of Ireland, Great Britain and Denmark, and it maintain a discreet presence in Eastern Europe.

In Italy there are not many finds, and the only specimen well documented is the one found in the deposit of the Cave of Beatrice Cenci (Valdiosera et al., 2007; Agostini et al., 2009).

5.7 The Holocene

The following time spam, which goes from 7.000 to about 5.500 ky BP, takes the name of Atlantic, and corresponds to a very hot period, defined by various authors as "Post-Glacial climatic Optimum", in which are recorded the highest temperatures which have ever occurred in the Holocene.

Evidence of this warming can be found in Denmark, with the expansion of the northern range limit of *Emys orbicularis*, and *Mitilus edulis* in Greenland and of the Hazel(nut) in Scandinavia (*Corylus avellana*). The temperatures suddenly increased between 5° and 7°C, and the sea rose about 120 m to its present level. An uninterrupted belt of coniferous trees (the taiga), extended throughout Europe and eastern Asia.

Despite the increase of temperatures, the European distribution of the bear decreases Fig. 40. Separate nuclei are recorded in Germany, central Italy and France, while it remains fairly evenly distributed in the Balkan peninsula.

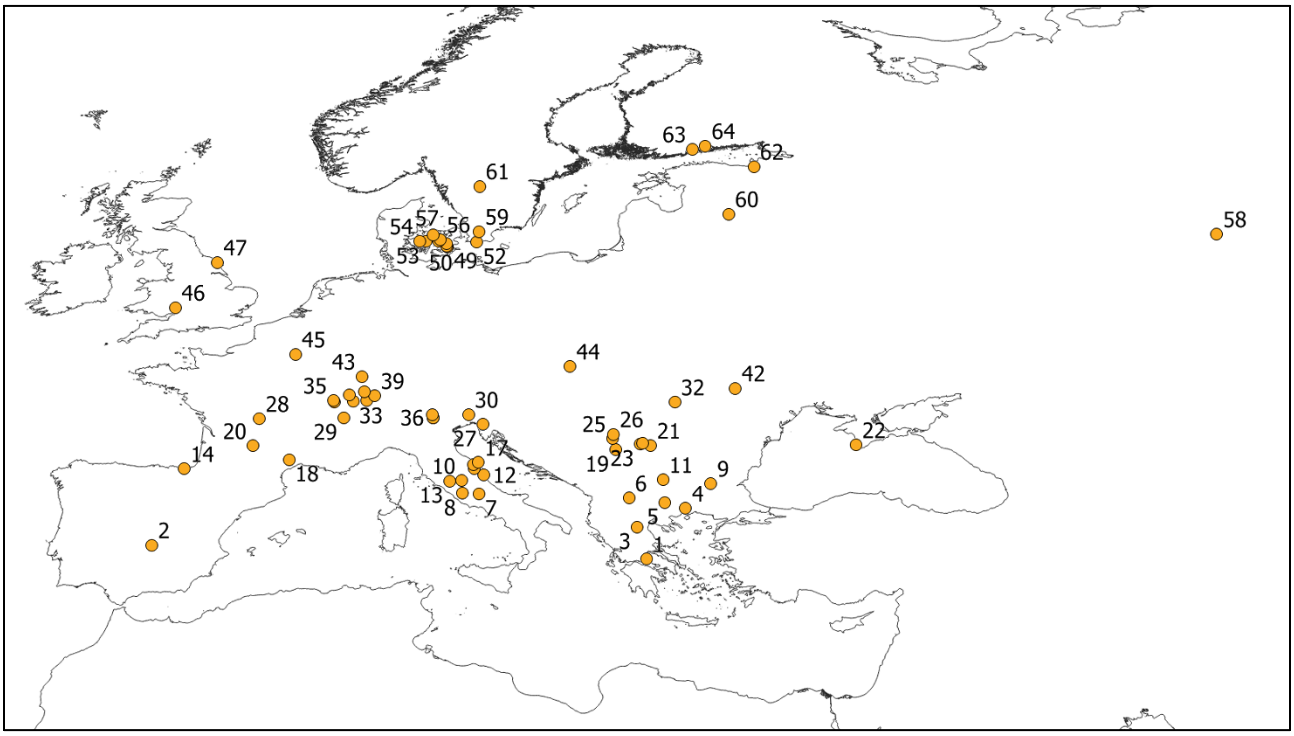


Figure 40: ***Distribution of the Ursidae during the Atlantic (7.000 – 5.500 ky BP).*** *(Deposit list in the Supplementary Information Table 15).*

After this period of optimum climate, the general temperatures in Europe are falling again and, with them, a slightly drier and colder climate is emerging.

This moment, which is between 4,000 y and 1,000 y BP, shows an increase in the distribution of the area of the brown bear that returns to be extremely abundant both in the territories of Central and Eastern Europe reaching its maximum expansion, especially in the Italian territory and in the Alps Fig 41.

This peculiar oscillation of the bear's range, for which, during colder periods, it increases and decreases during warmer periods, is certainly linked to an anthropic factor (Zedrosser et al., 2011; Wolf and Ripple, 2017); in fact, an increase in temperatures allows the exploitation of many areas previously inhospitable by man, with the consequent reduction of many of the local faunal populations.

Despite this, some of the causes are linked to an ecological factor typical of the bear. Studies on recent populations have shown that the bear, being an animal that hibernates, consumes much of the energy accumulated in summer during the winter period (Humphries et al., 2002).

Paradoxically, bioenergetic models predict that energy demands of hibernating mammals increase during warm winters, because the energetic costs of torpor increase (Humphries et al., 2002).

This factor inevitably affects the physiological and reproductive aspects of the animal, making it extremely less active during mild winters (Albrecht et al., 2017).

The presence of a prolonged period of mild winters would therefore have affected the suitability of the bear during the hot phases and instead re-established a demographic increase during the subsequent lowering of temperatures.

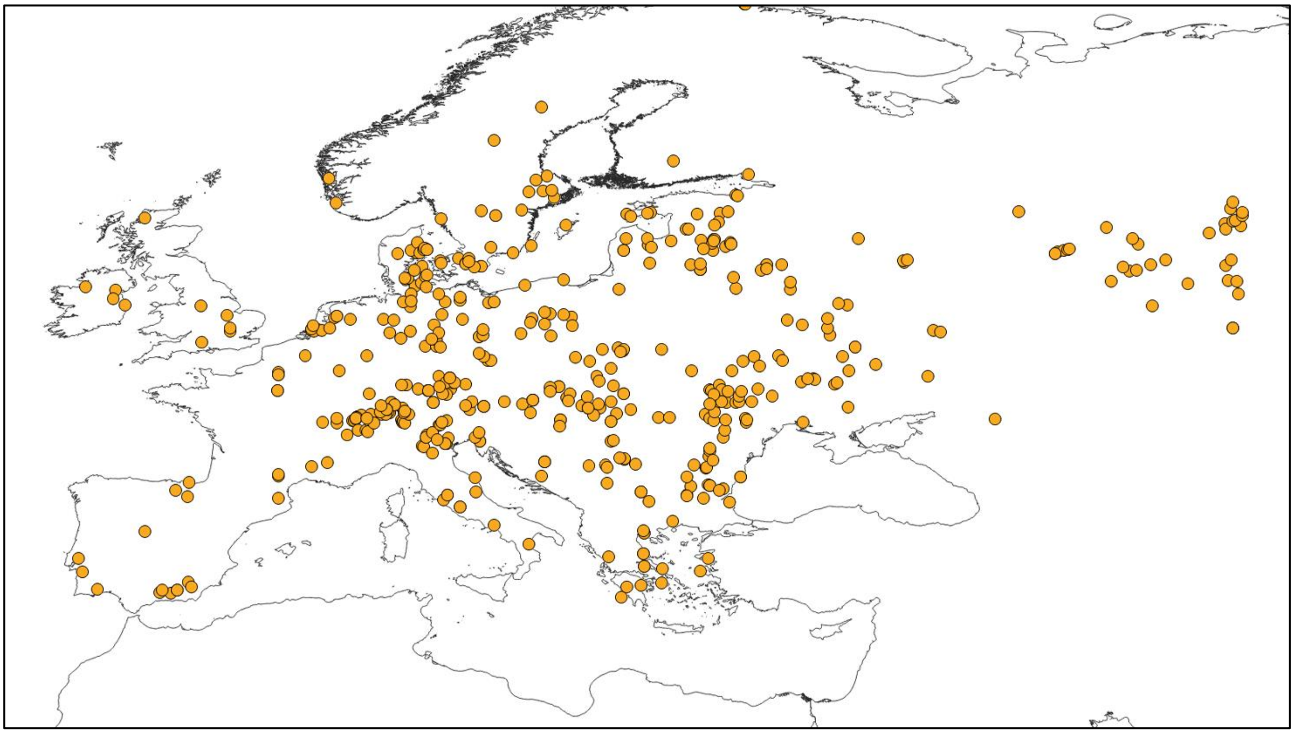


Figure 41: ***Distribution of the Ursidae during the Holocene until Recent (5.500 – 0).*** *(Deposit list in the Supplementary Information Table 16).*

Finally, the last crucial moment for the distribution of the European mammal fauna coincides with the last significant climate change that characterizes global temperatures about 1,000 years ago. Since the sub-Atlantic period, the climate has tended to improve, with a mild phase and an increase in average annual temperatures of a few degrees compared to today.

But it is not only the climate that determines many of the distributions of European wildlife. During this time, in fact, the foundation for the Roman civilization is established and with it the demographic increase of man. The results were: increasing in deforestation, more intense hunting and constant introduction of exotic species, captured by the numerous Asian and African colonies (Alroy, 2001; Stuart et al., 2004; Lorenzen et al., 2011).

This expansion of man also drastically affects the distribution of the brown bear, which is slowly relegated more and more in the areas of Eastern Europe, while it tends to disappear in the main anthropized territories Fig 42.

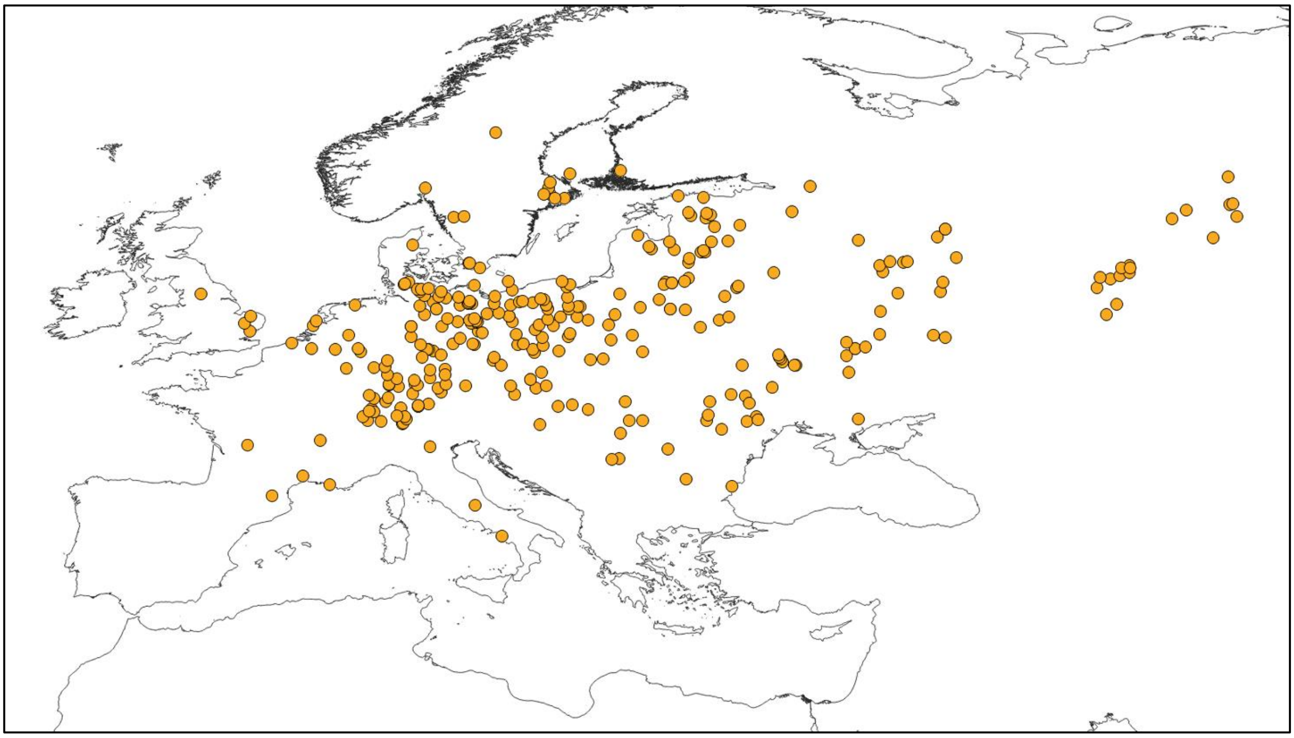


Figure 42: ***Distribution of the Ursidae during Recent period (0 – 1.500 DC).*** *(Deposit list in the Supplementary Information Table 17).*

5.8 Final remarks

From the study carried out it is easy to observe that the brown bear is a young species compared to some other extant carnivorian mammals, which had its maximum distribution during the last Late Pleistocene and, even more, during the Holocene, representing one of the most adaptable species in Holarctic ecosystems. Infact, its distribution has not suffered strong changes, even during the most drastic climatic variations or the most evident moments of faunistic turn over.

This factor can be justified by the flexibility of their diet, which can vary from nearly strict vegetarian to full carnivore, which has made it possible for this large mammal to exploit a wide spectrum of ecological niches. Despite this, it is good to consider that it is not certain that the forms of the Late Pleistocene are the direct ancestors of the populations after the Ice Age (Davison et al., 2011). In fact, some authors suggest (Zapfe, 1948; Mazza and Rustioni, 1994) that several times there may have been a recolonization of Europe by arctoid forms from Asian territories, a model that would also explain the replacement of the etruscan bear during the Late Villafranchian.

Today, the distribution of the bear in Europe is smaller than in the Pleistocene and Holocene Fig. 43 and divided in into two main mitochondrial lineages: Clade 1 and Clade 3 (Leonard et al., 2000) Fig. 44.

Figure 43: ***Present distribution of the brown bear (Ursus arctos L. 1758) in Europe***.
(http://ec.europa.eu/environment/nature/conservation/species/carnivores/conservation_status.htm)

The first one is composed of two subgroups, one believed to originate from the Iberian Peninsula, including southern Scandinavian bears and the Pyreneean populations (1a), and the other from the Italian–Balkan peninsulas (1b) (Taberlet and Bouvet, 1994). The second one is composed of Russian, northern Scandinavian and eastern European populations, and those carrying a western lineage (Valdiosera et al., 2007).

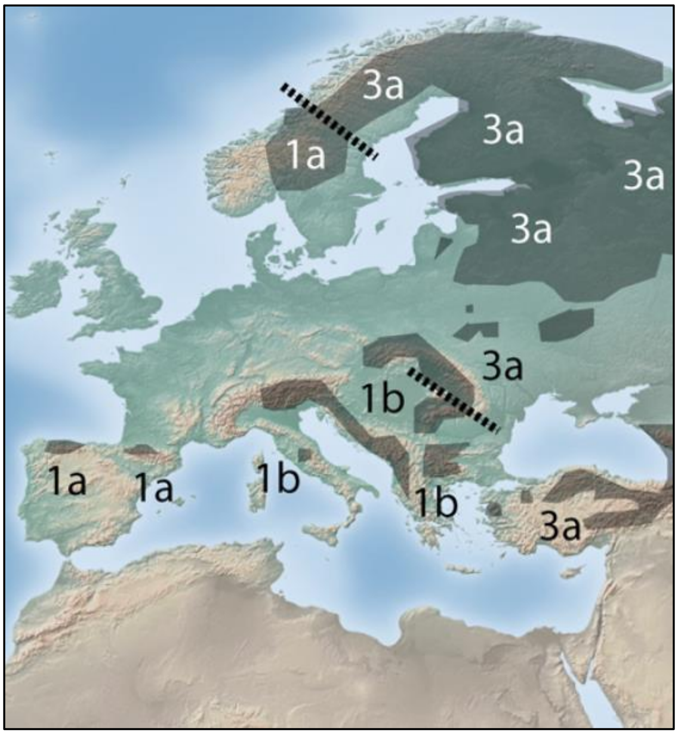


Figure 44: ***Different genetic population of brown bear in Europe.*** *Modified by Davison et al., 2011.*

In addition, a Carpathian refuge has also been proposed, based on the subfossil record in northwestern Moldova and mitochondrial DNA data from modern populations (Sommer and Benecke, 2005; Saarma et al., 2007).

A first hypothesis to explain this situation is represented by subsequent repopulation of the Europe after the Last Glacial Maximum, and that the different genetic traits have been imposed during the isolation in the glacial shelters.

The paleontological data shown in this thesis and recent genetic analyses demostrated that the genus *Ursus,* during the glacial maximum was still well distributed throughout Europe, and that there was still a discreet gene flow between the various populations showing some mixing of currently allopatric subclades 1a and 1b in southern refuge during the LGM (Valdiosera et al., 2007).

According Davison et al., (2011), the appearance of phylogeographical structure in modern brown bear populations may thus be the result of the high degree of female philopatry in brown bears and the severe reduction in population size during the Late Holocene (Servheen, 1990); consequently the different brown bear lineages in Europe would not represent evolutionary significant units and would instead be the result of a recent fragmentation caused by human activities.

6 The brown bear in Italy

The presence of brown bear in the Italian territory is documented since the Middle Pleistocene, as shown in the map proposed in the previous chapter. Many of the finds known today come from the central-southern area, an area that is extremely important regarding the current distribution of the bear in the Italian territory. In fact, as mentioned in the introduction of this work, in Italy two different subspecies lives: *Ursus arctos arctos* (L. 1745) related to the eastern Europe population which lives in the Alps region, and *Ursus arctos marsicanus* (Altobello 1921) distributed in Central Italy in the Appennine region (Ciucci et al., 2017) Fig. 45.

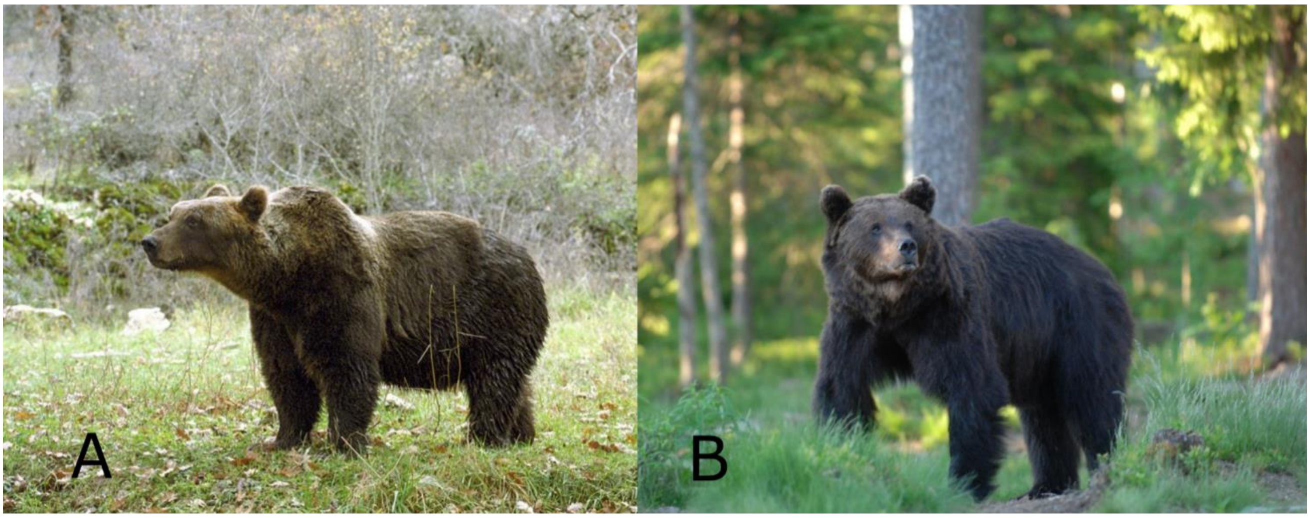


Figure 45: ***Italian brown bear. A) Ursus arctos marsicanus (Altobello 1921),*** *photo from* *http://www.parcoabruzzo.it*. ***B) Ursus arctos (Linnaeus 1758),*** *photo from Repubblica, Archivio servizio foreste e fauna, Provincia di Trento.*

It should be noted that the current population in the Alps, no longer represents the original genetic pool of brown bears that populated the areas of northern Italy in the last century. In fact, this population was decimated during the first half of the twentieth century until it almost reached extinction, and then reintroduced in the 1990s with Slovenian bears. Therefore, today's population can no longer be considered endemic to northern Italy but represents a continuum of the gene pool of the populations of continental Europe.

Instead, the small population of Marsican brown bear was characterized by a prolonged period of isolation. This results in a significant genetic and morphological differentiation from the populations of Alps and the rest of Europe, as already highlighted during the early years of the twentieth century (Altobello, 1921; Conti, 1954). Today, the Marsican bear counts about 60 individuals (55-85) inserted in the IUCN list as Critical Endangered (CR).

Due to its critical condition, the Italian Government established the Abruzzi National Park and for its conservation and monitoring. There are many studies carried out today on its ecological characteristics, but very little is known about the origin and isolation from other populations of this endemic bear and, to understand its adaptation, distribution and anatomical changes, a study of all available fossil material of the area is needed.

6.1 A look at the present

In order to fully understand the variability of the fossil material and to observe if there is a link with today's populations, it is necessary to analyze the morphologies and skeletal variability of these recent populations. Loy et al., (2008) and Colangelo et al., (2012) in their work, already highlighted the distinctive features on the mandible and skull between Marsican and the Alpine bear through analysis of geometric morphometry carried out on two-dimensional images.

Their results show that the Marsican bear is characterized by a wider and narrower skull, with a wider orbital region that forms almost a step in the frontal bone (similar to *U.* ex gr. *spelaeus)* and greater width of the occipital condyles. On the contrary, they described a higher jaw height, an increase in the length of the diastemas (upper and lower) and a more massive upper P4 in the population of Northern Italy.

However, these results are not sufficient to ensure to discriminate whether the fossil belongs to one or the other population (or to a third population that no longer exists).

The cause of this difficulty is always the scarcity of complete material in the fossil record. In fact, most of the material coming from Pleistocene and Holocene deposits is represented by isolated teeth, fragmented or diagenized skulls and incomplete mandibles.

To allow a clear comparison of the fossil material, it Is necessary to first analyze the recent material in more detail (especially in the dental elements) to allow, in a second step, a meaningful comparison of the fossil material.

In this regard, both the skulls and the molariform teeth (lower and upper) were analyzed by direct comparison of morphologies, with the analysis of morphometric data, and finally processed by geometric morphometry.

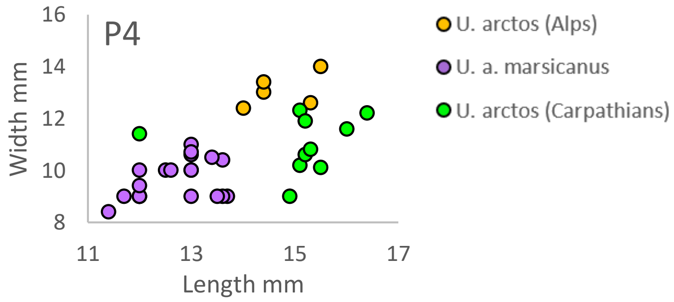
The two elements taken into consideration were treated with different methods; the first through the use of three-dimensional models, while for the second was used a study of two-dimensional morphologies and analysis of morphometric data.

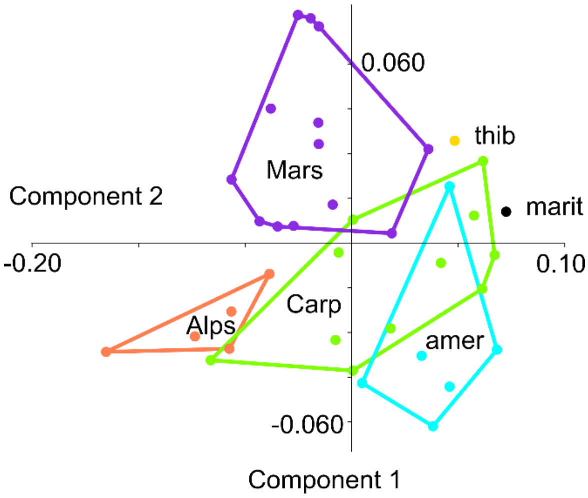
6.1.1 The teeth

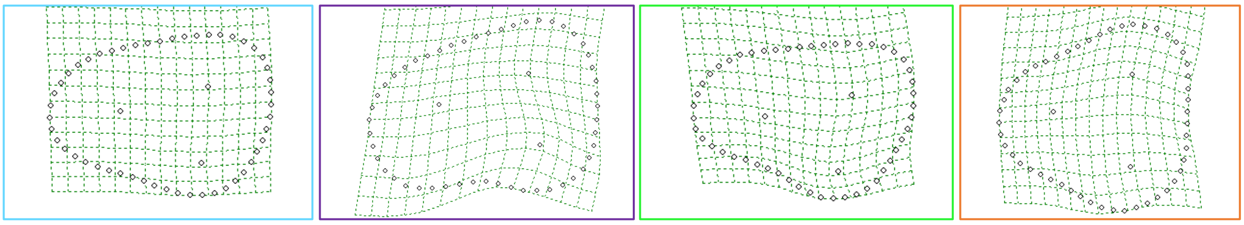
For the morphometric and morphological analysis of the dental elements, I used material coming from three different regions of Europe and representing three distinct brown bear populations currently living (Carpathians, Alps, and Apennines).

As outgroups, I used specimens referred to *U. thibetanus* (C 1546, from the National History Museum, Bratislava and abbreviated as "Thib”), *U. maritimus* (C 1529, from the National History Museum, Bratislava, with the abbreviation “Marit”) and *U. americanus* (C 1730 – C 1731 – C 1734 – C 1735 – C 1736 – C 1737, from the National History Museum, Bratislava, with the abbreviation “Amer”). *U.* ex gr., *spelaeus* has not been insert in the analysis to avoid the division of the plot in two well distinct group and focusing only in the morphological variability of brown bear teeth.

6.1.1.1 *Upper P4*







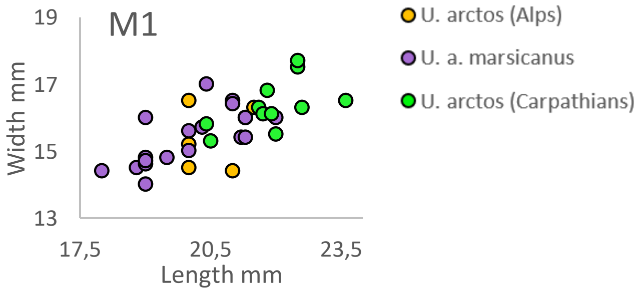
The analysis of the upper fourth premolar has given a rather clear result about the size of the tooth in the various populations, infact, it can be observed that the Marsican teeth are significantly smaller than those of other populations.

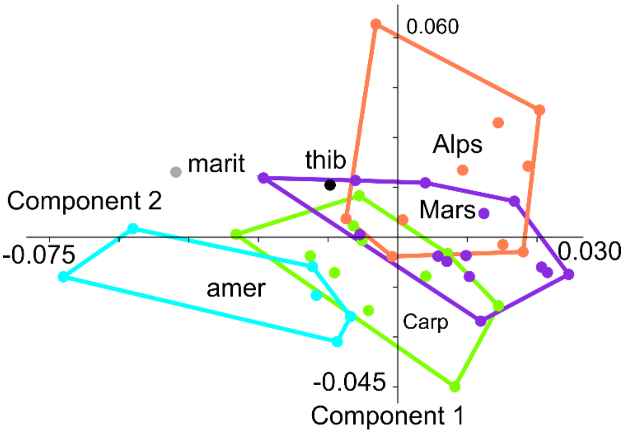
In addition, the graph shows that this tooth, generally in the population of the Carpathians, is longer and narrower than the brown bears in the Alps.

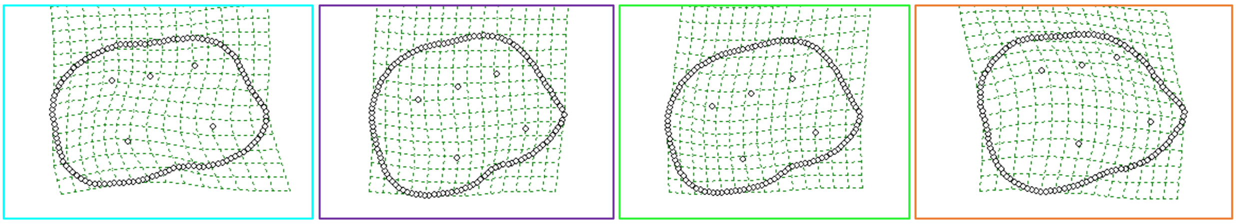
The morphology analysis is perfectly in line with the morphometric data. The first and second main components (64% of the total variability) indicate that the Marsican and the Alpine bears have different morphologies (longer in the first and wider in the second) and that the population of Carpathians remains distant from the other two forms of brown bear, being closer to the general morphology of the American black bear.

As expected, the polar bear and the Asian black bear remain outside the morphology of the brown bear populations.

6.1.1.2 *Upper M1*







The morphometric analysis of the first upper molar shows an extreme variability and a clear overlap of the average size between the various populations.

In spite of this, it is still possible to describe a pattern in which the smaller forms belong to the Marsican subspecies and the larger ones to the carpathian population.

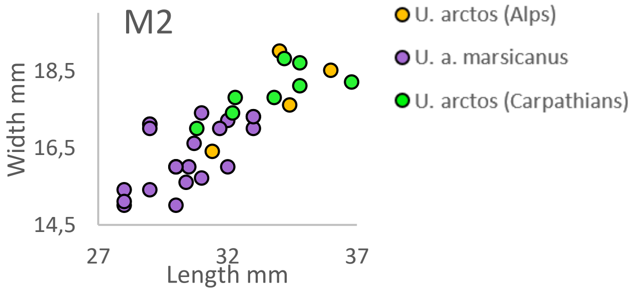
The Alpine bear stands in the middle of the graph, intersecting the extremes of the other two populations considered

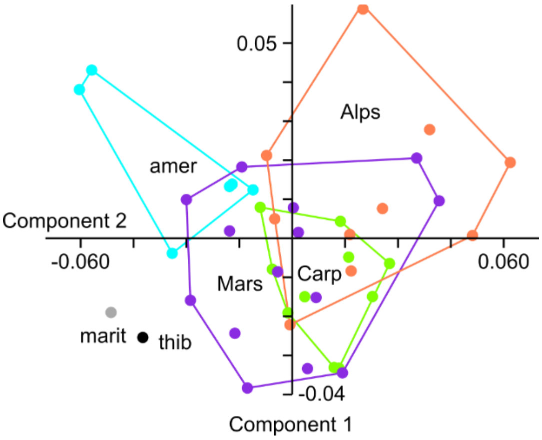
On the contrary, the diagram obtained from the geometric morphometry shows a greater morphological affinity between the Marsican and the Carpathian bear with a rectangular shape of the tooth, while Alpine bear are characterized by larger variability showing a rather high amplitude of the talon in comparison with the trigonid in some specimens.

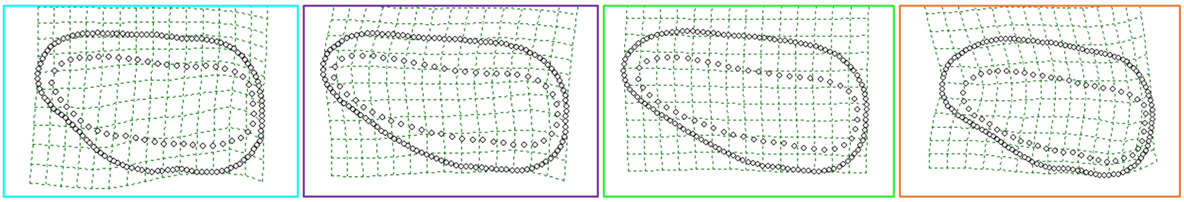
However, it should be pointed out that the first and second main components describe only 21% of the entire variability, so the distinction of the various populations through the morphological observation of this tooth element must be taken with the appropriate caution.

In spite of this, the presence of the American bear and the white bear in the most extreme portion of the graph shows us that the graph is quite consistent, and that in the brown bear this dental element tends to be plumper and less slender than their "cousins" from across the ocean.

6.1.1.3 *Upper M2*





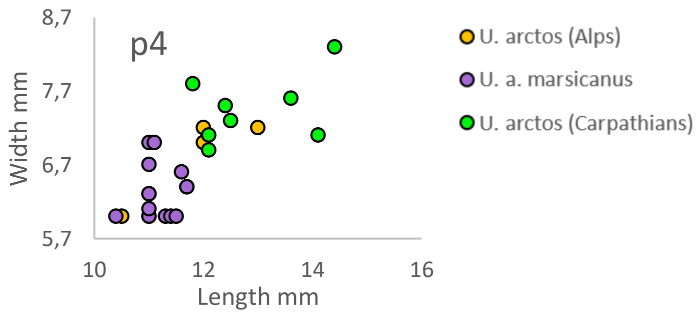


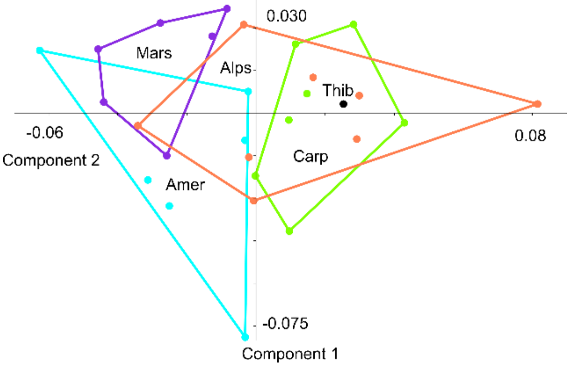
The second upper molar reflects the general characteristics also found in the other dental elements; the graph of the ratios between the length and maximum width of the tooth shows that there is a good overlap between the two continental brown bears, while the Marsican bears, show smaller average size.

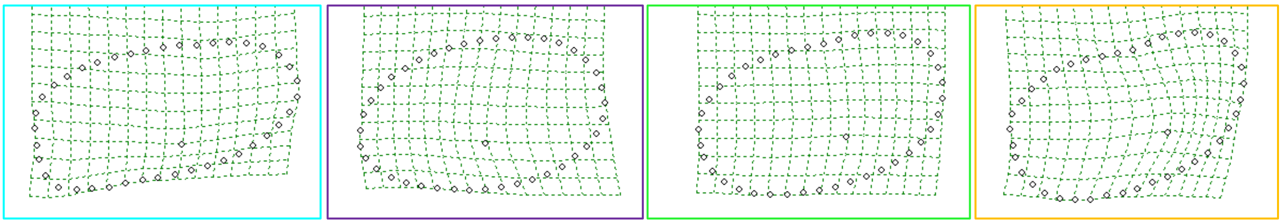
This similarity in size can also be observed in the morphology; in fact, even if some specimens of Alpine have a less elongated and stocky occlusal profile, all brown bear populations fall within the same morphological pattern.

In contrast, both the American, Tibetan and polar bears remain outside the standard morphology of the brown bear with a shorter tooth and a more undulated lingual profile. The graph of the two main components explains about 45% of the total variability.

6.1.1.4 *Lower p4*

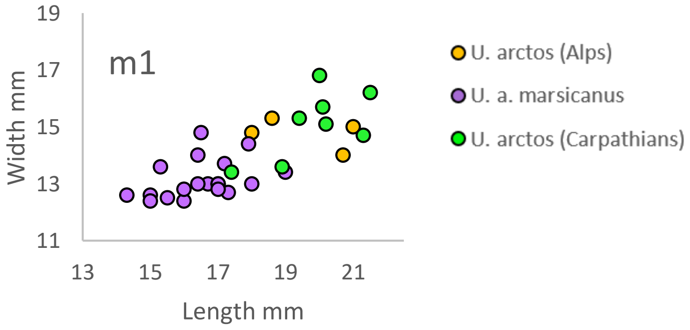


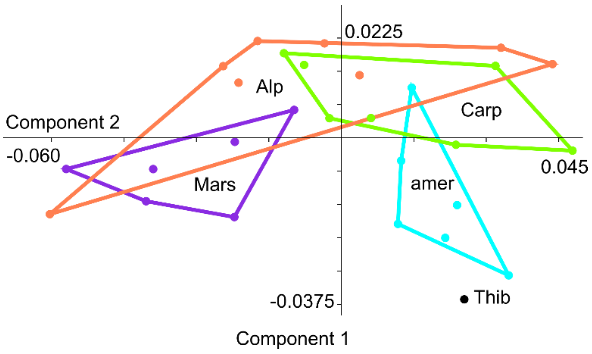


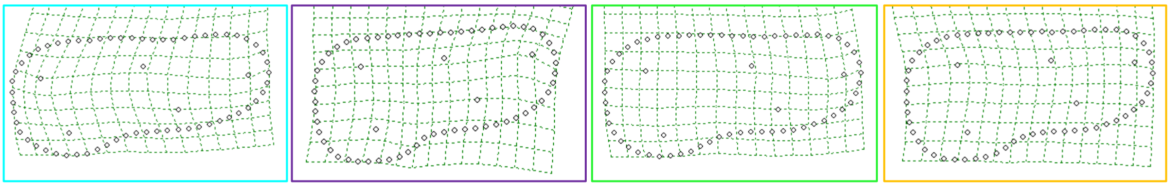


In the lower p4, the size of the Marsican is smaller than the rest of the populations analyzed, almost half the size of the carpathians. According to the morphometric data, the morphological data shows that there is a clear distinction between these two forms. This is mainly described by the more backward position of the protoconid and by the more regular profile of the lingual margin; on the contrary, both the alpine and Carpathians bear (and also the Tibetan in this case) possess the same morphological cluster, so it is impossible to describe a morphology typical of one or the other. The American black bear, on the contrary, is separated, showing a more elongated and angular morphology, rather distant from the populations of brown bear. The two main components are the first and the second and together represent about 76% of the total variability.

6.1.1.5 *Lower m1*

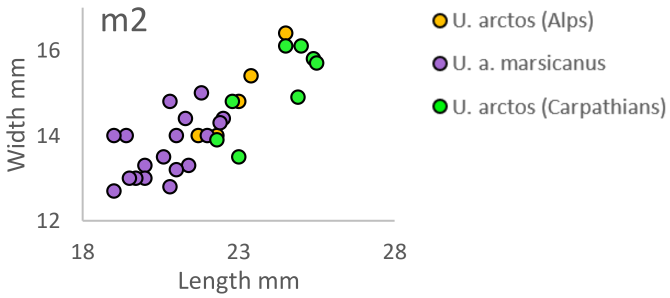


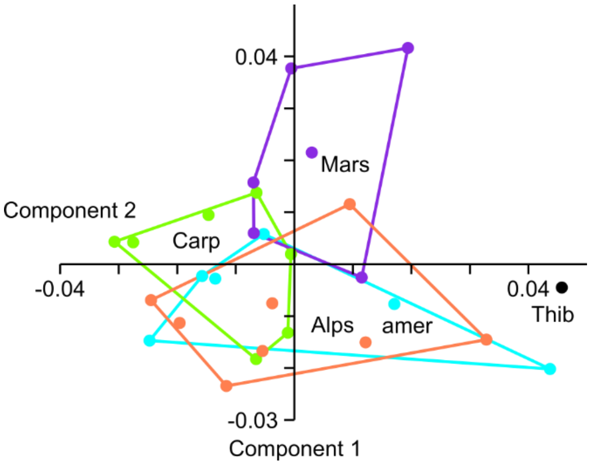


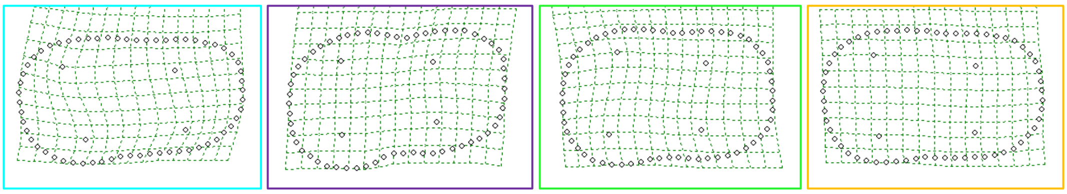


From the morphometric analysis, it is clear that the Marsican population tends to have a much lower ratio between length and width of the first molar than the other two modern populations. On the contrary, the morphology of the tooth gives a different result. The graph regards the first and the second main component (which explain respectively 38% and 22% of the variability) show some difference features between the population of Marsica region and that of the Carpathians, still overlapped by the variability of the Alpine bear. The Asian black bear (*U. thibetanus*), as expected, remains in a position rather distant from the populations of *U. arctos*. The American bear follow the same pattern, especially for reduced size of the talonid and the backward position of the cusps.

6.1.1.6 *Lower m2*

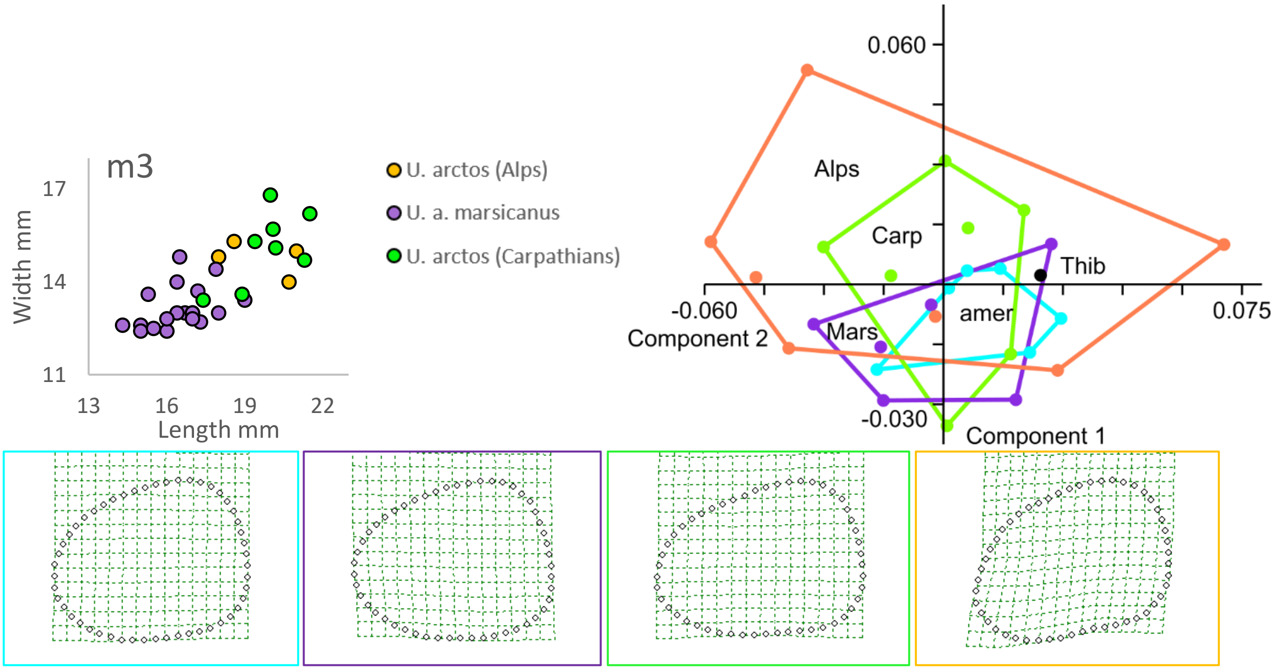






From the analysis of the second lower molar, a good morphomentric distinction emerges between the Marsican bear and the other European populations taken into consideration, with the latter larger and wider than the first. This pattern is also well described by the morphological analysis between the first and the second main component (43% of the total variance). In fact, although there is a slight overlap of morphologies showed in the graph, the dental element of the Marsican is less regular, with a profile generally more ondulated and a talonid often wider than the brown bear from continental region. In fact, these have a much more regular and quadrangular morphology, which can be found also in the American bear. However, the Asian black bear remains outside the general morphologies of the other forms taken into the analysis.

6.1.1.7 *Lower m3*



For the third lower molar, unlike the other dental elements, the position of the cusps was not monitored because, in many cases, they were rather small or even absent (a condition that makes it impossible to configure landmarks acceptable for the analysis of the main components). Despite this, the analysis clearly revealed that it is not possible to properly distinguish the various populations (and different species) from the morphology of this dental element, while the variability described by the Alpine brown bear covers substantially all that of the other forms. On the contrary, from the morphometric analysis it is possible to divide into two dimensional patterns the three populations, with the smaller Marsican bears and the larger Alpine and Carpathian bears.

6.1.2 Final remarks

Surely the major difference between the Marsican and the continental bear (Alpine and Carpathian) is represented by the morphometric ratios. In fact, apart from the lower fourth premolar and upper first molar, all the dental elements of the subspecies of the Apennines are smaller than the other bears considered. On the contrary, there is not a big morphometric difference between the Alpine bear and the Carpathian bear except for the upper P4 and, much less clearly, also in the first upper molar. Although it is not possible to establish a dimensional pattern between these two populations, it is good to highlight how the Carpathian bear reaches much more often higher dimensions than the dental elements than the Alpine brown bear.

Analyzing the data obtained, I have reason to believe that morphometry cannot clearly distinguish a phylogenetic trend, but only describes a different adaptation to different geographical (and demographic) conditions.

From the morphological analysis it is immediately clear that the different species of bears (U. *arctos, U. thibetanus, U. americanus* and *U. maritimus*) have quite different morphological dental characters, that fully justify the different specific attributions.

On the contrary, within the variability of *U. arctos* we can see many similarities but also some differences. In fact, by eliminating the effects of size and analysing only the morphology, it is quite evident that there is a differentiation between the Marsican bear and the other two populations, especially in the upper P4 and, to a lesser degree, for the lower m2.

6.1.3 The cranium

For the analysis of the morphology of the skull I decided to use the three-dimensional models of the recent specimens from the Carpathians (642, 1504, C4) from Alps (3361, 3362, 3400, 6583) and from the Appennines (157, 164, 167, 168, 173, 175, 176, 177, 178, 179, 181, 183, 212, 259); as outgroups were used a skull of a Asian black bear (1546) and one of *U. maritimus* (1529).

Subsequently, to observe how they were positioned within the recent bear morphologies, some skulls of cave bears (p 285-460397, p 1097, p 1918, Z941, Muse) and fossil brown bears were added.

The findings of brown bear have been further divided into *U. arctos* from Late Pleistocene-Holocene (2847-1, 2847-2, 4525, 46036, Nizke Tatry Mts, p 1085, MS/1451) and "*U. arctos priscus" (p 1085, 3iii, S.i)*, to observe a possible morphological difference in brown bear specimens. In contrast to the teeth, a single analysis was carried out for the skulls, in which all the digitalised elements representing a significant sample (undeformed or partially complete fossils) were inserted (Fig. 46-47).

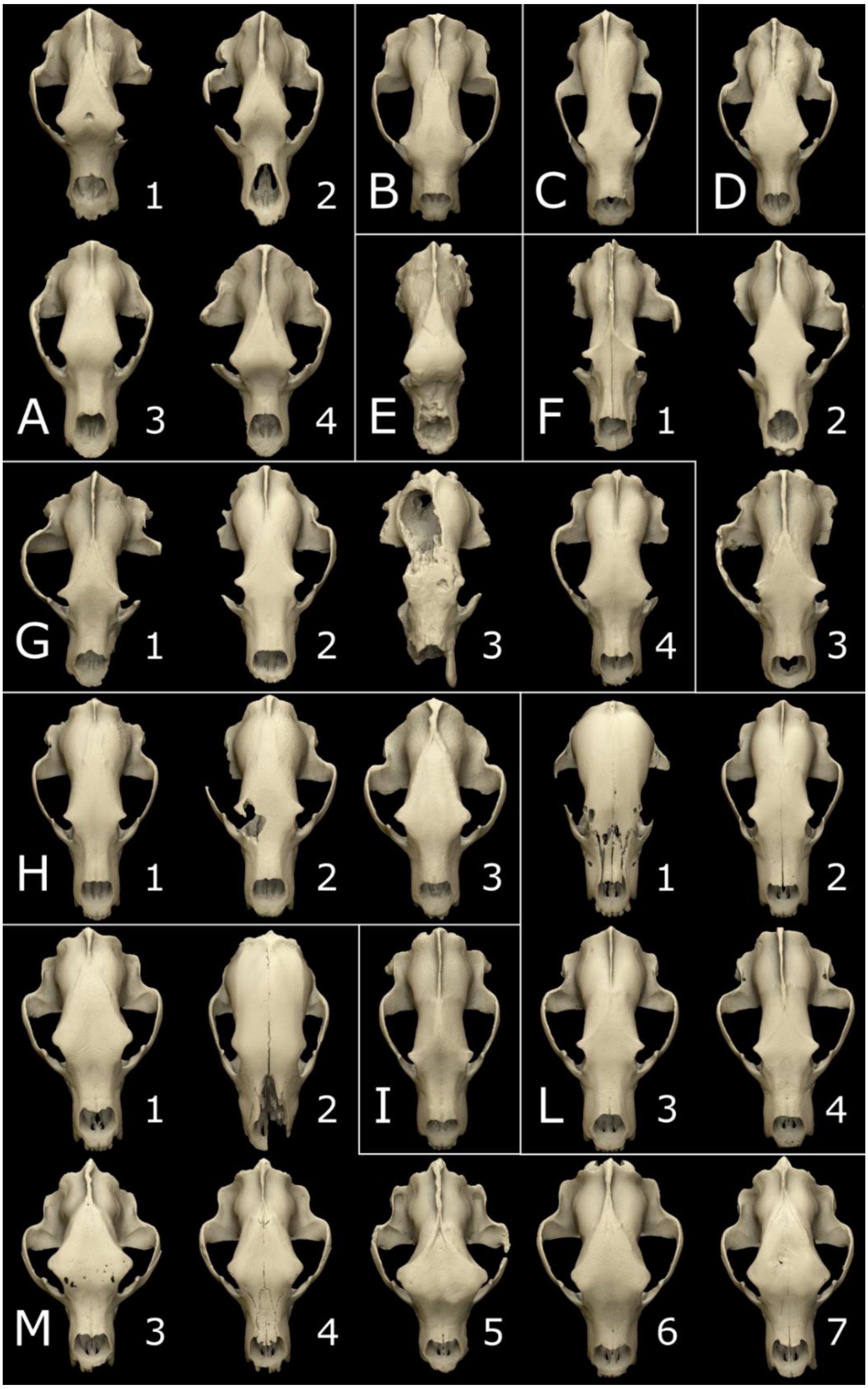


Figure 46: ***Part of the bears cranium for the 3D morphometric geometry and morphological analysis, dorasal view. A) U. spelaeus (Late Pleistocene). 1*** *– MJ-ZT U1 (Medvedia jaskyna),* ***2*** *– Z 941 (Medvedia jaskyna),* ***3*** *– p 285 (Caverna delle Fate).* ***4*** *– p 1925 (Caverna delle Fate).* ***B) U. thibetanus (Recent).*** *1546 (National History Museum, Bratislava).* ***C) U. maritimus (Recent).*** *1529 (National History Museum, Bratislava).* ***D) U. americanus (Recent).*** *1732 (National History Museum, Bratislava).* ***E) U. deningeri (Middle Pleistocene).*** *Hund II (Hundsheim);* ***F) "U. arctos priscus" (Late Pleistocene). 1*** *– p 1085 (Caverna delle Fate).* ***2*** *– 3iii (Winden),* ***3*** *– S.1 (Winden).* ***G) U. arctos (Late Pleistocene-Holocene). 1*** *– 570 (Vazecka jaskyna),* ***2*** *– 2847-2 (Laufenberghole).* ***3*** *– IGF 10961 (Bucine).* ***4*** *– MS 145/1 (Demanovska medvedia jaskyna).* ***H) U. arctos (Recent, Carpathians). 1*** *– C4 (Banskà Bystrica),* ***2*** *– 642 (Ocova), 3 – 1503 (Turany).* ***I) U. arctos syriacus (Recent).*** *1705 (Bojnice ZOO).* ***L) U. arctos (Recent, Alps). 1*** *– 3360 (Alps),* ***2*** *– 3361 (Alps),* ***3*** *– 3400 (Alps),* ***4*** *– 3362 (Alps).* ***M) U. arctos marsicanus. 1*** *– 131 (National Park of Latium, Abruzzi and Molise),* ***2*** *– 175 (National Park of Latium, Abruzzi and Molise),* ***3*** *– 486 (National Park of Latium, Abruzzi and Molise),* ***4*** *– 489 (National Park of Latium, Abruzzi and Molise),* ***5*** *– 173 (National Park of Latium, Abruzzi and Molise),* ***6*** *– 164 (National Park of Latium, Abruzzi and Molise),* ***7*** *– 179 (National Park of Latium, Abruzzi and Molise).*

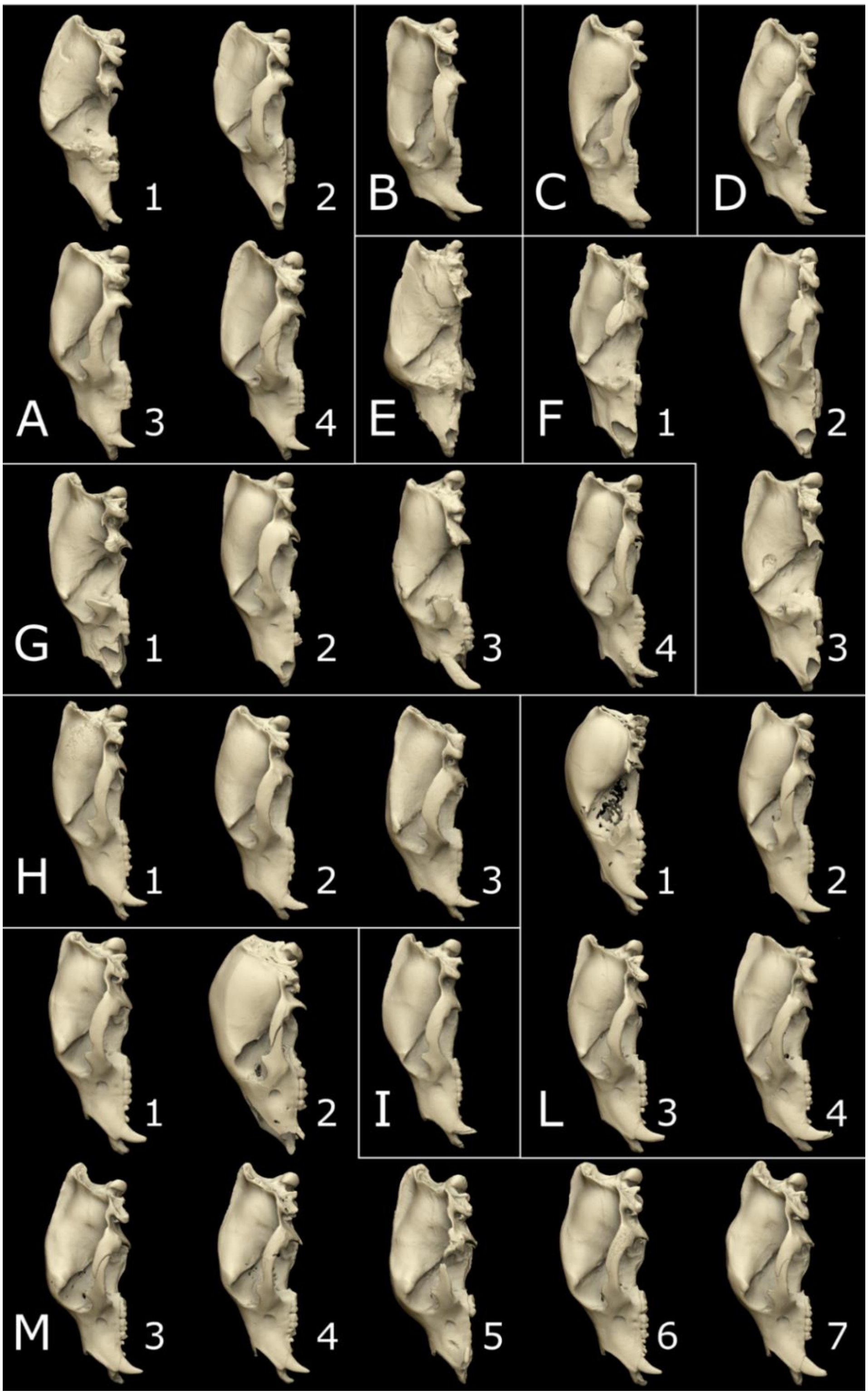


Figure 47: ***Part of the bears cranium for the 3D morphometric geometry and morphological analysis, lateral view. A) U. spelaeus (Late Pleistocene). 1*** *– MJ-ZT U1 (Medvedia jaskyna),* ***2*** *– Z 941 (Medvedia jaskyna),* ***3*** *– p 285 (Caverna delle Fate)* ***4*** *– p 1925 (Caverna delle Fate).* ***B) U. thibetanus (Recent).*** *1546 (National History Museum, Bratislava).* ***C) U. maritimus (Recent).*** *1529 (National History Museum, Bratislava).* ***D) U. americanus (Recent).*** *1732 (National History Museum, Bratislava).* ***E) U. deningeri (Middle Pleistocene).*** *Hund II (Hundsheim);* ***F) "U. arctos priscus" (Late Pleistocene). 1*** *– p 1085 (Caverna delle Fate),* ***2*** *– 3iii (Winden),* ***3*** *– S.1 (Winden).* ***G) U. arctos (Late Pleistocene-Holocene). 1*** *– 570 (Vazecka jaskyna),* ***2*** *– 2847-2 (Laufenberghole).* ***3*** *– IGF 10961 (Bucine).* ***4*** *– MS 145/1 (Demanovska medvedia jaskyna).* ***H) U. arctos (Recent, Carpathians). 1*** *– C4 (Banskà Bystrica),* ***2*** *– 642 (Ocova), 3 – 1503 (Turany).* ***I) U. arctos syriacus (Recent).*** *1705 (Bojnice ZOO).* ***L) U. arctos (Recent, Alps). 1*** *– 3360 (Alps),* ***2*** *– 3361 (Alps),* ***3*** *– 3400 (Alps),* ***4*** *– 3362 (Alps).* ***M) U. arctos marsicanus. 1*** *– 131 (National Park of Latium, Abruzzi and Molise),* ***2*** *– 175 (National Park of Latium, Abruzzi and Molise),* ***3*** *– 486 (National Park of Latium, Abruzzi and Molise),* ***4*** *– 489 (National Park of Latium, Abruzzi and Molise),* ***5*** *– 173 (National Park of Latium, Abruzzi and Molise),* ***6*** *– 164 (National Park of Latium, Abruzzi and Molise),* ***7*** *– 179 (National Park of Latium, Abruzzi and Molise).*

6.1.3.1 *The cranium (modern forms)*

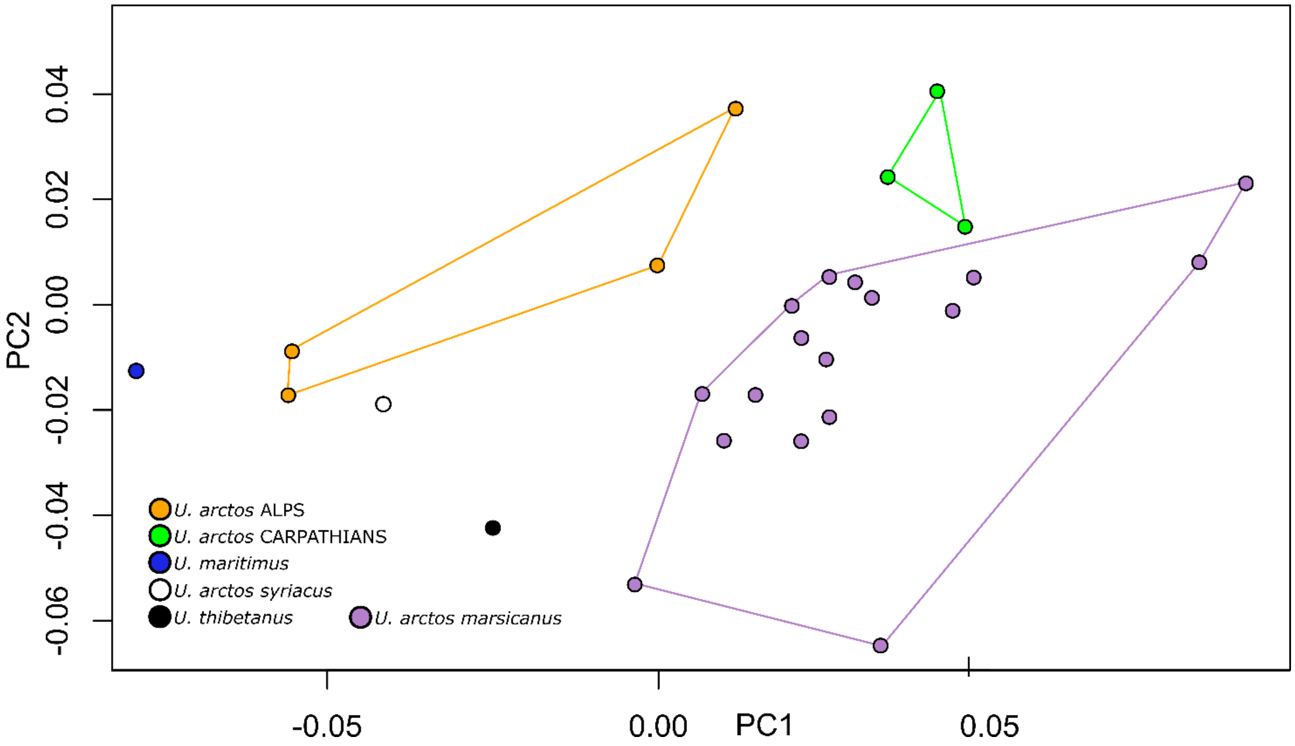


Figure 48: ***Morphometric geometry analysis, showing the graph of the first and the second principal components of the Recent bear cranium***

Both from the graph (showing the distribution of the three-dimensional configurations according to the first and second main components), and from the direct observation of the skulls, it is clearly possible to divide the modern brown bears from the other extant species (*U. maritimus, U. thibetanus* and *U. americanus*). *U. maritimus* has an extremely larger squamosal region, a very wide enlargement of the zygomatic arcs and an extremely reduced jaw region, giving the skull an elongated and squared morphology. Also *U. thibetanus* has a short maxillary region even if, the zygomatic arches are much less ample, showing much smaller dimensions than the polar bear or the brown bear. Finally, among the actual outgroups, the American black bear (*U. americanus*) has characters much more similar to the brown bear than the other species considered, maintaining rather wide zygomatic arches and a rather elongated maxilla in relation to the total size of the skull.

Looking instead at the other modern populations, and analyzing their various positions within the graph, it is clear that the Marsican bear is quite distinct from the two forms of brown bear. In fact, although it is the largest sample within the statistical analysis, this is well grouped confirming the peculiar morphological characteristics of this subspecies. These differences are concentrated mainly in the frontal and the zygomatic regions, as already pointed out by Colangelo et al., (2012) and Meloro et al., (2017). In fact, also analyzing the intraspecific variability, it is possible to observe a good repetition of the same character that occurs in many of the individuals (e.g. No. 3-5-6-7).

It is rather interesting to observe that this character is related to the skull of *U.* ex gr. *spelaeus*. Despite this, the graph shows that these two forms are extremely distant one from the other and, on the contrary, the speloid forms seem to overlap more with those of *U. arctos* (especially fossils).

Unlike the Marsican bear, which stands out clearly from the two morphologies of actual bear, the shape of *U. arctos* of the Alps and those of the Carpathians are rather similar at first sight but have peculiar characteristics that are arranged in two well distinct areas of the graph. Even if in the two population the morphology of the frontal is oblique, and the dimensions of the zygomatic arch are reduced (compared to the cave bear forms), they maintained different characters, mainly in the width of the ecnephalic area in proportion to the general dimensions of the skull.

6.1.3.2 *The cranium (modern and extinct forms)*

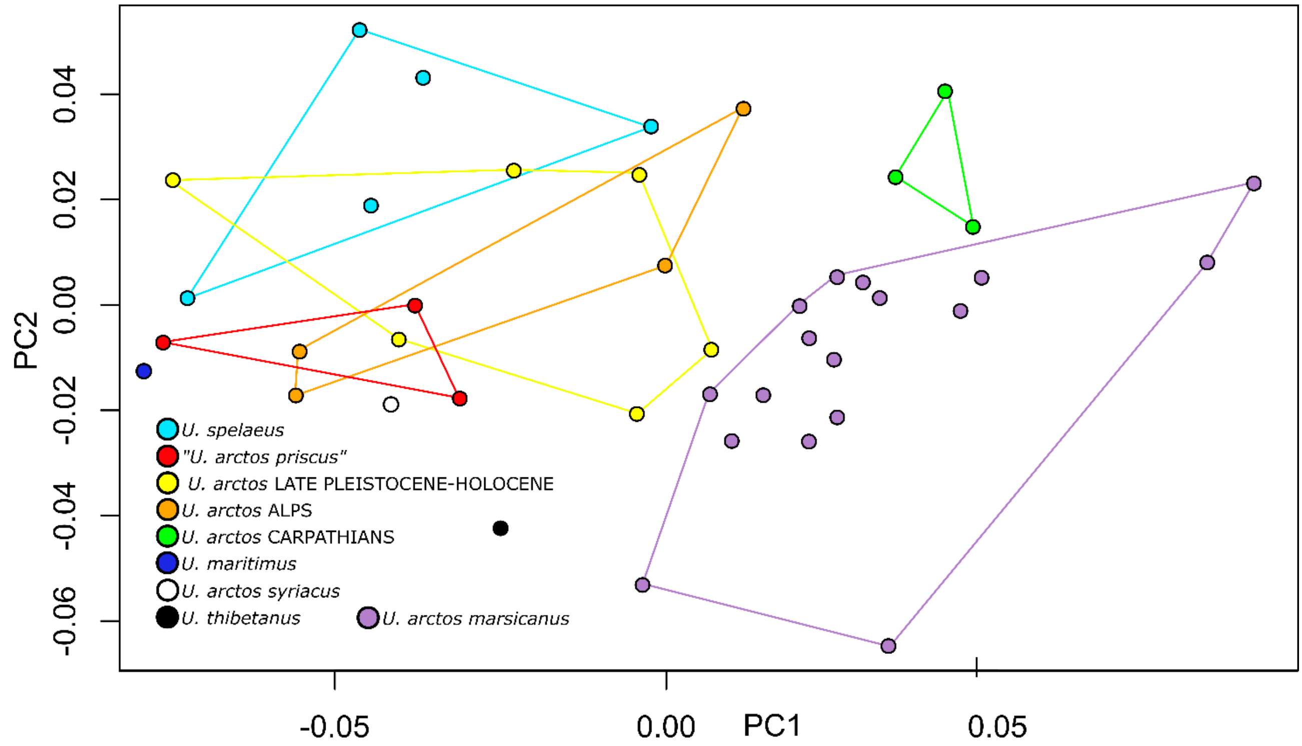


Figure 49: ***Morphometric geometry analysis, showing the graph of the first and the second principal components***

Cave bear represents a form rather distant from the recent ones, even if it intersects with the fossil forms of brown bear. In fact, observing the dorsal view of the skulls, it is possible to notice a greater amplitude of the zygomatic arch in the cave bear, followed by a shorter length of the nasal bone compared to the arcoid forms (Fig. 46, Group A). In lateral view, the cave bear shows a much narrower saggittal profile in addition to the typical conformation with the frontal step (Fig. 47 Group A).

I wanted to pay attention to the fossil finds of *U. arctos* and to those findings that are classified under the name of "*U. arctos priscus*". Although both groups are represented by fossil elements rather fragmented and in poor condition of conservation (the skull No. 1, Group F from the museum of Genova, is literally divided in half), it is quite clear that there is not a big morphological difference between them. In fact, analyzing both the lateral and occlusal norms of groups F and G, it is not possible to distinguish peculiar features such as to allow a different attribution (even subspecific) of the two brown bear fossil forms. This data is however slightly in disagreement with the statistical one; in fact, observing the graph, the two areas concerning "*U. arctos priscus*" (red) and *U. arctos* from Late Pleistocene-Holocene (yellow) overlap for a small part, even if both fit perfectly within the morphologies described by the recent brown bear.

6.1.4 Final remarks

The clearest evidence from the analysis carried out is the morphological difference of the Marsican brown bear compared to other forms of bear (both modern and fossil). In fact, in spite of the characters related to the cave bear, such as the width of the zygomatic arc and the presence of the frontal stop, it remains far outside the morphological range of *U.* ex gr. *spelaeus*.

Another character highlighted by this study is the rather evident difference between the brown bear skull of the Carpathians compared to the Alpine one. In fact, despite the general morphology of the two populations, they are clearly separated within the analysis of geometric morphometry.

This character supports the conclusions reported by Davison et al., (2011) regarding the division of current populations at the genetic level. In fact, as has been widely discussed above, the two nuclei of Eastern Europe and the Alps have different evolutionary stories, probably set during the reduction of the spatial distribution of the brown bear due to the continuous anthropogenic pressures (Chapter 5).

The pleistocenic brown bear show a huge spectrum of variability that largely overlaps with the current brown bear and the cave bear. It demonstrates and reaffirms the difficulty of recognising distinctive forms between and within the species of bear during the European Pleistocene and detect some distinctive characters. It should be remembered, however, that the analysis of geometric morphometry excludes the size factor from the statistical variables, therefore, it is true that there are not so clear differences in morphology, but still remain different trend in dimensions.

A further proof of the little morphological difference between fossil forms is represented by the inclusion in the analysis of "*U. arctos priscus*".

In fact, as mentioned in chapter 2, the taxonomic position of this subspecies is still very dubious; for some authors it represents an intermediate phase (or chronosubspecies) of the brown bear during the Late Pleistocene (Marciszak et al., 2015) while, other consider this term has an unvalid name. From my analysis, the two hypotheses are not at all in contrast with themselves; in fact, the graph shows some different features between the two groups (probably related to different environmental conditions), but not enough to separate them in two subspecies, like *U. arctos* from Alps and *U. arctos marsicanus* in Appennines

For this reason, I agree with Pacher 2007 considering *U. arctos priscus* as nomina delenda but do not reject the different morphological variability between fossil brown bears, for which a revision of detailed radimetrical data are required.

A final consideration concerns the cave bear. Although it is sometimes quite easy to distinguish the skull of *U.* ex gr. *spelaeus* from *U. arctos* according to the size and the presence or absence of premolars (see chapter 2), it is clear that the morphologies of these two species are not so different from each other (specially between a young female cave bear and an adult male brown bear).

In spite of the data presented and the results obtained, I want to underline that the work carried out represents only a first step towards the real understanding of the morphological relationships between the various species (fossil and recent); in fact, the increase in the sample of comparison and further statistical analysis, can certainly bring new important evidences, to delineate an increasingly clearer framework of the evolution and of the adaptive dynamics of the different bear forms that occurred throughout the Quaternary.

7 Fossil brown bear in Southern-Central Italy

One of the main objectives of my research was to identify, at a morphological level, a significative data of the presence of the Marsican subspecies within the fossil record and to identify the moment of its isolation.

In this regard, to understand the dynamics that led to the current distribution of *U. arctos marsicanus*, all the deposits of central-southern Italy have been selected, and the most significant dental elements (premolars and molars), skulls and mandibles have been studied.

The data obtained were compared with the analyses presented above, both morphometrically and morphologically, in order to describe any change in the brown bear over time, and to identify some features in common with the Marsican subspecies.

The deposits taken into consideration represent a broad look into the past, considering all the Late Pleistocene and Holocene.

These deposits are: Vigna San Carlo (Late Pleistocene, Monteverde, Rome), Ingarano (Late Pleistocene, northern Apulia), Grotta degli Orsi Volanti, Grotta del Cervo (Late Pleistocene, Abruzzi), Grotta della Lupa (Holocene, Abruzzi) and Gran Carro (Bronze Age, Latium) (Capasso Barbato et al., 1992; Petronio and Sardella, 1998a; Agostini et al., 2009; Petitti et al., 2013), Fig. 50.

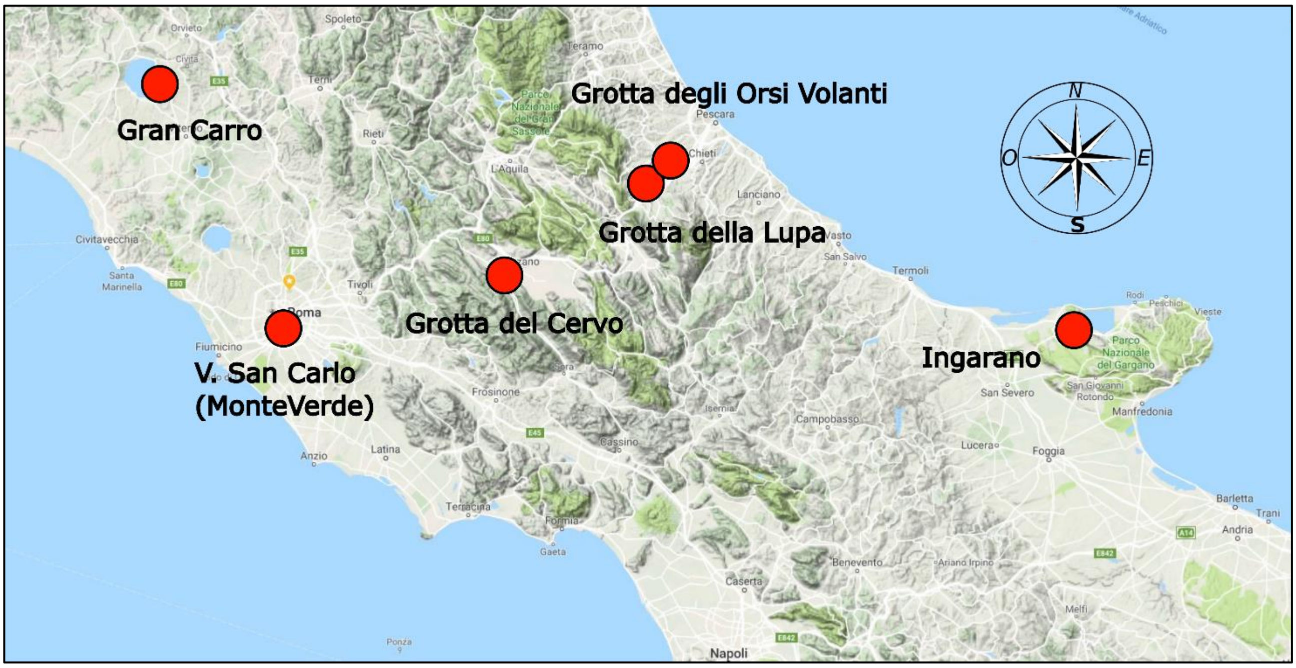


Figure 50: ***Maps of the brown bear fossil deposit analysed.***

7.1 Grotta del Cervo

7.1.1 The site

The Grotta del Cervo is located at Pietrasecca (Carsoli, AQ), its discovery is dated to 1984 and the studies inside the cave were carried out until 1994 by the Geological and Paleontological Service of the Superintendence for the Archaeological Heritage of Abruzzi, in collaboration with the Department of Earth Sciences of Sapienza, University of Rome.

The deposit is dated to the end of the Middle Pleistocene (about 130,000 y ago) with biochronological analysis. Besides faunal elements, also the occurrence of "modern" man is testified in the cave, thanks to the presence of 18 coins of the IV century A.D. (Agostini S. pers. comm.).

Within the site five species of mammals are recorded: the brown bear (*U. arctos*), the cave bear (*U. spelaeus)*, the cave lion (*Panthera leo spelaea*), the lynx (*Lynx sp.*), the red deer (*Cervus elaphus*) and part of Ursidae material referred to as *Ursus sp.*(Capasso Barbato and Gliozzi, 1994).

Contrary to the name of the deposit (Cervo means deer in italian), findings referable to the deer are represented only by 4 fragmented teeth, while the presence of brown bear is represented by various teeth, phalanges and a distal epiphysis of humerus.

By the type of fossilization, there has been no transport or remodeling traces on specimens, it is assumed that the death and consequent fossilisation took place in the same place (Agostini pers. comm.).

7.1.2 Material

The findings referable to *U. arctos* are 10 (between dental and post cranial elements), while other four teeth previously associated with *Ursus sp.* (Table 4); the rest of the bear material is attributed to *U. spelaeus*. Part of the material has been the subject of a publication (Capasso Barbato and Gliozzi, 1994) and of a specialist study for a master thesis (Candeloro, 1998).

Unfortunately, not all the published material has been made available, therefore the measurements and morphologies of the lower p4 (CP 63) derive from the analysis of the images proposed in the works cited and presented in the format of a drawing.

The material I observed is located at the depository of SABAP (Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Abruzzo) and has been measured (maximum length and maximum width) and digitized by photogrammetry following the technique "turn table" (See Chapter 4).

Considering the presence of numerous materials indicated only as *Ursus sp.*, I thought it necessary to include also this material in my analysis. In fact, with the aim of achieving a specific and precise attribution, these teeth have been measured and included in the morphometric analysis, but not into the analysis of geometric morphometry, in order to not alter the results.

Table 2: ***List and measurements of the Ursus material from the Grotta del Cervo deposit.*** *(Measure in mm)***.**

Inv. N°	*Element*	*Side*	*Ontogenetic Stage*	*Length*	*Width*
CP 33	*m3*	*Left*	*Prime adult (Class IV)*	*25,5*	*18,1*
CP 63	*p4*	*Right*	*Prime adult (Class IV)*	*16*	*9.5*
CP 66 (sp.)	*m2*	*Right*	*Juvenile (Class III)*	*32,5*	*20*
CP 115 (sp.)	*M2*	*Left*	*Juvenile (Class III)*	*43.5*	*21*
CP 116 (sp.)	*M1*	*Right*	*Juvenile (Class III)*	*31,4*	*23,1*
CP 117 (sp.)	*m1*	*Right*	*Juvenile (Class III)*	*30,5*	*15,1*
CP 119 (sp.)	*P4*	*Right*	*Juvenile (Class III)*	*17,4*	*12*
CP 137 (sp.)	*m1*	*Right*	*Prime adult (Class VI)*	*30,2*	*22,5*

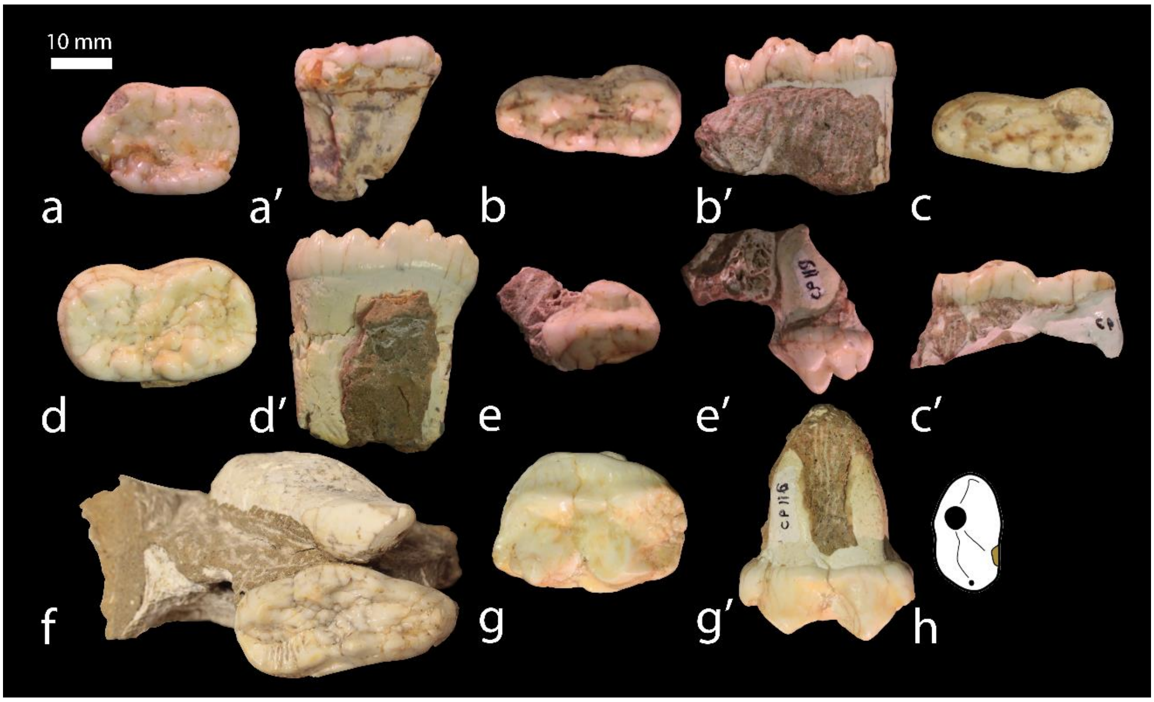
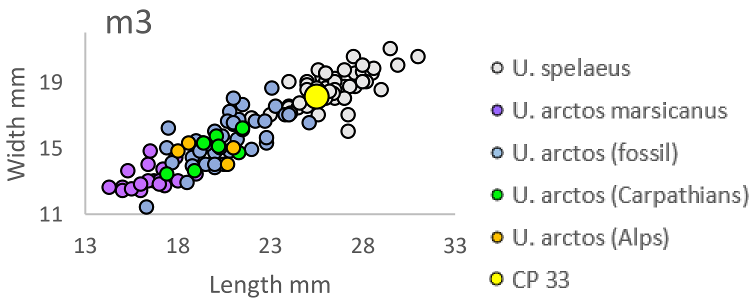
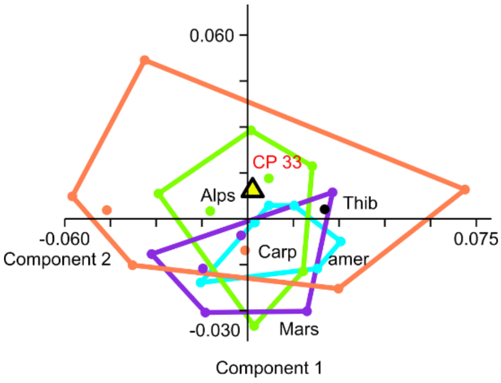


Figure 51: ***Grotta del Cervo Ursus material, occlusal view and lateral view (letter with apex): a-a’)*** *CP 33.* ***b-b’)*** *CP 137.* ***c-c’)*** *117.* ***d-d’)*** *CP 66.* ***e-e’)*** *119.* ***f)*** *CP 115.* ***g-g’)*** *CP 116.* ***h)*** *CP 63.*

7.1.3 Description

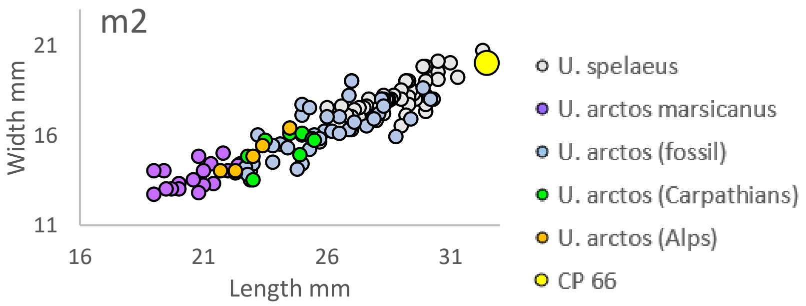
CP 33 – (m3 Left): The tooth has a subrectangular profile with the distal portion projected outwards and a slight central constriction on the labial side. Despite the presence of fractures on both the labial and lingual margins, it is possible to clearly observe the morphology of the chewing surface. The latter is poorly tuberculated, with the main cusps poorly developed and the talonid almost flat in the major of its surface. The metaconid is very low with the presence of three posterior accessory cusps, while the protoconid is little more developed and distinguishable. The hypoconid is formed by a single well visible cusp but, given the fracture of the tooth it is not possible to have the certainty that it is not divided into two main cusps. On the contrary, the enthypoconid is divided into three parts and its "ridge" reaches almost the center of the tooth. The wear is not very evident but present, for this reason the individual can be placed in the category Prime adult class IV. The cingulum is not present. From a morphometric point of view, it has rather large dimensions and, analysing the scatter plot, it is possible to observe that it falls within the variability of the speloid bear, close to the dimensional range of *U. arctos*. From the morphological analysis, on the other hand, the tooth has standard characters, which perfectly fit into an average morphology when compared to other forms of brown bear in both the Alps and the Carpathians.



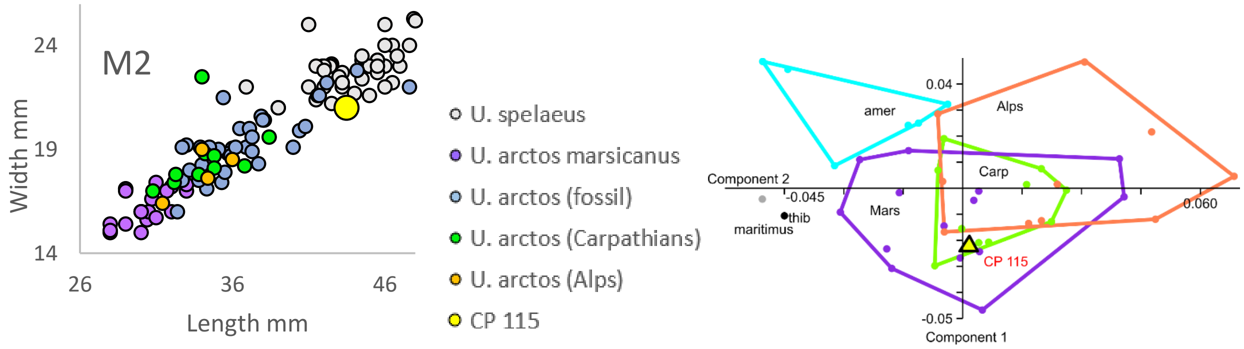


CP 63 - (p4 Left): The tooth has an elliptical profile with a slight constriction in the central portion. Even if the anterior root is fractured, the entire occlusal surface is still visible and preserved. The latter appears rather simple with a well-developed protoconid that occupies almost the entire tooth with a more inclined ridge in the mesial portion than in the distal portion; on the contrary, the paraconid and the hypoconid are poorly developed, but still evident. There are no accessory cusps.

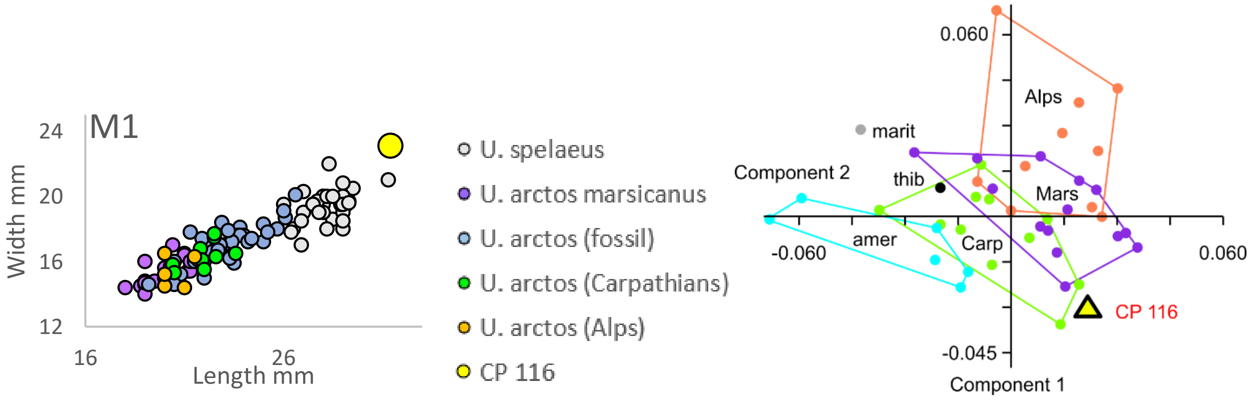
CP 66 - (m2 Right): The tooth is well preserved, has an elongated profile and a marked constriction between talonid and trigonid, mainly on the buccal side. In general, it has well developed cusps, the protoconid is rather backward with an anterior accessory cusp while the Metaconid is advanced and divided into two well delineated cusps. The occlusal portion of the tooth is remarkably rich in tubercles, in fact, the "ridge" of the two cusps of the trigonide do not intersect due to the presence of numerous accessory cusps placed in the central area of the tooth. The talonid is similar to the trigonide, with a rather developed hypoconid, consisting in a single cusp and the presence of a rather complex chewing surface. The ontogenetic stage of the individual it should be a juvenile (Class III) since there is no presence of wear on the surface. The morphometric analysis of the tooth tends to justify the complexity of the occlusal surface and the presence of the tubercles; in fact, the second lower molar not only fits perfectly within the variability of *U.* ex gr. *spelaeus*, but also represents one of the largest specimens of this species.



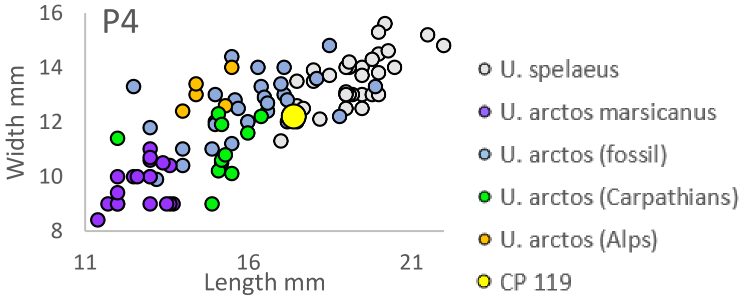
CP 115 - (M2 Left): The tooth is well preserved, although part of the root has been incorporated into a diagenized matrix containing also a canine. The tooth has an overall morphology rather simple, the talonid has few tubercles and most of the occlusal surface of the trigonid is occupied by the ridge of the protocone and the paracone. The main cusps are well developed and clearly recognizable; among these, only the protoconid is divided by three sinkings. The occlusal profile of the tooth is characteristic of the dental element, with a more ondulated buccal side and a straighter lingual side characterized by the presence of a rather evident cingulum. In general, the cusps do not show wear, so the tooth fits in the juvenile category, class III. Looking at the graph of the dimensions between the various species, it is immediately clear that the overlapping area of the dimensional range between *U. arctos* (fossil) and *U.* ex gr. *spelaeus* is extremely wide. Therefore, morphometric analysis is often ineffective for the attribution of the second molar higher than the brown bear or the speleal bear, and this specific case it is not an exception. The morphology of the tooth shows typical arctoid features, fitting into the variability of both the Marsican bear and the brown bear of the Carpathians, remaining far from the typical morphology of the american bear. The data obtained by morphometric and morphologic analisys leads me to attribute this element to *U. arctos* rather than *U.* ex gr. *spelaeus*.



CP 116 - (M1 Right): This tooth has a singular general shape, with rather square and irregular profiles. The main cusps are developed and well defined, also the lines of the two main ridges (para-metacone and proto-meso-hypocone) are parallel and very marked. The styles (metastyle and parastyle) are well visible, with the first more developed than the second. On the buccal side there is the presence of a very developed cingulum, which extends throughout the lingual profile of the tooth. The general morphology is not complex, in fact there is no presence of accessory cusps or a rather tubercolated occlusal surface, except for the distal portion. The tooth belonged to a young individual due to the almost non-existent wear; it can be placed in class III, juvenile category. The tooth is very large, much more than the standard dimensions observed in cave bears. Similarly, the analysis of geometrical morphometry shows that the tooth remains outside the standard morphologies analyzed, positioning itself out from the standard of the brown bears of the Carpathians and those of the central Apennines. Due these characteristics, it is appropriate to associate this tooth to *U.* ex gr. *spelaeus*.

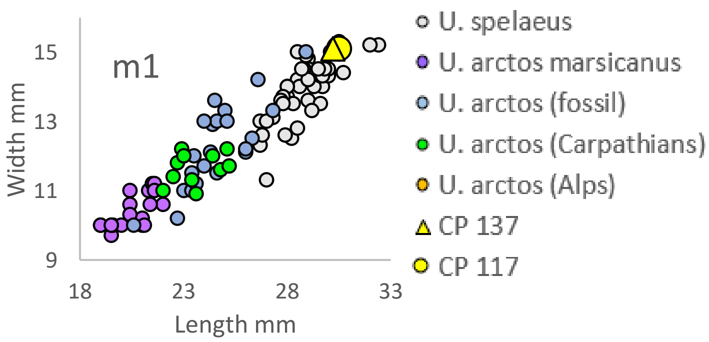


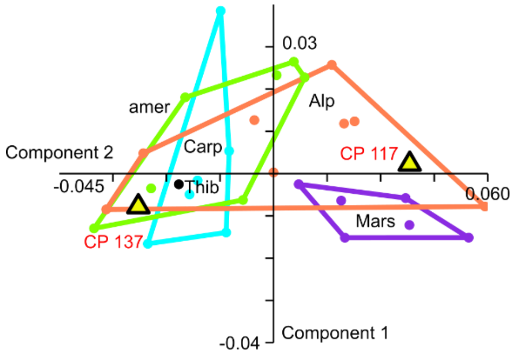
CP 119 - (P4 Right): Also in this tooth the cusps are very well developed; the metacone is higher than the other two, while the paracone is divided in two, with the presence of a small accessory cusp. The occlusal profile is almost rectangular, with the mesial portion forming almost two 90° angles, and the presence of a clear cingulum in the lingual portion. In general, the occlusal surface is simple but there are some additional cusps in both the anterior and posterior portions of the protocone. As for the other specimens analyzed, also this tooth does not present a high wear, so the individual had to be a juvenile (class III). The direct morphological analysis indicates quite clearly that the tooth falls within the variability of the cave bear (especially for the presence of the paracone divided) and this hypothesis is confirmed by the morphometric analysis even if, the overall size of the tooth is quite small. Due to the presence of clear characters, which highlight the attribution to *U.* ex gr. *spelaeus*, the tooth has not been considered in the analysis of geometric morphometry in order not to alter the data about the morphological variability of brown bears.



CP 117 - (m1 Right): The tooth has both the talonid and the trigonid larger in the distal portion than the mesial portion, showing a rather ondulated occlusal profile of the tooth. The cusps are well developed, with the metaconid occupying most of the trigonid, a paraconid slightly shifted in the lingual region and an entoconid divided in two main cusps. In general, the tooth does not show a huge tubercolosity, which is only slightly apparent in the central part of the tooth. As for most of the teeth analyzed there is no sign of significant wear, so the tooth is classified in the juvenile category, class III.

CP 137 - (m1 Right): The tooth has a rather slender general shape, with a straight lingual profile and a slightly undulated buccal profile. In contrast to the findings previously analyzed, this has a very high wear, which does not allow the detailed analysis of the cusps but indicates a rather advanced age of the individual at the time of death (category Prime adult, class VI). In the visible occlusal portion of the tooth, a slight tubercolation of the central portion can be seen, located at the height of the constriction at the beginning of the trigonid; but it is impossible to describe the general complexity of the entire chewing surface.
From a dimensional point of view, both teeth are very large, moving to an area of the graph represented mainly by the largest individuals of *U.* ex gr. *spelaeus*. On the contrary, the simplicity of the occlusal surface and the small presence of accessory cusps refer more to a morphology more similar to *U. arctos*. On the contrary, the general morphology of the tooth and the position of the cusps, gives us a rather ambiguous data, placing the two teeth at the extremes of the morphology of the Alpine bears, confirming both the low variability already found in the analysis of the modern species for the lower first molar, and the still uncertain taxonomic attribution of this tooth. Therefore, I prefer to keep the attribution to *Ursus sp.* for both dental elements.





7.1.4 Final remarks

From the analysis of the material coming from the site of Grotta del Cervo results that the characters between *U. arctos* and *U.* ex gr. *spelaeus* are often not distinguishable and most of the time even the information obtained from the dimensional relationships do not give a clear result. This is the case of the dental elements CP 117 and 137, which remain with the taxonomical attribution of *Ursus sp*. The presence of both evolutionary lines is certainly confirmed by the presence of teeth with clear characters of both the arctoid lineage (CP 33, CP 63 and CP 115) and the speloid lineage (CP 66, CP 116 and CP 119). An important data concerns the recorded dimensions of the dental elements; in fact, both in brown bear and speloid bear, the size are extremely high in relation to the registered standard trend for each species; this aspect could be related to the environmental conditions that characterized the central Apennines during a first general cooling started at the beginning of the Late Pleistocene, but the data can not confirm it. In fact, given the scarcity of material, the site is only a small piece of evidence regarding the morphology of the bear population that lived in this area at that time. New material and new studies are needed to reach more comprehensive conclusions about the brown bear from the early Late Pleistocene in central and southern Italy. The presence of only isolated material does not allow further analysis regarding the number of individuals or minimum age classes.

7.2 Grotta degli Orsi Volanti

7.2.1 The site

The Grotta degli Orsi Volanti is located near Rapino (Chieti), inside the Majella National Park. Its discovery is the result of an explosion produced by the extraction operations of a nearby quarry that revealed its entrance.

Its relevance comes from an interesting discovery of a left mandibular branch attributed to the genus *Macaca*, making it not only the first finding of the genus found in Abruzzi, but also the most southern evidence in relation to Italian material (Mazza et al., 2005).

The Cave infillings consist of a 30–70 cm thick homogeneous layer of dark grey–brown clays which are separated into two following layers by a stalagmitic crust. The lower horizon contains a rich amount of fossil bones, most covered by a black-reddish patina which is akin to that covering the surface of the stalagmitic crust (Mazza et al., 2005).

From the deposit come various faunistic finds datable to the Late Pleistocene and some Mousterian lithic industries. Among these there is also the presence of material of the genus *Ursus*, represented both by *U. arctos* and *U.* ex gr. *spelaeus*.

7.2.2 Material

The bear material from the site is abundant but, as often happens in cave deposits, only a few of these elements are attributable to *U. arctos*.

In fact, even in the Grotta degli Orsi Volanti, the finds referring to the brown bear are represented only by five isolated dental elements, catalogued with GOV followed by a progressive number (Fig. 52 and Table 5).

The material is stored at the SABAP in Chieti, and in the Lama dei Peligni Museum; although a preliminary study of the fossils has been made by other students, the material I examined has not been subject of specific publications. Measurements were taken of the maximum length and width, and the teeth digitized by photogrammetry (following the turn table technique illustrated in Chapter 4).

Table 3: ***List and measurements of the Ursus material from the Grotta degli Orsi Volanti deposit.*** *(Measure in mm).*

Inv. N°	*Element*	*Side*	*Ontogenetic Stage*	*Length*	*Width*
GOV 73	*P4*	*Left*	*Prime adult (Class IV)*	*17,2*	*12*
GOV 53	*m3*	*Left*	*Old adult (Class VIII)*	*24,4*	*17,7*
GOV 76	*M2*	*Left*	*Old adult (Class VIII)*	*37,7*	*18,3*
GOV 133	*M1*	*Left*	*Juvenile (Class III)*	*43.5*	*21*
GOV 134	*m1*	*Right*	*Prime adult (Class V)*	*28,9*	*15*

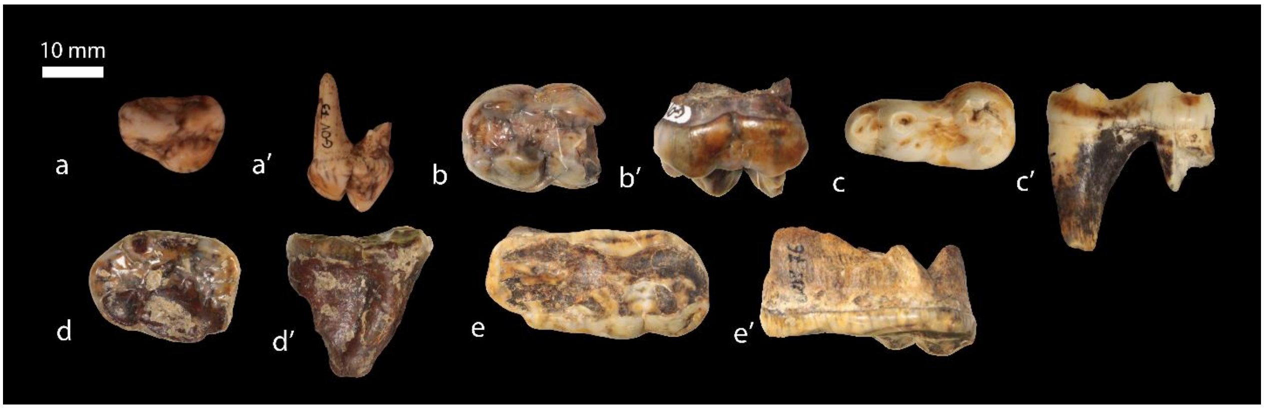
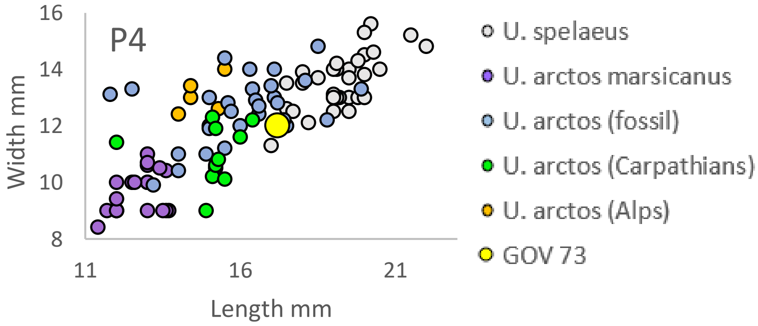
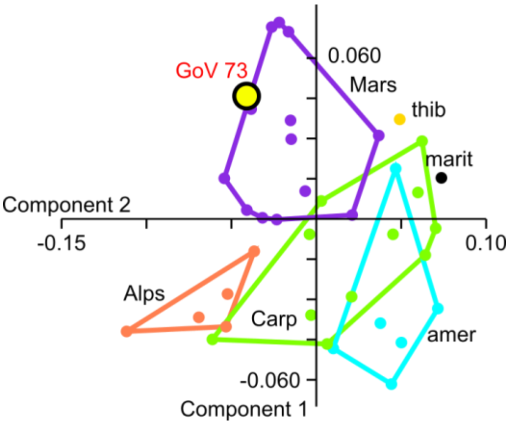


Figure 52: ***Grotta degli orsi Volanti Ursus material, occlusal view and lateral view (letter with apex): a-a')*** *GOV 73.* ***b-b')*** *GOV 133.* ***c-c')*** *GOV 154.* ***d-d')*** *GOV 53.* ***e-e')*** *GOV 76.*

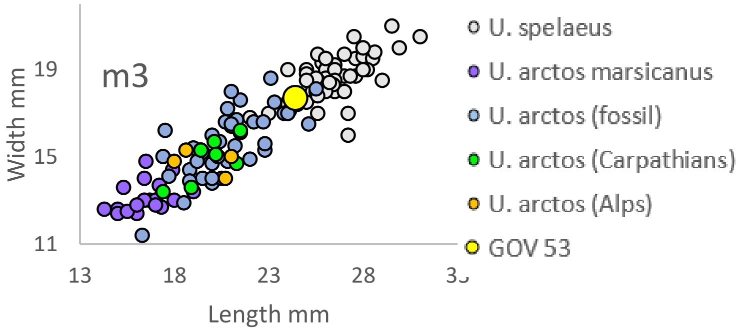
7.2.3 Description

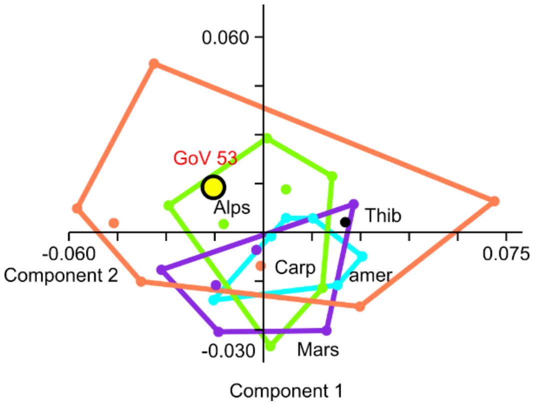
GOV 73 - (P4 Left): The fourth upper premolar has a rather elongated occlusal profile with the main cusps well outlined and a slight crest surrounding the buccal and lingual margin of the tooth. Between the cusps, the protocone is developed but not too sharp, while the paracone is low and looks like a small protuberance. The metacone has standard dimensions and occupies a backward position of the tooth. There are no tracks or accessory cusps and, the occlusal surface, does not show any tuberculated structures. The specimen belongs to a young or very young individual and is classified as Juvenile (Class III) because there is no presence of wear. From a dimensional point of view, it is clearly visible from the graph that the tooth fits perfectly within the dimensional range of the brown fossil bear, and is clearly separated from the forms currently living in Italy and Europe; despite this, the graph concerning the analysis of the external profile and the cusps, shows a very high affinity with the Marsican form and is quite clearly different from other populations and species of bear.



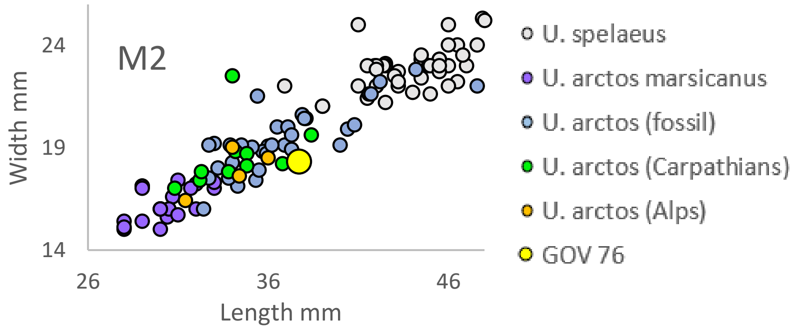


GOV 53 - (m3 Left): The third lower molar, unlike the tooth described above, is rather worn even if the ridges of the protoconid and part of the Mesolophid are still evident. In general, the tooth has a rather quadrangular morphology with an almost rounded distal margin; while the mesial one forms regular angles. As already mentioned, the wear is rather high, especially in the buccal portion of the tooth, that shows the margin and the Metaconid completely replaced by a deep groove. The tooth belongs to an Old adult individual (Class VIII). From a morphometric point of view, the tooth remains at the limit of the area of the graph occupied by the fossil brown bear specimens, in a dimensional range of transition between *U. arctos* and *U.* ex gr. *spelaeus*. From a morphological point of view, this is placed almost in the middle of the graph, within the morphology of the Alpine bears and the Carpathians, outside of the morphological range of *U. arctos marsicanus* and *U. americanus*.





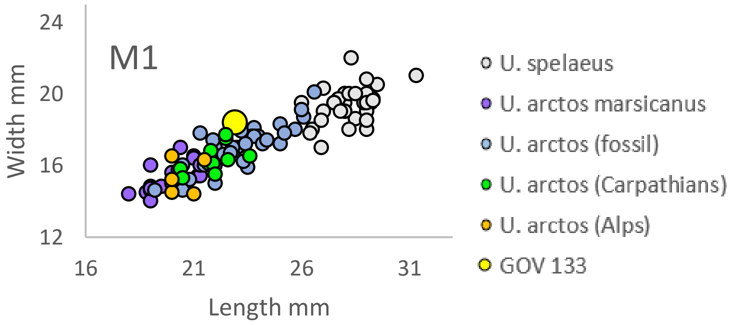
GOV 76 - (M2 Left): This tooth has an extremely characteristic occlusal profile; the lingual line is undulated, with a marked enlargement at the level of the hypocone due to the presence of a rather evident cingulum placed in an advanced position of the dental margin. Similarly, the buccal margin is equally irregular, both in the mesial portion of the tooth due to the presence of a paracone and metacone rather developed, and to the presence of a characteristic swelling in the buccal portion of the talon, probably due to a specific malformation of the individual. On the occlusal surface there are no accessory cusps or developed tubercolated portions, however, it should be stressed that the tooth is characterized by extreme wear and therefore a large part of the chewing surface and the cusps is remarkably worned. The tooth must to be placed in the category old adult (Class VIII). The morphometric analysis clearly shows that the tooth fits perfectly within the dimensional range of *U. arctos* fossil, reaching the maximum size of the brown Alpine bear and falling within the average dimensional range of the Carpathian bear. Given its peculiar morphology, the analysis with the geometric morphometry has not been carried out because for me it is a "peculiar" individual and therefore to be considered an exception to the usual variability.

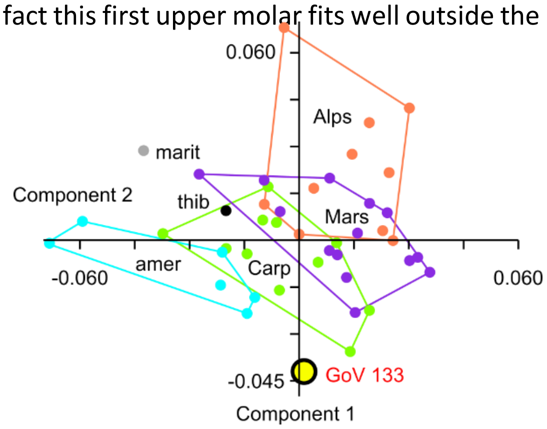


GOV 133 – (M1 Right): The tooth is not very well preserved and has an evident fracture in the mesial portion. It has an hourglass-shaped occlusal profile with a clear median throat and the width of talon and anterior portion of the tooth of the same size. The cusps are well developed, both the metacone and the paracone (even if partially fractured) appear, as usual, the highest cusps. The protocone, the mesocone and the hypocone are well outlined, not subdivided and form a rather rectilinear crest that runs along the longitudinal axis parallel to the main cusps and ends in an almost perpendicular distal crest.

There is the presence of a very evident metastyle while, given the fracture of the mesial portion, it is impossible to know whether or not there was the presence of the parastyle; the occlusal surface is quite large and has a slight tubercolation, especially in the posterior area of the talon, while the wear is almost absent making the tooth fall into the Juvenile category (Class III).

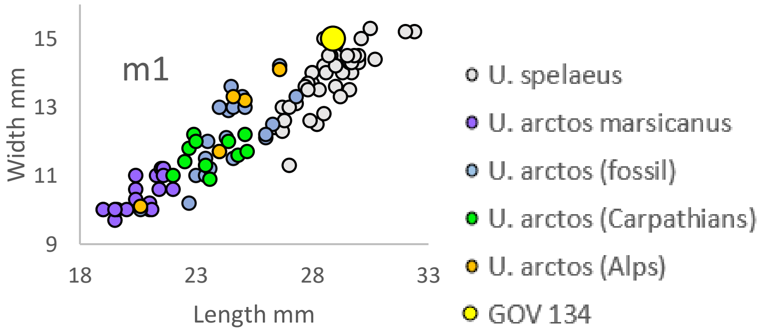
From a dimensional point of view, the tooth is very well within the range of U. arctos fossil placed just above the maximum size of the current bears (both the Alps and the Carpathians). On the contrary, the peculiar morphology of the tooth, is also found by statistical analysis, in fact this first upper molar fits well outside the standard morphology of both brown bear and American bear.

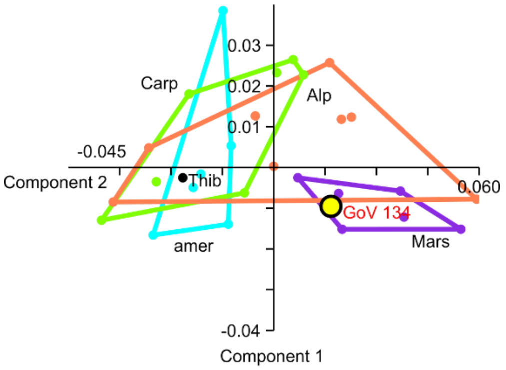




GOV 134 - (m1 Right): The tooth has a very simple general morphology, with distinct cusps and a characteristic occlusal profile, described by a slightly wavy lingual line near the main cusps and an almost straight buccal profile in the mesial portion, which enlarges in a wide curve at the beginning of the talonid. The cusps are easily recognizable even if the wear does not allow a precise positioning of them on the occlusal surface of the tooth. Despite this, an undivided entoconid and a rather large hypoconid are well evident. The occlusal surface of the tooth is rather simple, with a chewing surface occupied almost entirely by the cusps and without the presence of tubercles or accessory cusps. Wear indicates an individual who has reached adulthood and falls into the category Prime adult (Class V).

The simple morphology of the tooth shows rather standard characters and falls within the patterns of the Marsican and Alpine bear. On the contrary, the morphometric analysis gives opposite information; in fact, the tooth fits very clearly within the variability of the cave bear, showing above all an extremely high width. Given the evidence collected and the data analyzed, I think it is appropriate to attribute this find *to Ursus sp.* rather than *U. arctos*, considering it a peculiar element from a morphological point of view, since it remains outside the typical speloid morphology.





7.2.4 Final Remarks

The analysis carried out of the Grotta degli Orsi volanti material, reveal that not all the material attributed to *U. arctos* belongs to this species. In fact, for its morphological and morphometric characters, the first lower molar (GOV 134) must be assigned to *Ursus sp.*, underlining once again the difficulties to discriminate one from the other species.

As occurred in the Grotta del Cervo, the dental elements (both of *U. arctos* and *U.* ex gr. *spelaeus)* always show rather large dimensions in relation to the findings of the same species from other sites. This data is extremely curious, especially for the speloid bear; in fact, as already mentioned in the previous chapters, the two evolutionary lines of bear are characterized by reverse dimension trends, whereby the brown bear progressively decrease in size, while the cave bear shows an increasing dimension (both of the cranial and post cranial elements).

The Grotta degli Orsi volanti deposit, even if it does not have precise dates, is still within the time range of the tardiglacial (130,000 and 40,000 y), therefore it represents an exception to this pattern.

7.3 Vigna S. Carlo (Monteverde)

7.3.1 The site

Vigna S. Carlo (Monteverde) is a very old fossiliferous deposit located south of Rome, more precisely on the right bank of the Tevere river.

The site was discovered and excavated during the early years of the last century and, to date, there are no more traces of its precise location or photographic documentation of the deposit.

It is part of the so-called formation of Monte Verde, consisting of 8 layers: “Sabbioni e ghiaie, Tufo litoide da costruzione, Tufo vulcanico omogeneo stratificato, Argille marnose e travertino, Sabbie argillose, Ghiaie a piccoli elementi, Sabbie ed un complesso di strati alterni di argille sabbiose e sabbie”. Most of the fossiliferous material comes from “Sabbie argillose” and is biochronologically dated to the Late Pleistocene. Among the many faunal fossils have been identified various genera including *Felis, Histrix, Elephas, Rhinoceros, Hippopotamus, Cervus, Bos, Emys* and *Ursus* (Napoli, 1907; 1911).

7.3.2 Material

The genus *Ursus* is represented only by a complete hemimandible, accurately described by Professor Portis (Portis, 1907) and assigned to "*U. horribilis* or *ferox*".

The specimen is in perfect condition and is now stored at the MUST (University Museum of Earth Sciences) of Sapienza, University of Rome and catalogued as V.1152 (Fig. 53 and Table 4). Although the museum card still indicates the taxonomic attribution proposed by Portis, the specimen is to be considered within the species *U. arctos*, since *U. horribilis* and *U. ferox* have both fallen into synonymy, as evidenced in the chapter 2 of this thesis.

Table 4: ***List and measurements of the Ursus material from the V. San Carlo deposit.*** *(Measure in mm).*

Inv. N°	Element	Side	Ontogenetic Stage	m1	m2	m3	m4	m5	m6	m7
V. 1152	Hemimandible	**Left**	Juvenile (IV class)	235,6	31,2	48,1	46,3	51,9	16,6	21,4
				m8	**m9**	**m10**	**m11**	**m12**	**m14**	**m15**
				17	86,5	78	13,2	46,2	17	114

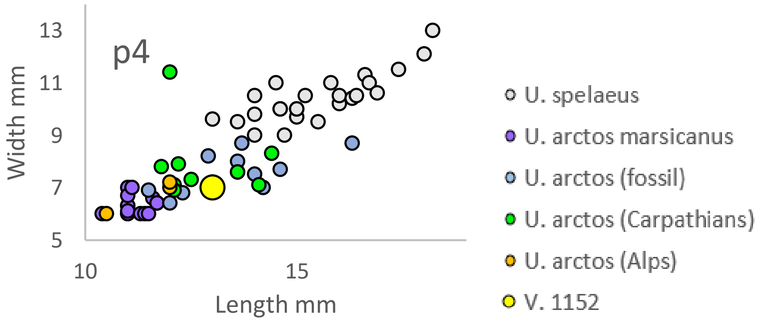
Inv. N°	Element	Side	Age	Length	Width
V. 1152	p4	Right	Juvenile (IV class)	13	7
V. 1152	m1	Left	Juvenile (IV class)	25	12
V. 1152	m2	Left	Juvenile (IV class)	26	15

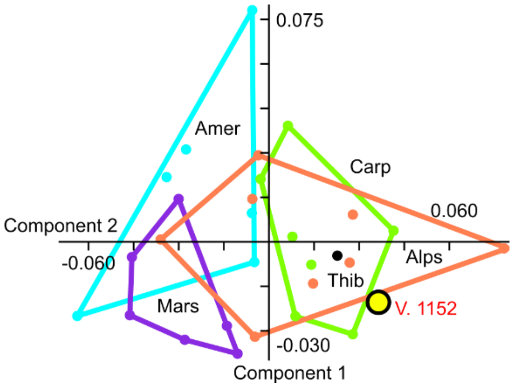
Figure 53: ***Emimandible from Vigna San Carlo (V. 1152). A)*** *Dorsal view* ***B)*** *Lateral view.*

7.3.3 Description

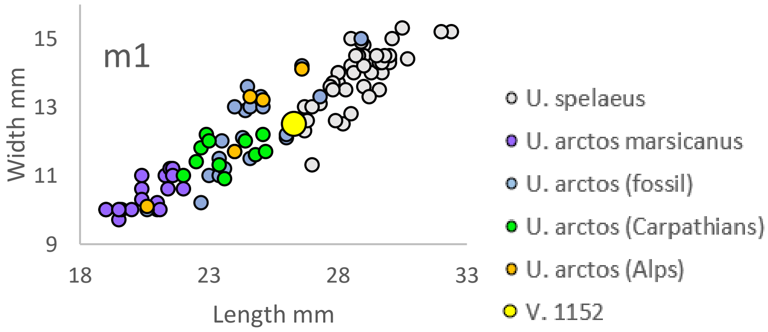
V. 1152: The specimen is represented by a left hemimandible in perfect state of preservation, with only a slight fracture on the coronoid process. The latter is wide, oriented at the back and with a narrow and shallow mandibolar incisura. The pterygoid process is clearly visible and has a cylindrical structure, with the lingual portion and the labial portion of the same size, which forms with the ramus mandibolae a very acute angle. At the base of the ramus mandibolae there is a very extended but weakly marked pterigoid insertion while the corpus mandibulae is relatively low (compared for example to a typical *U.* ex gr. *spelaeus* see Chap. 3). The specimen has a rather slender general structure, the fourth premolar, the first molar and the second molar are present, whilst, on the contrary, the third molar is missing, of which, however, the alveolus is well evident. In the distal portion it has a wide diastema ending with the partially fractured alveolus of the canine, on which a small alveum for the first premolar can be observed. It lacks incisors.

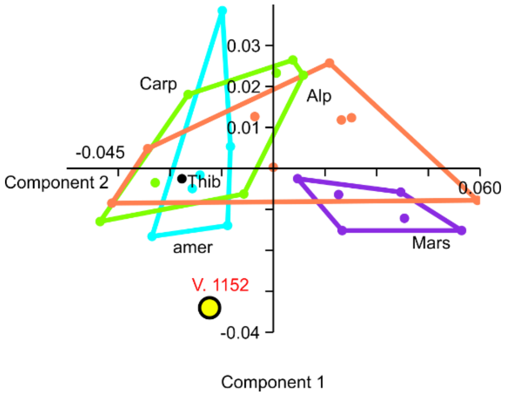
V. 1152 - (p4 Left): The tooth is slender, with an elliptical occlusal profile and a very simple general structure. In fact, there is only one main cusp (the protoconid) from which three ridges develop; two of them follow the longitudinal profile of the tooth up to the mesial and distal margin, the third one proceeds towards the lingual portion and then curves abruptly and stops in the central-distal portion of the tooth. There are no accessory cusps and the wear is very little evident.
From the graph of the dimensional ratios the tooth fits well within the dimensional range of brown bears, both fossil and modern; on the contrary, its morphology is rather outside the standards of other bears, although it is closer to the brown bear shapes of the Alps and Carpathians.





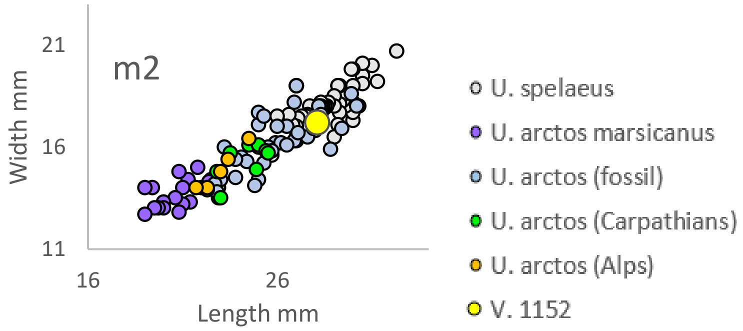
V. 1152 - (m1 Left): The tooth is slender, with a straight lingual profile course, while the constriction in the labial profile is rather pronounced. The occlusal surface is almost entirely occupied by the main cusps, which are very developed and poorly divided (apart from the entoconid which is formed by 2 cusps). There is no presence of tubercolation or accessory cusps, while wear is almost absent, reflecting the characters of the previous tooth, so the fossil represents an individual who belongs to the juvenile category (Class III). Although the geometric morphometry graph indicates that the tooth remains far outside the variability of the brown bear, on the contrary the morphometric data indicates a good affinity with the arctoid forms (all except *U. marsicanus*).

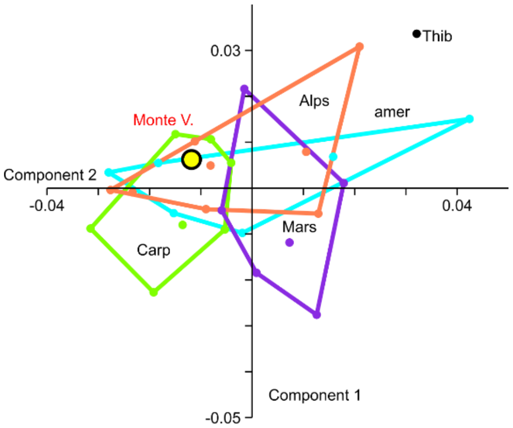




V. 1152 - (m2 Left): Also in this case the wear is consistent with the other dental elements indicating a juvenile individual, who has a rather simple occlusal surface, with the main cusps rather developed. In fact, the trigonid does not have a high tubercolosity and the crests of the protoconid and of the Metaconid encounter each other without the presence of further accessory cusps.

The talonid is also poorly tuberculated and the hypoconid forms a continuous crest along the distal profile of the tooth. The entoconid is not divided and the caterpillar is extremely poorly developed. In this case, rather than the other teeth of the mandible, it is extremely well evident the dimensional affinity of the finding analyzed with the fossil brown bears, rather than with the current ones. In fact, the second lower molar is remarkably big, reaching also the average dimensions shown by the variability of *U.* ex gr. *spelaeus*. From a morphological point of view, the tooth is part of the general pattern of most of the bears examined, falling within the graphic area occupied by both *U. arctos* Alpino and *U. arctos* of the Carpathians.





7.3.4 Final remarks

From the general analysis of the mandible the find has to be assigned to *U. arctos* and represents a rather peculiar form of the species, mainly about the shape of the first lower molar.

Despite this, only with an isolate hemimandible it is hard to discuss about evolutionary and adaptive features of the bear from this deposit. Moreover, as already mentioned, the site was discovered, excavated and studied only during the first years of 1900 and today there is no more precise information about it. Nevertheless, it is still one of the very rare findings referable to *U. arctos* in the central southern Italian area, so it is also an extremely important data for the morphological comparison.

An interesting feature of the mandible is that all the teeth of the lower jaw possess the same size and morphological features; in fact, observing the graphs of geometric morphometry, the teeth of V 1152 are always positioned in the common square between *U. arctos* from Alps and *U. arctos* from Carpathians, while, by a morphometric point of view, these always fit within the variability of the fossil brown bear.

7.4 Ingarano

7.4.1 The site

The site of Ingarano consists of a cave located in the north-west of the Gargano Promontory, is located 270 meters above sea level near Apricena (Foggia, Italy) which, since the 90s, has been the subject of numerous studies and excavation campaigns. The deposit contains a faunal assemblage referable to the Late Pleistocene (U.F. Ingarano) and the fossil remains are embedded in a conglomerate matrix present within what remains of a large karst cavity set in the limestones of Sannicardo (Petronio et al., 2006).

The site has been discovered thanks to the works for the adaptation of the Gargano railway and, even if it is chaotic, it is possible to distinguish various overlapping levels containing faunal remains in different chronological contexts (Petronio and Sardella, 1998a) whose depositional relationships are not very clear.

These levels can therefore be summarized in five depositional units (Fig. 54).

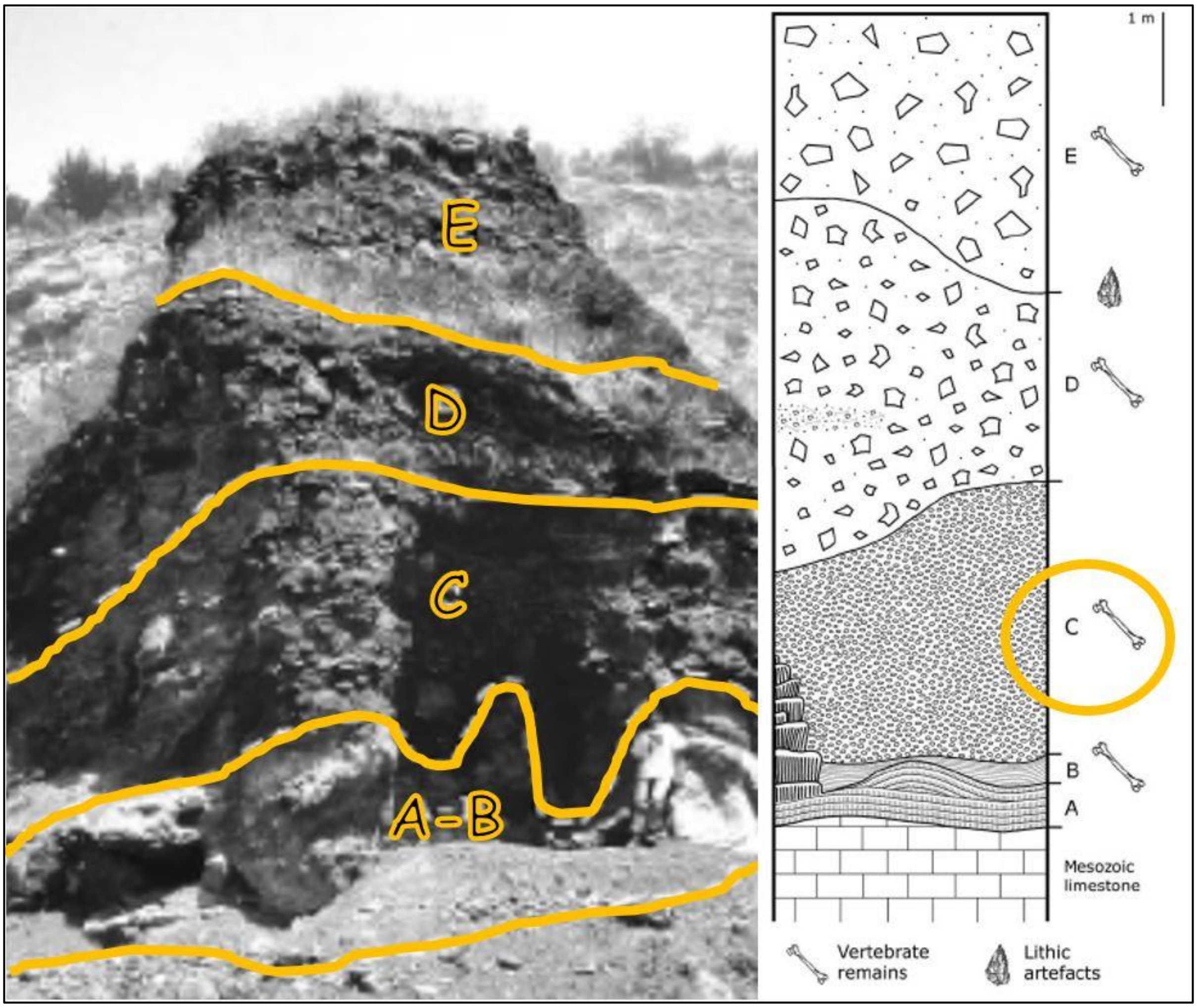


Figure 54: ***Ingarano deposits, the letters indacate the different leyer, the circle indicates the provenience of the brown bear fossil material.*** *Modified from Petronio et al., 1996.*

The first positional level (A) is composed of alabasters; it is characterized by a thickness varying from a few centimetres to about one meter deep and includes some fragments of speleothemes. This level is locally covered by a phosphate component interpreted as the product of the decomposition of guano from a colony of birds (Bedetti and Pavia, 2007). From this phosphatic product, it was possible to estimate an age of 40,000 +- 2,00 years BP using the geochemical method of 230Th/ 234U and 234 U/238U (Petronio and Sardella, 1998a).

The phosphate incrustations of the second depositional level (B), a few centimetres thick, are locally rich in medium and small vertebrates, including birds. The third compact conglomerate level (C) has a homogeneous texture with the presence of small limestone blocks and a reddish silt matrix with little local cement; its thickness varies from one to three metres and it is rich in vertebrate remains (micro-macromammals and birds).

A discontinuous surface indicates the passage to another conglomerate level (D) with a thickness between two and four meters. The deposition unit D is characterized by the presence of clasts with sharp angles, at the top of which are greater than 10 cm, and a predominantly calcareous matrix. This level is also rich in vertebrates with local concentrations of micro-mammals and birds (Bedetti and Pavia, 2007).

The succession ends with a conglomerate level (E) with a thickness of between two and three metres characterised by the presence of sharp-edged clasts cemented by a limestone matrix. From this level come some findings of lithic industry referable to the Levallois technique of the Middle Palaeolithic (Petronio and Sardella, 1998a).

The Ingarano deposit is characterized by a rich fauna of vertebrates; 41 species including amphibians, reptiles and other numerous fossils finds attributable to birds and macro and micro mammals have been found (Bedetti and Pavia, 2007). The most abundant component of mammals is associated with rodents, represented by *Microtus ex gr. arvalis/agrestis*.

Among the carnivores there are remains of *Canis lupus*, *Mustela nivalis* represented exclusively by a hemimandible and about 1400 bone remains referable to 54 individuals of *Vulpes vulpes* (Petronio et al., 2006) found at the base of the karst cavity. Belonging to the same order, there is the evidence of *Felis silvestris*, *Lynx lynx* and *Panthera spelaea* (Capasso Barbato et al., 1992). Among the artiodactyls is documented the presence of *Cervus elaphus*, *Dama dama*, *Capreolus capreolus*, *Rupicapra sp.* and *Bos primigenius*.

In the same way as the site of Vigna S. Carlo, the only representative of the genus *Ursus* is the brown bear.

7.4.2 Material

The material is kept at the Department of Earth Sciences of La Sapienza, University of Rome and is represented by some fossil elements of post cranial (a fragment of radium and a phalanx) and various cranial elements, including various teeth in anatomical connection and portions of cranial caps (Table 5, Fig. 55-56). From the site also comes a complete skull, with both hemimandibles in anatomical connection and supported by a concretional matrix. It is an extremely rare element, both because it represents one of the few complete skulls of the Italian Late Pleistocene, and because of the peculiarity of having been found in a fluvial-lacustrine deposit. Although the various faunas from the deposit have been the subject of numerous publications, the material of Ingarano bear is still unpublished, there is only one work by Capasso Barbato et al., (1998), in which the skull was only figured, but never described and studied in depth.

All the bear material concerning the cranial and mandibular elements referable to *Ursus arctos* coming from the site were measured and digitized by photogrammetry (according to the schemes proposed in Chapter 4). The only exception is the complete skull (INGND 1) which, because of its uniqueness and fragility, was subjected to a CAT scan.

The analysis of the tomographic images has allowed the acquisition of morphometric and morphological data of the teeth and of the internal portions of the skull; the three-dimensional models of the encephalic cavities and of the frontal sinuses has been also obtained (See Chap. 9). Despite this, the resolution of the images does not give the necessary resolution to acquire the data for the analysis of geometric morphometry. For this reason the teeth of the skull have been only described and measured, and does not appear in the morphological graphs.

Table 5: ***List and measurements of the Ursus material from the Ingarano deposit.*** *(Measure in mm).*

Inv. N°	Element	Side	Ontogenetic Stage	c2	c3	c9	c13	c14	c15	c18
INGND 1	cranium		Juvenile (Class III)	298	272,2	85	58,9	126,2	32,6	172,5
				c20	**c21**	**Mc2**	**Mc5**	**Mc6**	**Mc7**	**Mc8**
				94,2	69,8	55,1	146,2	109,6	81,7	66,1
Inv. N°	**Element**	**Side**	**Ontogenetic Stage**	**m1**	**m2**	**m3**	**m4**	**m5**	**m6**	**m7**
INGND 1	mandible		Juvenile (Class III)	219,3	33,8	42,1	42,3	48,8	13,8	22,3
				m8	**m9**	**m10**	**m11**	**m12**	**m14**	**m15**
				104	85,4	72,9	12,1	38,5	11,8	96,5
Inv. N°	**Element**	**Side**	**Ontogenetic Stage**	**Length**	**Width**					
INGND 1	P4	Left	Juvenile (Class III)	16	12					
INGND 1	M1	Right	Juvenile (Class III)	23,8	18,1					
INGND 1	M2	Right	Juvenile (Class III)	40	19,1					
INGND 1	p4	Left	Juvenile (Class III)	13	7					
INGND 1	m1	Left	Juvenile (Class III)	25	13,3					
INGND 1	m2	Right	Juvenile (Class III)	26,9	16,3					

INGND 1	*m3*	*Right*	*Juvenile (Class III)*	*21,3*	*18,3*
INGND 1	*P4*	*Left*	*Juvenile (Class III)*	*16*	*12*
INGND 1	*M1*	*Right*	*Juvenile (Class III)*	*23,8*	*18,1*

Inv. N°	***Element***	***Side***	***Ontogenetic Stage***	***Length***	***Width***
INGND 716	*M1*	*Left*	*Juvenile (Class III)*	*24*	*17,6*
INGND 717	*P4*	*Right*	*Juvenile (Class III)*	*13*	*11,8*
INGND 717	*M1*	*Right*	*Juvenile (Class III)*	*23,7*	*17,6*
INGND 717	*M2*	*Right*	*Juvenile (Class III)*	*35,9*	*18,8*
INGND 718	*m2*	*Left*	*Juvenile (Class II)*	*27*	*19*
INGND 719	*m2*	*Right*	*Juvenile (Class III)*	*29,9*	*18,6*

Figure 55: ***INGND 1 from the Ingarano deposit.*** *Lateral view.*

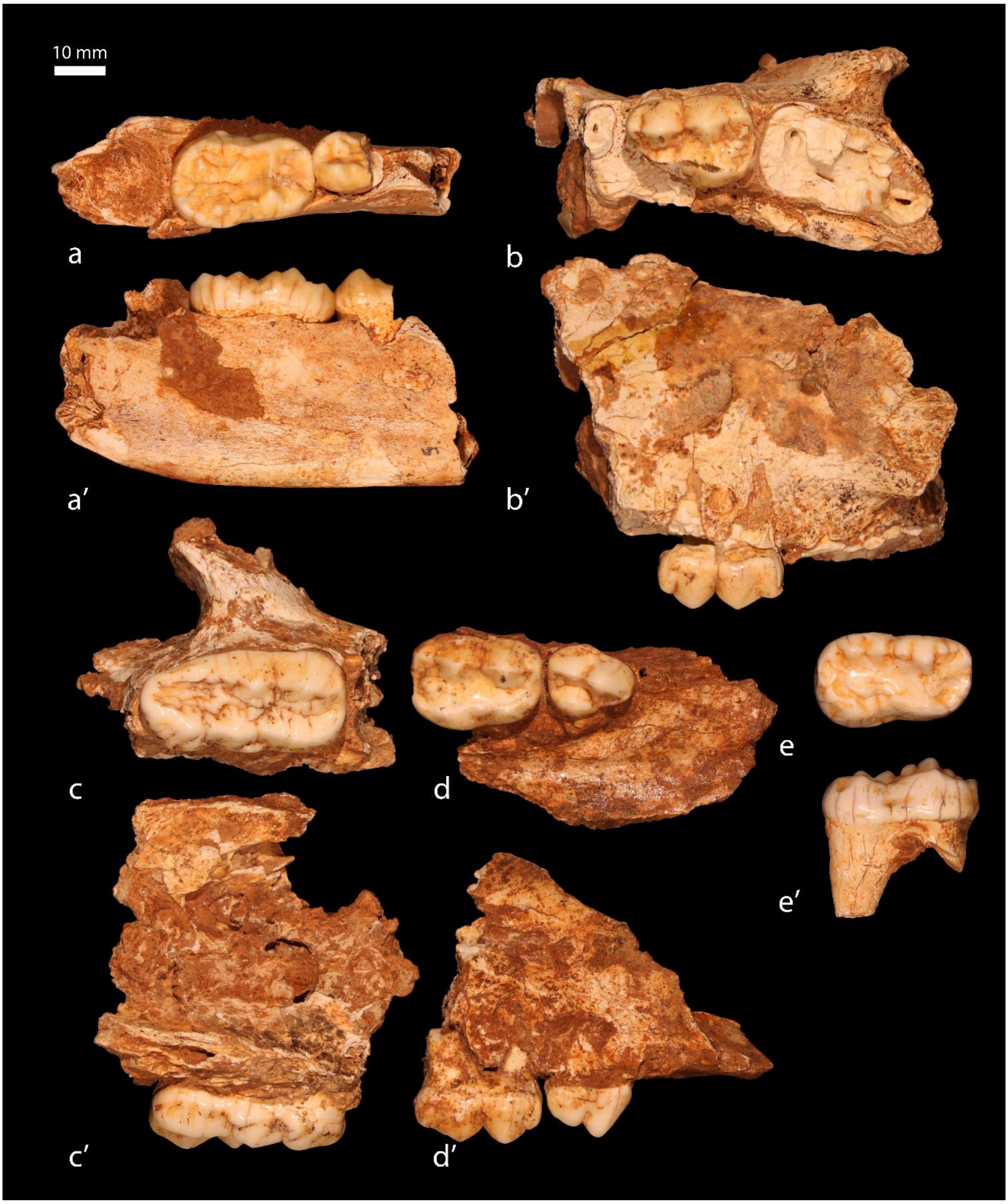


Figure 56: ***Ingarano Ursus material, occlusal view and lateral view (letter with apex): a-a')*** *INGND 718.* ***b-b')*** *INGND 716.* ***c-c')*** *INGND 717 b.* ***d-d')*** *INGND 717 a.* ***e-e')*** *INGND 719.*

7.4.3 Description

INGND 1: The skull is well preserved even though it has numerous fractures on various skeletal portions have been subjected to various restoration operations.

The general morphology is slender with thin structures and an anteroposterior development. The finding has a lateral crushing due to a diagenesis effect, which has led both to a deformation according to the saggittal plan, and to disarticulation and partial displacement of the hemimandibles.

Part of the two jugals are missing, which are however complete enough to allow the acquisition of morphometric and morphological data of the zygomatic bones, representative character of relatively small messeteric muscles.

Part of the left prefrontal is not present; probably the removal of this portion of the skull occurred after fossilization, since there is no sediment in the nasal cavity where it is possible to distinguish the nasal sinuses walls.

The frontal and the parietal are very well preserved, and it is possible to easily notice the rectilinear shape of this portion, typical of the arctoid species.

The rostral portion of the skull, on the other hand, is the most damaged and mineralized; however, it is possible to observe the right infra-orbital canal located perpendicular to the metacone of the first upper molar. Perfectly preserved are also the foramen magnum, the occipital condyles and, next to the mastoid process, the cavity of the acoustic meatus. The presence of a concreted rock does not allow the direct analysis of the palate and the vomeral portion.

In contrast to the left portion of the maxilla, the right portion lacks all the incisors (only the alveoli can be seen). All Canine, fourth premolars, and are present, both on the left and on the right side of the skull. Moreover, even if fragmented, the first and third premolars are visible.

Both hemimandibles are rather intact, although a large fragmentation is clearly visible in the central portion of the corpus of the right hemimandible, restored with plaster. The general morphology of the entire mandible is rather slender, with thin coronoid processes and a low mandibular body. The orientation of the coronoid branch is turned backwards, and the incisura is narrow and shallow. The articular condyle is cylindrical and forms a rather acute angle with the angulus mandibolae. The pterigoid insertion is long and poorly developed. On both hemimandibles there are molarforms (p4, m1, m2 and m3), canines and incisors (even if partially fragmented).

In the same way as the maxilla, both the first and third premolars are present, even if they are remarkably damaged. In contrast to the right hemimandible, the left hemimandible is disjointed from the skull due to diagenetic crushing and lacks the coronoid process.

Despite the possibility of observing the tooth profile by means of tomographic images, the disarticulation of the right jaw allows the observation of the occlusal surface of the various teeth taken into consideration in this study, therefore only the morphologies of the teeth on this side will be described here.

The only described tooth of the left portion is the upper and lower P4, since, in both cases, they are extremely damaged in the right dental row.

INGND 716: It is one of the two isolated portions of the maxilla from the deposit. The specimen is extremely fragmented and is represented by the dental row (only M1, M2 and part of the root of P4) and by the beginning of the zygomatic process. From the dimensions of the latter it is possible to understand that the total size of the skull did not have to be extremely high, such as to be able to treat a very young individual. The age is however confirmed by the dental wear, almost absent of the occlusal surface of the upper First Molar (the only tooth of which it is possible to observe the chewing portion). The other two teeth, partially present, consist exclusively of the root, which is still firmly embedded within the alveoli. In the distal part of the finding, the alveolar cavity of the canine is clearly visible, but without any trace of the tooth.

INGND 717: The specimen consists of two elements in anatomical connection but impossible to fisically assemble through restoration. It is a well-preserved fragment of the maxilla, with the presence of the fourth premolar, the first and the second molar.

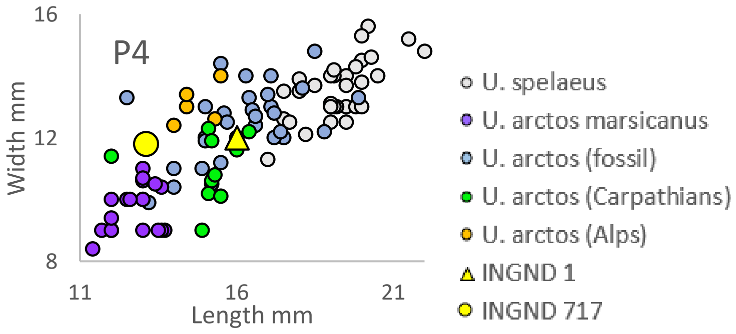
The first fragment (a) represents the largest portion, on which it is possible to observe a small part of the palatal, the fourth premolar, the first molar and the alveolus of the third premolar. Given the fragmentary contition of the specimen, it is impossible to deduce the size of the skull but, observing the internal portion of the fractured bone, it is possible to observe a certain sponginess that should characterize a rather young individual.

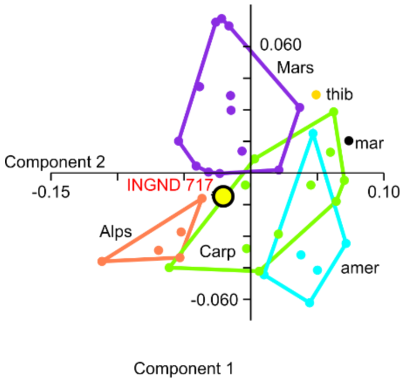
The second fragment (b) is represented only by the second upper molar and its top bone portion on which it is possible to observe the fragmented beginning of the jugal process.
In general, the presence of wear on the teeth is not much, so the maxilla fits into the category Juvenile, Class III.

INGND 719: The specimen consists of an extremely fragmented fragment of the left jaw, of which only the central portion of the mandibular body and a small part of the crest of the coronoid process remain. On the bone element there is still a fragment of the first lower molar and the second lower molar, while only the alveolus is present on the third lower molar.
It is very difficult to describe the general morphological characteristics of the finding as it represents a too small portion of the entire mandible, but it is easy to see how this should belong to a very young individual, both for the presence of teeth without wear and for the extreme backward position of the alveolus of the third molar, which does not exceed the margin of the coronoid crest.Therefore, the fragment had to belong to an individual who fits into the category Juvenile, Class II.

INGND 1 - (P4 Left): The upper premolar fourth has a rather thick morphology with a sub-triangular profile and very developed cusps. The paracone occupies a large part of the tooth surface and is almost twice as long as the protocone. The tooth, although rather large, has a simple morphology, without the presence of additional cusps or portions of tubercolated surface. The dimensions represent a singularity, as the width of the upper premolar quarter is greater than its length.

INGND 717 - (P4 Right): The tooth shows a sub-triangular morphology typical of the dental element, with rather well-developed cusps and a barely noticeable lingual girdle. There are no accessory structures on the main cusps, but it should be noted that there are two accessory cusps very close to each other located in the central portion of the distal region of the tooth. The wear, as then will be confirmed also for the other teeth of the series, is almost non-existent; therefore, the individual is to be considered in the juvenile category, class III.
Both dental elements fall within the variability of the fossil and actual brown bear, even if the tooth belonging to the jaw fragment (INGND 717) is positioned in a graphic area characterized mainly by the alpine forms of brown bear and instead, the one belonging to the skull is longer and narrower, a character found in the bears of the Carpathians. The morological analysis returns a rather ambiguous data, as the tooth analyzed fits perfectly in the area of graph that unites all three species of modern brown bear.



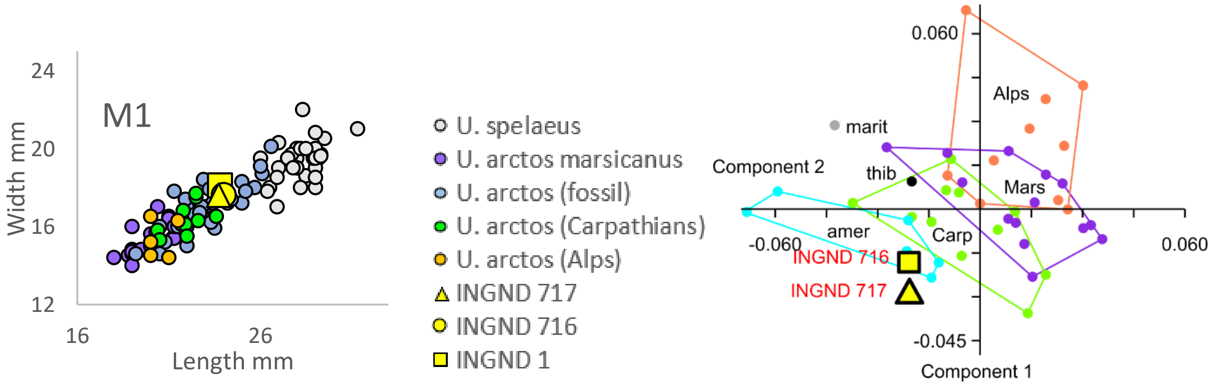


INGND 1 - (M1 Right): The tooth has a rather elongated external profile with the talon slightly wider than the triconid. The tooth has typical arctoid characters, in fact the cusps are well outlined and there is no presence of accessory structures or tubercles in the posterior portion of the occlusal surface. The metastyle and the parastyle are barely visible while the paracone and the metacone are wide and occupy a large part of the occlusal surface with their ridges. The proto-meso-hypocone line is rather straight and the cingulum is almost absent. On the tooth there is a slight wear, such as to make the specimen fit within the category Juvenile, Class III.

INGND 716 – (M1 Left): The thooth in the mesial portion is highly fragmented, showing only the buccal main cusp (the paracone). The metacone is well developed but doesn't reach the same high of the paracone. In this specimen the parastyle and metastyle are also well represented with the first more developed than the second. Due the lack of the protocone cusp is impossible to describe the Hypo-meso-protocone line but can be recognize a small and poorly developed lingual cingulum. There is no presence of tubercled areas. As already mentioned, the wear of the tooth is extremely reduced and concentrated exclusively on the top portion of the hypocone and mesocone, for this reason, the specimen is to be juvenile (Class III) according to the scheme proposed by (Stiner, 1998).

INGND 717 - (M1 Right): The tooth has a very simple general morphology, with a rather smooth occlusal surface and without the presence of accessory cusps. The parastyle and metastyle are clearly visible and the former is more developed than the latter. The distal portion has a slight fracture in the crown line, although the talon does not have any significant tubercolosity.

In contrast to the upper P4, the first upper molars coming from the site are almost identical in size and are positioned in the same portion of the graph occupied by most of the finds of brown bear fossil. According to the geometric morphometry graph, the two teeth analyzed remain very similar to each other, although outside the morphological patterns typical of other brown bears analyzed.



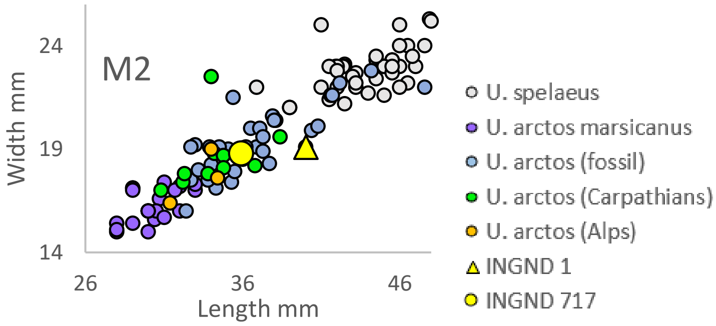
INGND 1 - (M2 Right): The tooth has an elongated and irregular profile, especially in the portion of the talonid. The cusps are clearly visible with an undivided paracone and metacone. The protocone and hypocone are formed by a single cusp that extends longitudinally, almost to form a crest.

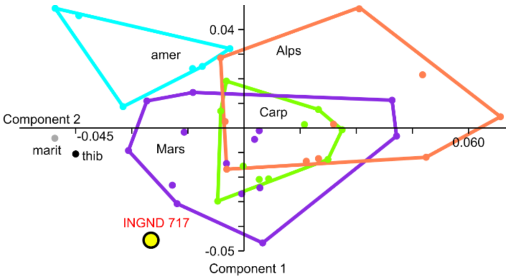
In contrast to what can be observed on a speloid tooth, the occlusal surface of the trigonid is almost completely occupied by the ridges of the main cusps, and a tubercled area is present only in the distal portion of the occlusal surface. The cingulum is present but formed by a single homogeneous crest without the presence of additional cusps.

INGND 717 - (M2 Right): The tooth also has a general morphology typical of the genus, with the main cusps well outlined and the presence of a rather developed lingual cingulum. The main cusps represent a large part of the occlusal surface, forming a series of small tubercles with a single groove that crosses the entire tooth. Wear is non-existent.

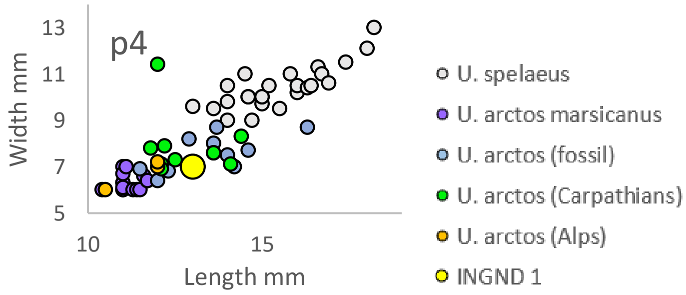
Also for the second upper molars, the characters indicated by the fourth upper premolar fourth are represented; in fact, while the tooth belonging to the skull is longer and narrower, that of the maxillary fragment is more stocky and short, while both remaining within the dimensional range of the Pleistocene brown bear.

The morphological trend described by the other dental elements is also confirmed by the second upper molar, in fact the specimen falls outside the typical morphologies, in a portion of the graph adjacent to the area occupied by Marsican teeth.





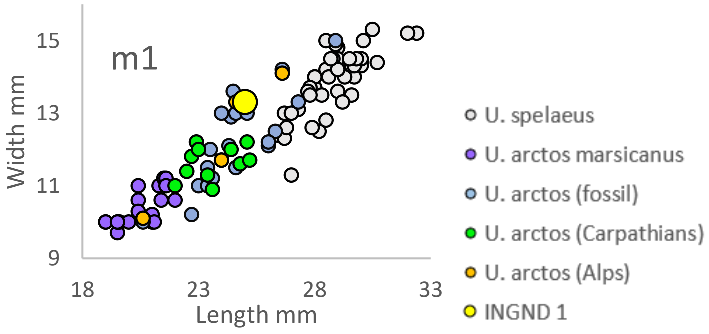
INGND 1 - (p4 Left): The tooth has an elongated, simple and ellipsoid-shaped profile; the paraconid, the main cusp, is well developed and placed in an advanced position with respect to the longitudinal axis of the tooth. Although they are much less marked, on the occlusal surface it is also possible to see a hint of protoconid and metaconid, placed at the mesial and distal extremities of the tooth and reduced to the size of small cusps. There is no tubercolation on the chewing surface and the wear of the tooth generally reflects that of the other upper elements. The lower fourth premolar fits perfectly within the size range of the fossil brown bear.



INGND 1 - (m1 Left): The first lower molar is elongated, has a rather straight lingual profile while the buccal one is wavier, shrinking to the height of the constriction. The latter is rather backward leaving the talonid only a third of the length of the entire tooth, leaving much of the occlusal surface occupied by the trigonid. The cusps are all well developed, the paraconid is placed in a central position of the mesial area of the tooth and the protoconid is well developed and formed by a single cusp. On the contrary, the Metaconid is lower than the other cusps and is divided into three distinct cusps; this division characterizes also the enthypoconid, even if it divides in two and not three cusps.

Almost all of the masticatory surface is occupied by the ridges of the cusps and there is no trace of tubercles or accessory cusps in the central portion of the tooth.

There is no evident wear on the cusps. The morphometric data of the tooth fall within the average size range of the fossil brown bear and brown bear of the Alps, while they are bigger than the standard brown bear of the Carpathians.



INGND 1 - (m2 Right): The second lower molar has a rather wide profile and is presented as a solid and stocky tooth. The occlusal surface is quite simple and there are no additional cusps or evident tuberculated structures.

On the contrary, the cusps are well outlined and occupy most of the chewing surface. Among these, the Metaconid and the paraconid are the most developed and, while the second is represented by a single cusp, the first is divided into two distinct cusps. The crests of the latter are congingent in the central axis of the tooth, clearly dividing the talonid from the trigonid. The distal cusps are less pronounced, with the entoconid reduced to a lateral crest and the hypoconid divided into three distinct cusps.

INGND 718 - (m2 Left): This second lower molar shows a rather enlarged occlusal profile with a peculiar thickening in the buccal portion of the talonid. In general, the tooth appears very robust even if it does not have an extremely complex occlusal surface; in fact, the few tubercles present are concentrated in the central portion of the talonid and almost completely absent in the portion of the trigonid.

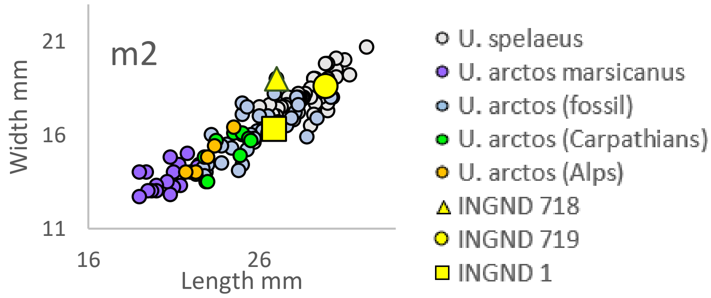
The main cusps are well developed, in the mesial portion the metaconid and the protoconid occupy a large part of the chewing area and their ridges join at the level of the longitudinal axis, and only the first of these is characterized by a secondary cusp placed at level of the constriction of the lingual profile of the tooth. As it normally happens in the teeth of *U. arctos*, between the two main cusps of the mesial area only the entoconid is divided, showing three cusps well distinct between them.

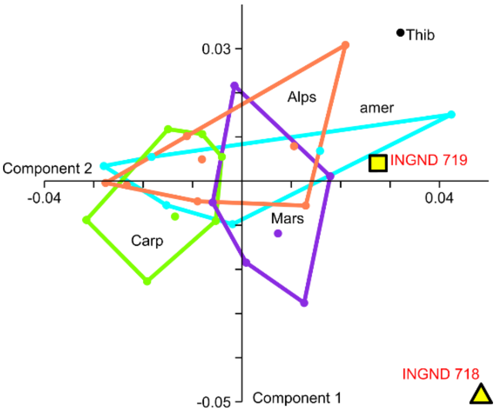
INGND 719 - (m2 Right): The second lower molar is the only molar-shaped bear tooth found isolated at the site. It shows an elongated occlusal profile, with the talonid slightly larger than the trigonide and a poorly developed central constriction.

The occlusal surface has quite developed cusps, especially on the lingual side of the tooth. In fact, both metaconid and entoconid are wide and high, and divided into several cusps (three cusps for metac. and two for entipoc.). Although the tooth has a peculiar large occlusal surface, there are no tubercles or additional cusps.

The wear is barely visible and present only on the crest of the protoconid and hypoconid; therefore, the tooth belongs to the category Juvenile, Class III.

The three lower molars are all rather large; the jaw fragment INGND 719 shows a tooth that falls almost within the size range of the cave bear, positioning itself at the end of the morphometric variability of the fossil brown bear; the other two elements are instead smaller but still outside the morphometric range of the modern bears. From a morphological point of view, the two teeth analyzed remain well outside the areas of the graph that delimit the morphologies of the brown bear, especially INGND 718.

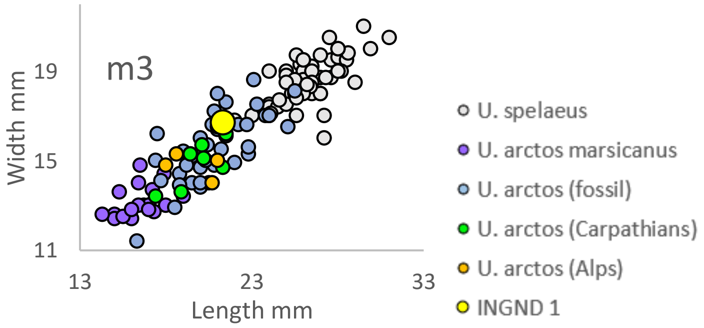




INGND 1 - (m3 Right): The tooth has a rather quadrangular profile, with an occlusal surface poorly tubercolated and rather simple.

Unfortunately, its backward position does not allow an in-depth analysis of the distal portion of the tooth; on the contrary, in the mesial area, it is possible to observe the Metaconid and the protoconid which are presented as single and well-developed cusps.

From the observable area, there does not seem to be any extreme complexity of the chewing surface and the dimensions shown in the morphometric graph are perfectly in accordance with the average size ratios of fossil brown bears.



7.4.4 Final Remarks

Regarding the study of the dental elements, the analysis of the bear material coming from the Ingarano deposit provide a good amount of information about ecological aspects of the species, and about peculiar characteristics of those specimens.

The morphology of the various dental elements shows a trend where all the findings studied remain outside the typical morphological ranges of the modern bears; especially INGND 718 and 719.

This character may be related to the geographical position of the site. In fact, the deposit of Ingarano, is located on the Gargano, a mountainous promontory almost surrounded by the sea. This geophysical conformation could have modified the eating habits or the adaptive dynamics of these bears, resulting in morphologies slightly different from continental bears.

The only element that does not have this characteristic is the upper P4. In spite of this, the morphometric analysis and morphology of this dental element still show an interesting data and a stimulus for reflection about the characteristics of shape and size of modern populations compared to fossil ones.

Regarding the graphs of the modern material (beginning of chapter) it is possible to observe that most of the morphological and morphometric differences between the various bears are represented by the upper fourth premolar, specially between the Alps and Carpathian populations.

The data concerning the teeth coming from the Ingarano deposit (INGND 717 and INGND 1) show that both of these falls within the dimensional ranges of the two distinct populations.

This evidence reveals that the difference between the two-modern population is not registered in Late Pleistocene material and have to be set up later.

The most interesting element of the site is certainly the complete skull. This presents indisputably arctoid characters both in morphology: 1) presence of the lower and upper premolars, 2) rather low frontal, 3) mandible with a rather wide angle between the coronoid process and the mandibular body, 4) general dimension, as demonstrated by the morphometric analysis of the dental elements.

Dental wear shows that it is a juvenile individual while some morphological features of the skull indicate that the find belonged to a female individual.

In fact, the sexual dimorphism in the bears of all species, both extinct and present, is rather accentuated (Kurtén, 1955). In the males, the zygomatic bone makes a wider arch and generally appears to be higher, whilst the sagittal crest is more pronounced, in order to allow the placing of big and powerful masseter muscles (Grandal-d'Anglade and López-González, 2005).

Females, on the other hand, have nasal bones, parietal bones and premaxillary bones longer than males; these traits are due to a more developed sense of smell, probably linked to the protection of the cubs. (Nezami et al., 2014).

In addition to the cranial characteristics, an important index of sexual dimorphism is the size of the canine (slenderer in the females) and its rapport with the length of the skull.

Unlike what happens in herbivores, this does not depend on the size of the animal but exclusively on eating habits and, above all, on sociality (solitary life, harem, herd).

The proportions of the carnassial teeth, on the other hand, seem to depend exclusively on the diet (Gittleman, 1997).

In this case, the general cranial dimensions and the shape of the zygomatic and the muzzle, give a considerable amount of data to confirm that the INGND 1 specimen belonged to a young female.

It is impossible to determine the genus of the other fossil elements coming from the site, but it remains clear that almost all the material represents juvenile individuals.

In fact, analyzing the number and morphology of the finds it is possible to hypothesize that there are at least four individuals even if, the taphonomy of the deposit, does not allow to determine if they all belonged to the same family nucleus or if they represent several isolated individuals.

Finding of many juvenile individuals within the same deposit is quite common and can be caused by many reasons.

The first one is related to the great mortality of the cubs during the hibernation, both for accidental causes and predation. Another reason is the rather common infanticide by adult males.

In fact, many dominant males, kill the cubs of the female before mating, in order to ensure that their progeny has the necessary parental care.

7.5 Grotta della Lupa

7.5.1 The site

The site is located in the Comune di Roccamorice (PE) and is represented by a karst cave located about 1040 meters above sea level, recently discovered (2015) by the activity of GRAIM (Research Group of Industrial Archaeology of the Maiella) and explored and studied by the Speleo Club Chieti. The Grotta della Lupa develops in the northern sector of the Maiella, surrounded by rocks belonging to two distinct formations, the first of the group of the Santo Spirito and the second by the Formazione Orfento.

In general, the cave can be described as a composite cavity, characterized by a first phase at full water regime and a second phase with water flows that affect only some portions of the cave with much lower flow rates. (Personal communication Dr. M. Adelaide Rossi and Dr. S. Agostini).

The fossiliferous deposit is located at the end of one of the two main branches called "lato a monte" from which have been found, in addition to the material of brown bear, also wolf remains (*Canis lupus*), deer (*Cervus elaphus*) and goat (*Capra hircus*).

The taphonomy of the deposit shows that most of the bone material comes from different periods, probably due to the deposition of carcasses already dismembered outside.

Although the state of fossilization and the presence of a thin layer of calcite on the surface of the findings indicates a time spam between the beginning of th Holocene and the recent period, it is not yet possible to have a more detailed dating; specific analyses are still in progress.

7.5.2 Material

The brown bear fossil material is entirely stored at the Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Abruzzi (Chieti) and is represented by both cranial and post-cranial elements (Fig. 57 and Table 6). The post-cranial material is composed by: 7 metatarsals (GL 131-137); 15 phalanges of which 6 first and 7 second (116-130); 4 fragmented femurs (GL 92,93,94,104); 3 tibias and 3 fragmented humerus, of which two left and one right (GL 95,96,97, 58,59,60); 3 well-preserved ulnas showing well welded articular surfaces (GL 57-66-68).

The cranial material is composed by: two fragments of a very small cranial dome (GL 109,138), an extremely damaged portion of neurocranium belonging to a subadult individual (GL 140), a left hemimandible (GL 1), a right hemimandible (GL 3), a non articulated complete mandible (GL 2 a-b), a fragment of the maxilla with a first upper right molar (GL 4), a second upper right molar (GL 5), two first lower right molars (GL 6,7).

The material analyzed is still unpublished and the most diagnostic elements have been digitized by photogrammetry with the technique "turn table".

Table 6: ***List and measurements of the Ursus material from the Grotta della Lupa deposit.*** *(Measure in mm).*

Inv. N°	***Element***	***Side***	***Age***	***m1***	***m2***	***m3***	***m4***	***m5***	***m6***	***m7***
GL 1	*Hemimandible*	*Left*	*Prime adult (Class VII)*	*X*	*39,3*	*44,9*	*45,1*	*43,9*	*15,7*	*23,5*
				m8	***m9***	***m10***	***m11***	***m12***	***m14***	***m15***
				143,7	*96,5*	*76,6*	*19,4*	*X*	*X*	*18,1*

Inv. N°	***Element***	***Side***	***Age***	***Length***	***Width***
GL 1	*m2*	*Left*	*Prime adult (Class VII)*	*23*	*14,4*
GL 1	*m3*	*Left*	*Prime adult (Class VII)*	*17,7*	*14,1*

Inv. N°	***Element***	***Side***	***Age***	***m1***	***m2***	***m3***	***m4***	***m5***	***m6***	***m7***
GL 2a	*Hemimandible*	*Left*	*Juvenile (Class II)*	*X*	*X*	*30*	*31,1*	*25,1*	*18,3*	*20,8*
				m8	***m9***	***m10***	***m11***	***m12***	***m14***	***m15***
				130,4	*98,8*	*83,6*	*X*	*X*	*X*	*X*

Inv. N°	***Element***	***Side***	***Age***	***Length***	***Width***
GL 2a	*m2*	*Left*	*Juvenile (Class II)*	*25*	*17,1*
GL 2a	*m3*	*Left*	*Juvenile (Class II)*	*22,2*	*16,6*

Inv. N°	***Element***	***Side***	***Age***	***m1***	***m2***	***m3***	***m4***	***m5***	***m6***	***m7***
GL 3	*Hemimandible*	*Right*	*Juvenile (Class II)*	*X*	*16,4*	*27,8*	*X*	*X*	*X*	*X*
				m8	***m9***	***m10***	***m11***	***m12***	***m14***	***m15***
				27,2	*X*	*X*	*X*	*X*	*X*	*X*

Inv. N°	***Element***	***Side***	***Age***	***Length***	***Width***
GL 3	*m2*	*Right*	*Juvenile (Class II)*	*27,6*	*16,5*

Inv. N°	***Element***	***Side***	***Age***	***Length***	***Width***
GL 4	*M1*	*Right*	*Juvenile (Class III)*	*26,1*	*18,7*
GL 5	*M2*	*Left*	*Juvenile (Class III)*	*35,1*	*18,4*
GL 6	*m1*	*Left*	*Juvenile (Class III)*	*26,8*	*12,3*
GL 7	*m1*	*Left*	*Juvenile (Class III)*	*24,9*	*12*

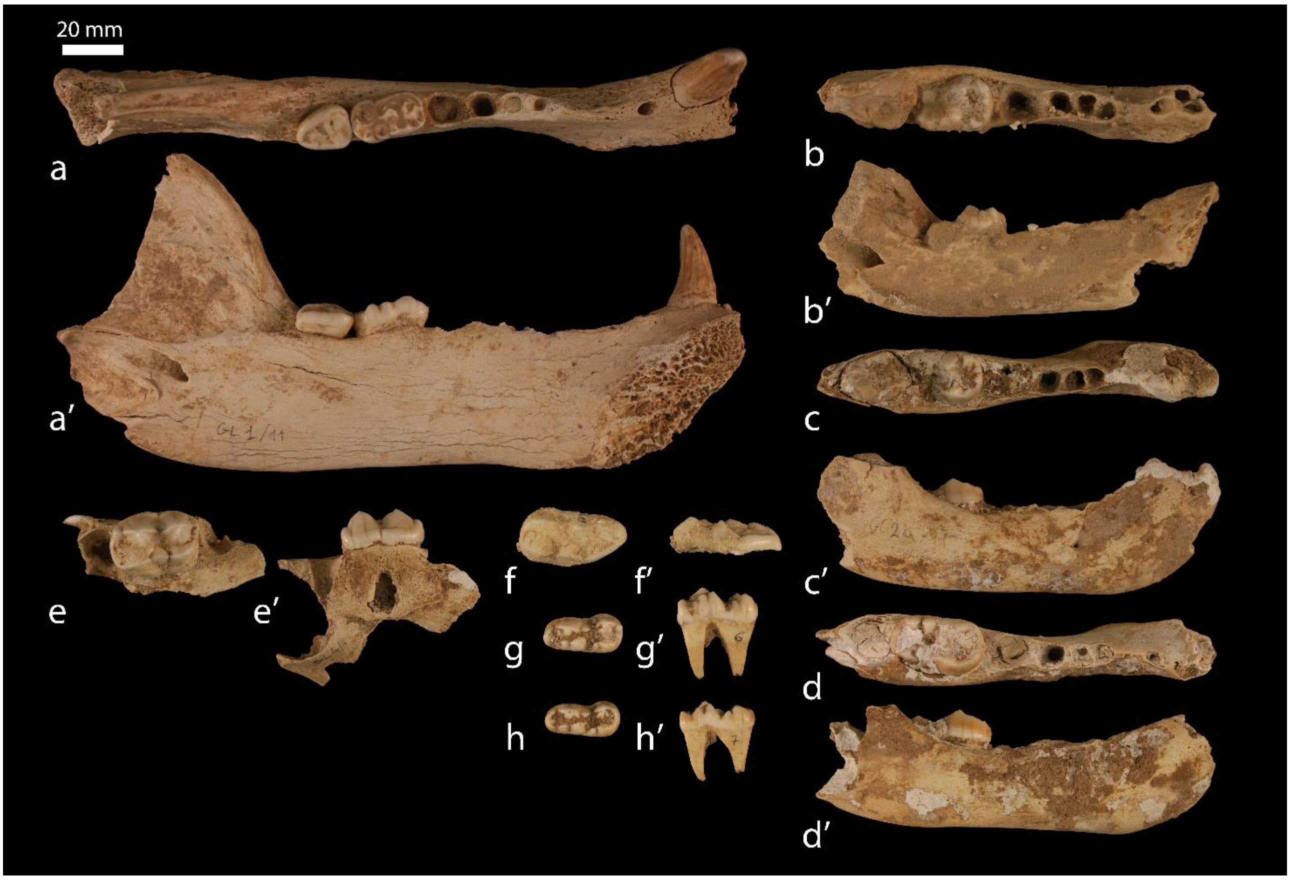


Figure 57: ***Grotta della Lupa Ursus arctos material, analysed in this paragraph;*** occlusal view *and lateral view (letter with apex):* ***a-a’)*** *GL 1.* ***b-b’)*** *GL 2a.* ***c-c’)*** *GL 2b.* ***d-d’)*** *GL 3.* ***e-e’)*** *GL 4.* ***f-f’)*** *GL 5.* ***g-g’)*** *GL 6.* ***h-h’)*** *GL 7.*

7.5.3 Description

GL 1: This is an almost complete left hemimandible, on which the canine, the second molar and the third molar are still present. The rest of the mandibular body is rather well preserved, missing only the proximal portion of the mandibular ramus and the top of the coronoid process. In general, it has a rather slender shape typical of the brown bear, with a low and narrow mandibular body and a thin mandibular ramus with the coronoid crest directed backwards.

The area of the insertion of the pterygoid muscle is wide and not pronounced while, due to the fragmentation of the distal portion, it is not possible to observe the morphology of the condyle and the angolar process. On the dystema is present and clearly visible the alveolus of the first lower molar.

GL 2 a-b: The specimen is to be considered as one, since they are two unarticulated hemimandibulars belonging to the same individual. In fact, in both dimensions and morphological characters are extremely similar, as well as the eruptive stage of the second and third lower molars. The mandible has a heavy fracturing of both the anterior portion and the entire mandibular ramus, therefore it is difficult to describe its peculiar characteristics, on the contrary it has a very thick, low and extremely short corpus.

The mandible belongs to an extremely young individual, given the small size of the find and the eruptive stage of the teeth present. The teeth are still partially incorporated inside the alveolus; however, it is possible to observe well-developed cusps and the presence of a large and rather complex chewing surface, especially in the lower third molar.

What is also noticeable is the size of the teeth in relation to the overall size of the mandible, which is extremely large. A huge part of the find is covered by the same alabaster concretion that characterizes all the dental elements coming from the site.

It should be noted that, despite the impossibility of describing the occlusal surface of the second and third molars, which did not allow a detailed morphological analysis, it was still possible to acquire measurements of length and width.

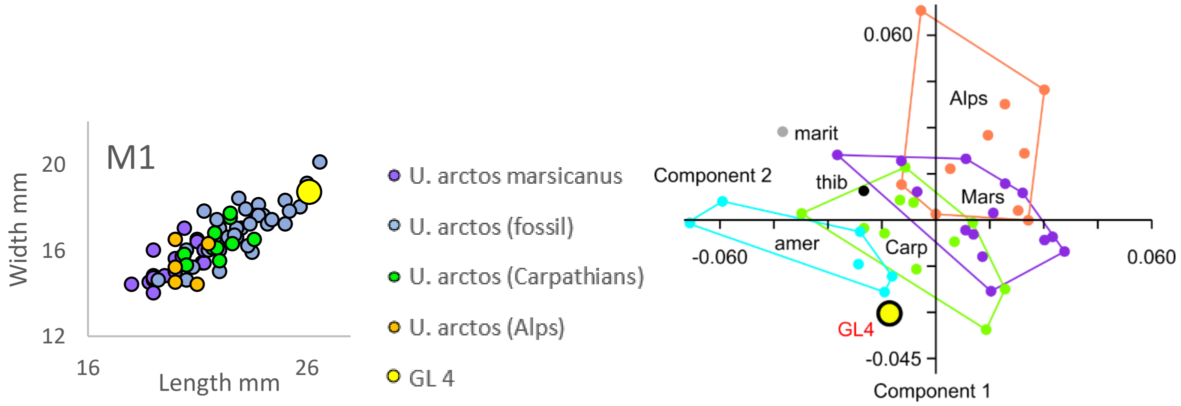
GL 3: Also in this case the specimen is referred to a right hemimandibola belonging to a juvenile individual. It is remarkably fragmented especially in the distal portion of the corpus and missing the mandibular branch. As in the previous specimen, also in this case there are the alveoli of the premolars and of the first molar, while the third molar is absent. The only clearly visible dental element is the second lower molar which, unlike the mandible described above, is almost completely erupted, suggesting that the ontogenetic stage of this individual should be more advanced than the previous one. Despite this, due to the very small general dimensions of the hemimandible, it is however a juvenile specimen which has not reached the full adult stage.

GL 4 - (M1 Right): The finding consists of a first upper molar, which is well preserved, and an extremely fragmented portion of the maxilla, which still shows part of the alveolus of the second upper molar and the fourth upper premolar.

The tooth has a general morphology of the occlusal profile rather thick and almost oval-shaped. In fact, both the lingual and buccal profiles are made up of curved lines interrupted by the central constriction. The cusps are very well developed and recognizable. The metacone and the protocone occupy a large part of the chewing surface and are formed by a single large pointed cusp. Also the cusps of the lingual side are well evident and form a well defined crest which runs perpendicularly to the crests of the other two main cusps. On the occlusal surface there are both the metastyle and the parastyle, (with the latter less developed than the latter) and a very evident cingulum on both the lingual and buccal surfaces.

The chewing surface is large but simple, there is in fact the presence of some tubercle only in the distal portion of the tooth and there is no evidence of accessory cusps. As in the elements already presented, the wear is not present, and the tooth is placed in the category Juvenile, Class III.

The only first upper molar coming from the site has rather large dimensions and is placed in an external position of the average dimensional range of the brown fossil bear; the morphology differs quite clearly from the modern standard forms of brown bear, coming closer to the American form rather than the Carpathians bears.



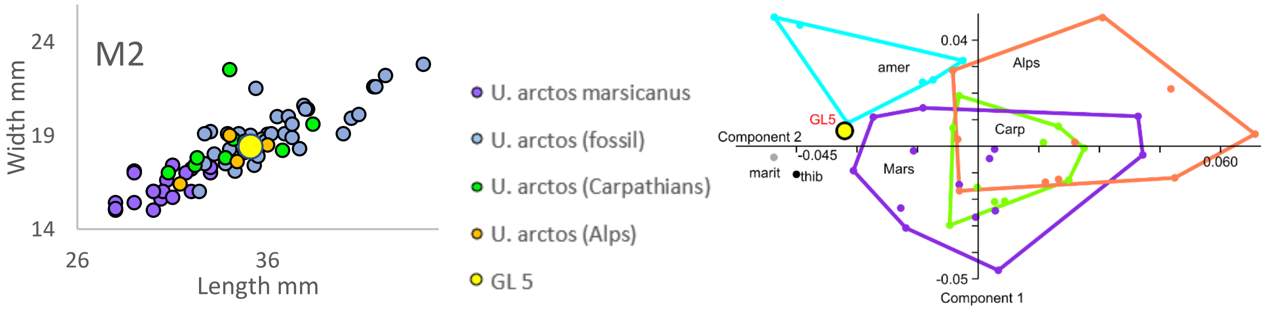
GL 5 - (M2 Left): This is a tooth consisting exclusively of the crown. Despite this, the element is in an excellent state of preservation and has a general morphology of the occlusal profile rather blunt, with the lingual profile straight and the buccal one which curves with a marked change of direction just below the end of the hypocone; on the contrary, the mesial portion of the margin line is rounded, while the distal one ends with a very acute angle.

The main cusps of the tooth are well developed and well recognizable. These occupy a large part of the occlusal surface and none of them is divided into several secondary cusps.

Despite the presence of numerous encrusted sediments in various portions of the tooth, the surface of the tooth has no accessory cusps or tubercles, being limited to a few units in the distal portion of the chewing surface of the tooth. The wear is not present, therefore the tooth belongs, as in the previous case to the Juvenile category, Class III.

The upper M2 has a rather average size, both within the size range of *U. arctos* fossil and for the current continental range (Alps and Carpathians).

Morphological analysis shows that the second upper molar from the Grotta della Lupa site remains outside the average shape of the current bears and is closer to the morphology of *U. americanus* than that of *U. marsicanus*.



GL 6 - (m1 Left): The tooth is rather small and has a simple morphology, with a straight lingual margin. The paraconid is moved towards the lingual profile, and the buccal margin is wide, so as to make the talonid a little wider than the trigonid.

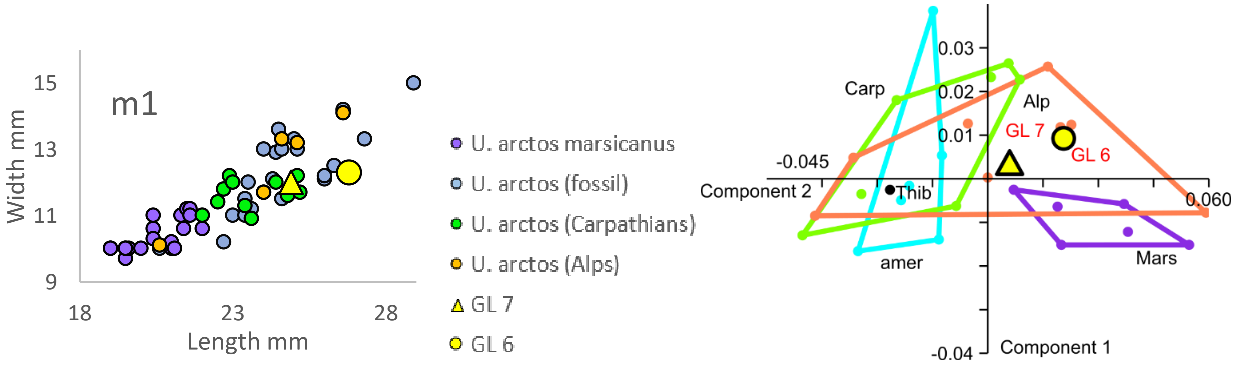
The occlusal surface is almost entirely occupied by the main cusps, which are extremely developed and pointed. Among these, the entoconid is divided in two cusps, with the anterior one clearly wider than the posterior one, forming almost a crest; the same character is shared also by the hypoconid and the protoconid. The metaconid is positioned rather posteriorly inside the trigonid, while the most advanced part is occupied by a poor developed metastylid.

The occlusal surface, even if partially covered by sediment, does not appear complex and there is no presence of tubercles or numerous accessory cusps. The wear is not present, and the tooth is placed in the category Juvenile, Class III.

GL 7 - (m1 Left): This dental element is very similar to the one previously described. The occlusal profile is slender with the trigonid much longer and narrower than the talonid.

The cusps of the buccal side are well developed and distinct; the protoconid is wide and divided into two portions, while the hypoconid remains solitary and forms a sort of crest that extends over the entire distal profile of the tooth until it coincides with the entoconid. The latter is characterized by a main cusp following the posterior crest, and which is divided in two in the most advanced portion of the talonid. The metaconid is wide and divided centrally by a groove which forms two cusps. The occlusal surface is mostly occupied by sediment, but it is possible to observe if there is no presence of accessory cusps or strong tuberculated structures. Wear is minimal, and the tooth is classified as Juvenile, Class III.

Both teeth have a size that fits with the average size of brown bear (fossil and current), positioning itself in the portion of the graph that unites all the fossil and modern populations (except Marsican bears). From a morphological point of view the data show the same plot, both teeth fit perfectly in the portion of the graph occupied by all the arctoid populations.

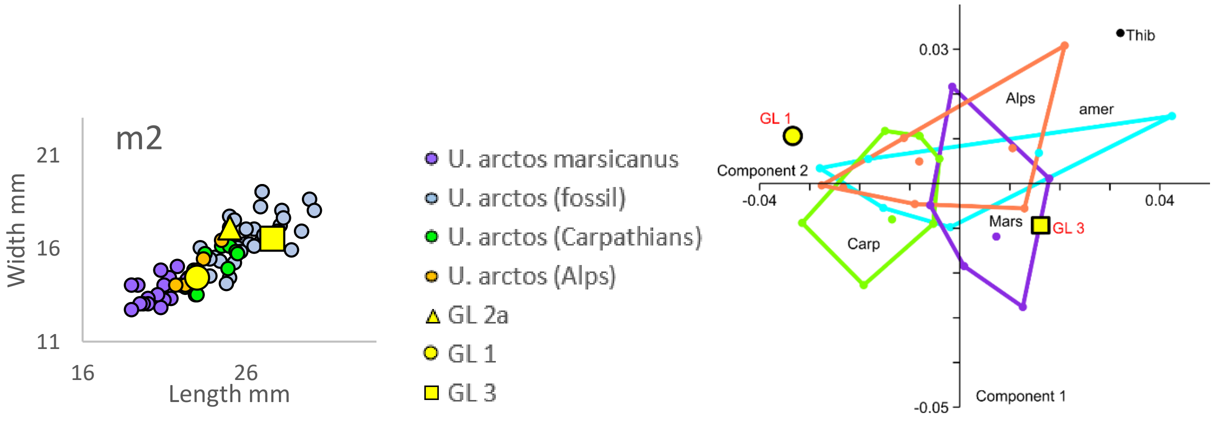


GL 1 - (m2 Left): The tooth is very small, with a rather regular outer profile interrupted only by a small cingulum in the buccal portion. Due to a developed wear of the occlusal surface (category Prime adult, class VII) it is not possible to observe the distinctive features of the cusps, the only interesting morphological feature is the division of the hypoconid into two separate cusps.

GL 3 - (m2 Right): The tooth has rather standard morphological features, with a quadrangular occlusal profile and well-developed, undivided cusps (except for the entoconid which is divided into two). The chewing surface has no tubercles and no additional cusps.

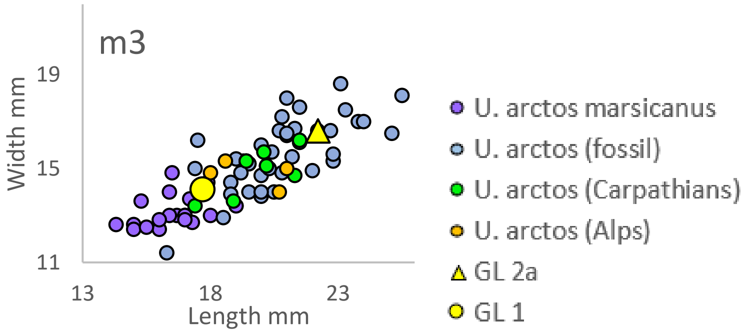
The dimensions of the lower second molars describe two distinct patterns. In fact, while the two elements show average measurements for fossil brown bear, the adult specimen is rather small, especially in relation to young specimens.

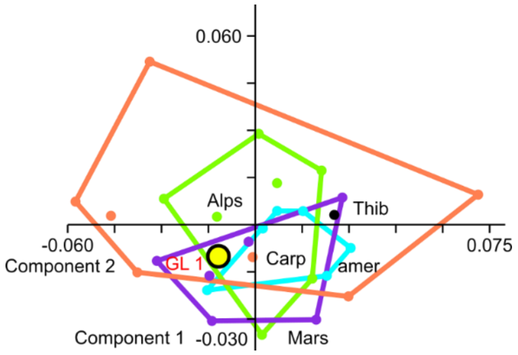
The same is indicated by the morphological analysis. in fact, it is possible to observe how the adult individual remains rather outside the area of the graph occupied by the modern bears, while the younger individuals enter, even if not completely, within the typical morphologies of brown bear.



GL 1 - (m3 Left): The tooth is extremely small and has a characteristic triangular shape, with a very sharp distal margin and a rather straight mesial margin. The occlusal surface is extremely simple and, although there is little wear, it is not possible to clearly distinguish any of the main cusps. The tooth falls into the category of Prime Adult (Class VII).

As for the second lower molar, also in this case the adult individual shows extremely reduced dimensional ratios in relation to those of the younger individual; however, unlike the previous dental element, the morphological analysis does not present any peculiar anomalies, since the finding perfectly fits within the average forms of almost all modern bears.





7.5.4 Final Remarks

The site of Grotta della Lupa returns some specific features about the fossil material both from a taxonomic and evolutionary point of view.

The analysis of the material showed that at least five distinct individuals were 2 cubs, 2 young and one adult. The first two are represented both by the cranial and post cranial fragments (see above), and by the hemimandibles analyzed in detail in the previous paragraph (GL2 - GL3).

One of the juvenile individuals is represented by a pair of complementary ulnas (GL 56-67) and at least three isolated teeth, including a lower left m1 (GL4-5-6).

The other young specimen is represented by a left ulna (GL 68) and by the other first lower left molar (GL 7).

The adult specimen is instead represented exclusively by the left hemimandible (GL 1).

Considering the similar conservation conditions of all bear material, it can be assumed that the various individuals died in the same moment.

This assumption, together with the analysis of the class ages, allows to refer the fossil material to a single family.

Normally, considering this scenario, it is easy to imagine that the adult individual is of feminine gender, considering that, also in the actual bears, it is the female which takes care of the young till their independence.

The morphometric study shows that the teeth fall within the variability of the brown bear fossil. While, from the analysis of geometric morphometry, it appears that the fossil material has some rather peculiar characteristics that, in more than one dental element, fall outside the general morphologies of the modern bear. Due to the scarcity of material it is not possible to elaborate any theory regarding these peculiar morphologies, but it is clear that the deposit does not present any material attributable to *U. arctos marsicanus*, despite the geographical location of the cave fits perfectly within the areal of the current Apennine bear.

7.6 Gran Carro

7.6.1 The site

The Gran Carro is a wide-spread settlement located on the backdrops of Lake Bolsena between the bathymetrich line of 301,9 m and 299,4 m above sea level, along the oriental lake shore.

The site is located in the middle of a large gulf bounded to the north by the Arlena stream and to the south by the Matempo stream. The chronology of the site of the Gran Carro is not entirely clear, despite this radiometric analysis carried out on some wooden rods, and the type of metal objects found suggest a time range between the end of the Bronze Age and the Early Iron Age (9th century BC).

The research activity was conducted from 1960 to 1980 under the settlement, in collaboration with the team of the engineer and the Superintendence of Southern Etruria, experimenting new methodologies of underwater excavation, electronic instrumentation for geomorphogical surveys and new scuba photography equipment.

Today, the deposit, is located at a depth of about 4/5 m and located about 100 meters from the current coast. New analysis starded since the 2012 revealing many other findings that have allowed an increasingly accurate understanding of the early villanovian community of Gran Carro and discover various aspects of their daily lives (Petitti et al., 2013). During this time the deposit has been devided in many sqares, nominated A1, B1, C1, A2, B2, C2 and C3 from which, in addition to numerous other archaeological remains, were found many specimens of different taxa, mostly represented by domestic species (dogs, cows, pigs and goats).

The bear bones were found in the squares A1, B1, C2, C3 from the excavations and researches of 2013 and 2015. They are now stored in the Earth Science Department of Sapienza, University of Rome and represent one of the very rare evidence of pre-Romanic bears specimens in the central-southern Italian area. The material, especially the faunal one, has not yet been totally catalogued; therefore, I have assigned a not definitive catalog number with the initials GrCa-U followed by a progressive number.

7.6.2 Material

The investigated specimens of *Ursus arctos* are represented by a left hemimandible from layer A1 (GrCa-U1), a right hemimandible from layer C2 (GrCa-U2), a left portion of maxilla from layer A1 (GrCa-U3), a fragmentary right maxilla with three molariforms from layer C3 (GrCa-U4) and a distal epiphysis of the right humerus from layer B1 (GrCa-U5) (Fig. 58 and Table 7). Due the underwater condition where specimens have been found, they have been firstly restored, to allow a good conservation under fresh air. Successively, all the specimens have been digitalized using both photogrammetry and CT scans. Tomographic images have been taken using a GE Optima CT660 scanner at "Studio radiologico Guidonia" (Guidonia) and processed with the free software Osirix, while the 3D photogrammetric models were made with a Canon EOS 500D camera and processed with Agisoft Photoscan using the "turn table" technique (See Chapter 4).

Table 7: ***List and measurements of the Ursus material from the Gran Carro deposit.*** *(Measure in mm)*.

Inv. N°	*Element*	*Side*	*Age*	*m1*	*m2*	*m3*	*m4*	*m5*	*m6*	*m7*
GrCa-U1	*Hemimandible*	*Left*	*Prime adult (Class VI)*	*X*	*X*	*41,5*	*40*	*X*	*13,6*	*16,2*
				m8	***m9***	***m10***	***m11***	***m12***	***m14***	***m15***
				X	*X*	*X*	*X*	*X*	*X*	*18,1*

Inv. N°	*Element*	*Side*	*Age*	*Length*	*Width*
GrCa-U1	*p4*	*Left*	*Prime adult (Class VI)*	*14,6*	*7,7*
GrCa-U1	*m1*	*Left*	*Prime adult (Class VI)*	*24,6*	*11,5*
GrCa-U1	*m2*	*Left*	*Prime adult (Class VI)*	*25,3*	*15,2*

Inv. N°	*Element*	*Side*	*Age*	*m1*	*m2*	*m3*	*m4*	*m5*	*m6*	*m7*
GrCa-U1	*Hemimandible*	*Left*	*Prime adult (Class VI)*	*X*	*27,1*	*35,6*	*34,7*		*11,1*	*14,3*
				m8	***m9***	***m10***	***m11***	***m12***	***m14***	***m15***
				85	*74,2*	*63*	*X*	*X*	*X*	*13,6*

Inv. N°	*Element*	*Side*	*Age*	*Length*	*Width*
GrCa-U2	*p4*	*Right*	*Prime adult (Class IV)*	*11,5*	*6,9*
GrCa-U2	*m1*	*Right*	*Prime adult (Class IV)*	*23*	*11*
GrCa-U2	*m2*	*Right*	*Prime adult (Class IV)*	*24,1*	*15,5*
Inv. N°	***Element***	***Side***	***Age***	***Length***	***Width***
GrCa-U3	*P4*	*Left*	*Prime adult (Class IV)*	*17,1*	*14*
GrCa-U3	*M1*	*Left*	*Prime adult (Class IV)*	*22*	*17*
GrCa-U3	*M2*	*Left*	*Prime adult (Class IV)*	*35,1*	*19*

Inv. N°	*Element*	*Side*	*Age*	*Length*	*Width*
GrCa-U4	*P4*	*Right*	*Old adult (Class VIII)*	*17,1*	*13*
GrCa-U4	*M1*	*Right*	*Old adult (Class VIII)*	*21,8*	*16,6*
GrCa-U4	*M2*	*Right*	*Old adult (Class VIII)*	*33,9*	*19,1*

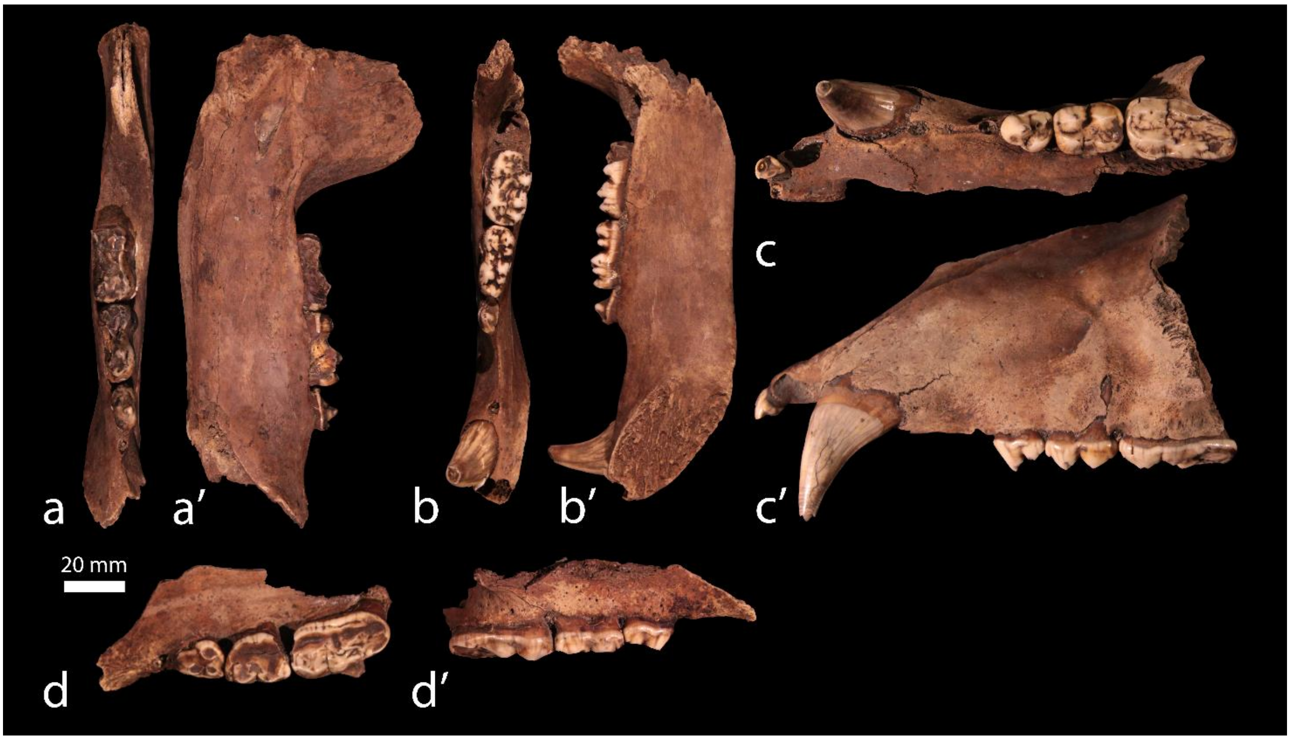


Figure 58: ***Gran Carro Ursus arctos material, occlusal view and lateral view (letter with apex): a-a')*** *GrCa-U1.* ***b-b')*** *GrCa-U2.* ***c-c')*** *GrCa-U3.* ***d-d')*** *GrCa-U4.*

7.6.3 Description

Inspite of the long permanence in an underwater environment, the specimens form the Gran Carro archaeological site show a quite good state of preservation. The ursid remains consisting of cranial and postcranial bone fragments of brownish colour whit irregular edges along the fractures. The bones surface is often crossed by many cracks of different size and deep that may remind the cuts made by human activity. The use of a digital microscope has made it possible to exclude this possibility, and to attribute the cause of these fractures exclusively to the underwater conditions of the deposit (Fig. 59).

Figure 59: ***Detail of a crack on the hemimandible GrCa-U1 produced by permanence underwater****. Image taken with the digital microscope DinoCapture 2.0.*

GrCa-U1: This is a left hemimandible, partially fractured both in the distal region of the corpus mandibule and in the proximal one; in fact, the entire portion below the canine and a large part of the mandibular condyle are missing. The rest of the specimen is well preserved and has a rather long general morphology, with a low, slender, slightly curved corpus mandibolae in the central portion of the basel line.

In the lingual portion is clearly visible both the inferior dental foramen, partially filled with sediment, and the portion of the pterygoid muscle insertion. The latter is partially consumed in the lower portion, probably due to water abstraction.

This specific type of wear is also visible on the posterior portion of the coronoid process and on the entire mandibular incision. Observing the specimen in lateral view, it is clearly visible how the coronary crest is moved towards a distal position, resulting in a rather wide angle with the mandibular body.

On the dorsal surface there are the third premolar, the first and the second molar, while the alveolus of the third premolar is clearly visible. A peculiar character of the specimen is represented by the absence not only of the lower third molar, but also of its alveolus. This character can be explained by two hypotheses: the individual was deformed when born, or the tooth was lost while the animal was still alive, and the bone healed covering the remaining hole.

The CT scan confirmed the second hypothesis, since the tomographic images show a lower bone density in the region of the alveolus of the lower third molar, therefore, there must have been a posthumous filling after the loss of the tooth. The general wear of the teeth classifyed the lower jaw as Prime adult, class VI.

GrCa-U2: This is a well-preserved right hemimandible missing the entire mandibular branch. On its occlusal profile it presents the lower canine, the lower fourth premolar, the first and the second lower molar; both the lower third molar and the first lower premolar are missing, of which only the alveoli remain.

In general, it has a slender and elongated morphology, even if quite small; the mandibular body is low and there is, in the anterior portion, a rather evident mandible foramen. Although the coronoid process is not present due to the fracture of the specimen, it is still possible to observe a portion of the coronoid crest, which maintains a curved profile, forming a rather wide angle with the mandibular corpus.

From the wear of the teeth it is clear that the mandible belonged to a young individual, probably about a one year old, since the cusps are well developed, pointed and not all the teeth are all completely erupted (Juvenile category, Class III).

GrCa-U3: The specimen is composed by a small anterior portion of the orbit, the beginning of the zigomatic process and part of the premascellar bone that forms the nasal canal of a rather small brown bear splancnocranium.

The general bone thickness is thin so much so that part of the surface of the bone that covered the teeth was consumed by diagenesis, leaving parts of the roots uncovered.

Moreover, most of the sutures are not completely ossified (mainly the maxillary-premaxillary suture), although the continuous persistence in the aquatic environment must have accentuated the processes of dislocation of one bone element from another. Despite this, those characters, together with the not consumed wear of the teeth, indicate that the individual died in the prime adult age (Stiner Class IV).

Among the teeth there are the second incisor, the canine, the fourth premolar and the two molars; on the contrary, the first and third incisor, the first, the second and the third premolar are missing, but their alveoli are still present.

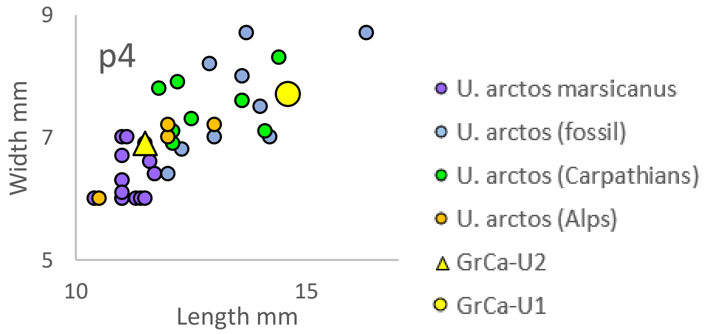
GrCa-U4: The specimen represents a small fragment of a right maxilla, only composed by the three molarifoms, a small portion of the palate, the alveolus of the third upper premolar and the distal crest of the first upper premolar alveolus. Despite the limited size of the finding, from the analysis of the advanced developed worn of the dental chewing surface, the find represents a very old individual, such as to be classified as Old adult, class VIII.

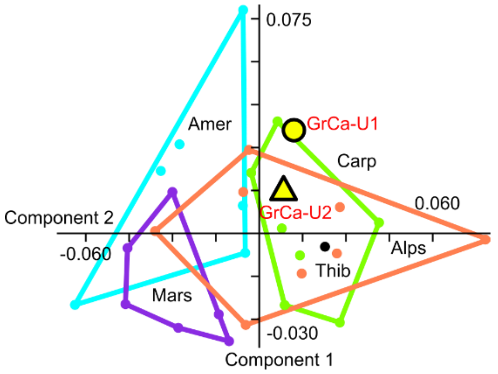
GrCa-U1 (p4 Left): The lower p4 has peculiar characteristics; the general shape of the tooth is very elongated with a slight constriction in the central portion.

Moreover, on the occlusal surface, besides an extremely developed protoconid, there are two accessory cusps, one close to the protoconid, in a more backward position, while the other one forms almost a poor developed paraconid. These characters are extremely rare in *Ursus arctos* and represent a peculiarity in the fossil record of the species. Despite the "complexity" of the tooth, there are no other ridges or tubercles on the chewing surface.

GrCa-U2 (p4 Right): unlike the previously described tooth, this p4 has a much simpler occlusal profile, with the only cusp represented by the protoconid, which is rather well developed and in a forward position in the middle of the tooth. Despite this, even on this tooth there is the presence of three small accessorious cusps much less developed and little visible than the other lower p4, placed in a backward area of the distal surface of the tooth.

The scatter plot clearly shows how the dimensions of the two fossil records are quite different; in fact, if the tooth belonging to the mandible GrCa-U1 falls perfectly within the size range of brown bears fossils, the other falls within the area of the graph occupied mainly by the Marsican bears. On the contrary, the geometric morphometry graph presents a rather different framework, bringing both teeth within the variability of the continental brown bear.





GrCa-U1 (m1 Left): The first lower molar shows a large part of the lingual line completely fragmented, so that the position of the Metaconid cannot be identified. Despite this, the buccal profile is rather sinuous, both in the trigonid and the talonid.

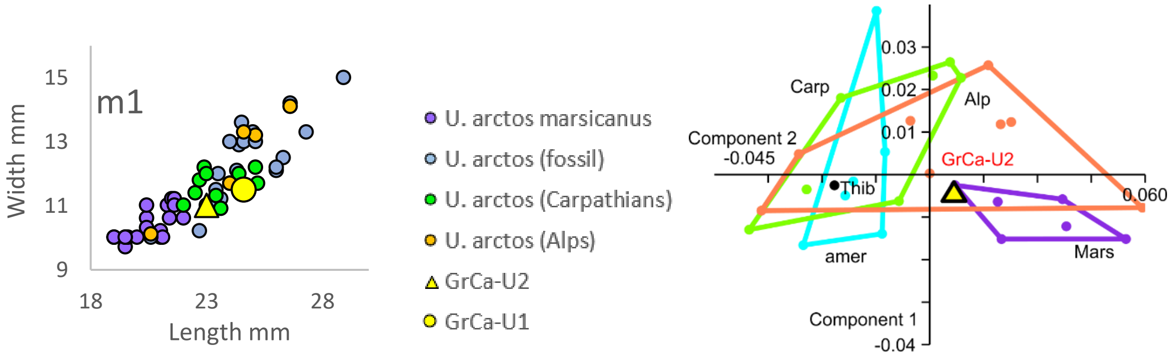
On the mesial portion of the tooth the paraconid is rather developed and occupies an internal position in respect to the axis of the tooth while, in the distal portion, the wear does not allow to distinguish precisely the main cusps. On the chewing surface there is no tubercolation or additional cusps.

GrCa-U2 (m1 Right): The m1 has a rather elongated occlusal surface morphology, with a straight lingual line and a slightly ondulated buccal line. In fact, the size of talonid is not remarkably high compared to triconid, giving the tooth a rather plump morphology.

The occlusal surface is characterized by the presence of extremely developed cusps, both in width and in height; both the protoconid and the hypoconid stand solitary in the buccal portion of the tooth, while the metaconid and the entoconid are divided into two separate cusps but equally developed. The paraconid is remarkably developed and it clutter a large part of the mesial portion of the tooth. The chewing surface is extremely simple and there is no presence of tubercolad structures or accessory cusps.

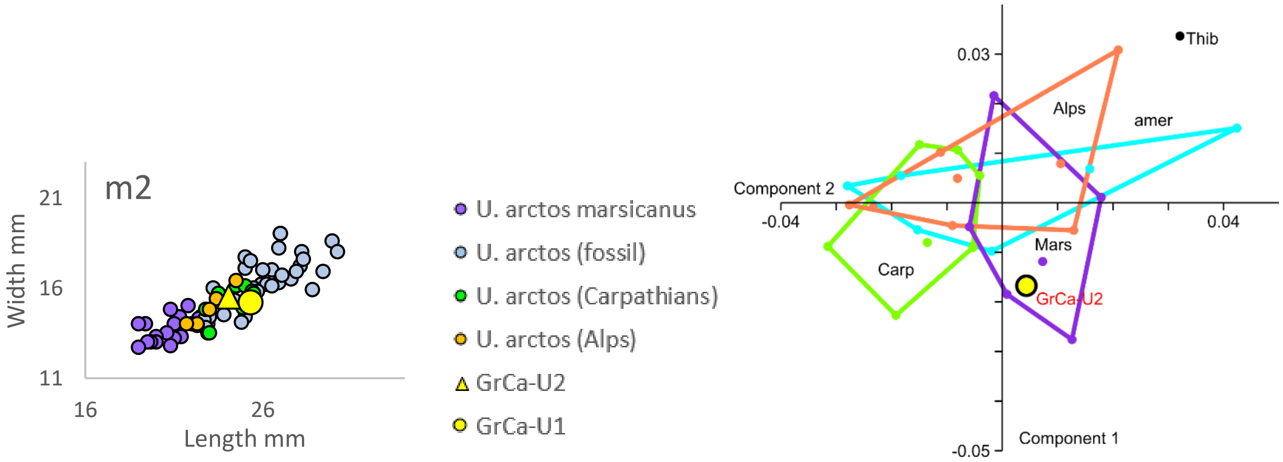
The tooth belonging to the GrCa-U2 manible fits perfectly within the average morphology of brown bears, on the contrary the tooth element belonging to GrCa-U1 has not been included in the morphological analysis because of its partial fracture of the occlusal line.

Nevertheless, the measurements of both teeth fit within the variability of *U. arctos* and perfectly fitting in the portion of the graph occupied by the brown bear of the Carpathians.



GrCa-U1 (m2 Left): The second lower molar is extremely damaged, in fact a good part of the lingual and distal portions is missing, therefore it is extremely difficult to describe the occlusal profile (it was also not possible to acquire the characters for the analysis of geometric morphometry). Despite this, the masticatory surface is quite evident, and shows neither a strong tuberculated structures nor any developed accessory cusps.
Unfortunately, due to the rather high wear and tear, it is not possible to describe the main cusps; in fact, both the protoconid and the hypoconids are remarkably worn. There is a barely hinted cingulum in the labial portion of the tooth.

GrCa-U2 (m2 Right): The second lower molar has a standard morphology of the tooth element and presents an occlusal profile elongated, and a well marked central constriction.
A small fragmentation of the distal portion (lingual side) does not allow the analysis of part of the entoconid; despite this, the other cusps are well evident and remarkably developed. In fact, a large part of the occlusal surface is occupied by a large metaconid divided into two main cusps, and by a pointed protoconid whose ridges join those of the metaconid. The hypoconid is formed by a continuous crest while it is possible to observe only one of the (probably) two cusps of which the entoconid is composed.
The chewing surface, although the sediment emphasizes the characters, is not remarkably complex and most of the tubercles are concentrated exclusively on the posterior portion of the talonid. Also the cingulum is not very developed but it extends on all the buccal line of the tooth.
Both teeth fall within the dimensional range of both the continental brown bear and that of U. arcos fossile. Only the tooth of the second manibola has been included in the morphological analysis and it fits into the average shape of the brown bear, even if it has more affinity with the Marsican bears than with other populations.



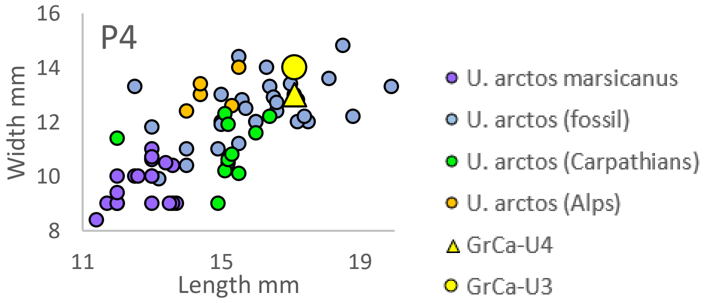
GrCa-U3 (P4 Left): The P4 shows a rather stocky occlusal profile, with the lingual line that forms a wide curve, due to a remarkably large protocone, positioned almost on the same line as the metaconid.

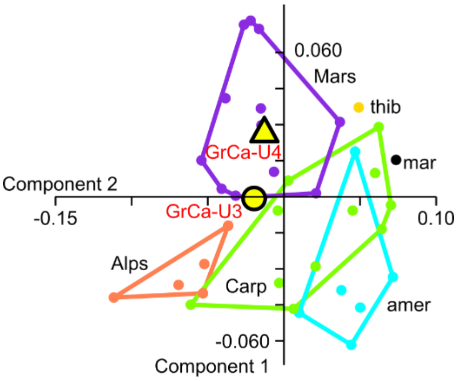
The chewing surface is occupied exclusively by the three main cusps and does not show acessories cusps or tubercles; the only noteworthy character is a slight crest that starts from the paracone, turns around the buccal profile of the tooth and then goes to join with the crest of the protocone

GrCa-U4 (P4 Right): the tooth shows a triangular dental profile, with a few pronounced cingulum in the buccal portion; despite the very high wear, it is possible to observe the presence of all the main cusps. A peculiar feature is represented by a small accessory cusp in the posterior portion of the metacone. Apart from this the occlusal surface is simple and there is no presence of tubercles or other complex structures.

Both teeth fit into the morphometric variability of the fossil brown bear and, unlike the other dental elements, remain outside the dimensional range of the modern populations.

The geometric morphometry data, on the other hand, shows a strong affinity with the Marsican subspecies in both GrCa-U3 and, above all, in GrCa-U4.





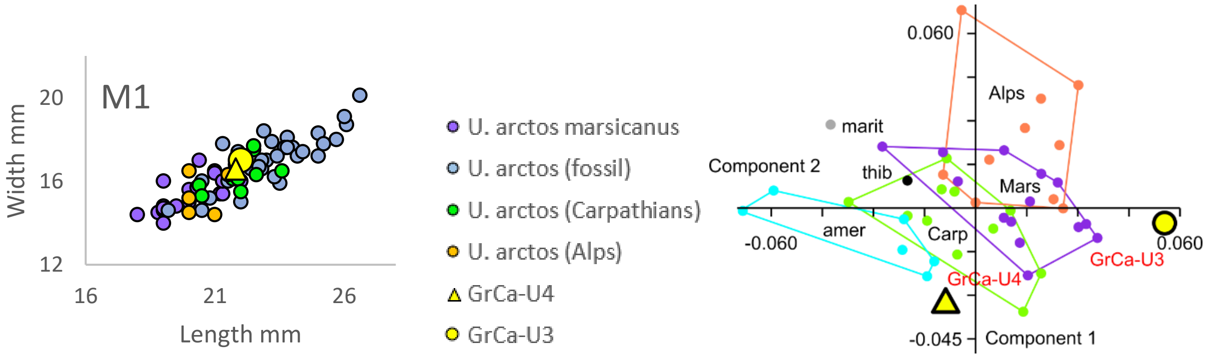
GrCa-U3 (M1 Left): The M1 has a straight occlusal line in both the mesial and distal portions, giving the tooth a rectangular shape.

The lateral lines are interrupted by the central constriction that divides a rather large talon from the anterior portion of the tooth. The main cusps are clearly visible and are all formed by a single main cusp.

The para-meso-hypocone line is oblique with respect to the ridges of the metacone and the protocone; it ends directly on the parastyle. Like the parastyle also the metastyle is present although less evident and developed than the first. The occlusal surface is extremely simple and does not shows a strong tubercolation or presence of accessory cusps.

GrCa-U4 (M1 Right): the M1 is is partially fractured, lacking the talon region, but is still possible to observe the general shape of the teeth. Infact, shows a more elongated morphology with the oblique mesial line typical of the dental element. It is not possible to accurately describe the dental cusps, given the extreme wear, but it is possible to observe a hint of paraconid in the mesial portion of the tooth and a small protuberance corresponding to the metastyle placed immediately behind the metacone.

Both dental elements fit within the morphometric standard size of brown bears and are perfectly positioned in the middle of the scatter plot; on the contrary, the morphology of the occlusal line and the position of the cusps of the two teeth do not have any specific affinity with modern bear shapes.



GrCa-U3 (M2 Left): the tooth shows a rather elongated and massive morphology of the occlusal surface, typical of the dental element; the distal line is rather wide while the mesial line is straighter, making, with the sides of the tooth, almost a right angle.

The buccal and lingual lines are rather undulated and follow the course of the main cusps of the tooth. The cusps are in fact very well developed and composed by a single element.

The protocone and metacone occupy almost the entire anterior surface of the tooth, while the hypocone and entocone are composed mostly by ridges that develop for almost the entire area of the talon.

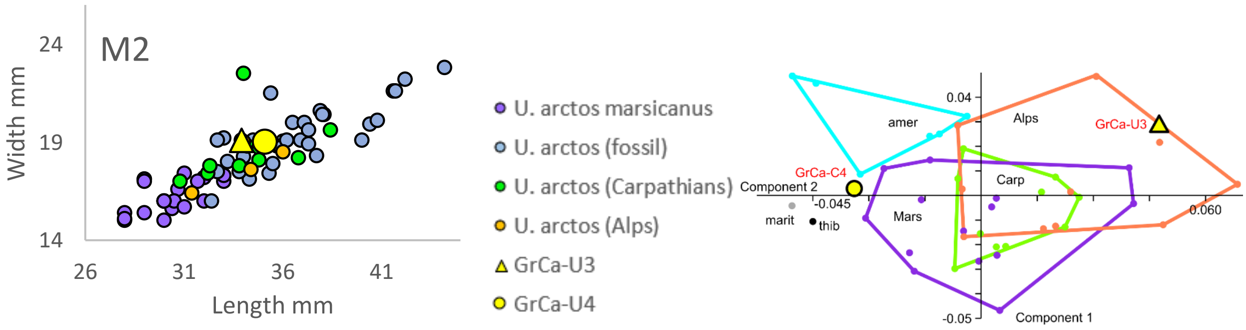
The chewing surface is large and not complex, there is the presence of a few tubercles (extremely small) only in the distal portion of the tooth, located mainly in the central area. There are no evident cingules.

GrCa-U4 (M2 Right): The M2 shows an almost ellipsoid occlusal profile, in fact, the main cusps are not so widely developed to alter the shape of the buccal and lingual lines; In general, this tooth has a plump and less elongated shape, with a talon that reaches almost the same size as the anterior portion of the tooth.

Although the occlusal surface is characterized by heavy wear, typical of the dental elements of this finding, it is curious to observe how much of the tooth is consumed only in the lingual border, leaving practically intact the cusps of the buccal line. The latter are well developed, and both composed by a single main cusp. The hypoconus, in the most distal portion of the crest, is interrupted by two grooves forming a small cusp.

The surfaces, although very consumed, do not have very complex morphology and shows few tubercles structures placed exclusively in the central portion of the talon. A well developed cingulum is present which extends along the entire lingual line of the tooth.

As with the first upper molar, the second upper molars fit within the standard size of both the modern brown bear and the fossil one. As already mentioned in the previous description, the two teeth show morphologies rather distant from each other, positioning themselves on the two opposite sides of the graph.



7.6.4 Final Remarks

Analyzing the proposed graphs, it seems clear that the findings from the deposit of the Gran Carro have different morphologies compared to the typical patterns of modern bears.

The only distinctive element is represented by the upper P4, which shows characters rather similar to *U. a. marsicanus*.

On the contrary, the morphometric analysis shows that some teeth are perfectly within the dimensional range of the fossil brown bear. Therefore, despite the dating of the site very close to the hypothetical split between the bear of the Apennines and that of the Alps, and the position very close to the current area of the Abruzzi bear, it is not possible to ascribe any fossil element to *U. arctos marsicanus*.

The number of findings and their morphology indicate that at least four different individuals come from the site, five if the found humerus does not belong to one of them.

Considering instead the ontogenetic stage and the taphonomic position of the finds inside the deposit, it is extremely unlikely that they represent a single family nucleus. For the same reasons, it is easier that the various individuals died from accidental causes or were hunted separately. The sedimentation may have occurred by transporting the lake water or by human transport, although there are no obvious anthropogenic signs.

The absence of cutmarks or direct evidence of human activity does not exclude the interaction between the latter and the bear; in fact, in the area of Bolsena (and in the site of the Gran Carro itself) there are many testimonies of human presence.

A special example comes from the Etruscan city of Bisenzio, located on the opposite side of the lake, and also dated to the end of the Bronze Age / early Iron Age.

In fact, from the necropolis of the city (Olmo Bello), a funerary urn with an inverted trochoconical shape has been found. On the cover of the urn there is a curious scene representing a beast chained with some men who surround it (Fig. 60).

Figure 60: ***Cinerary urn from the Olmo Bello necropolis, Bisenzio (****Villa Giulia, Etruscan National Museum, inv. 253686****). On the right, a focus of the beast on the top of the cover***

According to archaeologists, this decoration represents a ritual, and the creature in chains in the middle represents some non-anthropomorphic malignant deity (Torelli, 2000).

However, observing the object with a more "naturalistic" eye, it is clear that, if it were an animal, this could only be a bear.

The sitting posture, the elongated snout and the legs with the plantigrade articulation refer very much to a kind of ursid which, probaibly, could have been captured and carried to the collar for some funeral celebration.

The use of the bear as a symbolic animal is not rare. Already throughout the Late Pleistocene with *Homo neandertalensis* and *Homo sapiens* it is possible to find rupestrian paintings or tools representing this great mammal (Romandini and Nannini, 2011; Majkić et al., 2018).

The man-bear interaction has continued over time, with taming attempts, as evidenced by a peculiar hemimandible from the site of the Grande-Rivoire (France), which still bears the malformations due to the use of a horse bite placed between the first and second lower molars (Rubat Borel, n.d.; Chaix et al., 1997), or used as a duty for the lords of the fourteenth century (Ambrosi, 1952).

7.7 Discussion

As previously mentioned, the choice to study in a similar way all the fossil material coming from the deposits located in the central-southern Italian area, was intended to obtain results regarding: i) the evolution of the brown bear during the Late Pleistocene, trying to eliminate the environmental factors derived from different latitudes continentality; ii) the evolution of *U. arctos marsicanus*, analyzing in depth the fossil finds from the deposits located in its current area.

Analysing the general dimensions of the material coming from the most ancient sites, it is possible to observe a clear trend whereby the dimensions of the dental elements of the most ancient deposits (Grotta del Cervo, Grotta degli Orsi Volanti, Ingarano and Villa S. Carlo) are generally larger than those of the Holocene sites.

From the first study some peculiar characteristics have emerged about the intra- and infra-specific variability of both the morphologies and the dimensional ratios of *U. arctos*.

This evidence, despite the small number of finds, confirms the general decrease in size in the various forms of brown bear during the whole Late Pleistocene.

On the contrary, the findings coming from the Grotta della Lupa and from the underwater deposit of the Gran Carro, generally maintain intermediate dimensions, which often fit both in the dimensional range of the fossil bear and in that of the modern continental populations. At the same time, however, they have a dimensional pattern very distant from *U. arctos marsicanus*, which is always much smaller than other forms of brown bear.

Regarding the second point, the deposits analyzed do not show any characteristics such as to assume the presence of the Apennine bear in the fossil record.

Moreover, dating the site of the Gran Carro to the end of the Bronze Age, and assuming that it is impossible to have the presence of two subspecies of bear in the same area, it is clear that the split between the current Italian populations must have occurred in a time interval subsequent to that of the deposit.

8 The first occurrence of brown bear in Italy

In Italy, the presence of the Deninger bear, *Ursus deningeri*, is quite well documented (Palombo et al., 2002); its first occurrence is recorded in the latest Early Pleistocene sites of Monte Peglia (Umbria) (Colle Curti F.U. according the Italian biochronological scheme of (Gliozzi et al., 1997) and Viatelle (Veneto)

On the contrary the diffusion of the brown bear *Ursus arctos* is still unclear. Specimen of this species are documented in the Italian peninsula in the site of Bucine (Upper Valdarno, Tuscany) dated to late Middle Pleistocene (?early/middle Aurelian; ?Torre in Pietra/Vitina F.U.) (Masini et al., 1991; Ferretti, 1997; Gliozzi et al., 1997; Palombo et al., 2002), Acquedolci and Contrada Camillà in Sicily (Marra, 2003) referred to the *Elephas mnaidriensis* faunal complex.

In 1993, The Italian palaeontologist Augusto Azzaroli in his pioneer work on the Italian biochronological framework (1993) indicated the First Occurrence of *U. arctos* in the Italian peninsula in the Fontana Ranuccio F.U. even if, the remains from the deposit, were not described and figured.

Analysing the bibliography concerning the site prior to Azzaroli's work, some papers emerged that briefly describe only a first upper molar (Inv. 56574), a right third lower molar (Inv. 56575) and a third phalanx (Inv. 56576) all attributed to *U. deningeri*. (Biddittu et al., 1979; Cassoli and Segre Naldini, 1993).

Although new excavation campaigns have revealed new bear material still unpublished, the site of Fontana Ranuccio remains an ambiguous reference point for the first occurrence of *U. arctos*.

The FR deposit was discovered in the late 1970’s by Italian Institute of Human Palaeontology (IsIPU) researchers and dated approximately to 0.458±0.006 Ma (Biddittu et al., 1979; Segre, 1984) (Fig. 61). The specimens from the deposit consists of more than 20,000 faunal remains, besides four human teeth and several lithic and bone artefacts.

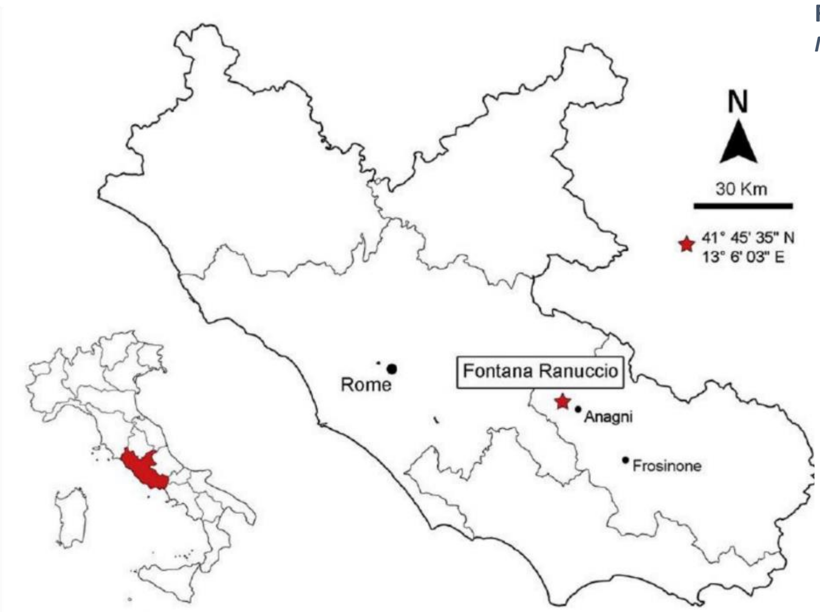


Figure 61: ***Geographical location of the Middle Pleistocene site of Fontana Ranuccio.***

In this chapter, I will describe for the first time the new (and the old) *Ursus* material coming from this deposit in order to investigate the first dispersal of the brown bear in Italian peninsula.

8.1.1 Material and methods

The *Ursus* teeth from Fontana Ranuccio consists in twelve isolated fossils (Fig. 62) wich were mostly discovered during the field activities carried out in the 1980s by the archaeologists and palaeontologists of the Istituto Italiano di Paleontologia Umana (IsIPU). Now it is stored at IsIPU laboratory at Anagni (Frosinone).

Table 8: ***List and measurements of the Ursus material from the Fontana Ranuccio deposit.*** *(Measure in mm).*

Inv. N°	*Element*	*Side*	*Ontogenetic Stage*	*Length*	*Width*
FR 06-411	*M1*	*Right*	*Juvenile/prime adult (III/IV class)*	*25.2*	*18.4*
FR 56574	*M1*	*Left*	*Prime adult (IV class)*	*27.6*	*18.3*
FR 89-1	*p4*	*Right*	*Juvenile*	*13.6*	*8*
FR sd-1	*m2*	*Left*	*Juvenile (III class)*	*28.5*	*16.2*
FR 56575	*m3*	*Right*	*Juvenile/prime adult (III/IV class)*	*26*	*18.4*
FR 82-2 Res	*i3*	*Left*	*X*	*9.9*	*10.3*
FR 85-2 P3	*i3*	*Right*	*X*	*9.8*	*10.1*
FR Sd-2	*I2*	*Right*	*X*	*10.7*	*0.85*
FR 85-1 S1	*c*	*Right*	*X*	*X*	*X*
FR 84-1	*m2*	*Left*	*X*	*X*	*X*
FR 96-33	*m1*	*Left*	*Prime adult (IV class)*	*10,8*	*X*
FR 84 inv 56576	*III Falanx*	*Right*	*X*	*X*	*X*

Figure 62: ***Fantana Ranuccio Ursus material, occlusal view and lateral view: a)*** *FR 06-411.* ***b)*** *FR 56574.* ***c)*** *FR 89-1.* ***d)*** *FR sd-1.* ***e)*** *FR 56575.* ***f)*** *FR 82-2 Res.* ***g)*** *FR 85-2 P3.* ***h)*** *FR Sd-2.* ***i)*** *FR 85-1 S1.* ***l)*** *FR 84-1.* ***m)*** *FR 96-33.* ***n)*** *FR 84 inv 56576.*

The teeth have been morphologically described and measured according the measurements shown in the Chapter 4 (Table 8), and the worn level has been used to stimate the ontogenetic stage according (Stiner, 1998). Furthermore, the FR *Ursus* material has been morphologically studied through a detailed comparative analysis with *U. deningeri*, *U.* ex gr. *spelaeus* and *U. arctos, U. dolinensis and U. thibetanus* from selected localities spanning from Middle Pleistocene to Holocene (Torres, 1984; Capasso Barbato et al., 1990; Rabeder et al., 2010; Wagner et al., 2017).

8.1.2 Comparison and description

8.1.2.1 *Fragmented elements (FR 85-1 S1, FR 84 inv 56576, FR 96-33)*

Very few features can be highlighted on the right lower canine FR 85-1 S1. In fact, the tooth is missing the top portion and part of the root such that it does not allow the acquisition of any linear measurement on it. The morphology of the tooth does not have the distinctive characters to define the belonging to the speloid or arctoid line.

As for the canine, also the third phalanx (FR 84 inv 56576) is rather worn both in the distal and in the proximal portion. In this case, however, it was possible to take some measures, but the lack of comparative data for the same time interval does not allow a more in-depth analysis of the dimensional relationships. Although the finding shows a rather slender morphology, the comparison data, also in this case, are not enough to determine the species of the bone element.

The last fragmented finding is the first lower molar (FR 96-33) of which only the talonid remains. The undamaged portion, also in this case, does not allow a specific attribution mainly because much of the occlusal surface and the cusps are remarkably consumed. However, it is possible to trace the tooth element to a prime adult individual (class VII of the Stiner 1998 diagram).

From the morphological data obtained it is clear that it has not been possible to identify any diagnostic character for a specific taxonomic attribution, therefore all these elements are assigned to *Ursus sp.*

8.1.2.2 *Incisors (FR 82-2 Res., FR 85-2 P3, FR Sd-2)*

In the deposit of Fontana Ranuccio, the bear incisors are represented by two thirds lower incisors (FR 82-2 Res. and FR 85-2 P3) and a second upper incisor (FR Sd-2) Fig. 63.

The first two are well preserved and maintain a rather typical morphology of the genus with a well-developed central cusp and the presence of two outlined lateral lobes, of which the distal one is less developed than the mesial one (Fig. 63 a-b).

On the contrary, the second upper incisor is extremely worn, making it impossible to delineate detailed morphological characteristics. Despite Torres outlines some distinctive features between *U. arctos* and *U.* ex gr. *spelaeus* (see Chapter 3) I have not been able to compare this tooth with material attributed to *U. deningeri*; therefore, I decided to attribute both the first two and the third to *Ursus sp.*

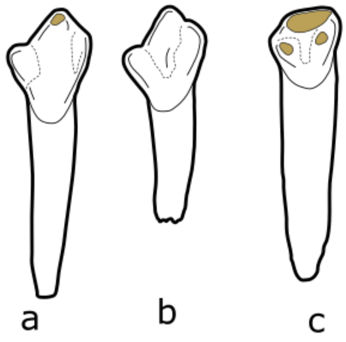
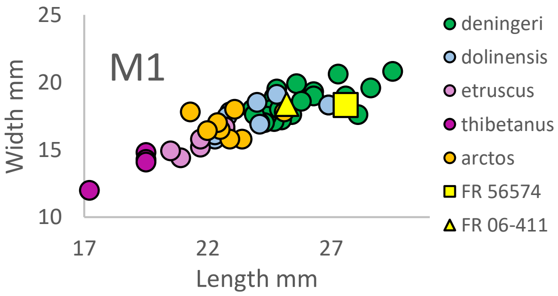


Figure 63: ***Drawing of the incisors from the Fontana Ranuccio deposit. a)*** *FR 82-2 Res* ***b)*** *FR 85-2 P3* ***c)*** *FR Sd-2****.***

8.1.2.3 *Upper first molars (FR 56574, FR 06-411)*



Considering the two first upper molars, the specimen FR 56574 shows some speloid features as the non-rectilinear non-rectilinear shape of the proto-ipoconid line and the presence and the presence of some tuberculated structure in the talonid surface.

On the contrary of the typical deningeroid morphology, the find does not show any developed styles, as instead it appears evident in the finds of U. deningeri coming from the site of Hundsheim (Fig. 64 e-f).

The central constriction of the tooth is rather accentuated especially in the lingual region, a character that is, however, found in both species. From a morphometric point of view, on the other hand, it falls perfectly within the dimensional range of the speloid forms of the Early-Middle Pleistocene.

The FR 06-411 specimen shows some unambiguous deningeroid features. Infact, the metastyle and the parastyle are well developed (the metastyle more than the parastyle) and the talon show a quite tubercleted surface, even more than FR 56574. Despite this, the teeth have a narrower shape with the same width in the distal and the proximal region and the proto-ipoconid line appear quite linear; according Torres 1984 and Capasso Barbato et al., 1990, those morphology, should rapresent more *U. arctos* than *U. deningeri*. But the comparison between the specimen proposed in the Fig. 64 shows that this line is straighter in the Hundheim theeth than all other brown bear fossil.

Also, the morphometric analysis indicate that this specimen is placed at the limit of the range dimension of *U. arctos* fitting much more with the variability of *U. deningeri* and *U.* ex gr. *spelaeus*.

According those analysis I attribute FR 06-411 and FR 56574 to *U. deningeri.*

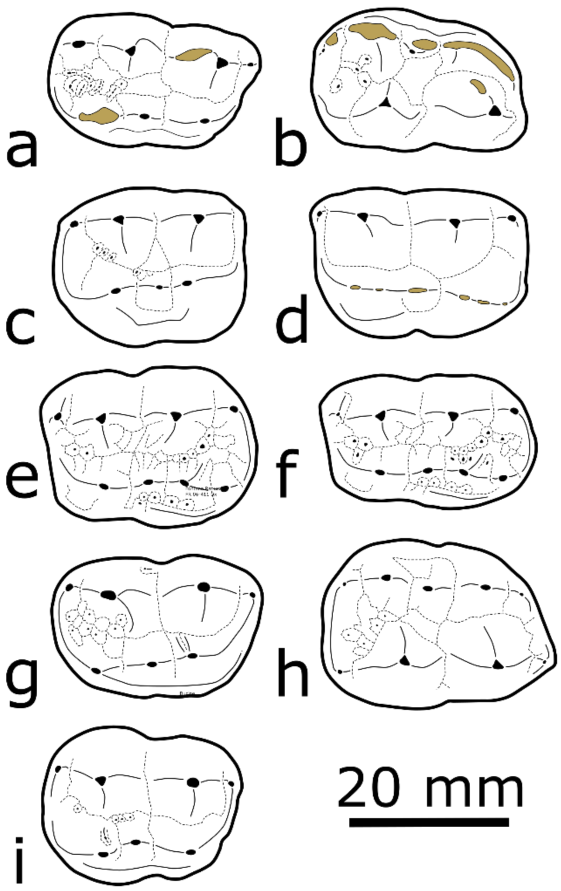
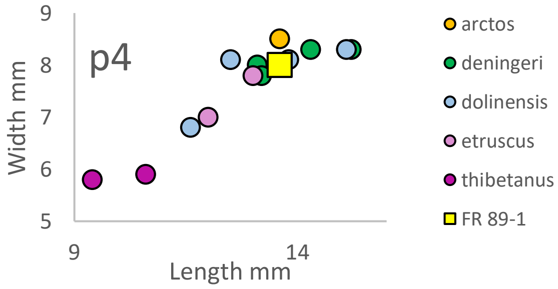


Figure 64: ***First upper molar comparison. a) FR 06-411*** *(right)*. ***b) FR 56574*** *(left).* ***c) U. arctos*** *(right),* ***DA4V/14*** *(Deutsch-Altenburg, Early Pleistocene).* ***d) U. arctos*** *(left),* ***DA4B/18*** *(Deutsch-Altenburg, Early Pleistocene).* ***e) U. deningeri*** *(left),* ***HH/5/398,*** *(Hundsheim, Middle Pleistocene).* ***f) U. deningeri*** *(left),* ***HH/5/342*** *(Hundheim, Middle Pleistocene).* ***g) "U. arctos priscus"*** *(right),* ***W S.1*** *(Winden, Late Pleistocene).* ***h) U. arctos*** *(left),* ***C. 4*** *(Banskà Bystrica, Recent).* ***i) U. arctos*** *(right),* ***IGF 10961*** *(Bucine, late Middle Pleistocene).* ***e - f - g - c) modified by Rabeder et al., 2010.***

8.1.2.4 *Lower p4 (FR 89-1)*



This tooth has a very simple morphology; the occlusal surface is narrow and has a vertical outline in the lateral view. The protoconid is the only cusp well developed and it is not divided; the metaconid and the entoconoid are small and poorly developed. There is no presence of accessories cusps. All those characters could describe well every arctoid teeth showed in the Fig. 65 (maybe also the etruscan one) (see chapter 3). On the contrary the deninger bear, and even more the Late Pleistocene cave bear, shows very complex morphology with a high tubercled surface and a much more elliptic external shape. An exception is represented by the HH 305 specimen from Hundsheim (early Middle Pleistocene). Infact the tooth has been ascribed to the *U. deningeri* despite its very simple morphology. I do not disagree with this attribution, (even if there is the presence of both *U. arctos* and *U. deningeri* in the deposit). In fact, during the first phase of the Middle Pleistocene, the variability of the two forms could be such that it could not distinguish one from the other form.

On the contrary, I have reason to think that, during the midst of the Middle Pleistocene, they must have already showed some dinstinctive morphology from each other (see Final remarks).

Unfortunately, even in this case the morphometry does not help (also because of an extreme lack of data) showing very similar dimensional patterns between *U. deningeri* and *U. arctos*.

From the data obtained, I have reason to believe that the tooth belonged to a brown bear, so I decided to assign it to *Ursus cf. arctos*.

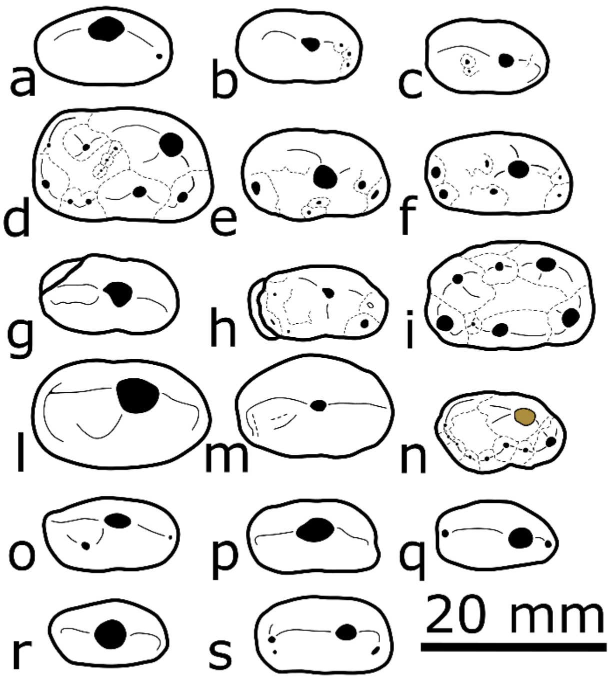
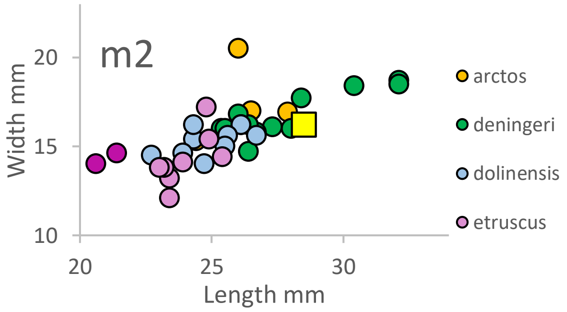


Figure 65: ***lower fourth molar comparison. a) U. etruscus*** *(right mirrored),* ***IGF 911*** *(Valdarno, Early Pleistocene).* ***b) U. etruscus*** *(Casa Frata, Early Pleistocene).* ***c) U. etruscus*** *(left),* ***IGF 4605*** *(Valdarno, Early Pleistocene)****. d) U. deningeri*** *(right mirrored),* ***Sapienza Museum no n°*** *(unknown, Middle Pleistocene).* ***e) U. etruscus*** *(left),* ***NM-Rv 20003*** *(C 718 Cave, Early Pleistocene)* ***f) U. deningeri*** *(left),* ***specimen H*** *(Sandalja, Middle Pleistocene).* ***g) U. deningeri*** *(left),* ***HH 305 (Hundsheim, Middle Pleistocene). h) U. deningeri*** *(left),* ***HH 306*** *(Hundsheim, Middle Pleistocene).* ***i) U. spelaeus*** *(left),* ***P3021*** *(Caverna delle Fate, Late Pleistocene).* ***l) U. arctos*** *(left),* ***V.1152*** *(Vigna S. Carlo, Late Pleistocene).* ***m) U. arctos*** *(left),* ***DA-4B 18-36*** *(Deutsch-Altenburg, Early Pleistocene).* ***n) U. savini nordostensis ssp.*** *(left),* ***IAM f-2365*** *(Ovrag, Late Pleistocene).* ***o) U. arctos*** *(left),* ***3399*** *(Alps, Recent).* ***p) U. arctos*** *(right mirrored),* ***3362*** *(Alps, Recent).* ***q) U. arctos*** *(left),* ***U. arctos*** *(left),* ***ZIN 34595*** *(Kudaro 3, Late Pleistocene).* ***r) U. arctos marsicanus*** *(right mirrored),* ***131*** *(National park of Latium, Abruzzi and Molise, Recent).* ***s) FR 89-1.***

8.1.2.5 *Lower second molar (FR 96-33, FR SD-1)*



The two second lower molars, FR9633 and FR SD-1 shows similar morphology (despite the first is composed only by the trigonid portion) (Fig. 66).

The morphology of the tooth and the high tubercolosity of the two findings from the site of Fontana Ranuccio represent well the typical morphology of *U. deningeri*. Furthermore, the metaconid is divided into three cusps in the second lower molar, a characteristic feature both in *U. deningeri* that in *U.* ex gr. *spelaeus*. (Torres P. , 1984) (Capasso Barbato, Minieri, Petronio, & Vigna Taglianti, 1990). The morphometrical analysis shows una overlap of dimensions between *U. deningeri* ed *U. arctos*, not allowing a good distinction between the two specs. Therefore, from the morphological data, both findings are attributed to *U. deningeri*.

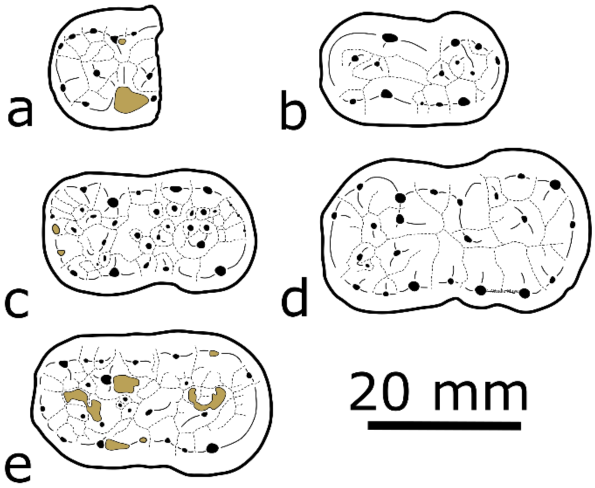
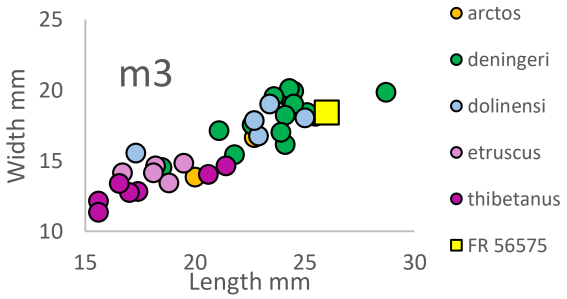


Figure 66: ***Lower second molar comparison. a) FR 84-1*** *(left).* ***b) U. arctos*** *(right),* ***3364*** *(Alps, Recent).* ***c) FR sd-1*** *(left).* ***d) U. deningeri*** *(right),* ***1889/5/4*** *(Hundsheim, Middle Pleistocene).* ***e) U. deningeri*** *(left),* ***MF/1346/37*** *(Kozi Grzbied, Middle Pleistocene), modified by Wagner 2012.*

8.1.2.6 *Lower m3 (FR 56575)*



The tooth from the Fontana Ranuccio deposit shows a quadrangular outline with a rounded talon. The occlusal surface shows a high tubercled surface, typical of the speloid lineage (Fig. 67). The tooth has a low worn so can be easily see the well developed entoconid and the two cusps formed metaconid. As it happened for the lower second molar, morphometrical analysis could not give us clear information about cluster dimension between the two Middle Pleistocene species; despite this I am quite confident to assign the specimen to *U. deningeri* concerning the morphological feature of the tooth.

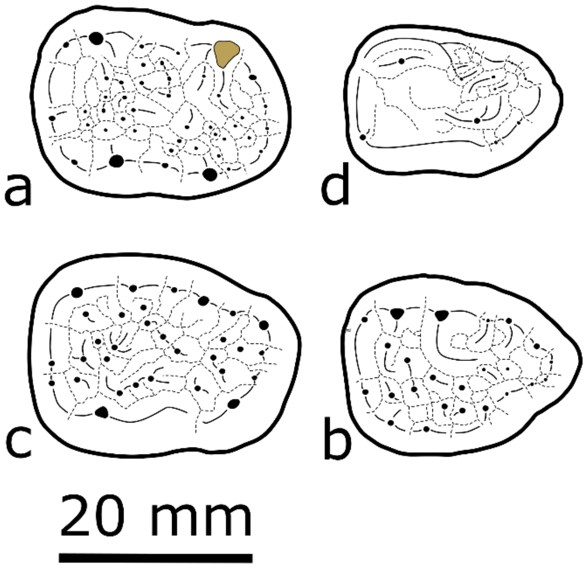


Figure 67: ***lower m3 comparison. a) FR 56575*** *(right).* ***b) U. arctos*** *(left)****, C.4,*** *Ursus arctos.* ***c) U. deningeri*** *(left),* ***MF/1346/45*** *(Kozi Grzbiet, Middle Pleistocene).* ***d) U. deningeri*** *(left),* ***Hund 382*** *(Hundsheim, Middle Pleistocene).*

8.1.3 Final remarks

As has been described above, it is very difficult to find confident characters that clearly distinguish the various species of bear, especially during the Middle Pleistocene and, above all, on isolated teeth (Wagner 2012). With our knowledge is today possible to recognize to identify some discriminating characters between *Ursus arctos* and *Ursus deningeri* during the Middle Pleistocene even if, as suggested by Wagner, (2010), new specimen and new analysis are necessary to clarify the morphological features that distinguish the two species. Despite this, our analysis suggests that there is presence of both *U. arctos* and *U. deningeri* in the site of Fontana Ranuccio as already highlighted by Azzaroli during the end of the last millennium. The deningeroid presence is confirmed by the specimen (FR 56574, FR 06-411, FR SD-1, FR 84-1, FR 84 Rec). The taxonomical attribution of FR 82-2 Res., FR 85-2 P3, FR Sd-2, FR 85-1 S1, FR 96-33, FR 84 inv 56576 remains uncertain, for which the attribution of *Ursus sp.* is proposed.

As far as the lower p4 is concerned (Fr 89-1), aware of the great variability referred to for this tooth, the taxonomic attribution of *U.* cf. *arctos* is proposed. In fact, the tooth shows very archaic characters as the narrower occlusal outline and the absence of the accessory cusps, which still remain in the Pleistocene and modern arctoid forms. On the other hand, the *deningeri – ex gr. spelaeus* lineage displays a different morphological feature (see Chap. 3) and an increasing of the occlusal surface width, reaching the greatest value in the LGM (Rabeder, 1999).

This assumption is more consistent considering the chronostratigraphic position of the site of Fontana Ranuccio, which is placed in the second part of the Middle Pleistocene. It should represent a period where it is possible to hypothesize that the archaic characters of the *U. deningeri* variability are less and less present, starting to show a more robust and complex morphology, which will characterize *U.* ex gr. *spelaeus* during the whole Late Pleistocene.

The occurrence of two bear species in the FR site plants interesting biochronological and palaeoecological questions.

In fact, the presence of both species during the Middle Pleistocene indicates an already strong subdivision of the ecological niches and of the feeding adaptations that characterize the speloid and the arctoid lineages, outlining a more herbivorous diet for the first and a strongly omnivorous one for the second. The site of Fontana Ranuccio, however, is not the first evidence of the presence of the two bears in the same deposit, according to the data collected from Deutch-Altenburgh and Hundsheim deposits (late Early Pleistocene and early Middle Pleistocene respectively).

Considering the chronostratigraphic position of the site of Fontana Ranuccio, it is possible to confirm the presence of the brown bear in Italy during the Middle Pleistocene (about 470 ky), representing the first occurrence of *Ursus arctos* in the Peninsula.

9 The brown bear brains

As has been mentioned several times in this paragraph, the use of tomographic scanning allows to obtain images of both the external portion and the internal portion of a specific object and, thanks to the treshold adjustment, it is possible to discriminate between some denser anatomical portions compared to others (as in the case of teeth compared to pneumatized areas of the bone).

In this case, through the use of specific software, it is possible to fill some cavities such as the frontal sinuses or the brain cavity, in order to obtain a virtual endocast.

Unfortunately, some fossil finds, especially the most diagenized, often have rather concrete bone surfaces, such as to make structures normally not very dense, extremely mineralized.

In this case, a simple discrimination of automatic density by the software, does not allow the acquisition of certain anatomical data and, to "restore" or "remove" the concreted portions, a manual intervent on the tomographic images is necessary, in order to obtain a digital data of the anatomical parts analyzed, perfectly coherent with the original.

This is the case of the study of the encephalic endocast of the bear skull from the Ingarano site (INGND 1, see Chap.7.4). The tomographic analysis has in fact shown both an enormous quantity of concretion minerals on the brain wall (probably phosphates), and the presence of sediment that fill the area of the cerebellum.

The CT scan was carried out with a 0.6 mm silce interval at the "Vannini" hospital in Rome, thanks to the collaboration with Dr. Massimiliano Danti and the Prof. Sabino W. Della Sala.

The preliminary analysis of the tomographic images has been made through the use of the open source software Osirix and has highlighted further characteristics of the specimen. In fact, it is possible to observe the presence of a thin metal bar inside the left jaw (probably used for an initial restoration) (Fig. 68).

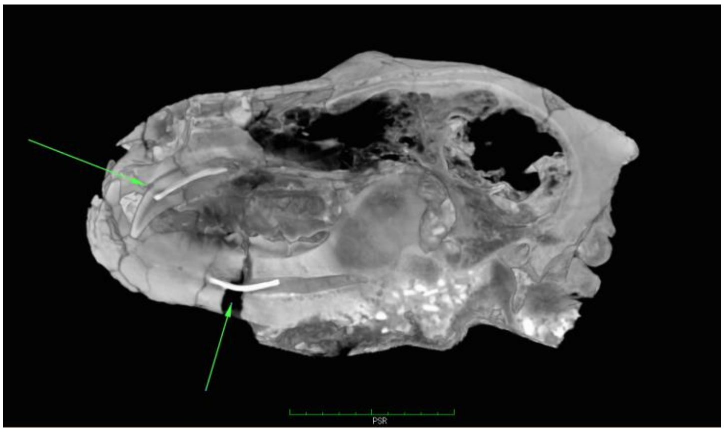


Figure 68: ***Detail of the iron bar in the mandible and in the Upper canine.***

After removing the non-anatomical elements, adjusting the treshold or cutting them out manually, the images were processed with the Mimics V. 10.1 software.

This second imaging software presents applications that normally allow the filling of some cavities (such as the one normally left by the brain after the decomposition of soft tissue) and to export the three-dimensional model. This operation is called Cavity fill (Fig. 69 A).

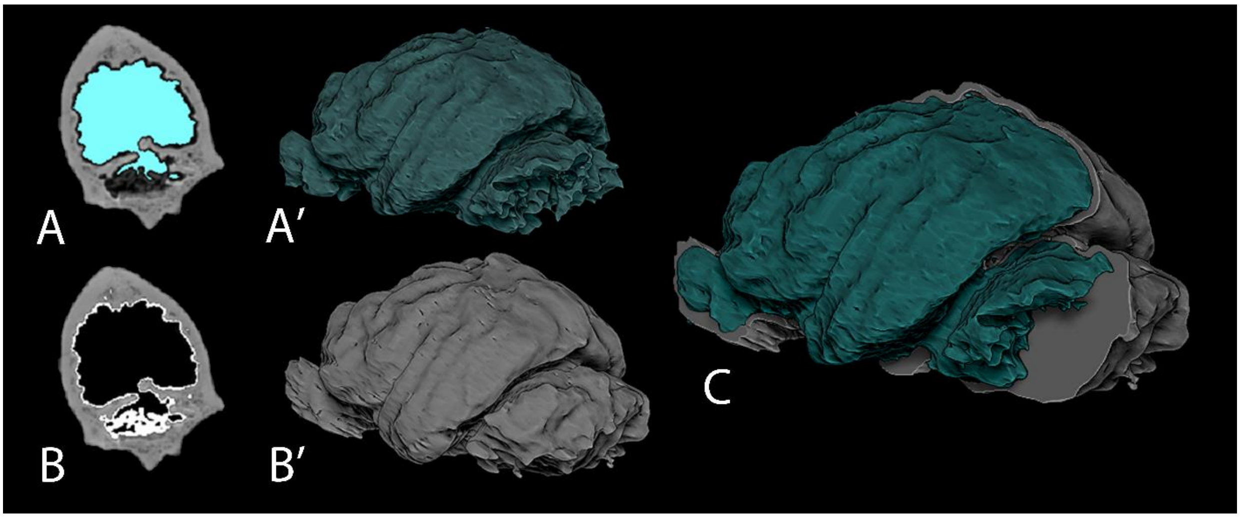


Figure 69: ***Cavity fill of the INGND 1 Braincase. A-A')*** *Model without the restoration.* ***B-B')*** *Model after the removal of the mineral concrection.* ***C)*** *Comparison of the two models.*

To do this, initially, both the anotimal cavities of the skull (passages in the cranial nerves, occipital foramen) and the fractures due to the processes of fossilization are digitally occluded. Then the software proceeds to fill the cavity of the object producing a virtual endocast of the area concerned. As already mentioned, the presence of encrusting mineral and rocky sediment inside the cavities of the fossil under study, have returned a virtual cast which reproduce a partial portion of the brain anatomy. It was therefore necessary to use filters and density masks to digitally remove the fill material, image by image. This has always been done with the Mimics V. 10.1 software (Fig. 69 B).

As a result of this long working process, it was possible to digitally reconstruct the entire encephalic endocast, also highlighting the distal portion of the cerebellum occupied by sediment.

The 3D model was then exported in PLY format (Polygon File Format) and converted to OBJ format. This step allowed the reading of the three-dimensional model by the virtual sculpture program ZBrush, necessary to obtain the final images of the brain of the Ingarano deposit (Fig. 69 C).

9.1 The brain

Although brains are almost never preserved in the fossil records, they leave a distinct impression on the inner surface of the braincase in the form of ridges and grooves. Is it possible although to find some “natural” fossil endocast, reproduce it with the use of silicon or obtain it virtually, with the using of Tomographic analysis (such the one presented below from the Deutsch-Altenburg deposit, Austria).

Although the endocast (both virtual and not) is not an exact copy of the brain of the fossilized animal (Franzosa and Rowe, 2005), the endocranial surface of the bear is conform to the animal's brain topography making it possible to reproduce the external morphology of the brain with a very high level of detail (García et al., 2007).

In vertebrates, the brain is divided into two portions: the cerebrum (the most advanced and developed portion) and the cerebellum (the posterior part that binds to the spine).

The external portion is called cerebral cortex and is divided into four different lobes: the frontal lobe dedicated to cognitive and movement issues, the parietal lobe dedicated to the somatosensory areas, the temporal lobe dedicated to hearing and memory and finally the occipital lobe linked to sight.

These areas are divided by deep furrows that take the name of "sulcus" and that follow a precise course by giving some circumvolutions that take the name of “gyrus”.

The gyrus and the sulcus represent most of the external surface of the brain and each pair takes different names according to its position (Fig. 70).

Each gyrus, sulcus or lobe is represented by two identical and mirrored elements, positioned on the right and left sides of the brain and divided by the Longitudinal Fissure.

The ventral area is also occupied by the innervation of the trigeminal nerve, the pons and the Medulla oblongata, which can occasionally be obtained from virtual cavity fill or found in the natural endocast.

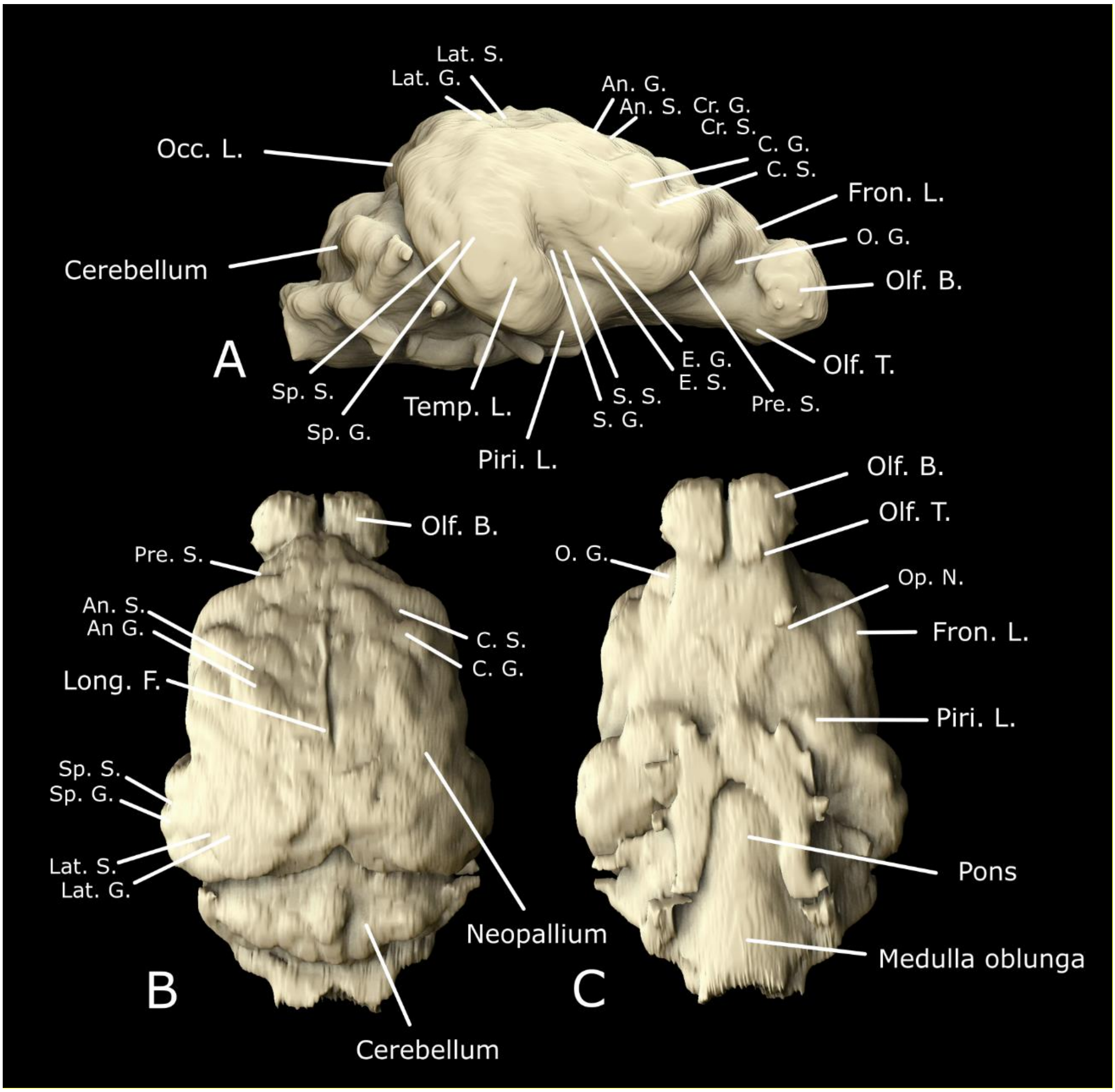


Figure 70: ***Anatomical portion of the brown bear brain endocast (U. arctos marsicanus) in lateral (A), dorsal (B) and ventral (C) view. An. G.)*** *Ansate gyrus;* ***An. S)*** *Ansate sulcus;* ***C. G.)*** *coronal gyrus;* ***C. S.)*** *coronal sulcus;* ***Cr G)*** *Crociate gyrus;* ***Cr S)*** *Crociate sulcus;* ***E. G.)*** *Ectosylvian gyrus;* ***E. S)*** *Ectosylvian sulcus;* ***Fron L.)*** *Frontal Lobe;* ***Lat. G.)*** *Lateral gyrus;* ***Lat. S.)*** *Lateral sulcus;* ***Long. F.)*** *Longitudinal Fissure;* ***Olf. B.)*** *Olfactory bulb;* ***O. G.)*** *Orbital Gyrus;* ***Olf. T.)*** *Olfactory tract;* ***Occ. L.)*** *Occipial Lobe;* ***Op. N.)*** *Optic nerve;* ***Pir. L.)*** *Piriform Lobe;* ***Pre. S.)*** *Presykvuab sulcus;* ***S. G.)*** *Sylvian sulcus;* ***S. S.)*** *Sylvian sulcus;* ***Sp. G.)*** *Suprasylvian sulcus;* ***Sp. S)*** *Suprasylvian sulcus;* ***Temp. L.)*** *Temporal Lobe.*

The brain of the Ursidae, concerning the morphology and topography of the sulcus and convolutions of the cerebral cortex, belongs to the carnivorous-ungulate type which has voluminous olfactory lobes and a wide and medium-pleated bark (Conti, 1954).

In comparison with an herbivorous like the sheep, which has a more oval side profile and the man, who presents a twist of the cerebellum and a more globular shape, the general morphology of ursidae brain results rather triangular, with the occipital lobe upraised and the frontal lobe forming an angle of about 45 degrees.

Normally, the ventral shape is rather roundish, with a good development of the temporal lobe rather than the frontal lobe which is generally narrower; this shape is generally much more similar to typical carnivores such as dogs and tigers.

9.1.1 Material

To observe the different morphologies of the brown bear endocast, three-dimensional models of various species and populations, both modern and fossil, were compared.

The recent material was obtained through cavity fills of tomographic scans and is represented by an endocast of *U. arctos* from Alps (C3361, Fig. 69-E) two brain of *U. arctos marsicanus* (female C 131, Fig. 53-2; male C 486, Fig. 53-C). The fossil brown bear is represented by the natural encephalic endocast coming from the site of Deutsch-Altenburg (DA-48 38-41, Fig. 69-A), digitized by photogrammetry with the "mobile camera" technique and the virtual endocast of the skull from Ingarano depoist (INGND1, Fig. 69-D). As comparison, the isosurface rendering of the *U. deningeri* from Sima de los Huesos has been used (SH99 T/U-13/14-68, Fig. 53-F; image taken by Garcia 2010).

All the 3d model have been measured following the modified scheme proposed by Garcia 2007 and the data are listed in the Table 9 and Fig 71.

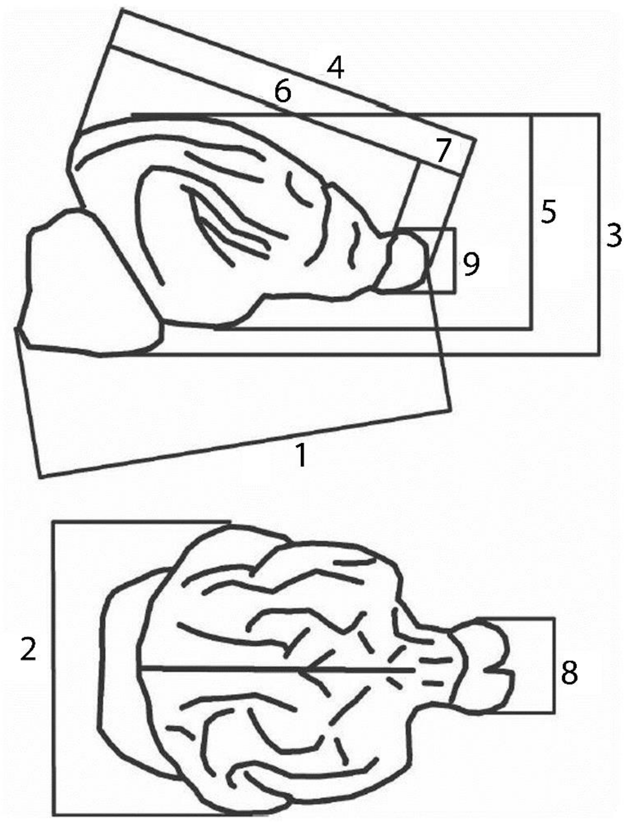


Figure 71: ***Measurement taken on the braincase. 1) Endocast length. 2) Endocast (and brain) width. 3)*** *Endocast height.* ***4)*** *Brain length.* ***5)*** *Brain height.* ***6)*** *Meopallium length.* ***7)*** *Combined olfactory bulbs lenght.* ***8)*** *Combined olfactory bulbs width.* ***9)*** *Combined olfactory bulbs height. Modified by Garcia 2010.*

Table 9: ***Measurements of the bear brain cited in the text.*** *Data in mm.*

Inv. N°	*Element*	*Species*	*m1*	*m2*	*m3*	*m4*	*m5*	*m6*	*m7*	*m8*	*m9*
INGND 1	*brain endocast*	*U. arctos*	*124*	*93,1*	*61,2*	*121,3*	*56,8*	*105,4*	*14,1*	*33,9*	*22,6*
DA-4B 38-41	*brain endocast*	*U. arctos*	*X*	*99,5*	*64,2*	*109,8*	*67,4*	*119,6*	*X*	*X*	*X*
C 131	*brain endocast*	*U. arctos marsicanus*	*115,4*	*83,9*	*64,4*	*113,4*	*58,9*	*102*	*16,2*	*34,9*	*23,1*
C 486	*brain endocast*	*U. arctos marsicanus*	*131,4*	*84,4*	*67,3*	*129*	*64,4*	*96,2*	*19*	*35,3*	*23,1*
C 3361	*brain endocast*	*U. arctos (Recent)*	*110,3*	*75,7*	*59,1*	*100,3*	*54,2*	*81,5*	*7,9*	*31,*	*20,5*
SH99 T/U-13/14-68	*brain endocast*	*U. deningeri*	*135,2*	*93,2*	*77,3*	*125,8*	*68,3*	*109,4*	*14,6*	*28,8*	*20,6*

9.1.2 Description

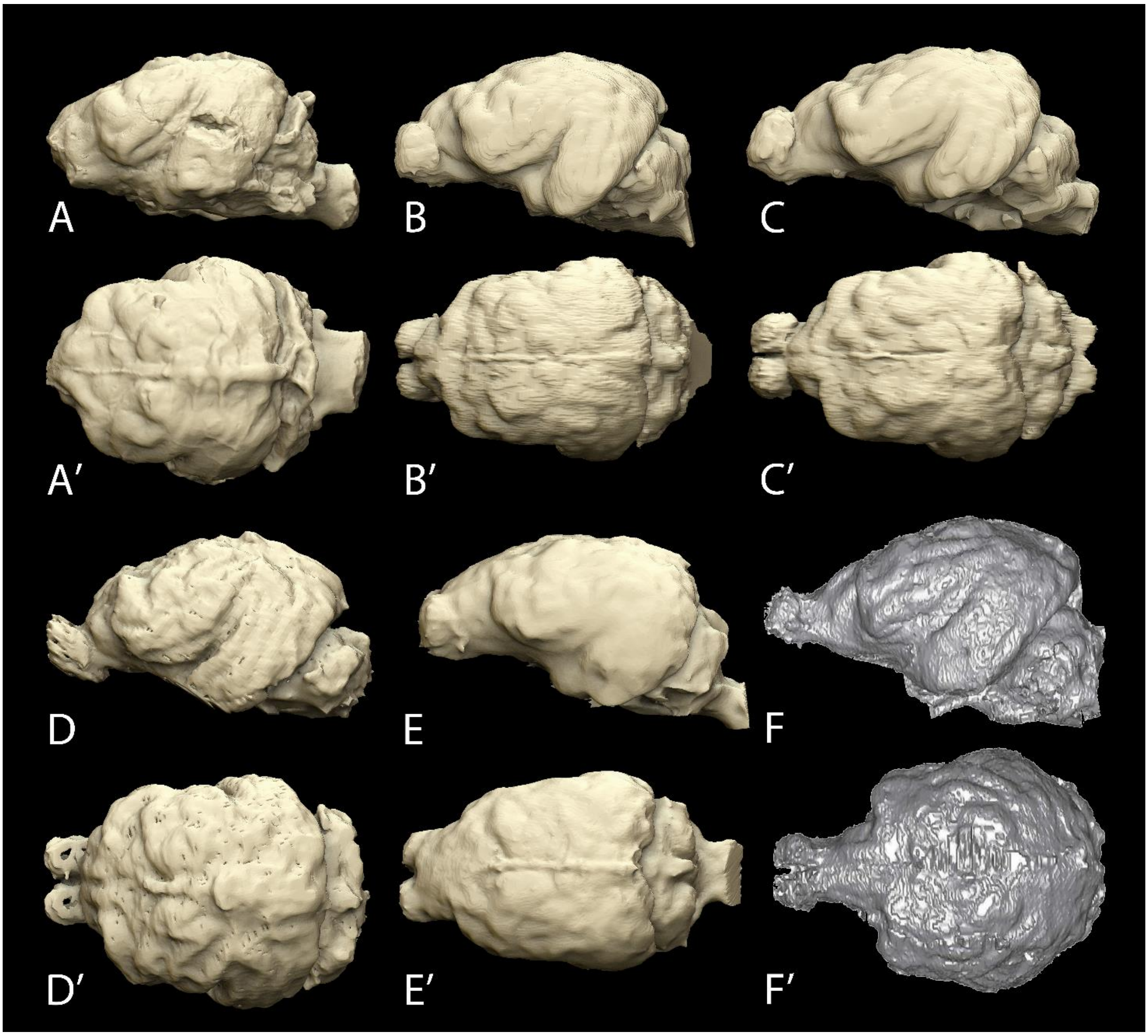


Figure 72: ***Brain endocast of Ursidae species, lateral and dorsal view (letter with apex). A-A') DA-4B 38-41, Ursus arctos*** *(Deutsch-Altenburg, Early Pleistocene).* ***B-B') C 131, Ursus arctos marsicanus*** *(National Park of Latium, Abruzzi and Molise, Recent).* ***C-C') C 486, Ursus arctos marsicanus*** *((National Park of Latium, Abruzzi and Molise, Recent).* ***D-D') INGND 1, Ursus arctos*** *(Ingarano, Late Pleistocene).* ***E-E') C 3361, Ursus arctos*** *(Alps, Recent).* ***F-F') SH99 T/U-13/14-68, Ursus deningeri*** *(modified from Garcia 2010, Sima de los Huesos, Middle Pleistocene).*

SH99 T/U-13/14-68 - The endocast shows a peculiar general morphology.

In fact, observing the profile in dorsal view it is possible to note a greater thickening of the occipital lobe compared to the frontal, and a strong restriction in the bulb area and of the olfactory tract until the beginning of the orbital gyrus.

In lateral view, on the contrary, it shows a rather straight anteroposterior line, such as to produce a rather concave lateral profile with a sub-triangular shape.

The sylvian sulcus is well defined and forms, thanks to the rather advanced position of the temporal lobe, an acute angle with respect to the longitudinal axis of the brain.

DA-4B 38-41 – Observing in dorsal view the endocast attributed to *U. arctos* coming from Deutsch-Altenburg, it can be noticed, a rather rounded morphology, with the portion of the occipital lobe wider than the frontal lobe.

Being a natural endocast and due to the deposition of minerals within the cavities of splanchnocranium, many of the raised portions, such as the Longitudinal Fossa, are remarkably pronounced; therefore, the brain shows some characteristic structures that are not part of the original anatomy of the brain.

The portion of the olfactory lobe is totally absent, while the lateral profile shows a rather curved trend even if, the absence of the anterior portion, does not allow an exhaustive analysis of the character. The sylvian groove is deep and maintains an oblique angle.

INGND 1 – The virtual endocast from the Ingarano deposit shows a very large frontal lobe, which reaches almost the size of the occipital lobe. The lateral line is rather curved, giving the brain a much more rounded shape than the other endocasts observed.

The olfactory lobes are developed and clearly divided (even if the groove shape could derive more from the deformed condition of the whole skul, than from a real morphological modification of the brain).

C 3361 – The brown bear from Alps, shows, in dorsal view, a rather elongated general morphology, with a curve profile, characterized by a gradual decrease of lateral amplitude from the occipital to the frontal lobes. In lateral view, the brain shows a rounded profile starting directly from the olfactory bulb; in fact, in this specimen, this last anatomical portion is rather wide and does not show a clear separation between the bulb and the olfactory sulcus.

The sylvian sulcus is poorly engraved and maintains an oblique line in relation to the longitudinal axis of the brain.

C 131 e C 486 – The two Marsican brown bear virtual endocasts show a very similar morphology, even if the dimensional ratios reveal a greater dimension of the male individual (C 486) rather than the female indivuum (C 131), see Table 9. Both have a general shape, in the dorsal view, rather elongated, with clear steps of the dorsal profile in concomitance with the passages between the occipital lobe and the frontal lobe, and between the frontal lobe and the olfactory bulb. The olfactory tract is wide and high, and the lateral profile shows a curved anteroposterior line (even if more accentuated in the female than in the male). Also in this case, unlike the alpine brown bear, the sylvian sulcus is quite deep and has an oblique course, a typical feature of the findings analyzed in this work.

9.1.3 Final Remarks

From the comparison of the various brain, some substantial differences have emerged between the speloid lineage and the arctoid one. In fact, as already described by García et al., (2007), in cave bears, the anterodorsal profile has a much straighter lateral line than that of brown bears, which instead tends to be rather curved, giving the brain a more rounded appearance.

This character is probably due to the difference in the width of the frontal sinuses (larger in *U. spelaeus* and *U. deningeri*, rather than in *U. arctos* which lead to a different development of the brain space. Another evident difference is represented by the rostral portion of the brain, narrower and elongated in the cave bears rather than in the brown bear. According to García et al., (2007) this sylvian solcos is deeper in the speloid lineage and more sinuous in *Ursus arctos*. I disagree with the authors, because from my analysis results that both evolutionary lines (and also within the brown bear) this anatomical portion shows low variability, and a quite deep groove.

The skull from Deutsch-Altenburg deserves a more in-depth discussion. As has been mentioned in chapter 2 of this thesis, the material coming from this deposit has not obtained, from the various experts, the same taxonomic validity. In fact, despite the fact that Rabeder et al., (2010) have done an excellent job of comparison, this material continues to raise many doubts and perplexities.

From the analysis of the natural endocast brain and its comparison with both *U. deningeri* and *U. arctos*, some ambiguous characters emerge.

In fact, analyzing the morphologies described above, the anteroposterior line of DA-B4 38-41 is rather curved, not reaching the typical conformation of *U. arctos* but, at the same time, the narrowing of the distal portion of the brain does not reuse accentuated as in *U. deningeri*.

Unfortunately, the absence of the olfactory lobe in the specimen, does not allow to be sure about the characters yet described. In fact, depending on the conformation of the latter, the brain could be more elongated, with a narrow olfactory trait, typical of *U. deningeri*, or maintain a shape more similar to *U. arctos*. The revision of the fossil bear from Deutsch-Altenburg is needed and was beyond the focus of the present study; in this thesis the specimen has been used only as a comparison with the endocasts of other Pleistocene bears.

Observing instead the brains of brown bear, it is possible to highlight some rather diagnostic characters which distinguish not only the modern species from the fossil ones, but also the two Italian modern populations. Most of the differences are observed in occlusal view where it is possible to notice how the general shape of the endocast tends to be more rounded in the fossil bear (INGND 1) and much more elongated in modern bears. Also, regarding the olfactory trait, it can be noted a considerable difference between the two groups, since it is much higher in the modern *U. arctos* than in the brain from the Ingarano deposit.

From a special focus on the morphology of the brain of the two currently living Italian populations (*U. arctos* and *U. arctos marsicanus*), it is possible to observe substantial differences in the area of the olfactory tract. In fact, while maintaining a rather elongated dorsal profile in both forms, the lateral profile shows a greater thickening of the dorsal area in the Alpine bear (C 3361), so as to make the sulcus of the frontal lobe almost invisible. On the contrary, there are no evident morphological differences between the two Marsican brown bear specimens (C 131 and C 486) which have both a very similar lateral and dorsal profile.

Lastly, observing the morphometric data, there are no dimensional differences linked to the specific attribution; in fact, both the brain of *U. deningeri* (SH99 T/U-13/14-68) and that of *U. arctos marsicanus* male (C 486) have very similar morphometric ratios.

On the contrary, there are considerable dimensional differences between the endocast of the female Marsican and that of the male, where the former is larger than the latter.

10 General Discussion

By making an overall analysis of all the work, it is possible to identify some rather clear evidence within the evolutionary history of the brown bear. These concern not only the morphological and morphometric features *U. arctos* during the Pleistocene, but also as regards in the modern population.

Starting from an evolutionary point of view, the first clear evidence about the origin of this species, is given by the analysis of the paleodistribution of the genus *Ursus* **(Cap 5).** Looking at the maps proposed I agree with the hypothesis advanced by Zapfe, (1946) and Mazza & Rustioni, (1994) that the phyletic line of *U. arctos* must have developed in Asia, and that it has exploited the different favourable environmental conditions during the Early and Middle Pleistocene to enter in different moments in the European territory. Therefore, I find myself thinking that *U. etruscus* represents an extinct lineage in Europe, which extinguished at the passage Villafranchiano Superiore - Galeriano. This fact is justified for me both by the absence of arctoid forms before this great faunistic turn over and by the subsequent total absence of the Etruscan form, which was however mainly bound in a few places of southern Europe **(see Fig. 13).**

Turning instead to the analysis of the first fossil evidence of *U. arctos* in Europe, and in specific to the encephalic endocast from the Deutsch-Altenburg deposit (Early Pleistocene), emerged some features that do not return a clear morphological pattern such as to eliminate any taxonomic doubt on this specific find. In fact, as discussed extensively in **Cap 8**, the finding from the Austrian deposit has ambiguous characters, for which it is not yet clear if they reflect more one or the other evolutionary lineage and must be considered as *Ursus sp*.

Obviously, not having had the opportunity to study in detail all the rest of the material (mostly isolated teeth and post cranial elements), I do not consider it appropriate to refute the taxonomic attribution proposed by Rabeder et al., (2010), but I believe that further analysis of comparison are necessary, mainly to delineate clearly what are the distinctive features of the two bears.

In fact, observing the descriptions proposed by the various authors, regarding the various fossil remains of the genus *Ursus* from the deposits of the late Early Pleistocene and the Middle Pleistocene, it is rather evident that the diagnostic morphologies between the two evolutionary lines are extremely ambiguous. In order to have a true framework of the adaptive dynamics, and to fully understand the causes and the model in which these two forms have split into two evolutionary lines so distant from each other (one herbivorous and the other omnivorous), I think it is necessary to review all the material of the Early and Middle Pleistocene, analyzing in full the variability of the genus during this period, maybe with the help of new statistical-informatics methodologies, made available by current technological development.

This problem is obviously encountered also in the first occurrence of the brown bear in Italy, making the taxonomic attribution of isolated dental elements extremely difficult.

This is the case of the material coming from the deposit of the Middle Pleistocene from Fontana Ranuccio. From the analyses carried out it was however evident that some arctoid morphologies are present since the Middle Pleistocene in Italy, mainly represented by a very simple and poorly tuberculated lower p4 (unlike the typical line of caverns for which these are more complex and often characterized by many accessory cusps) **(Cap 9)**.

The great variability can be found also on the fossil forms of the Late Pleistocene, even if in a much less evident way. In fact, this overlapping of morphological and morphometric patterns is mainly found on adult male brown bear and young female cave bear, often making it difficult to discriminate the specific attribution of some fossils. This is confirmed by the analysis of geometric morphometry developed on three-dimensional models of the skulls. By inserting some cave bear skulls into the statistical analysis, an overlap between the two forms is observed, making the distinctive features less clear **(Cap 6)** even if some anatomical portions of the cranial region maintain distinct morphologies and dimensions, such as the brain morphology and some dental features **(Cap 7-9).**

The inclusion of the "*Ursus arctos priscus*" inside the analysis, shows that the general morphology of those skulls has very similar characters both to the present forms and to the fossil ones. For this reason, according Pacher, (2007) I think that *U. arctos priscus* must be considered a synonym of *U. arctos*, even if can be still observe some morphometrical and morphological differences on skull, teeth and brain between modern and fossil brown bear **(Cap 6-9)**. A data that maintain a good morphological constancy within the entire evolutionary line of the brown bear are represented by the results of the geometric morphometry analysis, applied to the shape of the various dental elements. In fact, the morphological variability of the occlusal line, in relation to the position of the cusps, remains rather low throughout the fossil record **(Cap 6 – 7)**. The only tooth that shows a good intra- and inter-specific changes is the upper P4 that, both in the modern and in the fossil forms, tends to discriminate in a rather high way the different morphological patterns.

On the other hand, is confirmed the trend already highlighted by various authors (Kurtén, 1995; Marciszak et al., 2015) for which the Pleistocene forms of central Europe are generally larger than the Holocene forms and, subsequently, also than the extant ones **(Cap 6)**.

Focusing more closely at the modern variability, it was possible to recognize some morphological patterns that clearly distinguish not only the Marsican subspecies from the continental forms, but also, some different morphological differences between the populations of the Alps and the Carpathians. In fact, the shape of the skull and the morphology of the upper P4, indicate an accentuated distinction between these two populations. It is however important to underline that this evidence can and must be confirmed further by increasing the number of specimens within the analysis.

Regarding *U. arctos marsicanus*, the analyses carried out have brought new interesting data both about its morphological difference with the modern one and for its evolutionary history in the Italian territory.

The analysis of geometric morphometry on three-dimensional models further confirms the great morphological distance that exists between the Marsican subspeciesnot only with respect to the extant Alpine brown bear (Loy 2008, Colangelo 2012), but also with respect to the fossil bear (both brown bear and cave bear). This is further confirmed by the study of the shape of the brain **(Cap 9)** and the upper P4. Also, the general size of all the dental elements show some differences, resulting extremely smaller than other forms of brown bear **(Cap 6).** While, in contrast to what was highlighted in Colangelo et al., (2012), I have not found any difference between the two populations in the morphology of the first upper molar. For this reason, this character cannot be taken as a distinctive element of the two forms. Finally, I agree with the hipotesys suggested by Ciucci et al., (2017), that all these morphological and morphometric characters can be functionally associated with the high documented consumption of vegetable and fruits by Apennine bears.

11 Conclusions

At the beginning of my PhD, I immediately realized that there were many gaps in the knowledge about the evolution and the morphological and phyletic relationships between the various species of European bear.

During these years, this critical condition has been largely confirmed not only by my studies and researches, but also by all the experts that I had the pleasure and honor to met.

In these conclusions I do not want to repeat once again the specific results obtained from my work (which I hope to have presented in a comprehensive manner) but I would like to start from the beginning, from the first chapter, and take into account the "open questions" presented and the points that flowed from it, to make a final overview of what has resulted from this work.

First, I pointed out the lack of information about the Italian fossil brown bear material, the lack of descriptions and the problem that comes from publishing in non interantional journals (point A).

Facing this issue, the first real impression was that much of the bear fossil material is only mentioned in faunal lists or briefly described in some journals of limited visibility. Moreover, it was very unexpected to understand how few brown bear materials exists (often composed exclusively of post-cranial or a few cranial fragments) in relation to the extremely more abundant *U.* ex gr. *spelaeus*.

This was the main problem for my research, for wich I needed a high number of statistical data to recognize which characters morphologically separates the different modern and fossil species or subspecies, from what is simple intraspecific variability (huge in the present brown bear).

For this reason, I decided to approach the issue from a previous step, trying to census all the Italian material of *U. arctos* and, after, expanding it with European data. The result is a database with more than 3500 elements listing all the Italian material of the Italian brown bear and most of the European one.

Having the possibility to have a concrete data on the available material, the first question I asked myself was: when does the story of the brown bear begin in Italy? The information on the topic was extremely contrasting or not supported by concrete evidence (point B).

From my study emerged that the clearest evidence of arctoid bear in Italy is located at Fontana Ranuccio, deposit dated to Middle Pleistocene and located on south of Rome (Italy). The material has some characters in my opinion rather clear, but it is good to highlight once again that, having only a few teeth available to support this thesis, further material may disprove or confirm this evidence.

In fact, when dealing with the differences between the speleoid line and the arctoid line (point C), I had the impression that, very often, the two forms are distinguished without proper attention, considering as an example the most extreme characters of the two forms, without dwelling on how much the patterns of the two morphological variability are overlapped (as demonstrated by the analysis of geometric morphometry of the skull or as has been highlighted recently by genetics) (Barlow et al., 2018).

On the other hand, I do not want to say that these differences do not exist, the analyses proposed in this thesis have in fact shown clear morphological and morphometric patterns that clearly distinguish the two lines during the Late Pleistocene.

On the contrary, the separation of the two evolutionary lines during the Early and Middle Pleistocene still requires further studies, represented not only by an accurate review of all the historical material, but also by a greater number of specimens and therefore new excavation campaigns.

Despite this, from the analyses and comparisons carried out in this work, I think I have highlighted some discreet signals that open, in one way or another, to new perspectives for the understanding of the evolution of this large mammal during its first stages in Europe.

Finally, looking at the present, Italy represents an extremely interesting stage for the analysis of the evolutionary dynamics and dispersion of the brown bear. In fact, the presence of an endemic form on the territory allowed me to analyze even more deeply the intraspecific variability discussed earlier.

In this case the question "what is the origin of the Marsican?" has been echoing within the Italian scientific community since a long time.

My intention was to find fossil evidence that could provide some information on the dispersal dynamics of this small endemic population with peculiar morphological characters. The analysis of the fossil and sub-fossil material coming from the regions of the current Marsican bear range has not given the expected results, therefore no fossil element analysed shows any firm taxonomical identification to *U. arctos marsicanus*.

Despite this, the absence of fossil evidence until the end of the Bronze Age (the Gran Carro deposit) suggests that the split and isolation of the Marsican bear must have occurred after about 1,500 years, confirming at some genetic data, but still leaving a question mark about the precise timing of its geographical separation.

With the analyses carried out, it was not possible to highlight the fossil record related to the Marsican brown bear but, at the same time, it has been possible to establish the basis for a concrete morphological and morphometric comparison of both cranial and dental elements which, in the light of new findings, will be of great value for the identification of the endemic form of the Apennines in fossil and sub-fossil material.

12 References

Abella, J., Valenciano, A., Pérez-Ramos, A., Montoya, P., Morales, J., 2013. *On the Socio-Sexual Behaviour of the Extinct Ursid Indarctos arctoides: An Approach Based on Its Baculum Size and Morphology.* PLoS ONE 8. doi:10.1371/journal.pone.0073711

Agostini, S., Canzio, E. Di, Rossi, M.A., 2009. *Il rinvenimento di Ursus arctos di Grotta Beatrice Cenci (Cappadocia AQ) ed il significato paleoclimatico della successione del Pleistocene Superiore finale - Olocene antico.* In: Atti Del III Convegno Di Archeologia in Ricordo Di Walter Cianciusi, Avezzano, 13-15 Novembre.

Agustí, J., Antón, M., 2002. *Mammoths, sabertooths, and hominids: 65 million years of mammalian evolution in Europe.* Columbia University Press.

Aiello, L., Wood, B., Key, C., Wood, C., 1998. *Laser Scanning and Paleoanthropology.* In: Primate Locomotion. Boston, pp. 223–236. doi:10.1007/978-1-4899-0092-0_13

Akhremenko, A.K., Sedalishchev, V.T., 2008. *Specific ecological features of the brown bear (Ursus arctos L. 1758) in Yakutia.* Russian Journal of Ecology 39, 188–192. doi:10.1134/S1067413608030065

Albrecht, J., Bartoń, K.A., Selva, N., Sommer, R.S., Swenson, J.E., Bischof, R., 2017. *Humans and climate change drove the Holocene decline of the brown bear.* Scientific Reports 7. doi:10.1038/s41598-017-10772-6

Alferez, F., Molero, G., Maldonado, E., 1985. *Estudio preliminar del úrsido del yacimiento del Cuaternario medio de Pinilla del Valle (Madrid).* Col-Pa 40, 59–67.

Alroy, J., 2001. *A multispecies overkill simulation of the end-Pleistocene megafaunal mass extinction.* Science 292, 1893–1896. doi:10.1126/science.1059342

Altobello, G., 1921. *Mammiferi: IV. i carnivori (carnivora).* Tip. Giov. Colitti e Figlio.

Altuna, J., 1973. *Hallazgos de Oso Pardo (Ursus arctos, Mammalia) en cuevas del País Vasco.* Munibe XXV, 121–170.

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

Ambrosi, A., 1952. *Gli orsi nell'Appennino.* Rivista CAI 71, 1–35.

Andrews, C.W., 1922. *Note on a bear (Ursus savini, n. sp.).* Annals and Magazine of Natural History 204–207, 9.

Anyonge, W., & Baker, A. 2006. *Craniofacial morphology and feeding behavior in Canis dirus, the extinct Pleistocene dire wolf.* Journal of Zoology, 269(3), 309–316

Arbour, J.H., Brown, C.M., 2014. *Incomplete specimens in geometric morphometric analyses.* Methods in Ecology and Evolution 5, 16–26. doi:10.1111/2041-210X.12128

Argant, A., 1991. *Carnivores quaternaires en Bourgogne.* Doc. Lab. Géol. Lyon 115, 301.

Argant, A., 1996. *Sous-famille Agriotheriinae*. Masson, Paris.

Argant, A., 2001. *Cave Bear ancestors – Los antepasados del oso de las Cavernas.* Cadernos 26, 341–348.

Argant, A., 2010. *Carnivores (Canidae, Felidae et Ursidae) de Romain-la-Roche (Doubs, France).* 29, 495–601.

Argant, J., 2004. *Le gisement pliocène final de Saint-Vallier (Drôme, France): palynologie.* Geobios 37, 81–90.

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).*

Azzaroli, A., Giuli, C.De, Ficcarelli, G., Torre, D., 1988. *Late Pliocene to early mid-Pleistocene mammals in Eurasia: faunal succession and dispersal events.* Palaeogeography, Palaeoclimatology, Palaeoecology 66, 77–100.

Azzaroli, A., 1983. *Quaternary mammals and the 'End-Villafranchian' dispersal event - A turning point in the history of Eurasia.* Palaeogeography, Palaeoclimatology, Palaeoecology 44, 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.

Baltsavias, E.P., 1999. *A comparison between photogrammetry and laser scanning.* ISPRS Journal of photogrammetry and Remote Sensing, 54, 83–94.

Barlow, A., Cahill, J.A., Hartmann, S., Theunert, C., Xenikoudakis, G., Fortes, G.G., ... & García-Vázquez, A., 2018. *Partial genomic survival of cave bears in living brown bears.* Nature ecology & evolution, 1 1.

Bartolomei, G., Cesnola, A.P. di, Broglio, A., 1977. *Chronostratigraphie et écologie de l'Epigravettien en Italie. Centre national de la recherche scientifique.*

Baryshnikov, G., F., Boeskorov, G., G., 1998. *Brown bear Ursus arctos (Carnivora, Ursidae) from the Pleistocene of Yakutia. Byuleten' Moskovskogo Obshchestva Ispytateley Prirody, Ser*. Biol. 103, 3–9.

Baryshnikov, G.., Foronova, I., 2001. *Pleistocene small cave bear (Ursus rossicus) from the South Siberia, Russia.* Cadernos Laboratorio Xeolóxico de Laxe 26, 373–398.

Baryshnikov, G., 2008. *Taxonomical diversity of Pleistocene bears in northern Eurasia.* In 6th Meeting of the European Association of Vertebrate Palaeontologists,(Krempaská, Z., Ed.) 9–11.

Baryshnikov, G.F., Zakharov, D.S., 2013. *Early Pliocene Bear Ursus thibetanus (Mammalia, Carnivora) from Priozernoe Locality in the Dniester Basin (Moldova Republic).* Proceeding of the Zoological Institute RAS 317, 3–10.

Baryshnikov, G.F., 2007a. *The bears family (Ursidae).* Nauka,Sant-Petersburg, 147.

Baryshnikov, G.F., 2007b. *Ursidae. Fauna of Russia and Neighboring Countries. New Series, N147.* Mammals 1, 5.

Baryshnikov, G.F., Boeskorov, G.G., 2004. *Skull of the Pleistocene brown bear (Ursus arctos) from Yakutia, Russia.* Russian Journal of Theriology. Русский териологический журнал, 3, 71–75.

Bedetti, C., Pavia, M., 2007. *Reinterpretation of the Late Pleistocene Ingarano cave deposit based on the fossil bird associations (Apulia, South-Eastern Italy).* Rivista Italiana di Paleontologia e Stratigrafia 113, 487–507.

Bellucci, L., Mazzini, I., Scardia, G., Bruni, L., Parenti, F., Segre, A.G., Naldini, E.S., Sardella, R., 2012. *The site of Coste San Giacomo (Early Pleistocene, central Italy): palaeoenvironmental analysis and biochronological overview.* Quaternary International 276, 30–39.

Bellucci, L., Sardella, R., Rook, L., 2015. *Large mammal biochronology framework in Europe at Jaramillo: the Epivillafranchian as a formal biochron.* Quaternary International 389, 84–89.

Bellucci, L., Bidditttu, I., Brilli, M., Conti, J., Germani, M., Giustini, F., Iurino, D.A., Mazzini, I., Sardella, R., n.d. *First occurrence of the short-faced bear Agriotherium (Ursidae, Carnivora) in the Italian peninsula: biochronological and palaeoenvironmental implications.* Italian Journal of Geosciences.

Benazzo, A., Trucchi, E., Cahill, J.A., Maisano Delser, P., Mona, S., Fumagalli, M., Bunnefeld, L., Cornetti, L., Ghirotto, S., Girardi, M., Ometto, L., Panziera, A., Rota-Stabelli, O., Zanetti, E., Karamanlidis, A., Groff, C., Paule, L., Gentile, L., Vilà, C., Vicario, S., Boitani, L., Orlando, L., Fuselli, S., Vernesi, C., Shapiro, B., Ciucci, P., Bertorelle, G., 2017. *Survival and divergence in a small group: The extraordinary genomic history of the endangered Apennine brown bear stragglers.* Proceedings of the National Academy of Sciences 114, 201707279. doi:10.1073/pnas.1707279114

Bennett, K.D., Tzedakis, P.C., Willis, K.J., 1991. *Quaternary refugia of north European trees.* Journal of Biogeography 18, 103–115.

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.

Biknevicius, A. R., Van Valkenburgh, B., & Walker, J. 1996. *Incisor size and shape: implications for feeding behaviors in saber-toothed "cats".* Journal of Vertebrate Paleontology, 16(3), 510–521.

Binder, W. J., & Van Valkenburgh, B. 2000. *Development of bite strength and feeding behaviour in juvenile spotted hyenas (Crocuta crocuta).* Journal of Zoology, 252, 273–283.

Bon, C., Caudy, N., Dieuleveult, M. de, Fosse, P., Philippe, M., Maksud, F., Beraud-Colomb, E., Bouzaid, E., Kefi, R., Laugier, C., Rousseau, B., Casane, D., Plicht, J. van der, Elalouf, J., M., 2008. *Deciphering the complete mitochondrial genome and phylogeny of the extinct cave bear in the Paleolithic painted cave of Chauvet.* Proceedings of the National Academy of Sciences 105, 17447–17452.

Bona, F., Sala, B., 2016. *Villafranchian-Galerian mammal faunas transition in South-Western Europe. The case of the late Early Pleistocene mammal fauna of the Frantoio locality, Arda River (Castell'Arquato, Piacenza, Northern Italy).* Geobios 49, 329–347.

Bookstein, F.L., 1991. *Thin-Plate splines and the atlas problem for biomedical images.* in Lecture Notes in Computer Science (including subseries Lecture Notes in Artificial Intelligence and Lecture Notes in

Bioinformatics), 511, 326–342.

Bruner, E., Manzi, G., 2006. *Digital tools for the preservation of the human fossil heritage: Ceprano, Saccopastore, and other case studies.* Human Evolution 21, 33–44.

Buzi, C., Micarelli, I., Profico, A., Conti, J., Grassetti, R., Cristiano, W., Vincenzo, F. Di, Tafuri, M.A., Manzi, G., 2018. *Measuring the shape: performance evaluation of a photogrammetry improvement applied to the Neanderthal skull Saccopastore 1.* Acta Imeko.

Candeloro, M., 1998. *La fauna pleistocenica di Grotta del Cervo (Carsoli, AQ): un esempio di musealizzazione.* Master thesis. Sapienza, University of Rome.

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

Capasso Barbato, L., Gliozzi, E., 1994. *La fauna pleistocenica della Grotta del Cervo di Pietrasecca (Carsoli, AQ, Italia centrale).* Istituto Italiano di Speleologia1 5, 135–149.

Capasso Barbato, L., Cassoli, P.F., Minieri, M.R., Petronio, C., Sardella, R., Scarano, M., 1992. *Note preliminari sulla fauna pleistocenica di Ingarano.* Bollettino della Società Paloentologia Italiana 31, 325–334.

Casanovas-Vilar, I., Maderna, A., Albaa, D.A., Cabrera, L., Garcìa-Paredes, I., Hoek Ostend, L.W. van der, DeMiguel, D., Robles, J.M., Furió, M., Dam, J. van, Garcés, M., Angelone, C., Moyà-Solà, S., 2016. *The Miocene mammal record of the Vallès-Penedès Basin (Catalonia).* Comptes Rendus Palevol 15, 791–812.

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.

Chagneau, J., Prat, F., 1983. *Les Ursidés de l'aven de Vergranne (Doubs).* Annales scientifiques de l'Université de Franche-Comté 5, 83–109.

Chaix, L., Bridault, A., Picavet, R., 1997. *A Tamed Brown Bear (Ursus arctos L.) of the Late Mesolithic from La Grande-Rivoire (Ise`re, France)?* Journal of Archaeological Science 24, 1067–1074.

Christiansen, P., 2008. *Feeding ecology and morphology of the upper canines in bears (Carnivora: Ursidae).* Journal of Morphology 269, 896–908.

Christiansen, P., & Adolfssen, J. S. 2005. *Bite forces, canine strength and skull allometry in carnivores (Mammalia, Carnivora)*. Journal of Zoology 266, 133–151.

Ciucci, P., Altea, T., Antonucci, A., Chiaverini, L., Croce, A., Di, Fabrizio, M., Forconi, P., Latini, R., Maiorano, L., Monaco, A., Morini, P., Ricci, F., Sammarone, L., Striglioni, F., Tosoni, E., Regione, L.B.M.N., 2017. *Distribution of the brown bear (Ursus arctos marsicanus) in the Central Apennines, Italy, 2005-2014.* Hystrix, the Italian Journal of Mammalogy 86–91, 1.

Clot, A., 1980. La grotte de la Carrière (Gerde, Hautes-Pyrénées). Stratigraphie et paléontologie des Carnivores. Travaux du Laboratoire de Géologie de l'Université Paul Sabatier, 1–2, 1–263.

Colangelo, P., Loy, A., Huber, D., Gomerčić, T., Vigna Taglianti, A., Ciucci, P., 2012. *Cranial distinctiveness in the Apennine brown bear: Genetic drift effect or ecophenotypic adaptation?* Biological Journal of the Linnean Society 107, 15–26. doi:10.1111/j.1095-8312.2012.01926.x

Conti, J., Ciavatta, F., Iurino, D.A., Mecozzi, B., Sardella, R., 2017a. *A juvenile rhinocerotidae neurocranium from the Middle-Late Pleistocene site of Melpignano (Apulia, Italy): CT-Scan analisys and virtual restoration.* In: XVII Edizione Delle Giornate Di Paleontologia, Anagni, 24-26 Maggio.

Conti, J., Mazzini, I., Bellucci, L., Bona, F., Giustini, F., Massussi, M., Mecozzi, B., Brilli, M., Iurino, D.A., Lembo, G., Muttillo, B., Strani, F., Tucci, S., Voltaggio, M., Sardella, R., 2017b. *Toward the ward the Virtual reconstruction of Grotta Romanelli, Apulia (Southern Italy).* In: IMEKO International Conference on Metrology for Archaeology and Cultural Heritage Lecce, Italy, October 23-25.

Conti, J., Paparella, I., Iurino, D.A., Sardella, R., 2016. *Using the CT-scan as a tool to recover information from traded fossils: an example on a plesiosaur skull*. 88° Congresso SGI, Napoli.

Conti, S., 1954. *Morfologia comparata craniale ed encefalica degli orsi pleistocenici della Liguria.* Memorie del museo civico di storia naturale 'G. Doria' Genova.

Croitor, R., Brugal, J.P., 2010. *Ecological and evolutionary dynamics of the carnivore community in Europe during the last 3 million years.* Quaternary International 212, 98–108.

Crusafont, P.M., Kurtén, B., 1976. *Bears and bear-dogs from the Vallesian of the Vallés-Penedés basin, Spain.* Acta Zoologica Fennica.

Crusafont, P.M., Truyols, S.J., 1985. *A biometric study of the evolution of fissiped carnivores.* Evolution 10, 314–332.

Dalquest, W.W., 1986. *Lower jaw and dentition of the Hemphillian bear, Agriotherium (Ursidae), with the description of a new species.* J. Mammal 67, 623–631.

Davison, J.D., Ho, S., C., B.S., Korsten, M., Tammeleht, E., Hindrikson, M., Østbye, K., Østbye, E., Lauritzen, S.E., Austin, J., Cooper, A., Saarma, U., 2011. *Late-Quaternary biogeographic scenarios for the brown bear (Ursus arctos), a wild mammal model species.* Quaternary Science Reviews 30, 418–430.

Deperet, C., 1890. *Les animaux pliocènes du Roussillon.* Baudry.

Erdbrink, K., 1953. *A Review of Fossil and Recent Bears of the Old World: With Remarks on Their Phylogeny, Based Upon Their Dentition.*

Fabiani, R., 1923. *La fauna mammologica quaternaria della Buca del Tasso. Atti del Comitato per le ricerche di Paleontologia umana in Italia.* Arch l'Antropol e l'Etnologia 52, 10–21.

Ferretti, M., 1997. *Mammuthus cf. primigenius (Proboscidea, Mammalia), a new faunal element from the late Middle Pleistocene of Conca river (Cattolica, Romagna, Italy).* Boll. Soc. Paleont. It. 36, 391–398.

Ficcarelli, G., 1979. *Osservazioni sull'evoluzione del genere Ursus.* Bollettino della Società Paleontologica Italiana 18, 166–172.

Franzen, J.L., 1999. *The late Early Pleistocene teeth and bone accumulation of Dorn-Dürkheim 3 (Germany, Rheinhessen): natural or man-made.* Monographien des Römisch-Germanischen 42, 41–56.

Franzosa, J., Rowe, T., 2005. *Cranial endocast of the Cretaceous theropod dinosaur Acrocanthosaurus atokensis.* Journal of Vertebrate Paleontology 25, 859–864.

Freudenberg, W., 1914. *Die saugetiere des alteren Quartas von Mitteleuropa.* Geol. Paleont, Abh 12, 544–670.

Freudenthal, M., Meijer, T., Meulen, A.J. Van der, 1976. *Preliminary report on a field campaign in the continental Pleistocene of Tegelen (The Netherlands).* Rijksmuseum van Geologie en Mineralogie.

Frick, C., 1926. *The hemicyoninae and an American tertiary bear.* 56, 1–119.

Friess, M., Marcus, L.F., Reddy, D.P., Delson, E., 2002. *The use of 3D laser scanning techniques for the morphometric analysis of human facial shape variation.* BAR Int Series, 1049, 5–31.

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, 1007–1017.

García, N., Arsuaga, J.L., 2001. *Ursus dolinensis: a new species of Early Pleistocene ursid from Trinchera Dolina, Atapuerca (Spain).* Comptes Rendus de l'Académie des Sciences-Series IIA-Earth and Planetary Science 332, 717–725.

Gervais, P., 1859. *Zoologie et paléontologie françaises.* Paris.

Gittleman, J.L., 1997. *Sexual dimorphism in the canines and skulls of carnivores:* J. Zool., Land 242, 97–117.

Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Barbato, L.C., Stefano, D., 1997. *Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy*. The state of the art. 103.

Goldfuss, A., 1823. *Osteologische Beiträge zur Kenntnis verschiedener Säugethiere der Vorwelt.* Nova Acta Physico-Medica Academiae Caesarae Leopoldino-Carolinae Naturae Curiosorum 11, 451–490.

Grandal-d'Anglade, A., López-González, F., 2005. *Sexual dimorphism and ontogenetic variation in the skull of the cave bear (U. spelaeus Rosenmüller) of the European Upper Pleistocene.* Geobios 38, 325–337.

Grandal-d'Anglade, A., Vidal Romaní, J.R., 1997. *A population study on the Cave bear (U. spelaeus Ros.-Hein.) from Cova Eirós (Triacastela, Galicia, Spain).* Geobios 30, 723–731.

Green, S., Bevan, A., Shapland, M., 2014. *A comparative assessment of structure from motion methods for archaeological research.* Journal of Archaeological Science 46, 173–181.

Hendey, Q.B., 1972. *A Pliocene Ursid from South Africa.* Ann. S. Afr. Mus 59, 115–133.

Hendey, Q.B., 1980. *Agriotherium (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus.* Ann. South African Mus. 81, 1–109.

Hewitt, G.M., 1996. *Some genetic consequences of ice ages, and their role in divergence and speciation.* Biological journal of the Linnean Society 58, 247–276.

Hilpert, B., 2002. *New finds of Ursus arctos from the Cave ruin Hunas-A preliminary report.* In: Cave-Bear-

Researches/Höhlen-Bären-Forschungen.-Abh. Karst-Und Höhlenkunde. pp. 27–29.

Hofreiter, M., Serre, D., Rohland, N., Rabeder, G., Nagel, D., Conard, N., Munzel, S., Paabo, S., 2002. *Lack of phylogeography in European mammals before the last glaciation.* Proceedings of the National Academy of Sciences 101, 12963–12968.

Howell, F.C., 1987. *Observations on Carnivora from the Upper Neogene Sahabi Formation (Libya).* In: Neogene Paleontology and Geology of Sahabi Alan Liss. New York, pp. 153–181.

Humphries, M.M., Thomas, D.W., Speakman, J.R., 2002. *Climate-mediated energetic constraints on the distribution of hibernating mammals.* Nature 418, 313–316.

Iurino, D.A., Sardella, R., 2015. *Medical CT scanning and the study of hidden oral pathologies in fossil carnivores.* Paläontologische Zeitschrift 89, 251–259.

Iurino, D.A., Danti, M., Sala, W. Della Seta, Sardella, R., 2013. *Modern techniques for ancient bones: vertebrate palaeontology and medical CT analysis.* Boll. Soc. Paleontol. Ital 52, 14.

Jánossy, D., 1963. *Die altpleistozäne Wirbeltierfauna von Kövesvárad bei Répáshuta (Bükk-Gebirge).* Annales Historiconaturales Musei nationalis Hungarici, pars Mineralogica et Palaeontologica 55, 109–141.

Kahlke, R.D., García, N., Kostopoulos, D.S., Lacombat, F., Lister, A.M., Mazza, P.P., Spassov, N., Titov, V. V., 2011. *Western Palaearctic palaeoenvironmental conditions during the Early and early Middle Pleistocene inferred from large mammal communities, and implications for hominin dispersal in Europe.* Quaternary Science Reviews 30, 1368–1395.

Koby, F.E., 1944. *Un squelette d'ours brun du pléistocene italien.* Verhandlungen der naturforschenden Gesellschaft in Basel 56, 58–85.

Koufos, G.D., Konidaris, G.E., Harvati, K., 2017. *Revisiting Ursus etruscus (Carnivora, Mammalia) from the Early Pleistocene of Greece with description of new material.* Quaternary International 1–18.

Krause, J., Unger, T., Noçon, A., Malaspinas, A., S., Kolokotronis, S., O., Stiller, M., Soibelzon, L., Spriggs, H., Dear, P., H., Briggs, A., W., Bray, S., C., O'Brien, S., J., Rabeder, G., Matheus, P., Cooper, A., Slatkin, M., Pääbo, S., Hofreiter, M., 2008. *Mitochondrial genomes reveal an explosive radiation of extinct and extantbears near the Miocene-Pliocene boundary.* BMC Evolutionary Biology 8, 220.

Kukla, G.J., Clement, A.C., Cane, M.A., Gavin, J.E., Zebiak, S.E., 2002. *Last interglacial climates and early glacial ENSO.* Quaternary Research 58, 27–31.

Kurtén, B., Pairó, M.C., 1977. *Villafranchian Carnivores (nammalia) from la puebla de Valverde.* Commentationes Biologicae 85, 1–39.

Kurtén, B., 1955. *Sex dimorphism and size trends in the cave bear, U. spelaeus Rosenmüller and Heinroth* 90.

Kurtén, B., 1957. *The Bears and Hyenas of the Interglacials.* Quaternaria 4, 69–81.

Kurtén, B., 1966. *Pleistocene bears of North America I, Genus Tremarctos spectacled bears.* Acta. Zool. Fenn. 115, 1–120.

Kurtén, B., 1969. *Die carnivoren-Reste aus den Kiesen von süßenborn bei Weimar.* Paläontologische Abhandlungen 3, 735–756.

Kurtén, B., 1976. *Fossil Carnivora from the late Tertiary of Bled Douarah and Cherichira, Tunisia.* Notes du Service géologique de Tunisie 42, 177–214.

Kurtén, B., 1977. *Bären und Hyänenreste aus dem Pleistozän von Taubach.* Quartärpaläontologie 2, 361–378.

Kurtén, B., 1995. *The cave bear story: life and death of a vanished animal.*

Leonard, J.A., Wayne, R.K., Cooper, A., 2000. *Population genetics of Ice Age brown bears.* Proceedings of the National Academy of Sciences 97, 1651–1654.

Lì, Y., 1993. *On a new species of Pliocene Ursus (Carnivora: Ursidae) from Yinan, Shandong Province.* Vertebrata Palasiatica 31, 44–60.

Loreille, O., Orlando, L., Patou-Mathis, M., Philippe, M., Taberlet, P., Hänni, C., 2001. *Ancient DNA analysis reveals divergence of the cave bear, U. spelaeus , and brown bear, Ursus arctos, lineages.* Current Biology 11, 200–203.

Lorenzen, E.D., Nogués-Bravo, D., Orlando, L., Weinstock, J., Binladen, J., Marske, K.A., ... & Ho, S.Y., 2011. *Species-specific responses of Late Quaternary megafauna to climate and humans.* Nature 479, 359–364.

Lowe, D.G., 1999. *Object recognition from local scale-invariant features.* In Computer vision, 1999. The proceedings of the seventh IEEE international conference on 2, 1150–1157.

Loy, A., Genov, P., Galfo, M., Iacobone, M.G., Vigna Taglianti, A., 2008. *Cranial morphometrics of the Apennine* *brown bear (Ursus arctos marsicanus) and preliminary notes on the relationships with other southern European populations.* Journal of Italian Zoology 75, 67–75.

Lydekker, R., 1878. *Notices of Siwalik mammals.* Rec Geol Surv India 11, 103–104.

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, 969–974.

Magri, D., 2008. *Patterns of post-glacial spread and the extent of glacial refugia of European beech (Fagus sylvatica).* Journal of Biogeography 35, 450–463.

Majkić, A., D'Errico, F., Milošević, S., Mihailović, D., Dimitrijević, V., 2018. *Sequential incisions on a cave bear bone from the Middle Paleolithic of Pešturina Cave, Serbia.* Journal of Archaeological Method and Theory 25, 69–116.

Mallison, H., Wings, O., 2014. *Photogrammetry in paleontology–a practical guide.* Journal of Paleontological Techniques 12.

Marciszak, A., Socha, P., Nadachowski, A., Stefaniak, K., 2011. *Carnivores from Biśnik Cave.* Quaternaire, Hors-série 4, 101–106.

Marciszak, A., Krzysztof, S., Mackiewicz, P., Ridush, B., 2015. *Ursus arctos L. 1758 from Bukovynka Cave (W Ukraine) in an overview on the fossil brown bears size variability based on cranial material.* Quaternary International 357, 136–148.

Marra, A.C., 2003. *Ursus arctos from selected Pleistocene site of Eastern Sicily.* Bollettino della Società Paleontologica Italiana 145–150.

Martini, I., Coltorti, M., Mazza, P.P., Rustioni, M., Sandrelli, F., 2014. *The latest U. spelaeus in Italy, a new contribution to the extinction chronology of the cave bear.* Quaternary Research 81, 117–124.

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.* INQUA, Sottocomm. EOS.

Matheus, P.E., 1995. *Diet and co-ecology of Pleistocene short-faced bears and brown bears in Eastern Beringia.* Quat. Re. 44, 447–453.

Matheus, P.E., 2003. *Locomotor adaptations and ecomorphology of short-faced bears (arctodus simus) in Eastern Beringia.* Occas. Pap. Earth Sci. Paleontology Program, Government of the Yukon.

Mattson, D.J., 1998. *Diet and morphology of extant and recently extinct northern bears.* Ursus 10, 479–496.

Mäuser, M., 1987. *Geologische und paläontologische Untersuchungen an der altpleistozänen Säugetier-Fundstelle Würzburg-Schalksberg.* Müncher Geowissenschaftliche Abhandlungen Reihe A, Geologie und Paläontologie 11, 1–78.

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, 211–217.

Mazza, P., 1997. *Taphonomic analysis of late Middle Pleistocene mammal remains from Bucine.* Bollettino della Società Paleontologica Italiana 16, 381–390.

Mazza, P., Rustioni, M., 1994. *On the phylogeny of Eurasian bears.* Palaeontographica 230, 1–38.

McLellan, B., Reiner, D.C., 1994. *A review of bear evolution*. Bears: Their Biology and Management, 85–96.

McLellan, B.N., Servheen, C., Huber, D., 2008. *IUCN list*.

Medin, T., Martínez-Navarro, B., Rivals, F., Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Espigares, P.M., Figueirido, B., Rook, L., Palmqvist, P., 2017. *Late Villafranchian Ursus etruscus and other large carnivorans from the Orce sites (Guadix-Baza basin, Andalusia, southern Spain): Taxonomy, biochronology, paleobiology, and ecogeographical context.* Quaternary International 431, 20–41.

Meloro, C., Guidarelli, G., Colangelo, P., Ciucci, P., Loy, A., 2017. *Mandible size and shape in extant Ursidae (Carnivora, Mammalia): A tool for taxonomy and ecogeography.* Journal of Zoological Systematics and Evolutionary Research 55, 269–287.

Meloro, C., 2007. La fauna quaternaria di Grotta Milano (Petina, Salerno). Proc I Reg Congr Speleol "Campania Speleologica 1–3.

Miller, W.E., Carranza-Castañeda, O., 1996. *Agriotherium schneideri from the Hemphillian of central Mexico.* J. Mammal 77, 568–577.

Mitchell, E., Tedford, R.H., 1973. *The Elaliarctinae. A new group of extinct aquatic carnivora and a consideration of the origin of the Oteridae.* Bull. Amer. Mus. Nat. Hist. 151, 201–284.

Moigne, A., Interna-, C., Boulbes, N., Argant, A., Cr, E., Magniez, P., 2009. *Biochronologie Et Grands*

Mammifères Au Pléistocène Moyen Et Supérieur En Europe Occidentale Avant-Propos. Quaternaire 20, 413–414.

Moigne, A.M., Palombo, M.R., Belda, V., Heriech-Briki, D., Kacimi, S., Lacombat, F., Lumleya, M.A. de, Moutoussamyc, J., Rivals, F., Quilèsa, J., Testu, A., 2006. *Les faunes de grands mammifères de la Caune de l'Arago (Tautavel) dans le cadre biochronologique des faunes du Pléistocène moyen italienogique des faunes du Pléistocène moyen italien* 110, 788–831.

Montoya, P., Alcala, L., Morales, J., 2001. *Indarctos (Ursidae, Mammalia) from the Spanish Turolian (Upper Miocene).* Scripta Geology 122, 123–151.

Morales, A., 1984. *Long-term results and complications of intracavitary bacillus Calmette-Guerin therapy for bladder cancer.* 132, 457–459.

Morlo, M., Kundrát, M., 2001. *The first carnivoran fauna from the Ruscinium (Early Pliocene, MN 15) of Germany.* PalZ 75, 163–187.

Musil, R., 1964. *Die Braunbären aus dem Ende des letzten.* Acta Musei Moraviae 49, 83–106.

Musil, R., 1980. *U. spelaeus -der Höhlenbär.* Museum für Ur-und Frühgeschichte Thüringens 4–94.

Musil, R., 2001. *Die Ursiden-Reste aus der Unterpleistozän von Untermassfeld.* Monographien 40, 633–658.

Nagel, D., Koufos, G.D., 2009. *The Late Miocene Mammal Faunas of the Mytilinii Basin, Samos Island, Greece: New Collection.* Beitr. Paläont 31, 391–396.

Napoli, P.F., 1907. *Intorno alla formazione di Monteverde e di alcuni fossili rinvenuti.* Nota.

Napoli, P.F., 1911. *Di alcuni rinvenimenti di fossili a Monteverde presso Roma.* Nota.

Nezami, B., Eagdari, S., Barkhor, M., Sasanfar, Z., 2014. *Sexual dimorphism of Cranial shape in Iranian Brown Bear Ursus arctos Linnaeus, 1758 using Geometric Morphometric approach.* Bulletin of Environment, Pharmacology and Life Sciences 329–335.

Ogino, S., Egi, N., Takai, M., 2011. *New species of Agriotherium (Mammalia, Carnivora) from the late Miocene to early Pliocene of central Myanmar.* J. Asian Earth Sci. 42, 408–414.

Ohdachi, S., Aoi, T., Mano, T., Tsubota, T., 1992. *Growth, sexual dimorphism, and geographical variation of skull dimensions of the brown bear Ursus arctos in Hokkaido.* Journal of the Mammalogical Society of Japan 17, 27–47.

Oldfield, C.C., McHenry, C.R., Clausen, P.D., Chamoli, U., Parr, W.C.H., Stynder, D.D., Wroe, S., 2012. *Finite element analysis of ursid cranial mechanics and the prediction of feeding behaviour in the extinct giant Agriotherium africanum.* J. Zool. 286, 163–170.

Olive, F., 2006. *Évolution des grands Carnivores au Plio Pléistocène en Afrique et en Europe.* L'anthropologie 110, 850–869.

Pacher, M., Stuart, A.J., 2009. *Extinction chronology and palaeobiology of the cave bear (U. spelaeus).* Boreas 38, 189–206.

Pacher, M., 2007. *The type specimen of Ursus priscus GOLDFUSS, 1818 and the uncertain status of Late Pleistocene brown bears.* Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen 245, 331–339.

Palombo, M.R., Azanza, B., Alberdi, M.T., 2002. *Italian mammal biochronology from Latest Miocene to Middle Pleistocene: a multivariate approach*. 36, 335–368.

Peretto, C., Arnaud, J., Moggi-Cecchi, J., Manzi, G., Nomade, S., Pereira, A., Falguères, C., Bahain, J.J, Grimaud-Hervé, D., Berto, C., Sala, B., Lembo, G., Muttillo, B., Gallotti, R., Hohenstei, M., 2015. *A human deciduous tooth and new 40Ar/39Ar dating results from the Middle Pleistocene archaeological site of Isernia La Pineta, southern Italy.* PLoS One 10, e0140091.

Petitti, P., Sciancalepore, A., Severi, E., 2013. *The Gran Carro underwater settlement in Lake Bolsena, Italy*. Skillis 2, 225–232.

Petronio, C., Sardella, R., 1998a. *Remarks on the stratigraphy and biochronology of the Late Pleistocene deposit of Ingarano (Apulia, Southern Italy).* Rivista Italiana di Paleontologia e Stratigrafia (Research In Paleontology and Stratigraphy) 104.

Petronio, C., Petrucci, M., Salari, L., 2006. *La volpe nel Pleistocene superiore della Puglia: indicazioni paleoambientali.* Bollettino Museo Civico Storia Naturale di Verona 30, 59–78.

Petronio, C., Sardella, R., 1998b. *Remarks on the stratigraphy and biochronology of the Late Pleistocene deposit of Ingarano (Apulia, Southern Italy).* Rivista Italiana di Paleontologia e Stratigrafia 104, 287–294.

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, 89–94.

Petter, G., Thomas, H., 1986. *Les Agriotheriinae (Mammalia, Carnivora) néogènesde l'Ancien Monde présence du genre Indarctos dans la faune de Menacer (Ex-Marceau),* Algérie. Geobios 19, 573–586.

Petti, F.M., Petruzzelli, M., Conti, J., Spalluto, L., Wagensommer, A., Lamendola, M., Francioso, R., Montrone, G., Sabato, L., Tropeano, M., 2018. *The use of aerial and close-range photogrammetry in the study of dinosaur tracksites: Lower Cretaceous (upper Aptian/lower Albian) Molfetta ichnosite (Apulia, southern Italy).* Palaeontologia Electronica 21, 1–19.

Pilgrim, G.E., 1932. *The genera Trochictis, and Trocharion, with remarks on the Taxonomy of the Mustelidae.* P. Zool. Soc. London 845–867.

Portis, A., 1907. *Di due notevoli avanzi di Carnivori fossili dai terreni tufacei di Roma.* Boll. Soc. Geol. Ital. 26, 63–89.

Post, K., Mol, D., Reumer, J., Vos, J. De, 2001. *Zoogdierfauna uit het Bavelien.* Grondboor & Hamer 55, 2–22.

Prat, F., Thibault, C., 1976. Le gisement de Nauterie à La Romieu (Gers): fouilles de 1967 à 1973: Nauterie I. Éditions du Muséum.

Qiu, Z., Xie, J., Yan, D., 1991. *Discovery of late Miocene Agriotherium from Jiegou, Gansu, and its taxonomic implications.* Vertebrat Pal Asiatic 29, 286–295.

Qiu, Z.X., Qiu, Z.D., 1995. *Chronological sequence and subdivision of Chinese Neogene mammalian faunas*. Palaeogeography, Palaeoclimatology, Palaeocelogy 116, 41–70.

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).

Rabeder, G.., Withalm, G., 2006. *Brown bear remains (Ursidae, Mammalia) from Early Pleistocene cave fillings of Deutsch-Altenburg (Lower Austria).* In: 12th International Cave Bear Symposium (Abstract Book). Aridéa/Loutrá, pp. 47–48.

Rabeder, G., 1999. *Die Evolution des Höhlenbärengebisses.* Verlag der Österr. Akad. der Wiss. 11.

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.

Randi, E., 2003. *Conservation genetics of carnivores in Italy.* Comptes Rendus Biologies 326, 54–60.

Repenning, C.A., 1980. *Faunal exchanges between Siberia and North America.* Canadian Journal of Anthropology 1, 37–44.

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

Rode, K., 1935. *Untersuchungen über das Gebiß der Bären.* Monographien zur Geologie und Paläontologie 2, 1–162.

Romandini, M., Nannini, N., 2011. *Cacciatori epigravettiani nel Covolo Fortificato di Trene (Colli Berici, Vicenza): sfruttamento dell'Orso Speleo*. Preistoria Alpina 45, 7–9.

Rosa, M. La, Mazza, P., Mozzi-Cecchi, J., Rustioni, M., Vianello, F., 1992. *Paleolithic finds from the volcanoclastic Deposit of the Agro Pontino (Latium, Central Italy).* Abstract Symp. Quaternary Stratigraphy in volcanic areas, Rome 42.

Rowe, K.C., Heske, E.J., Brown, P.W., Paige, K.N., 2004. *No Surviving the ice: Northern refugia and postglacial colonization.* Proceedings of the National Academy of Sciences 101, 10355–10359.

Rubat Borel, F., n.d. *L'Orso e l'archeologia. Alcuni esempi dalla preistoria al medioevo.* L'Orso e l'archeologia. Alcuni esempi dalla preistoria al medioevo 2007, 53–86.

Saarma, U., Ho, S.Y., Pybus, O.G.., Kaljuste, M.., Tumanov, I.L., Kojola, I.., ... & Lyapunova, E.A., 2007. *Mitogenetic structure of brown bears (Ursus arctos L.) in northeastern Europe and a new time frame for the formation of European brown bear lineages.* Molecular Ecology 2, 401–413.

Sabol, M., 2001. *Fossil and subfossil findings of brown bears from selected localities in Slovakia.* Slovak Geological Magazine 7, 3–17.

Samuels, J.X., Meachen-Samuels, J.A.., Gensler, P.A., 2009. *The first mid-Blancan occurrence of Agriotherium (Ursidae) in North America: a record from Hagerman fossil beds National Monument, Idaho.* J. Paleont. 83, 597–603.

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, 104–109.

Segre, A.G., 1984. *Considerazioni sulla cronostratigrafia del Pleistocene laziale.* Atti della XXIV Riunione Scientifica dell’Istituto Italiano di Preistoria e Protostoria 149–154.

Servheen, C., 1990. T*he status and conservation of the bears of the world.* Int. Conf. Bear Res and Manage. Monogr. 2, 32.

Servheen, C., Herrero, S., Peyton, B., 1999. *Bears.* Status survey and conservation action plan. In: IUCN/SSC Bear and Polar Bear Specialist Groups. Gland, Switzerland.

Silvestri, L., 2017. *Caves and human lifeways in Middle Bronze Age Central Italy: a social bioarchaeology approach.* Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/12226/.

Slice, D., 2005. Modern Morphometrics in Physical Anthropology.

Smirnov, N.G., Golovachov, I.B., 1998. *Holocene history of small mammals in the Urals. In: Benecke, N. (Ed.)*, The Holocene History of the European Vertebrate Fauna. Berlin, pp. 210–221.

Soergel, W., 1926. *Der Bär von Süßenborn. Ein Beitrag zur näheren Kenntnis der diluvialen Bären.* Neues Jahrbuch für Mineralogie, Geologie und Paläontologie.(B) 115–156.

Sommer, R.S., Nadachowski, A., 2006. *Glacial refugia of mammals in Europe: evidence from fossil records.* Mammal Review 36, 251–265.

Sommer, R.S., Benecke, N., 2005. *The recolonization of Europe by brown bears Ursus arctos Linnaeus, 1758 after the Last Glacial Maximum.* Mammal Review 35, 156–164. doi:10.1111/j.1365-2907.2005.00063.x

Sorkin, B., 2006. *Ecomorphology of the giant short-faced bears Agriotherium and Arctodus*. Hist. Biol. 18, 1–20.

Sotnikova, M., 2008. *Carnivora assemblages of the Ruscinian Early Villafranchian transition: Eastern Europe (Ukraine) and Russia (Transbaikalia) similarity and distinctions.* In 6th Meeting of the European Association of Vertebrate Palaeontologists 30, 85–87.

Sotnikova, M. V., 1989. *Late Pliocene-early Pleistocene Carnivora. Stratigraphic significance.* Nauka Transactions 440, 1–123.

Sotnikova, M.V., Dodonov, A.E., Pen’Kov, A. V., 1997. *Upper Cenozoic bio-magnetic stratigraphy of Central Asian mammalian localities.* Palaeogeography, Palaeoclimatology, Palaeoecology 133, 243–258.

Stach, J., 1957. *The Apterygotan Fauna of Poland in Relation to the World-fauna of this Group of Insects: Families: Neelidae and Dicyrtomidae.* Państwowe Wydawnictwo Naukowe.

Stiner, M.C., 1998. *Mortality analysis of Pleistocene bears and its paleoanthropological relevance.* Journal of Human Evolution 34, 303–326.

Stuart, A.J., Kosintsev, P.A., Higham, T.F.G., Lister, A.M., 2004. *Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth.* Nature 431, 684–689.

Taberlet, P.., Bouvet, J., 1994. *Mitochondrial DNA polymorphism, phylogeography, and conservation genetics of the brown bear Ursus arctos in Europe.* Proc. R. Soc. Lond. B 255, 195–200.

Taberlet, P., Fumagalli, L., Wust-Saucy, A.G., Cosson, J.F., 1998. *Comparative phylogeography and postglacial colonization routes in Europe.* Molecular ecology 7, 453–464.

Tedford, R.H., Harington, C.R., 2003. *An Arctic mammal fauna from the early Pliocene of North America.* Nature 425, 388.

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 1–11.

Thenius, E., 1956. *Zur Kenntnis der fossilen Braunbären (Ursidae, Mammalia).* Sitzungsberichte der Österreichische Akademie der Wissenschaften. Mathematisch Naturwissenschaftliche Klasse, Abteilung 1: Biologie, Mineralogie, Erdkunde und Verwandte Wissenschaften 165, 153–172.

Thenius, E., 1959. *Indarctos arctoides (Carnivora, Mammalia) aus dem Pliozätn Osterreichs nebst einer.* Revision der Gattung. Neues Jahrb. GeoL Paliont. Abh., Stuttgart 108, 270–295.

Thenius, E., 1979. *Zur systematischem und phylogenetischen Stellungd es bambusbaren: Ailuropoda melanoleuca David (Carnivora, Mammalia).* Z. Saugetierk 441, 286–305.

Torelli, M., 2000. *Gli Etruschi.*

Torres, P., 1984. *Ursidos del pleistoceno-holoceno de la Península Ibérica.* Doctoral dissertation, Minas.

Torres, P.H., 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.

Torres Pérez-Hidalgo, T.J., 1992. *The European descendants of Ursus etruscus C. Cuvier (Mammalia, Carnivora, Ursidae).* Boletín del Instituto Geológico y minero de España 103, 632–642.

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., MacLarnon, A., Soligo, C., Rae, T.C. 2016. *Functional morphology of the cave bear (Ursus spelaeus) mandible: a 3D geometric morphometric analysis.* Organisms Diversity & Evolution 16(1), 299-314.

Viret, J., 1939. *Monographie paléontologique de la faune de vertébrés des Sables de Montpellier. III. Carnivora Fissipedia.* Travaux du Laboratoire de Géologie de la Faculté des Sciences de Lyon 37, 7–26.

Viret, J., 1954. *Le loess a bancs durcis de Saint-Vallier (Drome) etsa faune de mammiféres villafranchiens.* Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon 4, 1–200.

Vislobokova, I.A.., Agadjanian, A.K., 2015. *New data on large mammals of the Pleistocene Trlica fauna, Montenegro, the Central Balkans*. Paleontological Journal 49, 651–667.

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., 2004. *A taxonomic revision of bears from selected Biharian localities of the Czech Republic. A preliminary report: I. C 718, Chlum I, Chlum IV.* Cahiers scientifiques-Muséum d'histoire naturelle de Lyon 139–144.

Wagner, J., 2005. *A taxonomic revision of bears from selected biharian localities of the Czech Republic: A preliminary report. II.* Koneprusy caves-an old collection. Bulletin de la Société d'histoire naturelle de Toulouse 141, 51–54.

Wagner, J., 2010. *Pliocene to early Middle Pleistocene ursine bears in Europe: a taxonomic overview.* Journal of the National Museum (Prague), Natural History Series 179, 197–215.

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, 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, 533–544.

Wiszniowska, T., 1989. *Middle Pleistocene Carnivora (Mammalia) from Kozi Grzbiet in the Swietokrzyskie Mts., Poland.* Acta Zoologica Cracoviensia 32, 589–630.

Withalm, G., 2001. *Die Evolution der Metapodien in der Höhlenbären-Gruppe (Ursidae, Mammalia).* Beiträge zur Paläontologie 26, 169–249.

Wolf, C., Ripple, W.J., 2017. *Range contractions of the world's large carnivores.* Royal Society open science 4, 170052.

Yu, L., Li, Y.W., Ryder, O.A., Zhang, Y.P., 2007. *Analysis of complete mitochondrial genome sequences increases phylogenetic resolution of bears (Ursidae), a mammalian family that experienced rapid speciation*. BMC Evolutionary Biology 7, 198.

Zapfe, H., 1948. *Die altplistozanen Baren von Hundsheim in Niederosterreich.* Jb. Geol. Bundesanstalt 41, 95–164.

Zdansky, O., 1924. Jungtertiä Carnivoren Chinas. C2. *Palaeont Sin Ser*. 1, 16–28.

Zedrosser, A., Steyaert, S.M., Gossow, H., Swenson, J.E., 2011. *Brown bear conservation and the ghost of persecution past. Biological Conservation* 144, 2163–2170.

Zedrosser, A., Dhale, B., Swenson, J.E., Gerstl, N., 2001. *Status and management of the brown bear in Europe*. Ursus 12, 9–20.

13 Supplementary material

Table 10: ***Deposits list showed in the Fig. 32 and Fig. 33***

Latitude	***Longitude***	***Specie***	***Site***	***Catalog***	***References***
40.629158	23.484758	*etruscus*	Apollonia	1	KOSTOPOULOS 2006
45.167069	3.391613	*etruscus*	Blassac La Girondie	2	PALOMBO 2004 (Heintz et al., 1974; Bonadonna & Alberdi, 1987; Duvernois, 1990)
38.269829	21.835148	*cf. etruscus*	Kastritsi	3	KOSTOPOULOS 2006
43.942667	4.542178	*etruscus*	La Sartanette, porch d'entrée	4	PALOMBO 2004 (Duvernois, 1990; Crégut, 2002)
38.347123	21.733025	*cf. etruscus*	Makinia	5	KOSTOPOULOS 2006
42.424649	11.160901	*etruscus*	Monte Argentario	6	PETRUCCI 2009
43.949159	11.399299	*etruscus*	Mugello	7	PALOMBO 2002, Masini 1989-1994, Abbazzi 1995, Rook 1996, Benvenuti 1998
45.029247	8.364931	*etruscus*	Olivola	8	PALOMBO 2002, Azzaroli 1977, De Giuli 1984, Torre 1987, Masini 1991-1996, Ficcarelli 1996, Azzaroli 1992, Azzaroli & Mazza 1992, Torre 1993-1996, Caloi 1977, Giozzi 1997
42.988514	12.215362	*etruscus*	Pietrafitta	9	PALOMBO 2002, Moretti 1949, Ambrosetti 1987, Masini 1991-1996, Rustioni & Mazza 1992,1993 (testo Cartaceo), Mazza 1993, Abbazzi 1995, Gentile 1996, Torre 1996, Ferretti 1999
41.78257	15.45227	*etruscus*	Pirro Nord	10	Da inserire Personal measurements, PALOMBO 2002, De Giuli & Torre 1984, De Giuli 1987-1990, Masini 1989-1991-1996, Rook & Torre 1996, Pfeifer 1999, Rook & Sardella 2000
43.339312	19.360669	*etruscus*	Trlica Fauna	11	VISLOBOKOVA 2015
43.748953	11.247384	*etruscus*	Upper Valdarno (Casa Frata)	12	PALOMBO 2002, Virsekku 1980, De Giuli & Masini 1983-1987, Masini 1989-1990-1991-1994-1996, Ficcarelli 1996- Torre 1996, Gliozzi 1997
43.293050	11.857246	*etruscus*	Val di Chiana	13	PALOMBO 2002, Azzaroli 1984, De Giuli 1987, Torre 1992, Azzaroli & Mazza 1993, Masini 1991-1996, Abbazzi 1995
43.629330	11.462952	*etruscus*	Valdarno (Figline)	14	PALOMBO 2002, Masini 1991-1994-1996, Albianelli 1995-1997, Caloi 1997, Gliozzi 1997
43.746599	11.248988	*etruscus*	Valdarno (Tasso Sands)	15	PALOMBO 2002, Masini 1991-1994-1996, Albianelli 1995-1997
50.349100	19.315162	*sp.*	Zabia Cave - Kroczyce	16	Wolsan 1990, Nadachowsky 1990 (Testo "Lower Pleistocene Carnivores of Poland" Quartapalaontologie 277-280)
50.349100	19.315162	*sp.*	Zabia Cave - Kroczyce		Wolsan 1990, Nadachowsky 1990 (Testo "Lower Pleistocene Carnivores of Poland" Quartapalaontologie 277-280)
37.724445	-2.400412	*etruscus*	Barranco Leon, Orce, Guadix-Baza Basin	17	RIVALS 2015, BELLUCCI 2015
42.963068	12.935440	*sp.*	Colle Curti	18	PALOMBO 2002, Borselli 1988, Ficcarelli 1990-1990-1991, Masini 1991-1991-1996, Rook 1994-1996, Coltorti 1998, Abbazzi 1998
45.018075	9.993583	*dolinensis*	Frantoio, Fiume Arda, Piacenza	19	BONA 2016
37.724445	-2.400412	*etruscus*	Fuente Nueva-3, Orce, Guadix-Baza Basin	20	RIVALS 2015, BELLUCCI 2015
50.511418	20.203279	*deningeri*	Kozi Grzbiet - Kielce	21	Wolsan 1990, Nadachowsky 1990 (Testo "Lower Pleistocene Carnivores of Poland" Quartapalaontologie 277-280)
45.176368	6.281462	*aff. Deningeri*	Le Vallonnet	22	PALOMBO 2004 (de Lumley et al., 1988, 2000; Moullé, 1998; Moullé et al., 2000; Crégut, 2002; Bailon et al., 2003)
44.973341	4.117803	*deningeri*	Soleilhac	23	PALOMBO 2004 (Bonifay, 1971; Guérin, 1980; Thouveny & Bonifay, 1984; Bonadonna & Alberdi, 1987; Lister, 1990; Fosse 1992; Crégut 2002; Lacombat, unpublished data)
50.529377	10.400723	*rodei*	Untermassfeld	24	Tafel 2001, Musil 2001, Garcia 2004 (cartaceo Das Pleistozan von untermassfeld bei meiningen (thuringen))
37.724445	-2.400412	*etruscus*	Venta Micena, Orce, Guadix-Baza Basin	25	RIVALS 2015, BELLUCCI 2015
48.131231	16.904999	*arctos*	Deutsch-Altenburg	26	RABEDER 2010
48.131231	16.904999	*deningeri*	Deutsch-Altenburg	27	Nagel & Rabeder 1997, 233-235
49.349504	13.156409	*deningeri*	Moosbach	29	Personal measurements
42.379288	-3.500481	*dolinensis*	Trinchera Dolina, Atapuerca	30	GARCIA 2001

Table 111: ***Deposits list showed in the Fig. 34 and Fig. 35***

Latitude	***Longitude***	***Specie***	***Site***	***Catalog***	***References***
52.848622	1.462114	*deningeri*	Bacton	1	TURNER 2009 (Bishop 1982)
44.883133	-0.604096	*arctos*	Bruges	2	PALOMBO 2004 (Guérin, 1980; Crégut pers. comm.)
42.839282	2.754164	*deningeri*	Caune de l'Arago CM I	3	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006, KAHLKE 2011
42.839282	2.754164	*arctos*	Caune de l'Arago CM I	4	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006
42.839272	2.754161	*arctos*	Caune de l'Arago CM II	5	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006
42.839272	2.754161	*deningeri*	Caune de l'Arago CM II	6	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006
42.839272	2.754161	*arctos*	Caune de l'Arago CM III	7	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006
42.839272	2.754161	*deningeri*	Caune de l'Arago CM III	8	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006
44.806199	1.225815	*arctos*	Combe Grenal	9	PALOMBO 2004 (Grégut, 2002)
49.765940	8.276073	*deningeri*	Dorn-Dürkheim	10	KAHLKE 2011 (Franzen 2000)
33.003824	35.634233	*sp*	Gesher Benot Ya‘aqov	11	KAHLKE 2011 (RABINOVICH 2006)
43.353770	2.698448	*thibetanus*	Grotte d'Aldène, couche K	12	PALOMBO 2004 (Grégut, 2002)
43.353770	2.698448	*deningeri*	Grotte d'Aldène, couche K	13	PALOMBO 2004 (Grégut, 2002)
48.113054	16.946029	*arctos*	Hundsheim	14	Personal measurements
48.113054	16.946029	*deningeri*	Hundsheim	15	Personal measurements
48.113054	16.946029	*sp.*	Hundsheim	16	Personal measurements
46.842323	29.617667	*deningeri*	Kolkotova Balta	17	KAHLKE 2011
43.682742	5.392085	*deningeri*	L'escale a Saint Estève Janson	18	PALOMBO 2004 (Guérin, 1980; Lister, 1990; Brugal, 1992)
43.677115	4.097287	*cf. deningeri*	Lunel Viel, Grotte N 1	19	PALOMBO 2004 (Fosse, 1996)
41.489324	21.945725	*deningeri*	Manestirec cave	20	KAHLKE 2011 (Kurten et al.,1989)
43.727660	0.523677	*thibetanus*	Nautière	21	PALOMBO 2004 (Guérin, 1980; Brugal, 1992)
43.727660	0.523677	*cf deningeri*	Nautière	22	PALOMBO 2004 (Guérin, 1980; Brugal, 1992)
44.305657	4.433387	*deningeri*	Orgnac 3	23	PALOMBO 2004 (Aouraghe, 1999; de Lumley et al., 2000; Moigne &Valensi, 2000; Moigne, pers. comm.)
44.305657	4.433387	*thibetanus*	Orgnac 3	24	PALOMBO 2004 (Aouraghe, 1999; de Lumley et al., 2000; Moigne &Valensi, 2000; Moigne, pers. comm.)
52.454583	1.730155	*sp.*	Pakefield	25	(STUART 2001)
44.306034	1.476116	*deningeri*	Pech de l'Azé, couche 9	26	PALOMBO 2004 (Delpech & Prat, 1980)
44.306034	1.476116	*arctos*	Pech de l'Azé, couche 9	27	PALOMBO 2004 (Delpech & Prat, 1980)
48.056601	20.463305	*deningeri*	Tarko	28	KAHLKE 2011 (Jánossy, D., 1986)
46.380180	4.775587	*deningeri*	Verchizeuil	29	PALOMBO 2004 (Argant, 1991)
46.380180	4.775587	*thibetanus*	Verchizeuil	30	PALOMBO 2004 (Argant, 1991)
45.084333	1.518397	*deningeri*	Abimes de la Fage	31	PALOMBO 2004 (Mourer-Chouviré et al., 1975; Crégut, 2002) MOURER-CHOUVIRE 2003
45.733084	0.193065	*ex gr. spelaeus*	Abri Suard	32	PALOMBO 2004 (Guérin, 1980)
38.050115	14.591699	*arctos*	Acquedolci	33	MARRA 2003, VILLA 2001
53.056271	-0.773864	*arctos*	Balterton	34	TURNER 2009 (Lister 1991)
44.089770	5.403852	*arctos*	Bau de l'Aubesier, Couche 1-H	35	PALOMBO 2004 (Fernandez, 2001; Crégut, 2002)
44.089770	5.403852	*arctos*	Bau de l'Aubesier, Couche 4-H	36	PALOMBO 2004 (Fernandez, 2001; Crégut, 2002)
47.538110	6.632879	*ex gr. spelaeus*	Baume de Gonvillars	37	PALOMBO 2004 (Guérin, 1980)
50.316773	2.946604	*sp*	Biache Saint Waast	38	PALOMBO 2004 (Guérin, 1980)
40.472989	50.011171	*arctos (binagadensis)*	Binagady	39	BARYSHNIKOV 2002
50.43916	19.66741	*arctos*	Biśnik Cave	40	MARCISZAK 2015
43.476547	11.616161	*arctos*	Bucine	41	PALOMBO 2002, Masini 1991, Ferretti 1997, Gliozzi 1997, Mazza 1997, PETRONIO 2011
41.537332	12.730004	*sp.*	Campoverde	42	PALOMBO 2002, Mazza 1992, La Rosa 1993, Caloi 1995-1998
45.089877	5.137096	*ex gr. spelaeus*	Carrière Fournier, Chatillon Saint Jean	43	PALOMBO 2004 (Mourer-Chouviré, 1972; Poplin 1972; Brugal, 1992)
41.901268	12.303912	*sp.*	Castel di Guido km 20	44	CALOI 1998
42.839272	2.754161	*arctos*	Caune de l'Arago Complexe Sommital	45	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002), MOIGNE 2006
42.839272	2.754161	*ex gr. spelaeus*	Caune de l'Arago Complexe Sommital	46	PALOMBO 2004 (de Lumley et al., 2000; Crégut, 2002) MOIGNE 2006

36.879821	14.680559	*arctos*	Contrada Camillà	47	MARRA 2003, VILLA 2001
42.787243	19.815812	*ex gr. spelaeus*	Crvena Stijena Cave Crvena Stijena Cave V-XXXI	48	KHALKE 2011 (FORSTEN 2003)
42.208603	12.730865	*sp.*	Fara Sabina	49	PALOMBO 2002, Angelelli 1983, Caloi 1988-1995
43.482252	5.314309	*thibetanus*	Grotte des Cèdres	50	PALOMBO 2004 (Crégut, 2002), DEFLEUR 1994
43.482252	5.314309	*cf. ex gr. spelaeus*	Grotte des Cèdres	51	PALOMBO 2004 (Crégut, 2002),DEFLEUR 1994
43.482252	5.314309	*arctos*	Grotte des Cèdres	52	PALOMBO 2004 (Crégut, 2002), DEFLEUR 1994
43.690864	7.294876	*arctos*	Grotte du Lazaret CII	53	PALOMBO 2004 (Guérin, 1980; Valensi & Abbassi, 1998; Crégut, 2002), DEFLEUR 1994
43.690864	7.294876	*ex gr. spelaeus*	Grotte du Lazaret CIII	54	PALOMBO 2004 (Guérin, 1980; Valensi & Abbassi, 1998; Crégut, 2002)
43.690864	7.294876	*arctos*	Grotte du Lazaret CIII	55	PALOMBO 2004 (Guérin, 1980; Valensi & Abbassi, 1998; Crégut, 2002)
49.6285	11.45874	*arctos ?*	Hunas	56	MARCISZAK 2015 - Hilpert 2002
42.536997	43.643408	*deningeri (kudarensis)*	Kudaro 3 Cave (layer 4f)	57	BARYSHNIKOV 2002
42.536997	43.643408	*thibetanus*	Kudaro 3 Cave (layer 4f)	58	BARYSHNIKOV 2002
43.061751	0.413186	*sp*	Montoussé I	59	PALOMBO 2004 (Chaline et al., 2000)
44.306034	1.476116	*deningeri*	Pech de l'Azé, couche 9	60	PALOMBO 2004 (Delpech & Prat, 1980)
44.306034	1.476116	*arctos*	Pech de l'Azé, couche 9	61	PALOMBO 2004 (Delpech & Prat, 1980)
40.9306	-3.82991	*arctos*	Pinilla del Valle	62	MARCISZAK 2015 (ALFEREZ 1985)
40.549447	14.243954	*ex gr. spelaeus*	Quisisana (Capri)	63	PALOMBO 2002, Capasso Barbato 1995
41.927741	12.220587	*ex gr. spelaeus*	Torre in Pietra (lower beds)	64	PALOMBO 2002, Caloi 1978-1998, Malatesta 1978 a-b, Masini 1991
41.927741	12.220587	*sp.*	Torre in Pietra (Upper Beds)	65	PALOMBO 2002, Caloi 1978-1998, Malatesta 1978 a-b, Di Stefano 1997
43.496766	10.329242	*arctos*	Montignoso	66	PALOMBO 2002, Rustioni 1999, PETRONIO 2011, lMP (per MASETTI 2009)
41.402814	43.493543	*deningeri*	Akhalkalaki	67	BARISHNIKOV 2002, KAHLKE 2011
43.33142	2.71636	*thibetanus*	Aldène	68	CREGUT-BONNOURE 1996
42.376560	-3.510082	*deningeri*	Atapuerca - Sima de los Huesos	69	Garcia 2001 (testo Les carnivores des sites du Pleistocene ancien et moyen d'Atapuerca, L'Anthropologie 105 - 83-93)
51.498594	0.252430	*arctos*	Aveley	70	TURNER 2009
39.619174	46.988618	*aff. Arctos*	Azykh Cave (layer 6)	71	BARYSHNIKOV 2002
42.377138	-3.509622	*deningeri*	B Cueva Mayor, Atapuerca	72	TORRES 1984
51.367588	11.100870	*sp.*	Bad Frankenhausen	73	KAHLKE 2011 (KAHLKE 2008)
43.47123	3.71612	*thibetanus*	BalarucVII	74	CREGUT-BONNOURE 1996
44.046798	5.243943	*arctos*	Bau de l'Aubesier	75	LEBEL 2001
33.076232	35.150905	*deningeri*	Bear's Cave	76	(TCHERNOV 1997)
51.308128	-2.947136	*arctos*	Bleadon	77	TURNER 2009 (Currant and Jacobi, 2001)
43.22225	0.63686	*thibetanus*	Boule	78	CREGUT-BONNOURE 1996
45.73930	13.759754	*deningeri*	Bristie I° comune Sgonico	79	Lugli 2000 (Libro: Atti del Museo Civico di Storia Naturale di Trieste 48 35-58)
43.71351	6.59025	*thibetanus*	Cèdres	80	CREGUT-BONNOURE 1996, DEFLEUR 1994
43.15861	5.84609	*thibetanus*	Cimay	81	CREGUT-BONNOURE 1996
51.791789	0.992110	*arctos*	Cudmore Groove	82	TURNER 2009
41.133409	24.148826	*ex gr. spelaeus*	Drama	83	KOSTOPOULOS 2006
41.756220	13.102539	*arctos*	Fontana Ranuccio	84	Personal measurements, PALOMBO 2002, Biddittu 1979, Segre 1982-1984, Cassoli 1993, Di Stefano 1993, Sardella 1994, Moullé 2000, PETRONIO 2011
41.756220	13.102539	*deningeri*	Fontana Ranuccio	85	Personal measurements, PALOMBO 2002, Biddittu 1979, Segre 1982-1984, Cassoli 1993, Di Stefano 1993, Sardella 1994, Moullé 2000 PETRONIO 2011
41.591666	14.237649	*deningeri*	Isernia La Pineta	86	Personal measurements
43.651863	22.702367	*ex gr. spelaeus*	Kozarnika B2-1, -B1	87	KAHLKE 2011 (GUADELLI 2005)
43.651863	22.702367	*deningeri*	Kozarnika B2-1, -B1	88	KAHLKE 2011 (GUADELLI 2005)
42.526009	43.655415	*deningeri (praekudarensis)*	Kudaro 1 (layer 5c)	89	BARYSHNIKOV 2002
42.536997	43.643408	*thibetanus*	Kudaro 3 Cave (layer 5)	90	BARYSHNIKOV 2002
42.536997	43.643408	*deningeri*	Kudaro 3 Cave (layer 5)	91	BARYSHNIKOV 2002
49.338081	8.793096	*deningeri*	Mauer	92	CAPASSO 1987, Bonifay 1971, Ruger 1928
49.358021	9.165096	*deningeri*	Mosbach	93	CAPASSO 1987, Zapfe 1948
55.36069	50.43596	*arctos kamiensis*	Mysy	94	BARYSHNIKOV 2004 - Vereshchagin 1959
55.36069	50.43596	*sp.*	Mysy	95	BARYSHNIKOV 2004
38.05782	14.58126	*cf. arctos*	Non Specificato	96	MANGANO 2005

40.372936	23.167619	*deningeri*	Petralona	97	BARYSHNIKOV 2010
42.75652	10.39341	*thibetanus*	Reale	98	CREGUT-BONNOURE 1996
42.75652	10.39341	*thibetanus*	Reale	99	CREGUT-BONNOURE 1996
45.75602	13.65875	*deningeri*	Slivia	100	BON 1992, PALOMBO 2002, Ambrosetti 1979, Caloi 1990-1997, Masini 1991-1996, Bon 1991, PETRONIO 2011
44.657119	41.365637	*deningeri*	Treugolnaya Cave (layers 6-7)	101	BARYSHNIKOV 2002, 2007, KAHLKE 2011
43.339312	19.360669	*deningeri*	Trlica Fauna	102	VISLOBOKOVA 2015
44.165616	8.307534	*sp.*	Valdemino	103	PALOMBO 2002, Masini 1991, Sala 1992, Gliozzi 1997, Nocchi 1997
47.416732	6.391450	*arctos*	Vergranne	104	SOMMER 2005, MOIGNE 2006 (Chagneau J. Et Prat 1983)
47.613224	18.390085	*deningeri*	Vértesszölös 1	105	KHALKE 2011 (Kretzoi 1990)
45.778129	13.648077	*deningeri*	Visogliano	106	PALOMBO 2002, Cattani 1991, Masini 1991, Gliozzi 1997, Abbazzi 2000, Tozzi 2000
51.255519	-2.182189	*deningeri*	Westbury	107	TURNER 2009 (Bishop 1982)
50.85962	-0.710006	*deningeri*	Boxgrove	108	TURNER 2009 (Roberts 1990)
41.799827	12.327096	*ex gr. spelaeus*	Cava Rinaldi - Ponte Galeria	109	CAPASSO BARBATO 1987
48.113054	16.946029	*ex gr. spelaeus*	Hundsheim II	110	Personal measurements
48.113054	16.946029	*deningeri / ex gr. spelaeus ?*	Hundsheim II	111	Personal measurements

Table 12: ***Deposits list showed in the Fig 37***

Latitude	***Longitude***	***Specie***	***Site***	***Catalog***	***References***
43.00058	-2.433283	arctos	A Cueva de Arrikrutz	1	TORRES 1988 (Distribution)
42.95896	-2.32781	arctos	AK Cueva de Aketegui, Aizkorri	2	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
49.04557	9.31777	arctos	Beilsteinhohle	3	MARCISZAK 2015 - Roemer in Freudenberg 1914
50.5215	2.68323	arctos	Beuvry	4	MARCISZAK 2015 - Dubois, 1926
50.05887	14.46599	arctos	Bohdalec	5	MARCISZAK 2015 - Kafka 1901
55.94919	9.53613	arctos	Brown Bank	6	MARCISZAK 2015 - Erdbrink, 1967
45.71107	8.29058	arctos	Cava Ciota Ciara	7	BERTO 2015
43.271826	-3.256967	arctos	Cueva de Trúcios	8	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
43.75739	1.46916	arctos	Gargas	9	Baryshnikov, 2007
43.11288	-2.0129	arctos	Gaztelu Cave	10	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
43.749002	10.552231	arctos	Grotta Cucigliana	11	FARINA 2014, FARINA 2011
42.138671	13.120713	arctos	Grotta del Cervo	12	AGOSTINI 2011 Capasso Barbato 1994 - CANDELORO 1998 - Agostini 2004
40.011062	15.375505	arctos	Grotta du Poggio	13	SALA 1979
41.232898	13.096799	arctos	Grotta Guattari	14	STINER 1991, PETRONIO 2011
40.529076	15.372133	arctos	Grotta Milano	15	MELORO 2007
42.214414	14.171489	arctos	Grotta Orsi Volanti	16	MAZZA Personal measurements
41.67821	15.58876	arctos	Grotta Paglicci	17	CREZZINI 2015
43.749002	10.552231	arctos	Grotta Parignana	18	FARINA 2009, FARINA 2014, CATERINI 1921, MINIERI 1995
43.07591	-2.22473	arctos	Guipuzcoa	19	MARCISZAK 2015 - Torres Pérez Hidalgo 1988a
42.97702	-2.10731	arctos	Illobi Cave	20	MARCISZAK 2015 - Villaluenga, 2011
33.916667	35.600097	arctos	Ksar'Akil	21	CAPASSO BARBATO 1990, Kurten 1965
42.536997	43.643408	arctos	Kudaro 3 (layer 3)	22	BARYSHNIKOV 2002
42.96421	1.75437	arctos	L'Herm Cave	23	MARCISZAK 2015 - Filhol, 1878
43.016776	-2.962403	arctos	Las Grajas II	24	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
42.77725	1.3829	arctos	Malarnaud Cave	25	MARCISZAK 2015 - Lartet 1867
43.48854	11.83708	arctos	Maspino	26	MARCISZAK 2015 - Koby, 1945
43.104679	-2.124660	arctos	MK Mandabeko Koba, Artitzaga	27	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
43.3625	12.74165	arctos	Monte Cucco	28	CAPASSO BARBATO 1990
50.11	19.46	arctos	Nietoperzowa	29	WOLSAN 1989 (Testo Zarys Historii Badan)
53.748546	87.097397	arctos	Novokuznetsk	30	Baryshnikov 2007
42.97652	-2.62298	arctos	Pais Vasco	31	MARCISZAK 2015 - Torres Pérez Hidalgo 1988a
40.372936	23.167619	arctos	Petralona	32	KOSTOPOULOS 2006, BARYSHNIKOV 2010
43.453752	2.207518	arctos	Plo-del-May	33	Prat, 1976
48.99992	18.50526	arctos	Pružinská Dúpna	34	MARCISZAK 2015 - Káňa and Roblíčková 2013
43.149923	-3.759689	arctos	Saldarrano Cave	35	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
43.273977	-4.663791	arctos	ST Sima Tresviso, Tresviso	36	MARCISZAK 2015 - Torres Pérez Hidalgo, 1988a
40.881723	-3.453980	arctos	T Cueva del Reguerillo	37	TORRES 1988 (Distribution)
50.95085	11.3808	arctos	Taubach	38	CAPASSO 1987
43.905386	12.571909	arctos	Torrente Conca	39	PALOMBO 2002, Conti 1982, Biondi 1984, Nesci 1991, Ferretti 1997
50.13	19.47	arctos	Tunel Wielki Cave	40	WOLSAN 1989 (Testo Zarys Historii Badan)
37.926402	23.994280	arctos	Vraona	41	KOSTOPOULOS 2006

48.96737	19.58381	arctos	Vyvieranie Cave	42	MARCISZAK 2015 - Sabol 2001
47.95222	16.75689	arctos	Winden	43	MARCISZAK 2015 - Thenius 1956
47.88688	11.53015	arctos priscus	Zoolithen Cave	44	MARCISZAK 2015 - Wagner 1851 - Baryshnikov 2004
45.60272	13.85495	cf. arctos	Caverna degli Orsi	45	BERTO 2013, BERTO 2011
38.05809	14.59791	cf. arctos	Grotta di S. Teodoro	46	FERNANDEZ 2015
42.536997	43.643408	deningeri (kudarensis)	Kudaro 3 (layer 3)	47	BARYSHNIKOV 2002
40.987381	21.972986	ingressus/arctos	Loutra Arideas Cave A	48	KOSTOPOULOS 2006
42.138671	13.120713	sp.	Grotta del Cervo	49	AGOSTINI 2011 Capasso Barbato 1994 - CANDELORO 1998 - Agostini 2004
42.998880	-2.429258	spelaeus	A Cueva de Arrikrutz, Onate	50	TORRES 1984
39.018282	21.555083	spelaeus	Agrapha Cave	51	KOSTOPOULOS 2006
45.61019	10.23925	spelaeus	Cariadeghe	52	ROSSI 2013
44.168726	10.153147	spelaeus	Equi	53	CAPASSO BARBATO 1990
41.779421	13.857623	spelaeus	Fate	54	CAPASSO BARBATO 1990
45.52944	10.33813	spelaeus	Grotta Buco del Frate	55	ROSSI 2013
42.025914	13.260204	spelaeus	Grotta Cola	56	Personal measurements
43.749002	10.552231	spelaeus	Grotta Cucigliana	57	FARINA 2014, FARINA 2011
42.138671	13.120713	spelaeus	Grotta del Cervo	58	AGOSTINI 2011 Capasso Barbato 1994 - CANDELORO 1998 - Agostini 2004
42.777822	10.192824	spelaeus	Grotta del Reale	59	(AZZAROLI 1990, Segnalato da Nesti) (MOCHI 1911)
41.8804	13.02896	spelaeus	Grotta dell'Arco (Bellegra)	60	CAPASSO BARBATO 1981
42.214414	14.171489	spelaeus	Grotta Orsi Volanti	61	MAZZA Personal measurements
39.694603	20.846108	spelaeus	Ioannina Cave	62	KOSTOPOULOS 2006
43.3625	12.74165	spelaeus	Monte Cucco	63	CAPASSO BARBATO 1990
40.372936	23.167619	spelaeus	Petralona Cave	64	BARISHNIKOV 2010
45.757754	13.674825	spelaeus	Pocala	65	CAPASSO BARBATO 1990
41.8584733	15.6814140	arctos	Ingarano	66	PETRONIO 2011
42.214414	14.171489	arctos	Grotta Orsi Volanti	67	MAZZA inedito
42.737471	-7.456055	arctos	Arcoia Cave (1170)	68	GARCIA-VASQUEZ in press
45.84028	8.88244	arctos	Cava cima Paradiso	69	BONA 2010
46.894638	8.285949	arctos	Kerns neotektonik Höhle	70	NIELSEN 2013, Trüssel 2003
50.10	19.48	arctos	Mamutowa Cave	71	WOLSAN 1989 (Testo Zarys Historii Badan)
50.50	20.30	arctos	Raj Cave	72	WOLSAN 1989 (Testo Zarys Historii Badan)
47.95222	16.75689	arctos priscus	Winden	73	Da controllare, MISURE PERSONALI
45.60272	13.85495	cf. arctos	Caverna degli Orsi	74	BERTO 2013, BERTO 2011
47.95222	16.75689	ingressus	Winden	75	Misure prese personalmente
42.025914	13.260204	spelaeus	Grotta Cola	76	Di Canzio 2001
42.214414	14.171489	spelaeus	Grotta Orsi Volanti	77	MAZZA inedito
46.668915	7.453334	spelaeus	Oberwil Schnurenloch	78	NIELSEN 2013, Andris 1964
46.963288	6.802248	spelaeus	Rochefort Cotencher	79	NIELSEN 2013, Le Tensorer, 1998
47.01677	8.49437	spelaeus	Vitznau Steigelfadbalm	80	NIELSEN 2013, Amrein 1913
48.735185	18.413523	spelaeus	Medvedia jaskyna	81	Misure prese personalmente

Table 13: ***Deposits list showed in the Fig. 38***

Latitude	***Longitude***	***Specie***	***Site***	***Catalog***	***References***
43.134419	-1.221370	*arctos*	Oilascoa	1	VALDIOSERA 2007 - Clot et al. 1990
43.137109	-0.966151	*arctos*	Harzabaletako Karbia	2	VALDIOSERA 2007 - Clot & Duranthon 1990
43.533061	-1.054826	*arctos*	Duruthy	3	VALDIOSERA 2007 - Delpech 1983
45.760209	1.284221	*arctos*	Le Rond du Barry	4	VALDIOSERA 2007 - Evin et al. 1994
46.951537	15.713985	*arctos*	Grubgraben	5	VALDIOSERA 2007 - Damblon et al. 1996; Terberger & Street 2002; Musil 2003
48.080497	27.095060	*arctos*	Ciuntu	6	Borziac 1997 - VALDIOSERA 2007
48.323220	15.400106	*arctos*	Willendorf II	7	VALDIOSERA 2007 - Vogel & Zagwijn 1967; Haesaerts et al. 1996
48.602449	17.876382	*arctos*	Moravany Lopata II	8	Musil 2003 - VALDIOSERA 2007
51.594903	-4.174767	*arctos*	Paviland Cave	9	VALDIOSERA 2007 - Aldhouse-Green & Pettitt 1998

Table 14: ***Deposits list showed in the Fig. 39***

Latitude	***Longitude***	***Specie***	***Sito***	***Catalog***	***Referneces***
36,13	-5,35	*arctos*	Devil's Tower	1	Bate 1928
38,8	23,5	*arctos*	Kitsos "1972"	2	Jullien 1973; Chevallier 1973
40,47	-0,1333333333	*arctos*	Cova Fosca/Ares del Maestre	3	Estevez 1988; Vilette 1983 u. 1988; Oller 1988

41,2	-3,333333333	*arctos*	Cueva de Las Figuras/San Andrés de Congosto/Alcorlo	4	Alberdi u.a. 1977
42,75	-1,6666666667	*arctos*	Zatoya	5	Mariezkurrena/Altuna 1989
42.026632	13.268739	*arctos*	Grotta Beatrice Cenci	6	AGOSTINI 2011, VALDIOSERA 2007
43	1,65	*arctos*	Cueva de Abauntz	7	Altuna/Mariezkurrena 1983a
43,1	0,4166666667	*arctos*	Grotte du Bignalats/Arudy	8	Altuna/Marsan 1986
43,17	-2,1666666667	*arctos*	Cueva de Iruaxpe I/Aretxabaleta	9	Mariezkurrena 1987
43,25	-4	*arctos*	Cueva de El Castillo	10	Klein/Cruz-Uribe 1994
43,25	-2,5	*arctos*	Cueva de Santimamiñe	11	Altuna 1972
43,32	-5,666666667	*arctos*	La Riera/Peña Llabres	12	Altuna 1986
43,35	-2,5	*arctos*	Cueva de Lumentxa	13	Aranzadì/de Barandiarán 1935; de Barandiarán 1965; Altuna 1972; Elorza 1990
43,4	-4,8666666667	*arctos*	Cueva de La Riera	14	Straus u. a. 1981
43,53	1,5	*arctos*	Abri Dufaure	15	Altuna u. a. 1991
43.104679	-2.124660	*arctos*	MK Mandabeko Koba, Artitzaga	16	MARCISZAK 2015 - Torres Pérez Hidalgo 1988a
44,25	2,5	*arctos*	Roquemissou	17	Fontan 1991
44,6	22,25	*arctos*	Cuina Turcului (Schicht I)	18	A. Bolomey 1973; E. Kessler 1974
44,65	33,8166666667	*arctos*	Sjuren' I bei Tankovoe	19	A. Ja. Tugarinov 1937, M. A. Voinstvenskij 1967, E. A. Vekilova 1971; G. Baryshnikov & O. Potapova 1992
44.3869	4.41534	*arctos*	Chauvet Cave	20	MARCISZAK 2015 - Phillipe and Fosse 2003
45,22	4,333333333	*arctos*	Grotte de Cottier/Retournac	21	P. Bouchud/J. Bouchud 1953b; Mourer-Chauviré 1976
45,67	0,833333333	*arctos*	Grotte de La Chaise	22	P. Bouchud/J. Bouchud 1953a
45.52306	11.43805	*arctos*	Burwell fen	23	MARCISZAK 2015 - Adam 1880
46	6,3333333333	*arctos*	Vieille Église/La Baume de Thuy	24	Chaix/Olive 1984
46.60272	13.85495	*arctos*	Ballinamore	25	MARCISZAK 2015 - Adam 1880
46.763516	7.117871	*arctos*	Hauterive Champrèveyres	26	NIELSEN 2013, Leesch 2004
47,22	6,6333333333	*arctos*	Abri de Roche-Chêvre/Bretonvillers	27	Baudais u. a. 1993
47,28	7,7333333333	*arctos*	Rislisberg bei Oensingen	28	H. R. Stampfli 1983a, 1983b
47,8	12,3	*arctos*	Frasdorf	29	von den Driesch/Vagedes 1994
47,87	27,2666666667	*arctos*	Duruitor (Schicht 2)	30	A. I. David u. N. A. Ketraru 1978; A. I. David 1980; I. M. Ganja 1972
47.151253	6.890285	*arctos*	La Chaux de Fonds Grotte du Bichon	31	NIELSEN 213, Chauvière 2008
47.375775	7.932033	*arctos*	Winznau Käsloch	32	NIELSEN 2013, Leesch 2012
47.48844	13.2108	*arctos*	Grubenloch	33	MARCISZAK 2015 - Hilzheimer 1936 - Döppes 2014
48,23	28,2833333333	*arctos*	Cosauti I	34	A. I. David 1999
48,42	9,7833333333	*arctos*	Brillenhöhle	35	Boessneck/von den Driesch 1973; Lepiksaar 1973c
48,45	3,35	*arctos*	Noyen-sur-Seine	36	Vigne/Marinval-Vigne 1988; Marinval-Vigne u. a. 1989; Dauphin 1987
48,48	10,1333333333	*arctos*	Fohlenhaushöhlen b. Langenau	37	Boessneck 1978e; Storch 1978b; Lepiksaar 1978a; K. Brunnacker/M. Brunnacker 1978
48,8	27,1833333333	*arctos*	Brynzeny I	38	A. I. David 1980; I. M. Ganja 1972
48.09848	16.1063	*arctos*	Allander Tropfstein Cave	39	MARCISZAK 2015 - Döppes and Pacher, 2013 - Döppes 2014
48.99688	23.10527	*arctos*	Bukovynka Cave	40	MARCISZAK 2015
49.27654	11.47092	*arctos*	Neumark	41	MARCISZAK 2015 - Hilzheimer 1936 - Doppes 2014
50,4	7,4666666667	*arctos*	Kettig	42	M. Baales 1994
50,65	11,1666666667	*arctos*	Allendorf (Fst. Fuchskirche I und II)	43	R. Feustel & R. Musil 1977b
50,65	11,1	*arctos*	Königsee-Garsitz (Fst. Bärenkeller)	44	R. Feustel & R. Musil 1977a
50,67	11,3833333333	*arctos*	Obernitz (Fst. Teufelsbrücke)	45	R. Musil 1980; D. von Knorre 1980; G. Böhme 1980
50,7	11,65	*arctos*	Döbritz (Fst. Kniegrotte)	46	R. Musil 1974
50,85	11,6166666667	*arctos*	Oelknitz (Ot. von Rothenstein)	47	R. Musil 1985
51,28	-2,7666666667	*arctos*	Sun Hole	48	J.W. Jackson 1955, E.K. Tratman 1963, C. Grigson 1978
51.44659	-0.39409	*arctos*	Leitrim	49	MARCISZAK 2015 - Adam 1880
51.48159	-0.44494	*arctos*	Longford	50	MARCISZAK 2015 - Adam 1880
52.92184	20.93213	*arctos*	Wężewo	51	MARCISZAK 2015 - Degerbøl 1933
53,27	-1,2	*arctos*	Mother Grundy's Parlour	52	J.B. Campbell 1969
53,27	-1,2	*arctos*	Robin Hood's Cave	53	J.B. Campbell 1969, P.A. Mellars 1974, R. Burleigh, A. Hewson u. N. Meeks 1976, C. Grigson 1978
53.544994	-9.363992	*arctos*	Clonbourne	54	MARCISZAK 2015 - Adam 1880
54,3	-8,3333333333	*arctos*	Kesh Corran	55	F. McCormick 1999
54.23573	20.12781	*arctos*	Pieniężno	56	MARCISZAK 2015 - Degerbøl 1933
54.5625	21.80236	*arctos*	Chernyakhovsk	57	MARCISZAK 2015 - Degerbøl 1933

54.84353	10.69205	*arctos*	Kaedeby	58	MARCISZAK 2015 - Degerbøl 1933
55,5	11,2166666667	*arctos*	Mullerup	59	M. Degerbøl 1933, M. Degerbøl u. H. Krog 1959, G. Clark 1975
55,72	11,4166666667	*arctos*	Faurbo Knold	60	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55.36991	10.73055	*arctos*	Skalkendrup	61	MARCISZAK 2015 - Degerbøl 1933
56.67018	9.01273	*arctos*	Jebjerg	62	MARCISZAK 2015 - Degerbøl 1933
56.91712	8.88232	*arctos*	Hundsø	63	MARCISZAK 2015 - Degerbøl 1933
57,42	9,7666666667	*arctos*	Nørre Lyngby	64	P. Bondesen u. H. Lykke-Andersen 1978, K. Aaris-Sørensen 1995, K. Aaris-Sørensen u. T. Nord Andreasen 1997
61,55	60,05	*arctos*	Severnaya cave	65	KOSINTEV 2015
38,48	22,5	*arctos*	Delphi, Corycien-Höhle	66	Tranier 1973
42.59067	0.53124	*arctos*	Coume-Nere Cave	67	MARCISZAK 2015 - Chaix and Valton 2007
42.936902	-2.897548	*arctos*	GR Sima de las Grajas, Sierra de Guinijo	68	TORRES 1984
44,52	33,8333333333	*arctos*	Šan-Koba (Schicht 7-4) bei Peredovoe	69	A. Ja. Tugarinov 1937; V. I. Gromov 1948; M. A. Voinstvenskij 1967; E. A. Vekilova 1971
44,6	22,25	*arctos*	Cuina Turcului (Schicht II)	70	A. Bolomey 1973; E. Kessler 1974
44,65	33,8166666667	*arctos*	Sjuren' II bei Tankovoe	71	M. A. Voinstvenskij 1967; E. A. Vekilova 1971
46,92	7,5833333333	*arctos*	Birsmatten-Basisgrotte bei Nenzlingen	72	E. Schmid 1963a
47,22	7,5333333333	*arctos*	Günzberg (Fst. Balm, "Unter der Fluh")	73	H. G. Stehlin 1941
47,5	7,8333333333	*arctos*	Birseck (Fst. Schloßfelsen)	74	F. Sarasin 1918
47,95	28,1166666667	*arctos*	Frumušika I	75	A. I. David 1982, 1997
48,2	8,95	*arctos*	Jägerhaushöhle b. Fridingen	76	Boessneck 1978b; M. Brunnacker 1978; K. Brunnacker/M. Brunnacker 1978
48,8	9,2166666667	*arctos*	Falkensteinhöhle b.Thiergarten	77	Boessneck 1978c; Reichenbach-Klinke 1978; Lepiksaar 1978b; K. Brunnacker/M. Brunnacker 1978
52,42	-8,7	*arctos*	Lough Gur	78	F. McCormick 1999
52,73	12,5833333333	*arctos*	Friesack	79	L. Teichert 1993a, 1993b, 1994, 1999
52,97	-7,9666666667	*arctos*	Dunore Bog	80	F. McCormick 1999
53,27	-1,2	*arctos*	Robin Hood's Cave	81	J.B. Campbell 1969, P.A. Mellars 1974, R. Burleigh, A. Hewson u. N. Meeks 1976, C. Grigson 1978
53,73	-7,7833333333	*arctos*	Derrykeel Bog	82	F. McCormick 1999
53,78	11,5166666667	*arctos*	Hohen Viecheln	83	O. Gehl 1961; E. Soergel 1961; H. H. Wundsch 1961
54,1	12,7666666667	*arctos*	Tribsees	84	U. Lehmkuhl 1988c
55,47	13,25	*arctos*	Ugglarp	85	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55,78	52,9166666667	*arctos*	Deukovskaja stojanka II	86	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,5	16,5	*arctos*	Alby	87	E.S. Königsson, J. Lepiksaar u. L.-K. Königsson 1971
57,22	22,5	*arctos*	Suljagals	88	I. A. Loze 1988
58,43	24,6833333333	*arctos*	Pulli	89	L. Jaanits u. a. 1982; K. Jaanits 1991; L. Lõugas 1997
59,48	26,55	*arctos*	Kunda (Fst. Lammasmägi)	90	R. Indreko 1948; K. L. Paaver 1965; L. Lõugas 1996b, 1997; L. Lõugas u. a. 1996

Table 15: ***Deposits list showed in the Fig. 40***

Latitude	***Longitude***	***Site***	***Catalog***	***References***
38,48	22,5	Delphi, Corycien-Höhle	1	Tranier 1973
39,22	-3,9	Verdelpino	2	Morales 1977
40,18	22	Servia	3	Watson 1979
41,17	24,5833333333	Sitagroi	4	Bökönyi 1986
41,5	23,4833333333	Kovačevo	5	L. Ninov 1990a
41,72	21,55	Anza (Anzabegovo) (Periode III)	6	S. Bökönyi 1976b
41,95	13,55	Grotta Continenza/Trasacco	7	Wilkens 1989/90a
41,97	12,6666666667	Arene Candide	8	Rowley-Conwy 1997
42,5	25,9333333333	Karanovo bei Nova Zagora	9	S. Bökönyi 1992b; S. Bökönyi u. L. Bartosiewicz 1997
42,65	12,65	Grotta Sant'Angelo	10	Wilkens 1996b
42,7	23,3666666667	Sofia (Fst. Slatina, Bauhorizont I)	11	S. Bökönyi 1992c
42,95	13,8166666667	Monte Tinello/Acquaviva Picena	12	Wilkens 1989b
42.639952	11.983789	Gran Carro	13	Personal measurements
43,28	-2,1666666667	Herriko Barra/Zarautz	14	Elorza/Sanchez Marco 1993; Mariezkurrena/Altuna 1995
43,3	13,3166666667	Sta. Maria in Selva/Tréia	15	Wilkens 1987c
43,5	13,25	Coppetella/Iesi	16	Wilkens 1988b
43,62	13,5166666667	Piano Donatelli	17	Wilkens o. J. a

43,78	3,4166666667	Grotte IV, St. Pierre de la Fage	18	Bökönyi/Kretzoi 1983
44,3	20,8333333333	Divostin I	19	S. Bökönyi 1988b
44,5	1,5	Roucadour	20	Ducos 1957
44,52	22,7166666667	Ostrovul Corbului	21	S. Haimovici 1987a
44,55	33,6666666667	Murzak-Koba bei Čorgun'	22	V. D. Lebedev 1952; I. M. Gromov 1953; M. A. Voinstvenskij 1967; E. A. Vekilova 1971
44,6	22,166666667	Lepenski Vir (Phase II)	23	S. Bökönyi 1969b
44,65	22,3	Icoana	24	A. Bolomey 1973; E. Kessler 1985
44,88	20,6666666667	Starčevo bei Pančevo	25	A. T. Clason 1982
45,13	20,7333333333	Padina	26	A. T. Clason 1982
45,65	13,7666666667	Caverna dei Ciclami	27	Riedel 1968
45,95	1,833333333	Les Matignons/Juillac-le-Coq	28	Poulain 1956; Poulain-Josien 1966e
46	6,3333333333	Vieille Église/La Baume de Thuy	29	Chaix/Olive 1984
46,17	13	Cladrecis	30	Riedel 1983/84a
46,83	5,8333333333	Chalain/Museum Lons-le-Saunier	31	Chenevoy/Chaix 1985
46,83	24	Gura Baciului	32	G. El Susi & D. Rusu 1995
46,87	6,8333333333	Col des Roches, Gem. Le Locle bei Chaillexon	33	L. Reverdin u. M. P. Vouga 1930
46,92	7,5833333333	Birsmatten-Basisgrotte bei Nenzlingen	34	E. Schmid 1963a
46,92	5,7833333333	Grotte des Planches-près-Arbois	35	Chaix 1985
46.002798	11.107932	Riparo Pradestel	36	BOSCATO 1980
46.016828	11.103121	Riparo Romagnano III	37	BOSCATO 1980
46.152214	11.087438	Vatte di Zambana	38	BOSCATO 1980
47,17	7,9833333333	Schötz (Fst. 7) im Wauwilermoos	39	H. R. Stampfli 1979b
47,22	6,6333333333	Abri de Roche-Chêvre/Bretonvillers	40	Baudais u. a. 1993
47,4	7,4333333333	Liesbergmühle (Fst. VI)	41	H. R. Stampfli 1979a
47,57	27,2333333333	Pogoreşti	42	O. Necrasov 1964
48,2	7,3166666667	Hattstatt	43	Poulain 1980c
48.735185	18.413523	Medvedia jaskyna	44	Misure prese personalmente
49,38	3,7666666667	Cuiry-lès-Chaudardes, "les Fontinettes"	45	Hachem 1994; 1995a und b
51,87	-2,65	King Arthur's Cave	46	N. Noe-Nygaard 1983
54,27	-0,4166666667	Star Carr	47	F.C. Fraser u. J.E. King 1954b, M. Degerbøl 1961, N. Noe-Nygaard 1983, C.J.O. Harrison 1987, A.J. Legge u. P.A. Rowley-Conwy 1988
55,1	11,8833333333	Sværdborg (Fst. I)	48	K. Aaris Sørensen 1976
55,12	11,8833333333	Lundby (Fst. II)	49	K. Rosenlund 1980
55,15	11,8333333333	Lundby Mose	50	M. Degerbøl 1933, K. Aaris-Sørensen 1977
55,28	11,8166666667	Holmegaard	51	H. Winge 1924, M. Degerbøl 1962, G. Clark 1975, K. Rosenlund 1976, C. Willms 1987, E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55,35	13,4333333333	Skateholm I	52	L. Jonsson 1988
55,38	10,7333333333	Skalkendrup Mose	53	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55,4	10,3833333333	Odense	54	N. Noe-Nygaard 1983
55,42	11,4	Maglemose	55	G.F.L. Sarauw 1903, Winge 1903, H. Winge 1904a, H. Winge 1905, K. Rosenlund 1976
55,5	11,5	Verup	56	M. Degerbøl u. H. Krog 1951, K. Andersen 1960
55,72	11,1	Dyrhøjgårds Mose	57	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55,78	52,9166666667	Deukovskaja stojanka II	58	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,92	13,55	Ageröd (Fst. I:B)	59	J. Lepiksaar 1978c
56,85	26,8833333333	Zvidze	60	J. Sloka 1975, 1986a; A. Strazdinja 1986; I. A. Loze 1988
58,33	13,5833333333	Hornborgasjön	61	A. Arnesson-Westerdahl 1983, A. Arnesson-Westerdahl 1983/84, A. Arnesson-Westerdahl 1985
59,37	28,2166666667	Narva I (Schicht 3 u. 2)	62	K. L. Paaver 1965; E. A. Cepkin 1984a; L. Lõugas 1996c, 1997
60,3	24,95	Vantaa	63	A. Forstén u. L. Blomqvist 1974
60,47	25,6333333333	Askola	64	A. Forstén 1972, H. Matiskainen 1989

Table 16: ***Deposits list showed in the Fig. 41***

Latitude	*Longitude*	*Site*	*Catalog*
54,33	10,1333333333	Ellerbek (Ot. von Kiel)	C. Kurck 1917, H. Lüttschwager 1954
56,17	10,1833333333	Braband	C. Willms 1987, E. Iregren, B. Ringberg u. A.-M. Robertsson 1990, N. Benecke 1993

56,2	10,25	Flynderhage	K. Aaris-Sørensen 1980a
56,47	10,5	Dyrholmen	M. Dergerbøl 1942
50,95	10,7166666667	Gotha (Fst. Siebleben)	H.-J. Barthel 1987
48,5	10,8666666667	Pestenacker-Nord	Vagedes 1998
48,5	10,9	Pestenacker	Vagedes 1996; Vagedes 1998
46,13	11,1166666667	Grotta d'Ernesto	Riedel 1994b
52,15	11,2166666667	Eilsleben	H.-J. Döhle 1994
50,98	11,333333333	Erfurt (Fst. Nordhäuser Str.)	H.-J. Barthel 1983
51,3	11,3333333333	Großobringen	H.-J. Barthel 1985a
51,7	11,4666666667	Quenstedt (Fst. Schalkenburg)	H.-H. Müller 1985a
46,53	11,5	Fingerhof/Völser Aicha	Riedel 1985b; 1986b
55,75	11,55	Gislinge Lammefjord	K. Aaris-Sørensen 1980a
52,72	11,65	Schönstedt	M. Teichert 1972
48,92	11,9	Hienheim	Clason 1977c
42.639952	11.983789	Gran Carro	Personal measurements
49,2	12,1166666667	Regensburg, Bajuwarenkaserne	Brink 1990
48,55	12,15	Ergolding, Fischergasse	Neumann 1990
48,93	12,2666666667	Tiefbrunn	Boessneck/Schäffer 1985
55,87	12,5833333333	Henriksholm-Bøgebakken	K. Aaris-Sørensen 1980a, K. Aaris-Sørensen 1980b, E. Iregren, B. Ringberg u. A.-M. Robertsson 1990, K. Aaris-Sørensen u. T. Nord Andreasen 1992/93
41,97	12,6666666667	Arene Candide	Rowley-Conwy 1997
53,52	12,6833333333	Waren (Fst. Stinthorst)	O. Gehl 1976
53,7	12,6833333333	Basedow	O. Gehl 1974, 1976
52,48	12,8	Zachow (Fst. Gallberg)	L. Teichert 1990a
48,83	12,9666666667	Künzing-Unternberg	Ott-Luy 1988
55,6	13	Segebro	J. Lepiksaar 1982
47,42	13,2166666667	Bischofshofen (Fst. Götschenberg)	J. Peters 1992
47,87	13,35	Mondsee (Fst. See), Gem. Innerschwandt	E. Pucher & K. Engl 1997
51,5	13,75	Dresden (Ot. Cotta)	N. Benecke 1999
55,42	13,8333333333	Bredasten	L. Jonsson 1985/86
50,15	14,2166666667	Makotřasy	A. T. Clason 1985
53,38	14,2666666667	Glasow (Fpl. 5)	O. Gehl 1980
50,17	14,4	Roztoky	L. Peške 1989, 1991b
53,42	14,5833333333	Szczecin-Ustowo (Fst. 1)	M. Kubasiewicz 1958b; Z. Chełkowski 1960a
47.59479	14.01076	Brunnenschacht	MARCISZAK 2015 - Döppes and Pacher, 2013 - Döppes 2014
47.87012	15.15169	Burian Cave	MARCISZAK 2015 - Döppes and Pacher, 2013
51,67	16,1	Głogów-Nosocice	M. Sobociński 1961a; A. Kulczycka-Leciejewiczowa 1993
47,72	16,1833333333	Pitten	K. Bauer & P. Wolff 1985
54,38	16,3166666667	Dąbki (Fst. 9), Gem. Darłowo	M. Sobociński 1984b, 1986b; M. Iwaszkiewicz 1985, 1989; J. Ilkiewicz 1989
52,52	16,7	Mrowino	Z. Schramm 1987a
47.95222	16.75689	Winden	Da controllare, MISURE PERSONALI
52,22	17,4	Szlachcin bei Środa Wlkp.	K. Świeżyński 1966b
48,7	18,2	Nitriansky Hrádok (Ot. von Šurany, Fst. Zámeček)	C. Ambros 1986c, unpubliziert
48,1	18,6333333333	Šarovce	C. Ambros 1958c, unpubliziert
48,32	18,833333333	Nitra (Fst. Mlynárce)	C. Ambros 1961, 1986c, unpubliziert
52,6	18,9	Brześć Kujawski (Fst. 3 und 4)	P. Bogucki 1981, 1982; D. Makowiecki (unpubliziert)
52,13	18,9666666667	Pikutkowo (Fst. 6)	L. Radomski & K. Świeżyński 1967
47,65	19,5	Aszód (Fst. Papi Földek)	S. Bökönyi 1974a
48,12	19,8166666667	Salgótarján (Fst. Pécskő)	S. Bökönyi 1968a
48,47	2,4333333333	Videlles	Poulain-Josien 1958f
43,7	2,4833333333	Abri Jean-Cros/Lacamp/Labastide-en-Val	Andre 1979; Vaquer u. a. 1979; Heintz/Ginsburg 1979; Poulain 1979a; Desse 1979; Jourdan 1979; Cheylan 1979; Guilaine 1979
49,38	2,5	Catenoy, "le camp de César"	Méniel 1984a
49,5	2,5	Mont d'Huette/Jonquières	Poulain 1984d
47,5	20,5	Kisköre (Fst. Gát)	S. Bökönyi 1974a; I. Vörös 1986a
44,3	20,8333333333	Divostin II	S. Bökönyi 1988b
47,87	21,1166666667	Polgár (Fst. Csőszhalom)	S. Bökönyi 1974a; S. Bökönyi u. D. Jánossy 1965; Ch. A. Schwartz 1998
45,63	21,1333333333	Parţa (Sch. 4)	G. El Susi 1995a
49,7	21,1333333333	Šarišské Michal'any (Fst. Fedelemka)	C. Ambros unpubliziert
45,67	21,25	Parţa, Gem. Şag (Horizont 6)	A. Bolomey 1988

50,88	21,5166666667	Ćmielów	K. Krysiak 1951, 1952a
50,7	21,8	Kamień Łukawski bei Sandomierz	K. Krysiak & A. Lasota 1971
48,3	21,833333333	Tiszalúc (Fst. Sarkad)	I. Vörös 1987a
50,8	21,85	Zawichost-Podgórze	K. Krysiak 1967a; K. Krysiak &. A. Lasota 1973a
44,65	21,9	Liubcova	O. Necrasov u. a. 1977
44,37	22,4833333333	Mihajlovac-Knjepište	S. Bökönyi 1992a
42,8	22,8	Goljamata Peščera bei Ilija	V. Vasilev u. V. Nikolov 1980
39,37	22,95	Dimini	Halstead 1992; 1993
40,5	23	Dikili Tash	Jullien 1992; Karali-Yannacopoulou 1992
42,3	23,2666666667	Kremenik bei Sapareva Banja	L. Ninov 1986
46,98	23,8	Iclod	G. El Susi 1994a
50,8	23,95	Gródek Nadbużny (Fst. 1C) bei Hrubieszowo	K. Krysiak 1956c
38,5	24	Skoteini-Höhle, Tharrounia	Kotjabopoulou/Trantalidou 1993
41,17	24,5833333333	Sitagroi	Bökönyi 1986
61,33	24,6333333333	Luopioinen (Fst. Hietaniemi)	J.-P. Taavitsainen 1980
42,62	25,4	Kazanlăk	R. Dennell 1978
43,13	25,6	Samovodene	L. Ninov 1993
44,3	25,8	Izvoarele	O. Necrasov & G. Gheorghiu 1970
38,38	26,1166666667	Emporio	Clutton-Brock 1982
55,25	26,1166666667	Žemaitiškės 3B	L. Daugnora u. A. Girininkas 1996
47,15	26,4166666667	Tîrpeşti	O. Necrasov & M. Bulai-Ştirbu 1965; O. Necrasov & M. Ştirbu 1979, 1981; O. Necrasov u. a. 1967
44,13	26,4666666667	Căscioarele	A. Bolomey 1968a; E. Kessler 1985
43,2	26,5833333333	Poljanica	S. Bökönyi 1978a, 1988a
44,8	26,6333333333	Gumelniţa	O. Necrasov & S. Haimovici 1966
43,18	26,65	Ovčarovo (Fst. Gorata)	G. Nobis 1986b
43,17	26,6666666667	Ovčarovo (Fst. Platoto)	V. Vasilev 1981a, 1981b, 1983, 1985
46,93	26,6666666667	Ghelăieşti, Gem. Bîrgăoani	S. Haimovici & C. Stan 1985
48,52	26,6666666667	Bernovo Luka	V. I. Bibikova 1963; L. D. Voronenkova 1964; M. A. Voinstvenskij 1967
48,5	26,75	Lenkovcy	V. I. Bibikova 1963; M. A. Voinstvenskij 1967
46,82	26,8666666667	Traian (Fst. Dealul Viei)	O. Necrasov & S. Haimovici 1962b, 1970; O. Necrasov & M. Bulai-Ştirbu 1965
56,85	26,8833333333	Zvidze	J. Sloka 1975, 1986a; A. Strazdinja 1986; I. A. Loze 1988
47,28	26,9333333333	Cucuteni	S. Haimovici 1969b
48,8	27,1833333333	Brynzeny III (Fst. Cyganka)	G. D. Čemyrtan 1978; A. I. David 1982
47,85	27,2166666667	Kostešty IV	A. I. David 1982
48,53	27,333333333	Polivanov Jar bei Komarovo	V. I. Bibikova 1963; M. A. Voinstvenskij 1967
43	27,4166666667	Goljamo Delčevo	St. Ivanov & V. Vasilev 1975
47,8	27,6166666667	Jablona I	A. I. David 1982
48,43	27,6666666667	Merešovka-Četėcue	A. I. David 1986
42,25	27,7666666667	Kiten (Fst. Ourdoviza)	Z. Boev & G. Ribarov 1990; G. Ribarov 1991a
49,57	27,9	Sandraki	I. G. Pidopličko 1956; A. M. Voinstvenskij 1967
59,43	28,1166666667	Riigiküla I (Ot. v. Narva)	K. L. Paaver 1965; N. N. Gurina 1967; E. A. Cepkin 1968
47,83	28,1333333333	Putinešty I bei Lutinešty	G. D. Čemyrtan u. A. I. David 1975, A. I. David 1982
59,37	28,2166666667	Narva I (Schicht 1)	K. L. Paaver 1965; E. A. Cepkin 1984a
47,88	28,3	Florešty I	A. I. David 1982
48,15	28,3	Soroki I (Schicht 1a)	A. I. David 1969; A. I. David u. V. I. Markevič 1970; I. M. Ganja 1972; V. I. Markevič u. E. A. Cepkin 1969; E. A. Cepkin 1970a; V. I. Markevič 1974
43,67	28,3833333333	Durankulak (Horizont V)	H. Manhart 1998c
48,45	28,4166666667	Stena	V. I. Bibikova 1963
50,1	28,5333333333	Trojanov	V. I. Bibikova 1963; M. A. Voinstvenskij 1967
46,93	28,65	Novye Rusešty I, mittlere Schicht	A. I. David u. V. I. Markevič 1967, I. M. Ganja 1972
60,57	28,833333333	Liljendal (Fst. Kvarnbacken)	J.-P. Taavitsainen 1980
47,85	29	Solončeny I	V. I. Bibikova 1963, V. I. Calkin 1970, A. I. David 1982
50,38	29,1666666667	Gorodsk	I. G. Pidopličko 1956; M. A. Voinstvenskij 1967
48,57	29,35	Mit'kov ostrov bei Skibincy	V. N. Danilenko 1969
49,87	29,45	Pavoloč'	V. I. Bibikova 1963
55,5	29,8333333333	Osovec I	V. I. Bibikova 1972
48,17	30,1833333333	Sabatinovka I	I. G. Pidopličko 1938, 1956
50,42	30,5	Podgorcy I	V. I. Bibikova 1963
55,52	30,7166666667	Krivina	V. I. Bibikova 1972
50,17	30,75	Luka-Vrubleveckaja	V. I. Bibikova 1953

49,13	32,4833333333	Moljuchov Bugor bei Novoselicy	V. I. Bibikova 1963
51,57	33,4	Pogorelovka-Vyrčišče (Horizont 2)	O. P. Žuravl'ov & N. S. Kotova 1996
48,85	33,6666666667	Berezovs'koe	V. I. Calkin 1970; O. P. Žuravl'ov 1997b
48,92	33,7833333333	Dereivka	V. I. Bibikova 1963
50,92	34,8166666667	Lisogubovka	O. P. Žuravl'ov & N. S. Kotova 1996
49,3	38,9	Podgorovka bei Starobel'ska	Ju. G. Gurin 1992
51,85	39,2166666667	Čerkasskaja	I. E. Kuz'mina & A. K. Kasparov 1987
37,17	-4,15	Cueva del Coquino/Loja	Ruiz Bustos 1992
44,23	4,3333333333	Grotte de l'Aigle/Méjannes-le-Clap	Poulain 1979b
52,57	5,6333333333	Swifterbant	D.C. Brinkhuizen 1976, A.T. Clason u. D.C. Brinkhuizen 1978b, D.C. Brinkhuizen 1979, J.T. Zeiler 1991b, J.T. Zeiler u. A.T. Clason 1993, J.T. Zeiler 1995a
58,97	5,7333333333	Viste	H. Winge 1908, M. Degerbøl 1951
46,67	5,7833333333	Chalain 3	Arbogast 1997; Eisenmann/Arbogast 1997
53,2	51,45	Vilovatoe, Vilovatovskaja stojanka	A. G. Petrenko 1984
54,47	53,45	Mullino II	A. G. Petrenko 1984
52	56	Ivanovskoe bei Ivanovki	A. G. Petrenko 1995
53,28	-6,1	Dalkey (Fst. II u. V)	T. Hatting 1968, G.F. Mitchell 1968, P.C. Woodman 1978
46,78	6,65	Yverdon (Fst. Garage Martin)	L. Chaix 1976c
46,8	6,75	Yvonand (Fst. IV)	J. Clutton-Brock 1990
46,87	6,8333333333	Col des Roches, Gem. Le Locle bei Chaillexon	L. Reverdin u. M. P. Vouga 1930
46,97	6,8666666667	Auvernier (Fst. La Saunerie, Sch. III)	Th. Josien 1955a
47	6,9166666667	Saint-Aubin (Fst. Port Conty, Schicht III)	L. Reverdin 1921, 1928, 1930
46,27	6,95	Collombey-Barmaz I	L. Chaix 1976a
47,1	7,15	Twann	C. Becker & F. Johansson 1981
46,25	7,4166666667	Saint-Léonard (Fst. "Sur le Grand Pré")	L. Chaix 1976a
46,92	7,5833333333	Lüscherz	Th. Josien 1956
47,15	7,6666666667	Seeberg (Fst. Burgäschisee-Süd)	J. Boessneck u. a. 1963
37,37	-7,6666666667	Castro do Zambujal	von den Driesch/Boessneck 1976
47,23	8,2666666667	Hitzkirch (Fst. Seematte-Gelfingen, oben)	K. Hescheler & J. Rüeger 1940
38,33	-8,5	Rotura	Lentacker 1990/91
47,4	8,55	Zürich (Fst. AKAD/Pressehaus, Sch. J)	H. Hüster-Plogmann & J. Schibler 1997
47,28	8,65	Feldmeilen-Vorderfeld (Gem. Meilen)	F. Eibl 1974; W. Förster 1974
47,23	8,7166666667	Stäfa (Fst. Uerikon, Zürichsee)	J. Rüeger 1944
47,62	8,7166666667	Ossingen	E. Kuhn 1932
47,8	8,833333333	Egolzwil (Fst. 2, Schicht II)	K. Hescheler & J. Rüeger 1939, 1942
47,67	8,9833333333	Steckborn-Schanz	D. Markert 1985a
46,83	9,4	Tamins (Fst. "Crestis")	M. Primas 1979, 1985
46,72	9,4333333333	Cazis (Fst. Petrushügel)	M. Primas 1985
47,22	9,5333333333	Eschen (Fst. Borscht)	E. Kuhn 1937; H. Hartmann-Frick 1965
47,13	9,5666666667	Alt-Schellenberg, Gem. Schellenberg	R. Mittelhammer 1982
54,7	9,6333333333	Bondebrück	H. Lüttschwager 1967
48,8	9,65	Ödenahlen	Kokabi 1995
56,3	9,95	Ringkloster	I. Bødker Enghoff 1994-95, P. Rowley-Conwy 1994-95
		Rebensteiner Mauer	S. Bökönyi 1974a
		Brückler Mauer	S. Bökönyi 1974a
55,5	29,83333333	Osovec II	V. V. Š?eglova 1975
50,45	3,983333333	Spiennes	A.T. Clason 1971b
44,5	17,41666667	Pod bei Bugojno	M. Sachenbacher-Palavestra 1986
44,5	17,41666667	Pod bei Bugojno	M. Sachenbacher-Palavestra 1986
42,47	26,33333333	Ezero	St. Ivanov & V. Vasilev 1979
43,67	28,38333333	Durankulak (Holocene, Late Bronze Age)	H. Manhart 1998c
50,38	13,98333333	Levousy, Gem. K?esín	L. Peške 1975
		Homolka	G. M. Allen 1968; C. Ambros 1968; P. Bogucki 1979
55,23	10,1	Voldtofte	G. Nyegaard 1993
56,77	10,3	Bundsø	M. Degerbøl 1939
54,87	10,73333333	Lindø	K. Rosenlund 1976, G. Nyegaard 1985
55,62	11,6	Øgaarde	M. Deberbøl 1943, M. Degerbøl u. H. Krog 1951
56,37	10,61666667	Kolind	M. Degerbøl 1942, K. Rosenlund 1976
56,38	10,81666667	Ørum Aa	S. Müller 1888a, H. Winge 1903, H. Winge 1904a
56,2	10,43333333	Holme Skanse	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
56,45	10,7	Ørum Å	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
55,45	10,53333333	Dræby Mark	E. Iregren, B. Ringberg u. A.-M. Robertsson 1990
56,15	9,166666667	Ikast	N. Noe-Nygaard 1983

56,38	10,81666667	Kainsmore	N. Noe-Nygaard 1983
56,42	10,75	Kainsbakke (Fst. A47)	J. Richter 1986a, 1986b, 1987, 1991
54,93	10,83333333	Spodsbjerg	G. Nyegaard 1985
57,93	27,16666667	Kääpa	K. L. Paaver 1965; K. Jaanits 1991
58,5	27,66666667	Villa	K. L. Paaver 1965
58,37	25,96666667	Valma	K. L. Paaver 1965
58,4	27,23333333	Akali (frühe Schicht)	J. Lepiksaar 1938, 1984; K. L. Paaver 1965; L. Lõugas 1997
58,45	23,33333333	Ridala	K. L. Paaver 1965; E. A. Cepkin 1984a; K. Jaanits 1991; L. Lõugas 1997
57,73	26,91666667	Tamula	K. L. Paaver 1965; K. Jaanits 1991
58,35	22	Loona	K. L. Paaver 1965; E. A. Cepkin 1984a; K. Jaanits 1991; L. Lõugas 1993, 1997; L. Lõugas u. a. 1996
58,23	22,23333333	Naakamäe	K. L. Paaver 1965; E. A. Cepkin 1984a; K. Jaanits 1991; L. Lõugas 1993, 1997
44,2	20,9	Ljuljaci bei Kragujevac	
43,32	20,91666667	Livade bei Mala Vrbica	H. J. Greenfield 1986
46	6,333333333	Vieille Église/La Baume de Thuy	Chaix/Olive 1984
		Beaussement	Poulain-Josien 1965c
46,92	5,783333333	Grotte des Planches-près-Arbois	Chaix 1985
53,87	9,95	Nützen (Fst. Grab II / Hügel o 13)	E. Schmid 1981b
47,63	13	Karlstein	von den Driesch 1979
51,35	11,1	Bad Frankenhausen (Fst. Kyffhäuser)	M. Teichert & J. Lepiksaar 1977; M. Teichert 1981, 1978, 1985a, 1985b, 1987; G. Böhme 1987
48,92	12,35	Riekofen	Busch 1985
54,27	10,75	Wangels (Fst. LA 505)	D. Heinrich im Druck b
48,32	11,68333333	Mintraching	Boessneck/Schäffer 1985
48,92	11,9	Hienheim	Clason 1977c
52,47	8,366666667	Hüde I	J. Boessneck 1978g, H. Hüster 1983, K.-D. Hübner, R. Saur u. H. Reichstein 1988
54,78	9,766666667	Neukirchen-Bostholm	H. Reichstein 1985
51,8	9,883333333	Odagsen (Fst. I)	C. Schulze-Rehm 1993
51,72	8,75	Wewelsburg (Fst. I)	K. Steppan 1992
49,2	12,11666667	Regensburg-Pürkelgut	Boessneck 1958
54,5	10,48333333	Heidmoor / Berlin	J. Lüttschwager 1953, B. Mueller 1983, J. Ewersen 1992
50,93	11,58333333	Jena	A. T. Clason 1969
47,83	11,16666667	Polling	Blome 1968
49,28	11,48333333	Griesstetten	König 1993
48,57	10,33333333	Altheim	Boessneck 1956a
48,25	11,93333333	Altenerding, Fuchsberg	Boessneck 1956a
48,5	10,9	Pestenacker	J. Boessneck 1956a
47,83	11,16666667	Polling	J. Boessneck 1956a
53,43	11,85	Parchim (Fst. Löddigsee)	U. Lehmkuhl 1989; N. Benecke (im Druck)
53,9	11,46666667	Wismar (Fst. "Wolfsburger Moor")	R. Beltz 1910
47,83	11,16666667	Polling	Boessneck 1956a
58,15	-4,98333333	Inchnadamph	N. Noe-Nygaard 1983
54,1	-6,61666667	Annaghmare	J.E. King 1965, P.A. Mellars 1974
52,68	-0,4	Barholm	M. Harman 1993a
51,17	-1,78333333	Ratfyn	J.W. Jackson 1935b
53,2	-1,85	Fox Hole Cave	D. Bramwell 1971
40,5	23	Dikili Tash	Jullien 1992; Karali-Yannacopoulou 1992
39,37	22,95	Magula Pevkakia	Jordan 1975; Lepiksaar 1975c; Hinz 1979; Amberger 1979
39,37	22,95	Magula Pevkakia	Amberger 1979; Hinz 1979
39,37	22,95	Magula Pevkakia	Jordan 1975; Lepiksaar 1975c; Hinz 1979; Amberger 1979
39,37	22,95	Magula Pevkakia	Jordan 1975; Lepiksaar 1975c
36,92	21,7	Pylos	Nobis 1993b
37,73	23,98333333	Samos, Heraion	Boessneck/von den Driesch 1981; 1983; 1988
40,63	22,96666667	Kastanas	Becker 1986
37,57	22,8	Tiryns	von den Driesch/Boessneck 1990
38,65	23	Kalapodi	Stanzel 1991
46,83	18,28333333	Mez?komárom (Fst. Alsóhegy)	S. Bökönyi 1974a; S. Bökönyi u. D. Jánossy 1965
47,1	20,15	Tószeg (Fst. Laposhalom)	S. Bökönyi 1952a, 1959a; S. Bökönyi u. D. Jánossy 1965
47,75	20,41666667	Füzesabony	S. Bökönyi 1959a; S. Bökönyi u. D. Jánossy 1965
48,3	21,83333333	Tiszalúc (Fst. Dankadomb)	S. Bökönyi 1960b, 1974a; S. Bökönyi u. D. Jánossy 1965

46,83	18,28333333	Mez?komárom (Fst. Alsóhegy)	S. Bökönyi 1978a
46,77	21,13333333	Békés (Fst. Városerd?)	S. Bökönyi 1974a; S. Bökönyi u. D. Jánossy 1965
46,5	18,26666667	Nagyárpád (Fst. Vár)	S. Bökönyi 1978a
47,5	19,83333333	Budapest (Fst. Remete barlang)	S. Bökönyi 1959a
47,5	19,83333333	Budapest (Fst. Csepel-Háros)	S. Bökönyi 1974a
47,5	19,83333333	Budapest (Fst. Csepel-Hollandi utca)	S. Bökönyi 1978a
46,77	21,13333333	Békés (Fst. Várdomb)	J. Banner & I. Bóna 1974
47,18	21,45	Bakonszeg (Fst. Kádárdomb)	S. Bökönyi 1988a
54,3	-8,33333333	Keshcorran / Carrowkeel	R.A.S. Macalister, E.C.R. Armstrong u. R.L. Praeger 1912
53,62	-6,78333333	Newgrange	P.A. Mellars 1974, L.H. van Wijngaarden-Bakker 1974, L.H. van Wijngaarden-Bakker 1986b
45,65	13,76666667	Caverna Cotariova	Riedel 1976b
46,78	11,91666667	Sonnenburg	Riedel 1984c; 1985b
46	10,83333333	Fiavè	Jarman 1975
45,37	10,56666667	Barche Solferino	Riedel 1952; 1955; 1976d; 1977
45,88	10,75	Ledro	Riedel 1976f; 1977
45,33	10,65	Isolone della Prevaldesca	Riedel 1975b; 1977
		Balm' Chanto	Riedel 1987a
46,13	11,11666667	Riparo del Santuario	Riedel/Tecchiati 1992; Riedel/Tecchiati im Druck.
44,97	11,11666667	Poggio Rusco	Catalani 1984a
46,72	11,66666667	Albanbühel/Brixen	Riedel/Rizzi 1995
42,8	13,55	Paludi di Celano	De Grossi Mazzorin 1989b
45,83	12	Cornuda	Riedel 1988
41,97	12,66666667	Grotta Cardini	Tagliacozzo u. a. 1989
40,97	14,6	Mulino Sant'Antonio	Albarella 1987/88
45,5	11,83333333	Val Liona	Riedel 1948a
45,5	11,83333333	Fimon	Riedel 1948a
45,52	11,93333333	Colombare di Negrar	Riedel 1976e; 1977
56,85	26,88333333	Zvidze	J. Sloka 1975, 1986a; A. Strazdinja 1986; I. A. Loze 1988
56,9	26,16666667	Zvejnieki	K. L. Paaver 1965
56,93	26,86666667	Abora I	Ja. Ja. Sloka 1975; I. A. Loze 1979
56,75	27,83333333	Jurisdika	K. L. Paaver 1965
56,33	26,83333333	Lejmaniški	K. L. Paaver 1965
56,97	21,96666667	Sarnate (späte Schicht)	K. L. Paaver 1965
56,55	27,56666667	Budjanka	K. L. Paaver 1965
56,67	27,86666667	Krej?i (frühe Schicht)	K. L. Paaver 1965
56,65	23,2	Lejas-Cijskas	K. L. Paaver 1965
56,67	27,86666667	Krej?i (späte Schicht)	K. L. Paaver 1965
57,52	25,33333333	Kaulenkalns	K. L. Paaver 1965
56,97	23,16666667	Silin'upe	K. L. Paaver 1965
57,53	25,48333333	Rinnjukalns	K. L. Paaver 1965
56,72	26,78333333	Malmuta	K. L. Paaver 1965
56,93	26,93333333	Piestinja	K. L. Paaver 1965
47,22	9,533333333	Eschen (Fst. Lutzengüetle, Schicht III)	H. Hartmann-Frick 1960
47,22	9,533333333	Eschen (Fst. Borscht)	E. Kuhn 1937; H. Hartmann-Frick 1965
55,25	26,11666667	Kretuonas 1C bei Reskutenai	L. Daugnora u. A. Girininkas 1995, 1996
55,5	25,6	Nark?nai Didysis bei Utenos	L. Daugnora u. A. Girininkas 1996
56,3	21,83333333	Švjantoji	E. A. Cepkin 1984
55,25	26,11666667	Kretuonas 1D bei Reskutenai	L. Daugnora u. A. Girininkas 1996
55,25	26,11666667	Kretuonas 1A bei Reskutenai	L. Daugnora u. A. Girininkas 1996
55,63	23,28333333	Daktarišk?s 5	L. Daugnora u. A. Girininkas 1996
56,3	21,83333333	Šventosios 6	L. Daugnora u. A. Girininkas 1996
55,25	26,11666667	Kretuonas 1B bei Reskutenai	L. Daugnora u. A. Girininkas 1995, 1996
46,7	28,7	Gura-Galbenej	A. I. David 1982
48,25	26,88333333	Slobodka-Šireucy	A. I. David 1969, 1982
47,85	27,31666667	Petru?eni (Fst. "La Cigoreanu")	O. G. Levitschkii u. E. N. Sava 1993
51,97	5,35	Wijk bij Duurstede-De Horden	F.J. Laarman 1996b
51,82	4,483333333	Mijnsheerenland (Fst. Hofweg)	R.M. van Heeringen u. R.C.G.M. Lauwerier 1996
51,83	4,333333333	Hekelingen	A.T. Clason 1967a
51,92	4,333333333	Vlaardingen	P.J.H. Van Bree 1961, A.T. Clason 1967a, D.C. Brinkhuizen 1979
52,65	5,75	Noordoostpolder (Fst. P14)	E.F. Gehasse 1992
51,83	4,333333333	Hekelingen III	W. Prummel 1987a, J.T. Zeiler 1995a
52,13	4,433333333	Voorschoten	W. Groenman, A. Voorrips u. L.H. van Wijngaarden 1968, M.J. van Maren u. L.H. van Wijngaarden-Bakker 1972, J.T. Zeiler 1995a
51,87	4,7	Hazendonk	J.T. Zeiler 1991b

52,65	5,75	Noordoostpolder (Fst. P14)	E.F. Gehasse 1992
51,85	4,916666667	Molenaarsgraaf	A.T. Clason 1977b, D.C. Brinkhuizen 1979
60,35	5,333333333	Ruskenesset	A. Brinkmann 1920
70,1	28,61666667	Gropbakkeengen	H. Olsen 1967, M.A.P. Renouf 1989, H. Olsen unveröff.
52,3	16,6	Bruszczewo (Fst. 5)	M. Soboci?ski 1977d
50,67	21,68333333	Z?ota (Fst. Gajowizna) bei Sandomierz	K. Krysiak & A. Lasota-Moskalewska 1977; A. Lasota-Moskalewska 1977
50,12	19,95	Kraków-Witkowice (Fst. 2)	J. Rydlewski & P. Valde-Nowak 1980
50,8	20,66666667	Nowa Huta-Zes?awice (Fst. 1), Ot. von Kraków	M. God?owska 1968a, 1968b
51,55	17,78333333	D?bnica bei Trzebnica	M. Soboci?ski 1973d
54,7	18,46666667	Rzucewo (Fst. 1) bei Puck	E. Lubicz-Niezabitowski 1928; D. Makowiecki & W. van Neer 1996
39,1	-8,71666667	Leceia	Lentacker 1990/91
47,43	22,23333333	Otomani	S. Haimovici 1968b
44,72	21,61666667	Moldova Veche (Fst. Ostrov)	G. El Susi 1995b
44,68	21,86666667	Gornea (Fst. P?z?ri?te)	G. El Susi 1995b
45,13	26,65	S?rata-Monteoru	S. Haimovici 1994a
46,25	27,5	Mîndri?ca	S. Haimovici 1980b
45,85	27,43333333	Gîrbov?? bei Tecuci	S. Haimovici 1991
46,85	27,55	Rate?u Cuzei, Gem. Rebricea	V. E. Ionescu-Rusu & M. Br?ileanu 1979a
56,35	46,71666667	Achmylovskaja stojanka II	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,23	46,13333333	Majdanskaja stojanka	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,13	46	Vasil'surskoe poselenie (Schicht 3)	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
		Loban' I	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,82	55,53333333	Zajur?im	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,8	52,23333333	Kumys, Kumysskaja stojanka	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
54,58	49,16666667	Gul'kinskaja stojanka bei Zelenovka	V. I. Calkin 1958a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
53,88	56,3	Inzelga	A. G. Petrenko 1984
54,63	55,7	Žukovskaja stojanka bei Ufa	A. G. Petrenko 1984
56,32	46,5	Udel'no-Šumeckaja stojanka III	A. G. Petrenko 1984
52	56	Ivanovskoe bei Ivanovki	A. G. Petrenko 1995
47,92	18,75	Malé Kosihy (Fst. Törökdomb)	C. Ambros unpubliziert
48,7	18,2	Nitriansky Hrádok (Ot. von Šurany, Fst. Záme?ek)	C. Ambros 1971, unpubliziert
49,3	20,33333333	Gánovce	C. Ambros 1959, unpubliziert
48,73	21,26666667	Košice (Fst. Barca)	C. Ambros unpubliziert
49	20,48333333	Spišský Štvrtok (Fst. Myšia hôrka)	C. Ambros unpubliziert
48,65	17,73333333	Podolie	C. Ambros unpubliziert
37,33	-3,18333333	Cuesta del Negro/Purullena	Lauk 1976
43,35	-2,51666667	Cueva de Txotxinkoba	Altuna 1967b; 1972
40,58	-5	Aldeagordillo	Garnica Queseda, unpubl.
37,32	-4	Las Peñas de los Gitanos/Montefrío	H. P. Uerpmann 1978
37,75	-2,55	Cerro de la Virgen	von den Driesch 1972b
37,13	-3,53333333	Cerro de la Encina/Monachil	Lauk 1976
37,33	-3,18333333	Cuesta del Negro/Purullena	Lauk 1976
		Cueva de Guetaleuta I	Altuna 1967b; 1972
37,5	-2,36666667	Terrera Ventura	von den Driesch/Morales 1977
58,1	11,6	Huseby Klev	A. Cardell 1995
55,87	13,16666667	Fjelie	A. Cardell 1995
59,65	17,33333333	Apalle	A. Cardell 1995
59,27	17,95	Hallunda	A. Cardell 1995
60,25	16,91666667	Grangärde	J. Ekman u. E. Iregren 1984
56,5	14,41666667	Gualöv	H. Berlin 1941, J.E. Forssander 1941, R. Liljegren 1975, E. Iregren 1988
59,6	16,53333333	Äs	J. Lepiksaar 1974
59,7	17,8	Korsnäs	K. Aaris-Sørensen 1978
55,37	13,45	Rävgrav	L. Larsson 1985
60,5	17,55	Sotmyra	G. Ekholm 1918, L. Hedell 1935-37
55,43	13,85	Herrestad bog	E. Iregren 1988
55,57	12,98333333	Hindby bog	E. Iregren 1988

64,33	17,25	Åsele (Fst. 1023-1024)	J. Ekman u. E. Iregren 1984, E. Iregren 1985
58,27	14,66666667	Alvastra (Fst. westlicher Graben)	E. During 1988
58,27	14,66666667	Alvastra (Fst. östlicher Graben)	E. During 1986, E. During 1987
62,47	14,58333333	Rätan	J. Ekman u. E. Iregren 1984
46,68	7,683333333	Spiez (Fst. Bürg)	W. Küenzi 1941
47,52	9,433333333	Arbon (Fst. Bleiche)	E. Kuhn & A. Güller 1946
46,75	9,5	Scuol-Munt Baselgia (I-III)	B. Kaufmann 1983
46,75	9,5	Scuol-Munt Baselgia (I-II)	B. Kaufmann 1983
		Crestaulta	J. Rüeger 1942
46,97	6,866666667	Auvernier (Fst. La Saunerie, Sch. II)	Th. Josien 1955a
46,97	6,866666667	Auvernier (Fst. La Saunerie)	H. R. Stampfli 1976b
47,8	8,833333333	Egolzwil (Fst. 2, Schicht I)	K. Hescheler & J. Rüeger 1939, 1942
47,4	8,55	Zürich (Fst. Utoquai)	E. Kuhn 1932
47,67	8,983333333	Steckborn-Turgi	J. Winiger & A. Hasenfratz 1985
47,4	8,55	Zürich (Fst. Seefeld, Sch. E)	H. Hüster-Plogmann & J. Schibler 1997
47,4	8,55	Zürich (Fst. Pressehaus, Sch. C2)	H. Hüster-Plogmann & J. Schibler 1997
47,4	8,55	Zürich (Fst. Mythenschloß, Sch. 2.4)	H. Hüster-Plogmann & J. Schibler 1997
47,4	8,55	Zürich (Fst. Mythenschloß, Sch. 2.3-2)	H. Hüster-Plogmann & J. Schibler 1997
47,4	8,55	Zürich (Fst. Mythenschloß, Sch. 2.1)	H. Hüster-Plogmann & J. Schibler 1997
47,28	8,65	Meilen (Fst. Rohrenhaab)	M. Sakellaridis 1979
47,17	8,516666667	Zug (Fst. Sumpf)	L. Reverdin 1927; J. Schibler 1996
47,17	8,283333333	Hochdorf (Fst. Baldegg)	K. Hescheler & J. Rüeger 1940
37,5	22	Messene, Heroen- u. Demeterheiligtum	Nobis 1997
38,65	23	Kalapodi	Stanzel 1991
39,1	26,5666666667	Mytilene	Ruscillo 1993
39,17	20,9833333333	Kassope	Friedl 1984
39,87	16,5333333333	Broglio di Trebisacce	Tagliacozzo 1994b
42,38	11,75	Poggio Cretoncini/Tarquinia	De Grossi Mazzorin 1995c
42,45	2,5	Lo Lladre, Llo	Vigne 1978; 1983
42,55	-2,5833333333	La Hoya	Altuna 1980; Altuna/Mariezkurrena 1983b; 1986
42,58	25,4	Slavčova bei Rizovo	L. Ninov 1996b
42,63	11,9833333333	Gran Carro/Lago di Bolsena	De Grossi Mazzorin 1995a
42,8	22,8	Goljamata Peščera bei Ilija	V. Vasilev u. V. Nikolov 1980
42,9	27,2166666667	Sašova bei Jasenovo	L. Ninov 1996b
42,92	-3,25	Castro de las Peñas de Oro	Altuna 1965; 1972
43,62	13,5166666667	Ancona, Colle dei Cappuccini	Azzaroli 1979; Wilkens 1990b
43,67	25,3666666667	Zimnicea	S. Haimovici 1972b
43,72	17,2166666667	Gradina bei Duvno	J. Boessneck u. M. Stork 1972
43,8	2,5	Le Laouret	Vigne 1996
44,2	26,5	Radovanu	M. Şt. Udrescu 1982, 1984, 1985a, 1989
44,27	19,8833333333	Petnica bei Valjevo	
44,43	5,2166666667	Les Gandus/St. Ferréol-Trente-Pas	Columeau 1991
44,5	17,4166666667	Pod bei Bugojno	M. Sachenbacher-Palavestra 1986
44,6	26,85	Piscul Crăsani	M. Şt. Udrescu 1984, 1989
45,23	26,6833333333	Cîrlomăneşti, Gem. Verneşti	M. şt. Udrescu 1977, 1984, 1985a, 1989
45,65	13,7666666667	Cattinara	Riedel 1974; 1975a
45,73	11,3833333333	Santorso	Cassoli/Tagliacozzo 1989
45,88	13,5	Gradisca sul Cosa	Petrucci 1990
46,15	13,7333333333	Most na Soči	L. Bartosiewicz 1985, 1986
46,17	7,5	Vex-le-Château	L. Chaix 1990b
46,57	11,5666666667	Castelrotto	Riedel 1985a
46,67	7,833333333	Châtillon-sur-Glâne	L. Chaix u. a. 1991
46,68	9,5666666667	Lantsch/Lenz (Fst. Bot da Loz)	E. Heizmann 1983
46,7	31,9	Ol'vija bei Parutino	I. G. Pidopličko 1956; V. I. Calkin 1959, 1960
46,72	4,95	Curtil Brenot/Ouroux-sur-Saône	Poulain 1973e
46,72	11,6666666667	Stufels/Brixen	Riedel 1985b; 1986c
46,83	28,75	Chanska II bei Gansk	V. I. Calkin 1962c, 1966; A. I. David 1982
46,88	42,666666667	Lužki	V. I. Calkin 1962a, 1963, 1966
46,93	6,85	Cortaillod-Ost	L. Chaix 1986
46,95	7,4666666667	Bern (Fst. Engemeistergut)	M. A. Nussbaumer/E. Büttiker 1989
46,98	24,4	Piscu Crăsani	M. Şt. Udrescu 1985a
47,15	9,8166666667	Bludenz	W. Amschler 1939b
47,22	9,5333333333	Eschen (Fst. Lutzengüetle, Schicht II)	H. Hartmann-Frick 1960
47,23	16,6166666667	Velemszentvid bei Szombáthely	S. Bökönyi 1974a
47,3	8,2166666667	Hallwil (Fst. Rostbau)	P. Steinmann 1923, 1925
47,32	9,5666666667	Montlingerberg, Gem. Oberriet	F. E. Würgler 1962
47,4	8,55	Zürich (Fst. Alpenquai)	E. Wettstein 1924; K. Hescheler & E. Kuhn 1949
47,5	19,833333333	Budapest (Fst. Csepel-Háros)	S. Bökönyi 1974a

47,57	34,4166666667	Čertomlyk bei Čkalovo	O. P. Žuravlev 1991b, 1997a
47,62	8,2333333333	Dangstetten	M. Uerpmann 1973; H.-P. Uerpmann 1977
47,73	26,65	Stînceşti bei Botoşani	S. Haimovici 1963c, 1974b; S. Haimovici & G. Ghiorghiu 1971
48,3	7,6	Breisach-Münsterberg, Hotel am Münster	Arbinger-Vogt 1978
48,42	17,7166666667	Bučany	C. Ambros 1984
48,47	2,4333333333	Videlles	Poulain-Josien 1958f
48,72	11,5166666667	Manching	Switzerlander 1961; Boessneck u. a. 1971
48,8	9,4	Heuneburg	Geringer 1967; Gerlach 1967; Graf 1967; Reiss 1967; Braun-Schmidt 1983; McEneaney-Schneider 1984; von den Driesch/J. Boessneck 1989
48,97	31,8	Šarpovka bei Pastyrskoe	I. G. Pidopličko 1956; V. I. Bibikova 1963
49,1	32,55	Subbotovo	I. G. Pidopličko 1956; V. I. Bibikova 1963; M. A. Voinstvenskij 1967
49,15	32,15	Žabotin	V. I. Bibikova 1963
49,2	12,1166666667	Regensburg-Harting	von den Driesch 1995b
49,38	2,5	Catenoy, "Le camp de César"	Méniel 1987a
49,57	34,45	Zol'nik 5 bei Mačucha	I. G. Pidopličko 1956, V. I. Calkin 1966
49,58	25,65	Zales'e	O. P. Žuravlev 1997c
49,6	5,8833333333	Clémency	M. Schönfelder 1994
49,95	35,9666666667	Ljubotin	V. I. Calkin 1966
50,33	19,15	Grodziec bei Będzin	M. Kubasiewicz & J. Gawlikowski 1976
50,4	34,1166666667	Basovka	V. I. Bibikova 1963; V. I. Calkin 1966
50,43	7,4666666667	Heimbach-Weis (Ot. von Neuwied)	E. Schmid 1973a
50,57	13,7166666667	Jenišův Újezd	M. Beech 1993a
50,92	34,8166666667	Širjaevo	I. G. Pidopličko 1956; V. I. Calkin 1966
51,42	9,3333333333	Altenbauna	M. Schönfelder 1994
51,5	13,75	Dresden-Coschütz (Fst. Heidenschanze)	C. Ambros 1986b
51,58	13,95	Saalhausen (Fpl. 2)	L. Teichert 1990b
51,77	39,5833333333	Čardymskoe bei Čardym	V. I. Calkin 1966
51,8	-0,2166666667	Welwyn Garden City	M. Schönfelder 1994
51,87	13,9666666667	Lübbenau (Fst. "Batzlin")	L. Teichert 1973, 1976b
51,98	-0,2	Baldock	M. Schönfelder 1994
52	33,2666666667	Juchnovskoe bei Novgorod-Severskij	V. I. Calkin 1956, 1962a
52,17	31,833333333	Čaplinskoe bei Čaplin	V. I. Calkin 1956, 1962a
52,4	8,9666666667	Döhren (Ot. von Petershagen)	E. Schmid 1981a
52,42	31	Goroškov	V. I. Calkin 1962a
52,47	6,5333333333	Linderbeek	D.A. Hooijer 1947
52,5	33,25	Južnoe Dolbatovo	V. I. Calkin 1962a
52,73	18,4833333333	Konary (Fst. 28)	M. Sobociński 1987b
52,77	17,7333333333	Biskupin (Fst. 4) bei Żnin	E. Lubicz-Niezabitowski 1936, 1938, 1948; K. Krysiak 1950; J. Kaj 1950; A. Lasota-Moskalewska 1989
52,88	17,4166666667	Smuszewo (Fst. 1)	S. Godynicki & M. Sobociński 1979
53,17	9,9	Putensen	M. Schönfelder 1994
53,25	34,3666666667	Krasnoe bei Brjansk	V. I. Calkin 1956, 1962a
53,37	33,8666666667	Ovstug	V. I. Calkin 1956, 1962a
53,45	9,4833333333	Harsefeld	M. Schönfelder 1994
53,48	9,9166666667	Ehestorf-Vahrendorf	M. Schönfelder 1994
54,13	21,5833333333	Tarławki	A. Lasota-Moskalewska 1979a
54,17	31,1666666667	Kubliči	V. V. Ščeglova 1969a
54,18	28,15	Labenščina	I. G. Pronina u. V. E. Garutt 1957
54,55	31,166666667	Burakovo	V. V. Ščeglova 1969a
54,57	56,2	Šipovo, Šipovskoe	A. G. Petrenko 1984
54,77	9,5666666667	Husby	I. Kühl 1984
54,8	28	Dvorišče	V. V. Ščeglova 1969a
55,17	50,166666667	Kurgan	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,2	29,5333333333	Kostrica	V. V. Ščeglova 1969a
55,23	50,5666666667	Kirovskoe	V. I. Calkin 1966, 1969a
55,3	29,8666666667	Zaronovo	V. V. Ščeglova 1969a
55,37	49,8333333333	Gremjačij ključ bei Šuran	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,48	55,5833333333	Biktimirovskoe (Schicht 2) bei Novo-Biktimirovo	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,52	51,3833333333	Svinogorskoe (Schicht 2)	V. I. Calkin 1962a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,58	26,15	Sokiškiai bei Dūkšto-Salako	E. Grigalavičienė 1986b

55,67	37,55	Kruglica	V. I. Calkin 1962a
55,72	13,1666666667	Önsvala (Fst. Grab 2, 6, 18)	L. Larsson 1982
55,75	37,5	Staršee Kaširskoe (Ot. von Kašira)	V. I. Calkin 1956, 1961a, 1962a
55,77	37,7166666667	Mamonovskoe (Ot. von Moskau)	V. I. Calkin 1956, 1961a, 1962a
55,8	55,9	Ochlebininskoe (Schicht 1) bei Ufa	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,13	46	Vasil'surskoe (Schicht 2)	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,2	15,65	Avelsgärde	E. Iregren 1988, B. Petré 1980
56,35	46,7166666667	Malachajskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
56,4	46,8	Arda, Ardinskoe	A. G. Petrenko 1984
56,42	26,3333333333	Asote	K. L. Paaver 1965
56,48	23,3833333333	Tervete	K. L. Paaver 1965
56,58	16,6666666667	Gårdby (Fst. Ålebäck)	B. Petré 1980
56,67	50,65	Bujskoe	A. G. Petrenko 1984
56,83	24,5166666667	Mukukalns	K. L. Paaver 1965
56,97	50,35	Rojskij Šichan	T. M. Kulaeva 1965, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57	35	Pekunovskoe	V. I. Bibikova 1950; V. I. Calkin 1956, 1961a, 1962a
57,3	54,6333333333	Kalinovskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,5	55,5666666667	Gremjačanskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,6	48,9	Pižemskoe	V. I. Calkin 1962a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,7	56,4333333333	Altyn-Tau	V. I. Calkin 1962a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,75	18,6	Tingstäde (Fst. Nystu)	B. Petré 1980
57,95	56	Polovinnoe I	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
58	56,1333333333	Kultaevskoe bei Perm	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
58,25	56,5333333333	Galkinskoe	V. I. Calkin 1962a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
58,42	23,166666667	Asva	J. Lepiksaar 1935, 1938, 1984; K. L. Paaver 1965; L. Lõugas 1993, 1997
58,43	56,5333333333	Konecgorskoe	V. I. Calkin 1962a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
58,5	44	Odoevskoe	A. N. Formozov 1951; G. V. Nikol'skij 1935b
58,52	13,85	Horn (Fst. Kyrkbacken)	B. Petré 1980
58,58	16,1333333333	Ö. Eneby (Fst. Fiskeby)	B. Petré 1980
58,67	55,8666666667	Skorodum	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
59	56	Gorjuchalichinskoe	E. G. Andreeva u. A. G. Petrenko 1976
60,35	5,3333333333	Ruskenesset	A. Brinkmann 1920
70,1	28,6666666667	Gressbakken (Fst. Haus 1,3,5,9,11,12,21-23)	M.A.P. Renouf 1989, H. Olsen unveröff.

Table 17: *Deposits list showed in the Fig.42*

Latitude	***Longitude***	***Site***	***References***
40,42	15	Paestum	von den Driesch/Boessneck 1969b
42,13	13,5166666667	S. Potito/Ovindoli	Bökönyi 1986c
43,22	27,9166666667	Odercy bei Varna	M. Sobociński & M. Gajowy 1991
43,3	5,3666666667	Marseille, La Bourse	Jourdan 1976
43,62	25,3333333333	Novae, Ot. von Svištov (Grabung 1977, 1979)	W. Chrzanowska & O. Molenda 1983; A. Waluszewska-Bubień & A. Krupska 1983
43,8	3,8666666667	Grotte de l'Hortus/Valflaunès	Poulain 1972a
44,77	21,5666666667	Divici, Gem. Pojejena	G. El Susi 1992
45,3	24,3	Stolniceni (Fst. Vîlcea)	M. Şt. Udrescu 1979a, 1984, 1990
45,5	0,75	Aulnay-de-Saintonge - Aunedonnacum	Caillat 1983; Lignereux/Peters 1997a
46,17	21,666666667	Pecica (Fst. Oppidum Ziridava)	S. Haimovici 1969c
46,4	27,333333333	Răcătău	S. Haimovici 1989a
46,83	8,2333333333	Alpnachdorf	E. Kuhn 1932
46,87	7,5	Avenches (Aventicum)	C. Ambros 1979c, 1990
46,88	22,9166666667	Bologa	P. Georoceanu u. a. 1979
46,88	22,1333333333	Drăgeşti, Gem. Todireşti	S. Haimovici 1981-1982

46,9	26,4833333333	Izvoare	S. Haimovici 1987c
47,12	9,5166666667	Schaan	F. E. Würgler 1959
47,12	29,3	Delakeu I	V. I. Calkin 1962c, 1966; A. I. David 1969
47,53	7,7166666667	Augst ("Augusta Raurica")	E. Schmid 1970, 1984; J. Schibler u. A. R. Furger 1988; J. Schibler u. E. Schmid 1989; Ph. Morel 1988; E. Grädel 1989; S. Deschler-Erb 1991a, 1991b, 1991c, 1992; G. Breuer 1992
47,58	9,3333333333	Ütliberg (Fst. Uto-Kulm)	H. Hartmann-Frick 1991
47,7	10,333333333	Isny - Vemania	Piehler 1976
47,7	18,166666667	Ács (Fst. Vaspuszta)	S. Bökönyi 1974a; L. Bartosiewicz 1989
47,73	10,3166666667	Kempten - Cambodunum	Boessneck 1957; 1958
47,82	10,9	Epfach, Lorenzberg	Boessneck 1964
47,93	8,5	Hüfingen	Dannheimer 1964; Sauer-Neubert 1969
47,97	21,9333333333	Apagy (Fst. Peckés rét)	I. Vörös 1993
48,12	7,85	Sponeck/Jechtingen	Pfannhauser 1980; von den Driesch 1986a
48,17	8,6333333333	Rottweil	Kokabi 1988a
48,25	28,666666667	Sobar	A. I. David 1982
48,3	7,6	Breisach/Münsterberg	Schmidt-Pauly 1980
48,35	15,7333333333	Traismauer (Fst. "Augustiana")	A. Riedel 1993d
48,5	11,6166666667	Unterhaching, "Am Rodelberg"	von den Driesch 1995/96
48,72	11,45	Oberstimm	Stettmer 1997
48,75	30,1666666667	Sachnovka	I. G. Pidopličko 1956
48,8	9,2333333333	Cannstatt	Hilzheimer 1920
48,83	12,9666666667	Künzing	Swegat 1976
48,88	8,6833333333	Pforzheim	Kuss 1958
48,92	10,1666666667	Rainau-Buch	Gulde 1985
48,92	8,7	Pforzheim	S.E. Kuss 1958
49,18	16,6	Brno (Fst. Starý Lískovec)	L. Peške 1978b
49,23	9,1333333333	Bad Wimpfen	Frey 1991
49,3	11	Weißenburg - Biriciana	Sachenbacher-Palavestra 1991
49,47	8,6	Ladenburg - Lopodunum	Lüttschwager 1968; Teichert 1994
49,7	11	Ellingen - Sablonetum	von den Driesch/Liesau 1992
49,75	11,833333333	Eggolsheim	Breu 1986
49,85	7,8666666667	Bad Kreuznach	F. Johansson 1987
49,92	8,4833333333	Groß-Gerau	I. Kühl 1984
50,25	14,5333333333	Mlékojedy	L. Peške 1994b
50,27	8,5833333333	Saalburg	M. Hilzheimer 1924
50,3	19,9833333333	Kraków (Fst. Wola Duchacka)	H. Hoyer 1928
50,73	7,1166666667	Bonn	W. Wendt 1967
50,8	11,1666666667	Dienstedt	H.-J. Barthel 1987a
50,85	5,7	Maastricht	A. Ervynck 1997
50,87	10,9	Haarhausen	H.-J. Barthel 1987a
50,87	10,8333333333	Mühlberg	M. Teichert 1990
50,92	34,8166666667	Besedovka	I. G. Pidopličko 1956
51,67	6,45	Colonia Ulpia Traiana / Xanten (Fst. Thermen)	K. Waldmann 1967
51,88	13,7	Gießmannsdorf	L. Teichert 1980b
51,9	0,9	Sheepen	R.-M. Luff 1982
52,15	9,95	Hildesheim-Bavenstedt	M. Missel 1987, S. Hanik 1997
52,17	11,6666666667	Magdeburg-Cracau	R.-J. Prilloff 1993
52,18	4,4333333333	Valkenburg	A.T. Clason 1967a, P.J.H. van Bree u. A.T. Clason 1971, W. Prummel 1977
52,32	13,3166666667	Genshagen	H.-H. Müller 1996c
52,33	0,6	West Stow	P.J. Crabtree 1990b
52,37	13,6166666667	Waltersdorf	M. Teichert & R. Müller 1987
52,48	4,6166666667	Velsen (Fst. 1)	A.T. Clason 1967a, W. Prummel 1987b, L.H. van Wijngaarden-Bakker 1988, D.C. Brinkhuizen 1989
53,35	6,7666666667	Eenumerhoogte	A.E. van Giffen 1913
53,55	11,1833333333	Parum	U. Lehmkuhl 1987
54,33	28,1666666667	Novoselki	I. G. Pronina u. V. E. Garutt 1957
54,4	28,25	Kimija	I. G. Pronina u. V. E. Garutt 1957
54,63	9,7833333333	Süderbrarup	I. Wahl 1988
54,65	24,1666666667	Migonis	K. L. Paaver 1965
54,85	25,45	Nemenčine	K. L. Paaver 1965
55,2	36,3833333333	Nikolo-Lenivec	V. I. Calkin 1961a, 1962a
55,55	36,166666667	Svinuchovskoe	V. I. Calkin 1956, 1961a, 1962a
55,58	50,1666666667	Čerepaš'e	A. G. Petrenko 1988
55,75	37,5	Troickoe	V. I. Calkin 1961a, 1962a
55,77	37,7166666667	Barvicha (Ot. von Moskau)	V. I. Calkin 1962a

55,8	36,75	Ogubskoe	V. I. Calkin 1956, 1962a
56	40,5	Kondrakovskoe bei Murom	V. G. Andreeva 1940; V. I. Calkin 1956, 1961a, 1962a
56,7	10	Stilling	U. Møhl 1978b
57	35	Gorodnenskoe bei Kaljazin	V. I. Calkin 1962a
57,1	54,8666666667	Machoninskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
57,18	39,4166666667	Gorodišče	V. I. Calkin 1956
57,62	39,8666666667	Krasnyj Cholm bei Jaroslavl	V. I. Calkin 1956, 1961a, 1962a
58,32	56,1833333333	Ust'-Tujskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
59,57	17,7333333333	Uppgården	B. Johnsen-Welinder u. S. Welinder 1973
59,92	17,6333333333	Uppsala (Fst. Östhög)	S. Lindqvist 1936
60,23	17,7166666667	Ottarshögen	S. Sten u. M. Vretemark 1988, S. Sten u. M. Vretemark 1992
60,87	21,6666666667	Vainionmäki	T. Formisto 1996
42,7	2,1166666667	Château d'Usson/Rouze/Quérigut	Lignereux u. a. 1995a
44,72	21,1833333333	Kostolac (Fst. Castellum Pontes)	L. Bartosiewicz 1996a
45,43	11	Verona	Riedel 1994a
45,77	4,8333333333	Lyon, Sainte-Croix	Forest 1987
46,67	17,1666666667	Zalavár (Fst. Kövecses)	S. Bökönyi 1963b; I. Vörös 1984a
46,72	9,4333333333	Cazis (Fst. Niederrealta)	G. Klumpp 1967
46,75	9,5	Sagogn (Fst. Schiedberg)	W. Küpper 1972; E. Scholz 1972
46,83	28,75	Chanska II bei Gansk	I.M. Ganja 1972; A. I. David 1969, 1982
46,92	29,3833333333	Kalfa I	A. I. David 1982
46,98	35	Gočevo	V. I. Calkin 1963, 1969b
46,98	9,6833333333	Schiers	H. Hartmann-Frick 1975
47,12	7,2333333333	Nidau	E. Büttiker & M. A. Nussbaumer 1990; M. A. Nussbaumer & J. Lang 1990
47,13	9,5666666667	Neu-Schellenberg, Gem Schellenberg	H. Schülke 1965
47,17	9,1333333333	Starkenstein	F. E. Würgler 1956
47,2	26,5833333333	Borniş (Fst. Măleşti)	S. Haimovici 1987d
47,37	7,8666666667	Trimbach (Fst. Frohburg)	D. Markert 1989
47,42	7,5833333333	Rickenbach	H. R. Stampfli 1972
47,5	19,833333333	Budapest (Fst. Vár)	S. Bökönyi 1958, 1963a, 1964b
47,68	10,35	Sulzberg	von den Driesch 1995a
47,73	10,3166666667	Kempten	H.-P. Uerpmann 1987
47,78	18,9833333333	Visegrád (Fst. Kálvária)	S. Bökönyi 1974a; S. Bökönyi u. D. Jánossy 1965
47,87	28,8833333333	Alčedar	V. I. Calkin 1962c, 1972a
47,93	26,666666667	Siret	S. Haimovici u. a. 1993; S. Haimovici & L. Bejenaru 1994; L. Bejenaru & C. Tarcan-Hrişcu 1996
48,35	27,8833333333	Rud'	A. I. David 1989
48,4	10	Ulm-Weinhof	Anschütz 1966
48,7	16,9333333333	Pohansko	Z. Kratochvíl 1969a, 1969b
48,82	17,5	Mikulčice	Z. Kratochvíl 1978, 1980d, 1980e, 1980f, 1980g, 1980h, 1980i, 1981a, 1981b, 1981c, 1982a, 1982b, 1987d, 1987e, 1988a; C. Ambros u. H.-H. Müller 1980
48,85	15,5	Raabs a.d. Thaya (Fst. Flur Sand)	E. Pucher u. M. Schmitzberger 1999
48,88	10,2666666667	Lauchheim	Kokabi/Rösch 1991
48,92	11,9	Kelheim	Schäffer/von den Driesch 1983
49,15	10,1	Unterregenbach	H. Schatz 1963
49,18	16,6	Brno (Fst. Orlí Gasse 16)	Z. Kratochvíl 1987c
49,45	11,833333333	Nürnberg	Boessneck/von den Driesch-Karpf 1968; Lepiksaar 1968a
49,57	34,45	Opošnja	V. I. Calkin 1969b
49,58	17,2333333333	Olomouc (Fst. Prior)	Z. Kratochvíl 1985a, 1985b
49,83	6,2833333333	Château de Beaufort	A. Ervynck u. A. Lentacker 1996a
49,97	28,5	Rajki	I. G. Pidopličko 1956; M. A. Voinstvenskij 1967
49,97	31,5	Čučin bei Ržiščeva	N. G. Timčenko 1970, 1972b
49,98	31,3833333333	Monastyrek	N. G. Belan 1978
50	14,9833333333	Kouřim	L. Peške 1986b
50,17	30,75	Komarovka	N. G. Timčenko 1970, 1972a
50,33	30,6666666667	Poloveckoe	N. G. Timčenko 1970, 1972a
50,35	20,6833333333	Wiślica	M. Sobociński 1970b; A. Waluszewska-Bubień 1968
50,42	10,5333333333	Haina	H.-H. Müller 1996b
50,42	30,55	Kiev (Fst. Gora Kiselevka)	V. I. Zubareva 1940; I. G. Pidopličko 1956; V. I. Bibikova 1963; N. G. Timčenko 1972a

50,43	14,5833333333	Hradsko	L. Peške 1986b
50,53	34,3333333333	Novotroickoe	V. I. Calkin 1969b
50,57	11,6	Weisbach (Fst. Wysburg)	H.-J. Barthel 1996
50,57	30,5	Vyšgorod	V. I. Zubareva 1940; I. G. Pidopličko 1956; V. I. Bibikova 1963; M. A. Voinstvenkij 1967; N. G. Timčenko 1970, 1972a
50,68	16,85	Niemcza (Fst. 2)	K. Myczkowski (unpubliziert); P. Wyrost & W. Chrzanowska 1985
50,75	22,8833333333	Sąsiadka	K. Krysiak 1966
50,8	18,2	Racibórz-Ostróg	P. Wyrost & W. Chrzanowska 1985
50,88	16,75	Strachów bei Sobótka	M. Kubasiewicz 1967; J. Lodowski 1980; P. Wyrost & W. Chrzanowska 1985
50,92	34,8166666667	Petrovskoe	I. G. Pidopličko 1956
50,93	4,3666666667	Senecaberg	A. Gautier u. V. Rubberechts 1978
50,93	6,95	Köln (Fst. Albansviertel)	H. Berke 1992b
51	35,4	Šuklinka	V. I. Calkin 1956, 1963, 1969b
51,1	17,333333333	Wrocław (Fst. Ostrów Tumski I)	W. Chrzanowska 1986; P. Wyrost & W. Chrzanowska 1981; A. Waluszewska-Bubien 1981
51,12	15,9166666667	Rzymówka, Gem. Złotoryja	O. Molenda 1984a
51,15	10,45	Niederdorla	M. Teichert & R. Müller 1993, 1996
51,15	13,4833333333	Meißen	H.-H. Müller 1982
51,17	12,2833333333	Groitzsch	H.-H. Müller 1977b
51,2	13,4	Zehren	H.-H. Müller 1980a
51,2	16,2	Legnica	P. Wyrost u. a. 1980; P. Wyrost & W. Chrzanowska 1985; A. Waluszewska-Bubien 1985
51,22	3,2333333333	Brügge (Fst. Burgplatz)	A. Ervynck 1991a
51,27	34,333333333	Volyncevo	I. G. Pidopličko 1956; V. I. Bibikova 1963
51,42	21,15	Radom (Fst. 2)	K. Krysiak u. a. 1975
51,5	12,666666667	Kretzschau-Groitzschen (Fst. "Der Kessel")	H.-H. Müller 1969a
51,53	17,2666666667	Kaszowo (Fst. 1)	M. Sobociński 1973a
51,55	39,8833333333	Titčicha	V. I. Calkin 1963, 1969b
51,58	9,9166666667	Burg Plesse / Bovenden	R. Schoon 1993
51,6	18,75	Sieradz	M. Kubasiewicz 1963b
51,67	39,2166666667	Borševo I bei Voronež	V. I. Gromova 1948; A. N. Svetovidov 1948; V. I. Calkin 1956, 1963, 1969b; M. A. Voinstvenskij 1967
51,68	22,3166666667	Poznań (Fst. ul. Garbary)	M. Sobociński 1977a; A. Waluszewska-Bubień 1977a
51,7	36,2	Lipino bei Kursk	V. I. Calkin 1956, 1963, 1969b
51,73	15,8333333333	Bytom Odrzański (Fst. 1)	P. Wyrost 1994; D. Makowiecki (unpubliziert)
51,75	18,833333333	Kalisz	P. Wyrost 1994
51,82	13,9333333333	Vorberg	H.-H. Müller 1966b
51,97	16,9	Lubiń (Phase I-II)	M. Sobociński 1991b; M. Sobociński & D. Makowiecki 1991a; A. Krupska 1991; M. Iwaszkiewicz 1991a
52,12	26,1166666667	Pinsk	V. V. Ščeglova 1969b, V. V. Ščaglova & P. F. Lysenka 1977
52,15	9,95	Hildesheim (Fst. Domhügel, Leunishof)	R. Schoon unveröff. a
52,22	17,9	Ląd bei Słupca	Z. Schramm 1983; Z. Schramm u. a. 1991; Z. Schramm & W. Kruszona 1992; D. Makowiecki (unpubliziert)
52,23	17,1	Bnin (Fst. 2a) bei Śrem	M. Sobociński 1975c; A. Waluszewska-Bubień 1975a; M. Iwaszkiewicz 1975a
52,25	21	Warszawa (Fst. Bródno Stare)	K. Krysiak 1956b
52,4	13,666666667	Potsdam	H. Enderlein 1930
52,42	12,55	Brandenburg (Fst. Dominsel)	L. Teichert 1988b
52,43	15,5833333333	Międzyrzecz Wlkp.	P. Wyrost 1994
52,45	13,5666666667	Berlin-Köpenick (Fst. Schloßinsel)	H.-H. Müller 1962, unpubliziert
52,5	27,2166666667	David-Gorodok	V. V. Ščeglova 1969b
52,52	19,8666666667	Szeligi (Fst. 1 und 2)	S. Godynicki 1967; M. Iwaszkiewicz 1967
52,53	13,2166666667	Berlin-Spandau	H. Pohle 1961a, 1967; C. Becker 1993
52,55	17,6	Gniezno (Fst. 47)	M. Sobociński & Z. Schramm 1972; A. Waluszewska-Bubień 1969b
52,6	13,45	Berlin-Blankenburg	H.-H. Müller 1977a
52,6	11,9833333333	Hämerten	R.-J. Prilloff 1988
52,68	18,3	Kruszwica (Fst. 4)	M. Sobociński 1964a; J. Mackiewicz 1989
52,7	27,7333333333	Turov	V. V. Ščeglova 1969b
52,7	19,2166666667	Łęczyca (Fst. 1)	K. Krysiak 1955b

52,73	0,9333333333	Spong Hill	J.M. Bond 1994
52,73	15,4166666667	Santok (Fst. 1)	Z. Schramm & I. Kranz 1978a, 1978b; M. Sobociński 1979e, 1979f, 1983b; A. Waluszewska-Bubień 1979a; A. Krupska 1985; D. Makowiecki (unpubliziert)
52,73	15,4166666667	Santok (Fst. 2)	Z. Schramm & I. Kranz 1978a, 1978b; M. Sobociński 1979e, 1979f, 1983b; A. Waluszewska-Bubień 1979a; A. Krupska 1985; D. Makowiecki (unpubliziert)
52,8	21,333333333	Czersk (Fst. 1) bei Piaseczno	P. Wyrost 1994; J. Mackiewicz 1989
52,83	10,7	Burg Bodenteich	D. Heinrich 1994a, H. Reichstein 1996a, D. Heinrich 1999, H. Reichstein 1999a
52,83	48,8833333333	Muranskoe	V. I. Calkin 1958a, E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
52,87	14,2	Cedynia (Fst. 1)	M. Kubasiewicz & J. Gawlikowski 1961; S. Nogalski 1977
52,92	14,8666666667	Myślibórz	P. Wyrost & O. Molenda 1987
53	36,25	Lebedka	V. I. Calkin 1956
53,1	25,3166666667	Slonim	V. V. Ščeglova 1969c
53,12	18,8	Gronowo (Fst. 2)	D. Makowiecki & A. Leszczyszyn 1990; D. Makowiecki (unpubliziert)
53,15	24,45	Volkovysk I (Fpl. Švedskaja gora)	V. V. Ščeglova & Ja. G. Zverugo 1967, 1969; N. I. Burčak-Abramovič & Ja. G. Zverugo 1969; V. V. Ščeglova 1969b; E. A. Cepkin 1969
53,15	24,45	Volkovysk II (Fpl. Zamčišče)	V. V. Ščeglova & Ja. G. Zverugo 1967, 1969; N. I. Burčak-Abramovič & Ja. G. Zverugo 1969; V. V. Ščeglova 1969b; E. A. Cepkin 1969
53,15	11,333333333	Weinberg / Hitzacker	B.-M. Kocks 1978, H.F. Walcher 1978, J. Boessneck 1982b, A. von den Driesch 1982a
53,15	11,333333333	Weinberg / Hitzacker	B.-M. Kocks 1978, H.F. Walcher 1978, J. Boessneck 1982b, A. von den Driesch 1982a
53,15	17,6	Nakło	M. Sobociński & S. Godynicki 1975; A. Waluszewska-Bubień 1975d
53,2	22,7833333333	Tykocin (Fst. 1)	A. Lasota-Moskalewska 1984
53,25	19,4	Brodnica	M. Sobociński 1977b; A. Waluszewska-Bubień 1977b
53,28	19,2833333333	Bobrowo (Fst. 1)	D. Makowiecki 1990b
53,3	10,4	Bardowick (Fst. Kirchenhügel St. Wilhadi)	H. Reichstein 1983, I. Ulbricht 1983
53,3	18,75	Lubicz	E. L. Niezabitowski 1949
53,33	12,6833333333	Vipperow	N. Benecke 1993b
53,33	15,5	Stargard Szczecinski (Fst. 1)	J. Gawlikowski & J. Stępień 1984b
53,35	17,5	Więcbork	Z. Schramm 1974c
53,35	17,5166666667	Jezioro Więcborskie	Z. Schramm 1974c
53,4	49,4833333333	Muromskoe bei Žigulevska	A. G. Petrenko 1984
53,42	14,5833333333	Szczecin (Fst. Gemüsemarkt)	M. Kubasiewicz & J. Gawlikowski 1967, 1969; S. Nogalski 1984; M. Rulewicz 1994
53,43	13,35	Teschendorf	R.-J. Prilloff 1994a
53,45	13,1333333333	Bacherswall bei Prillwitz	R.-J. Prilloff 1994a
53,47	13,2	Hanfwerder bei Krickow, Ot. von Groß-Nemerow	R.-J. Prilloff 1994a
53,48	13,1666666667	Fischerinsel bei Wustrow	R.-J. Prilloff 1994a
53,5	16,75	Ujście bei Chodzież	K. Chmielewski 1961b
53,53	16	Złocieniec	J. Gawlikowski 1971
53,58	13,2	Zirzow	R.-J. Prilloff 1994a
53,58	16,1666666667	Stare Drawsko	M. Sobociński 1980e, 1986a, 1986c, 1994b; J. Janaszek 1980; A. Sosnowski 1981; A. Krupska & A. Waluszewska-Bubień 1984; D. Makowiecki (unpubliziert)
53,67	17,3666666667	Gwieździn (Phase II) bei Człuchów	M. Sobociński 1977a, 1980a; A. Waluszewska-Bubień 1978
53,68	23,8333333333	Grodno	V. I. Calkin 1954b, 1956
53,72	17,2	Krępsk (Fst. 1) bei Człuchów	M. Sobociński 1980a; A. Waluszewska-Bubień 1978; M. Iwaszkiewicz 1980
53,73	11,8666666667	Groß Raden, Ot. von Sternberg	O. Gehl 1981
53,78	12,5833333333	Teterow	H.-H. Müller (unpubliziert)
53,8	18,7	Jedwabno (Schicht III)	M. Sobociński 1980b
53,85	27,5	Minsk	V. V. Ščeglova 1967, 1969b
53,85	11,4666666667	Mecklenburg	H.-H. Müller 1984; H.-H. Müller u. R. Müller 1988; N. Benecke 1994a
53,85	14,6166666667	Wolin (Stadt, Fst. 4)	M. Kubasiewicz 1959a; S. Nogalski 1984

53,88	10,6833333333	Alt Lübeck	B. Schröder 1984
53,97	-1,833333333	York (Fst. Coppergate 16-22)	J.M. Bond u. T.P. O'Connor 1999
53,98	21,6333333333	Jeziorko bei Giżycko	K. Krysiak 1952b, 1958b
54	37,2	Suprut'	V. I. Calkin 1969b
54,1	11,6166666667	Rerik	M. Hilzheimer 1939
54,12	10,4333333333	Bischofswarder / Bosau	H. Reichstein, K.-C. Taege u. H.-P. Vogel (mit Beitrag von D. Heinrich) 1980
54,12	39,6166666667	Pronsk	E. G. Andreeva 1972; E. A. Cepkin 1981
54,18	15,5833333333	Kołobrzeg (Fst. 1)	M. Kubasiewicz & J. Gawlikowski 1965; S. Nogalski 1975, 1984; M. Rulewicz 1994
54,23	10,2833333333	Scharstorf	D. Heinrich 1985
54,25	10,5	Giekau	H. Requate 1956a, H. Requate 1956b
54,33	48,35	Maklaševskoe II	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
54,35	18,6666666667	Gdańsk (Fst. 2)	M. Kubasiewicz 1977
54,47	13,45	Ralswiek	N. Benecke 1983
54,5	18,8166666667	Gorzędziej (Fst. 1) bei Tczew	M. Kubasiewicz 1964b; S. Nogalski 1979b; J. Mackiewicz 1989
54,52	9,55	Haithabu	H. Reichstein 1991b
54,52	24,1	Punja	K. L. Paaver 1965
54,53	9,5666666667	Schleswig (Fst. Schild)	N. Spahn 1986, D. Heinrich 1987a, H. Hüster 1990, D. Heinrich 1991b, D. Heinrich 1995b, H. Pieper u. H. Reichstein 1995, H. Reichstein 1995c
54,58	24,5333333333	Aukštadvaris	K. L. Paaver 1965
54,58	24,5333333333	Aukštadvaris	K. L. Paaver 1965
54,63	39,75	Rjazan'	V. I. Calkin 1956; V. D. Lebedev 1960
54,7	25,25	Vil'njus	K. L. Paaver 1965
54,7	18,3666666667	Junkrowy	M. Sobociński 1979g
54,7	15,3833333333	Kędrzyno (Fst. 1) bei Kołobrzeg	P. Wyrost 1965; Z. Chełkowski & B. Chełkowska 1964a
54,8	49,1166666667	Tankeevka, Tankeevskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
54,88	48,55	Ščerbet'skoe I	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
54,97	49,666666667	Bolgary, Bolgarskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
54.288967	10.889692	Oldenburg	H.R. Stampfli 1961c
55,17	30,2333333333	Vitebsk	V. V. Ščeglova 1969b
55,17	50,166666667	Kurkul'skoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,42	49,7333333333	Imen'kovo, Imen'kovskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,43	13,8	Tankbåten (Ot. von Ystad)	M. Strömberg 1981
55,45	50,2333333333	Troickij Uraj, Troicko-Urajskoe I	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
55,7	13,1666666667	Södertull	E. Iregren 1988
55,7	13,2	Lund	J. Ekman 1973
55,75	25,45	Juodonis	K. L. Paaver 1965
55,98	25,5333333333	Petrašjunaj r.	K. L. Paaver 1965
56,3	26,1833333333	Dignaja	V. I. Calkin 1958b, 1961b, 1962b; K. L. Paaver 1965
56,33	26,3833333333	Olinkalns	K. L. Paaver 1965
56,42	26,3333333333	Asote	V. I. Calkin 1958b, 1961b, 1962b; K. L. Paaver 1965
56,45	24,666666667	Mežotne	V. I. Calkin 1958b, 1961b, 1962b; K. L. Paaver 1965; J. Sloka 1986b
56,48	23,3833333333	Tervete	K. L. Paaver 1965
56,63	23,2666666667	Dobele	K. L. Paaver 1965
56,88	24,4166666667	Kenteskalns	K. L. Paaver 1965
56,9	26,75	Daugmale	V. I. Calkin 1958b, 1961b, 1962b; K. L. Paaver 1965
56,92	27,6666666667	Kišukalns	K. L. Paaver 1965
57,25	22,6166666667	Talsy	V. I. Calkin 1958b, 1961b, 1962b; K. L. Paaver 1965
57,62	39,8666666667	Popad'inskoe bei Jaroslavl'	V. I. Calkin 1962a
57,73	26,9166666667	Ryuge	V. I. Calkin 1962b; K. L. Paaver 1965
57,83	28,3333333333	Pskov	V. I. Calkin 1956
58,2	52,5833333333	Idna-Kar bei Glazova	A. G. Petrenko 1984
58,23	26,45	Peėdy	K. L. Paaver 1965

58,28	12,3333333333	Ekholm	J. Lepiksaar 1991
58,3	12,9166666667	Gudhem	J. Lepiksaar 1975a
58,37	25,6166666667	Naanu	K. L. Paaver 1965
58,38	26,7166666667	Tartu	K. L. Paaver 1965
58,5	26,5	Otepja	V. I. Calkin 1962b; K. L. Paaver 1965
58,55	25,4666666667	Lõhavere	J. Lepiksaar 1938, 1984; K. L. Paaver 1965; L. Lõugas 1997
58,57	31,2833333333	Novgorod	V. I. Calkin 1956; E. K. Syčevskaja 1965
58,68	53,3666666667	Charinskoe bei Averino	A. G. Petrenko 1984
58,98	55,8	Anjuškar	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
59	56	Sandijak	E. G. Andreeva u. A. G. Petrenko 1976
59,33	18,5	Skopintull	S. Sten u. M. Vretemark 1988, S. Sten u. M. Vretemark 1992
59,33	18	Birka	P.G.P. Ericson, E. Iregren u. M. Vretemark 1988, B. Wigh 1998
59,37	26,3333333333	Rakvere	K. L. Paaver 1965
59,47	24,9	Iru	H. Moora 1971
59,53	17,35	Viby	S. Sten u. M. Vretemark 1988, S. Sten u. M. Vretemark 1992
59,92	10,7166666667	Oslo (Fst. Gamlebyen, Mindets Tomt I)	R.W. Lie 1988
60	32,3	Staraja Ladoga	V. I. Calkin 1956; V. D. Lebedev 1960
60,52	55,7166666667	Redikorskoe	E. G. Andreeva u. A. G. Petrenko 1976, A. G. Petrenko 1984
60,7	18,833333333	Alsike (Fst. Tuna)	B. Petré 1980, W. Prummel 1992a
63	14,6666666667	Hedningagärdet	E. Iregren 1997

14 Acknowledgement

This path has certainly been the longest and most challenging of my life. In these 3 years there have been moments of joy, pain, satisfaction, worry, that give to me the opportunity to grow from human and working point of view.

Obviously, it would not have been possible for me to reach this moment, without the people that have been by my side and which I have here the pleasure of thanking.

The first thanks go to the people who have made this work possible more than any other: my mother Liana, my father Stefano, my grandmother Elena and my sister Francesca. They have always been the fulcrum of support and sharing during difficult and happy times.

A big "thank you" goes to my partner, Francesca, who supported me and endured in writing this manuscript and without which I would not have come out healthy from this path, and another huge thanks to all the friends who have always been available in every moment of need.

I really thank Professor Raffaele Sardella, who has supported and helped me not only in the scientific field but also in the human one (and musical) during the last ten years; years that I could summarize in three words: daje daje and daje!

A special thanks goes to the two reviewers of the thesis. To Dr. Kunst, who was very helpful both in sharing his knowledge and in correcting the manuscript, and to Professor Sabol with whom I spent one of the most serene moments of my entire training, with the only regret of not having had the opportunity to meet him before.

Thanks to Fabio Massimo Petti, inexhaustible source of energy and work, who has always encouraged me to do better and more.

A big thank you goes to all the PaleoFactory lab: Flavia, Dawid, Cristina, Federico, Gian, Edoardo, Veronica, Alessio, Alfio, Costantino, Antonio, Beniamino, Ilaria and Lucone that in these years have been like a second family for me. Among these, I will never stop to thank Roberta, for having shared with me madness and frustrations always coming out with big laughter and Bart, who has fueled always the passion and dedication for paleontology, constantly reminding me of the words of Prof. Molà.

I must and want to thank the various institutes that allowed me to collect data for this project:

- Museo di storia Naturale di Genova, G. Doria (Genova, Italy)
- Dipartimento di Studi Umanistici, Università degli Studi di Ferrara
- Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Abruzzo
- Museo di Paleontologia, Dipartimento Scienze della Terra, Sapienza, Università di Roma
- Museo di Storia Naturale, Sez. Geologia e Paleontologia, Università degli Studi di Firenze
- Museo Lama dei Peligni (Chieti, Italy)
- Parco Nazionale della Majella (Abruzzi, Italy)
- Parco Nazionale d'Abruzzo Lazio e Molise (Italy)
- Museo Naturalistico, Fara San Martino (Chieti, Italy)
- MuSe, Museo delle Scienze, (Trento, Italy)
- Is.I.P.U., Istituto Italiano di Paleontologia Umana (Anagni, Italy)
- National History Museum, (Bratislava, Slovakia)
- Department of Geology and Paleontology, Comenious University (Bratislava, Slovakia)
- Slovak museum of nature protection and speleology (Liptovsky Mikulas, Slovakia)
- National History Museum (Wienn, Austria)
- Department of Palaeontology, Wien University (Wienn, Austria)

and especially all the people who work within them: Dr. Spartaco Gippoliti, Dr. Maria Chiara Deflorian, Dr. Maria Adelaide Rossi, Dr. Silvano Agostini, Prof. Marcello Tropeano, Dr. Elisabetta Cioppi, Dr. Fabio Bona, Prof. Marta Arzarello, Prof. Paul Mazza, Prof. Gernot Rabeder, Dr. Mario Rossi, Prof. Augusto Vigna Taglianti and Prof. Paolo Ciucci who have all shown themselves to be extremely helpful and collaborative.

In part, I want to dedicate this work to Prof. Mauro Cristaldi, who more than anyone else has taught me and pushed me to never stop being curious.

In writing these thanks, I asked myself whether to include at the beginning or at the end, the people who more than any other have contributed to this result, so I decided to put them in both positions, and I want to dedicate this thesis to my family, the people I admire and esteem most in this world, and a little also to myself, for fulfilling a six-year-old's dream of becoming a paleontologist.

Questo percorso è stato sicuramente quello più lungo e impegnativo della mia vita. In questi 3 anni si sono susseguiti momenti di gioia, dolore, soddisfazione, preoccupazione, che mi hanno fatto crescere sia da un punto umano che lavorativo.

Ovviamente non sarebbe stato possibile per me arrivare a questo momento se non fosse stato anche per le persone che mi hanno accompagnato e incentivato, sia lavorativamente che psicologicamente e che qui ho il piacere di ringraziare.

Il primo ringraziamento va senz'altro a quelli che più di tutti hanno reso possibile questo lavoro: mamma Liana, babbo Stefano, nonna Elena e la sorellina Francesca. Loro sono stati fulcro e sostegno durante i momenti difficili e fonte di gioia e condivisione durante quelli felici.

Un grazie enorme va alla mia compagna, Francesca, che mi ha supportato e sopportato nella scrittura di questo manoscritto senza la quale non sarei uscito sano da questo percorso.

Grazie a tutti gli amici, che sono sempre stati disponibili in ogni momento di bisogno.

Ringrazio davvero di cuore il prof Sardella che in tutti questi anni (10 oramai) mi ha appoggiato ed aiutato non solo in campo scientifico ma anche in quello umano (e musicale), anni che forse potrei riassumere in tre parole: daje daje e daje!

Un particolare ringraziamento va ai due revisori della tesi. Al dott. Kunst che è stato disponibilissimo sia nel condividere le sue conoscenze, sia nella correzione del manoscritto, ed al professor Sabol con il quale ho passato uno dei periodi più sereni del mio percorso formativo, con l'unico rammarico di non aver avuto la possibilità di conoscerlo prima.

Grazie a Fabio Massimo Petti, fonte inesauribile di energia e di lavoro, che mi ha sempre spronato a fare meglio e di più.

Un grazie enorme va a tutto il laboratorio di PaleoFactory: Flavia, Dawid, Cristina, Federico, Gian, Edoardo, Veronica, Alessio, Alfio, Costantino, Antonio, Beniamino, Ilaria e Lucone che in questi anni sono stati come una seconda famiglia per me. E poi a Roberta, per aver condiviso con me pazzie e frustrazioni uscendone sempre con grosse risate e a Bart, che ha alimentato in ogni momento la passione e la dedizione per la paleontologia, ricordandomi costantemente le parole del prof. Molà.

Devo e voglio ringraziare i vari istituti che mi hanno permesso di raccogliere i dati per questo progetto: il Museo di storia Naturale di Genova, G. Doria; il Dipartimento di Studi Umanistici, dell'Università degli Studi di Ferrara; la Soprintendenza Archeologia, Belle Arti e Paesaggio dell'Abruzzo; il Museo di Paleontologia, Dipartimento Scienze della Terra, Sapienza, Università di Roma; il Museo di Storia Naturale, Sez. Geologia e Paleontologia, Università degli Studi di Firenze; il Museo Lama dei Peligni; il Parco Nazionale della Majella; il Parco Nazionale d'Abruzzo Lazio e Molise; il Museo Naturalistico di Fara San Martino; il MuSe, Museo delle Scienze di Trento; l' Is.I.P.U., Istituto Italiano di Paleontologia Umana; il National History Museum, (Bratislava, Slovacchia), il Dipartimento di Geologia e Paleontologia, Comenious University (Bratislava, Slovacchia); lo Slovak museum of nature protection and speleology (Liptovsky Mikulas, Slovacchia); il National History Museum (Vienna, Austria); il Dipartimento di Paleontologia, della Wien University (Vienna, Austria) e soprattutto tutte le persone che lavorano al loro interno: il dott. Spartaco Gippoliti, la dott.ssa Maria Chiara Deflorian, la dott.ssa Maria Adelaide Rossi, il dott. Silvano Agostini, il prof. Marcello Tropeano, la dott.ssa Elisabetta Cioppi, il dott. Fabio Bona, la prof.ssa Marta Arzarello, il prof. Paul Mazza, il prof. Gernot Rabeder, il dott. Mario Rossi, il prof. Augusto Vigna Taglianti ed il prof. Paolo Ciucci che si sono mostrate tutte estremamente disponibili e collaborative.

In parte voglio dedicare questo lavoro al prof. Mauro Cristaldi che più di chiunque altro mi ha insegnato a non smettere mai di essere curioso.

Nello scrivere questi ringraziamenti, mi sono chiesto se inserire all’inizio o alla fine le persone che più di ogni altro hanno contribuito a questo risultato; per non sbagliare ho fatto tutti e due.

Voglio quindi dedicare questa tesi alla mia famiglia, e a me stesso, per aver esaudito il sogno di un bimbo che già a sei anni aveva deciso di voler diventare un paleontologo.