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The Late Pleistocene site of Equi (Massa, Apuane Alps): revaluation of historical data and new discoveries.

Morphological comparison of Italian and European Felids

Il sito del Pleistocene superiore di Equi (Massa, Alpi Apuane): rivalutazione dei dati storici e nuove scoperte.

Comparazione morfologica dei felidi italiani ed europei

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levan di terra al ciel nostr'intellecto

Il Canzoniere, Canto X
Francesco Petrarca (1304-1374)

1. Contents

1. Contents **1**

2. Introduction **5**

2.1. Purposes of the study 5

2.2. Organization of the text 7

2.3. Pleistocene and the large carnivore assemblage of MIS3 9

3. Materials and Methods **13**

3.1. Materials 13

3.2. Comparative materials 16

3.3. Methods 18

- Recording of paleontological data 18
- Georeferenting of European sites 21
- Tools for the dimensional and morphological analysis 22
- Abbreviation 23

4. The Late Pleistocene site of Equi **25**

4.1. Early studies 25

4.2. New research 31

4.3. Stratigraphical analysis of De Stefani's historical collection 33

- Metods 38
- Results 41
- Discussion 45

5. Carnivorans from Equi **49**

5.1. The faunal guild 49

5.2. Family Felidae Fischer Von Waldheim, 1817 52

5.2.1. The remarkable *Panthera Pardus* (Felidae, Mammalia) record: taphonomy, morphology, and paleoecology 55
- Anatomical description 56
- Taphonomy 73
- Bites 79
- Sex determination 80
- Body size 83
- Cubs 95

5.3. Family Canidae G. Fischer de Waldheim, 1817 99

5.3.1. *Cuon alpinus* (Pallas, 1811) (Mammalia, Carnivora): anatomical analysis and palaeoethological contextualisation 105
- Anatomical description 105
- The dhole within the carnivore guild 118
- Concluding remarks 120

6. Focused studies on Felids 123

6.1. Critical overview about cranial variability of European and African lions (*Panthera leo*) 125
- Different scholars for the European lion 127
- General overview 130
- Cranial description 134
- Results 135

6.2. Lynx remains from the Pleistocene of Valdemino Cave (Savona, Northwestern Italy), and the best preserved occurrence of *Lynx spelaeus* (Carnivora, Felidae) 142
- The Valdemino Cave 144
- Taphonomical remarks 147

- Description 147
    - *Lynx spelaeaus* (Boule, 1919) 147
    - *Lynx* sp. 151
- Discussion 152
- Evolutionary implications 155

7. Summary and Conclusions 159

8. References 169

9. Appendix 205

10. About the author 227

10.1. Future research 232

11. Acknowledgments 235

2. Introduction

2.1. Purposes of the study

This study focuses on the morphological and systematic description of the outstanding historical collection from the Late Pleistocene site of Equi, Apuane Alps (northwestern Tuscany). Historical collections usually do not preserve information about the stratigraphical context, thus lack basic information for understanding and decoding the significance of a particular site or faunal association. Today, many collections represent just a proof of the richness of the sites, but data on bones distribution within the deposit is unknown, and the represented species result as a mixture from different layers, preventing the interpretation of many aspects of the record (from taphonomy, to palaeoecology, to climatic changes, etc.). The very large collection dug out from the Equi site in the 1910s by De Stefani represents a great exception, and in this study we reevaluate, with new interpretations and discoveries, the careful and “modern” professional work of De Stefani and his team.

The main part of the study concerns the leopards from Equi, for its exquisite amount of specimens, both from young and adult individuals and for the general paleontological debate about its presence in caves and its role as bone accumulator.

The other determined carnivores from Equi are not considered in detail within this study, with the exception of the dhole, a member of the family Canidae which sporadically appears in Italy and Europe and even more rarely is described for its postcranial bones. As a fortunate excetion, dhole is found in the De Stefani collection from Equi with several cranial and postcranial remains, and their features deserved a deeper analysis.

Finally, additional studies have been performed on lion and lynx from other Italian Middle to Late Pleistocene sites, taking into account their scarce frequency at Equi.

The modern knowledge about morphology, taxonomic position and the evolution of the family Felidae in Europe are sufficiently advanced for the last half million of years (from mid Middle Pleistocene up to the Holocene), with the general presence of large lions as top predator, and leopard, small lynx, and wild cats as subordinate species. In this thesis, I also analyze the paleoecological relationships among these large carnivores in order to clarify their behaviour in the cold climatic conditions of the MIS3.

2.2. Organization of the text

This study is divided into four main parts.

The first one is a general introduction on the paleontological context, the fossils used for comparisons and the methodology. The second (and main) part focuses on Equi and its exceptional finds, while the third one concerns more specifically on concurrent studies brought out during the elaboration of this thesis. Finally, a conclusive chapter underlines and resumes the main results.

In the introduction, the Italian Middle and Late Pleistocene is summarily presented (Chapter 2.3). In Materials and Methods (Chapter 3) are described the sites and fossils used for my comparative analysis. The main stock of studied material comes from Equi, which represent the core of this manuscript. Few other remains from Middle and Late Pleistocene European sites were evaluated, and compared to fossil and modern osteological collections (Chapter 3.1, 3.2). The fossils were analyzed using a traditional comparative method (morphologically and dimensionally), and each find was measured, recorded and described. The huge amount of information recoded was reorganized in a standard matrix-database explained in Chapter 3.3 and also using software for distributional analysis, which allows a graphical return of the paleontological information and intra and inter-site analysis. I took advantage from the possibility to retrieve the geographical coordinates of the sites, georeferencing the data.

Chapters 4 and 5 focus on Equi and the fossil record form historical excavation (De Stefani's collection, excavated in 1910-1917). I described the historical investigation before (Chapter 4.1) and after 1996 (Chapter 4.2). In order to allow an objective and continuative comparison between the historical and modern investigations, I set a link between the osteological labels (which accompany each fossil) and the exhaustive publication published by De Stefani in 1917. Chapter 4.3 explain in detail approach and results. The stratigraphic relocation of the fossils allowed reconsidering also the whole faunal association from Equi, and in Chapter 5.1 are briefly described the carnivorans dug out from the site (in fact, about the entire collection is composed by such kind of animals), focusing the attention on the two main species: the leopards (Chapter 5.2.1) and the dhole (Chapter 5.3.1), which represents exceptional and exciting discoveries in the European paleontological panorama.

Chapter 6 is entirely devoted to collateral studies, about the taxonomical position of the European lion (Chapter 6.1.1) and the exquisite preservation of lynx remains from the Middle and Late Pleistocene site of Valdemino Cave (Chapter 6.1.2).

Finally, the conclusions (Chapter 7) summarize the different analyses about the main species of Italian felids, evaluating the progresses of the knowledge and new interpretations and perspectives pointed out along these three years of study.

Chapter 9 shows the matrixes and table of my database (with the catalog and measurements) and Chapter 10 briefly describe the author and proposes for future paleontological researches about the exciting faunal guild from Equi.

Finally, acknowledgments are reported in the Chapter 11, even though one paragraph will never be enough for express all my gratitude.

2.3. Pleistocene and the large carnivore assemblage of MIS3

The term Pleistocene was proposed by Charles Lyell in 1839 and is characterized by the presence of modern fauna, quite similar to the extant species. It includes a time range from 2,588 My up to 11,7 ky ago. The Plio-Pleistocene boundary was related to the first climatic deterioration, determined for the appearance of typical "cold-water neighbours" such as *Arctica islandica* and *Hyalinea baltica* at the end of the Neogene. The GSSP for the beginning of Pleistocene was nailed down at Monte San Nicola (Sicily, Italy) (Gibbard, 2004; Pillars and Gibbard, 2012).

The Pleistocene is usually divided into three subdivision, used for the first time in 1930s with a chronological significance of Early, Middle and Late Pleistocene (Masini and Sala, 2007). The Early-Middle boundary was placed at the Brunhes-Matuyama paleomagnetic reversal epoch (781 ky) while the Middle-Late boundary is not yet identified, but it is generally recognised with the Eemian Stage from the 2nd INQUA Congress in 1932 and in 1996 it was posed in a little younger time, at the base of the Marine Isotope Stage 5 (at about 129 ky) (Gibbard, 2004; Pillars and Gibbard, 2012).

Mammal paleontologists divide each subepochs of the Pleistocene following the composition of faunal association (Small and Large Mammal Ages). In this thesis I refer to Italian chronology and use Villafranchian, Galerian and Aurelian Ages according to the biochronological unit determined by Azzaroli et al. (1982, 1988), Gliozzi et al. (1997), and Rook and Martínez-Navarro (2010). The former authors identified the Faunal Unit Biochronological Scale (Figure 1), describing characteristic faunal associations for each time unit. The name of each unit is the most significant site for each fauna. All the paleontological sites can be generally referred to one of such Faunal Units (FU).

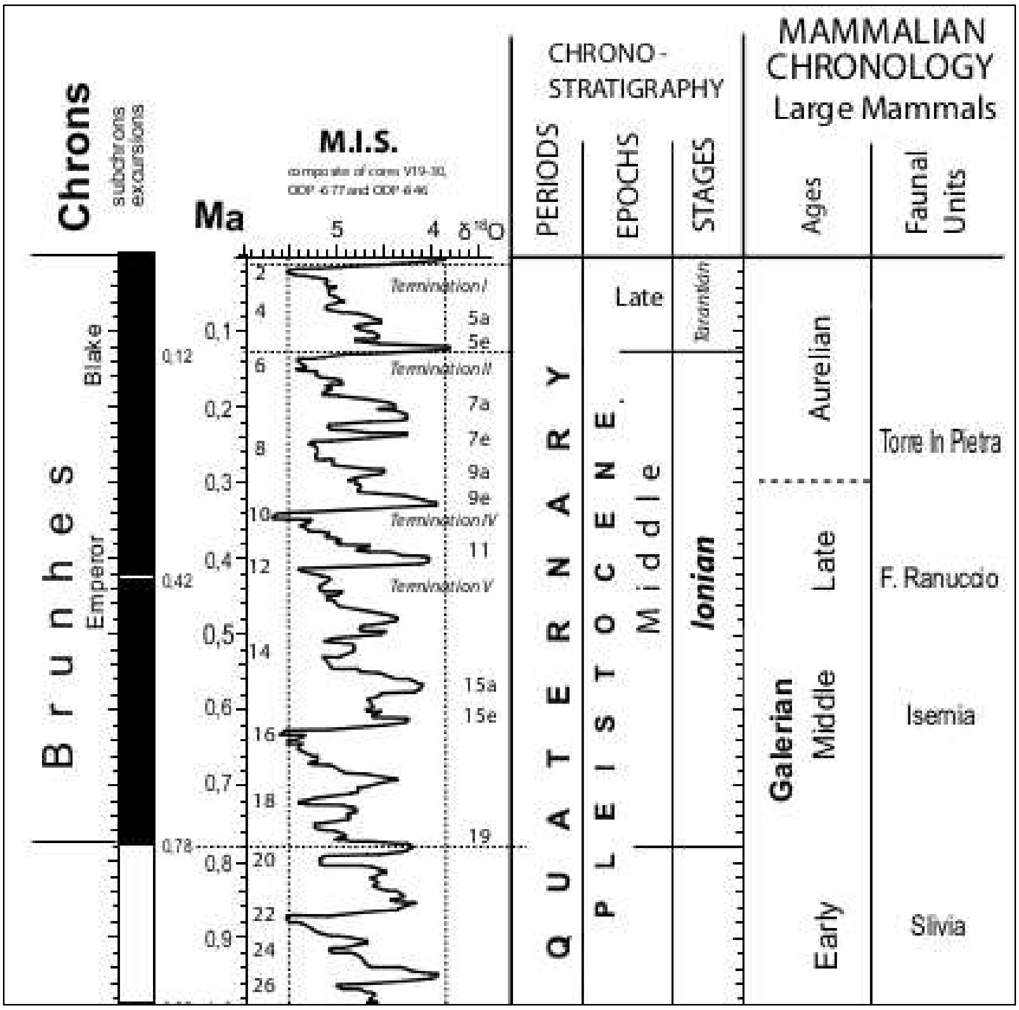

Figure 1: Time scale of the last 1 My. The right coloumns report the Faunal Units recognized by Gliozzi et al. (1997) included in the Galerian and Aurelian Mammal Ages. The large mammal chronology is ordered within the Chronostratigraphy, the Marine Isotope Scale and Paleomagnetism.

For the Late Pleistocene, the chronology is best identifiable using the Marine Isotopic Stage (MIS). The MIS are calculated using the $\delta^{18}O$ ‰, i.e. the variation of oxygen isotope 18 and 16. These two isotopes have a different number of neutron and consequently a little but sufficient different mass and weight, changing with a different velocity their physic state in relation to the temperature. As result, the $^{16}O/^{18}O$ ratio change across the time and the oscillation can be read in ice cores and are correlated to the temperature.

The MIS3 (spanning from about 56 up to 24 ky ago; Siddall et al., 2008) is generally referred to an interstadial, i.e. a warmer phase compared to the previous and follow intervals, but the $\delta^{18}O$ ‰ shows a continue and progressive decreasing of temperature per year through the time, even colder than today.

In Italy, the large mammal fauna of MIS3 was characterized by the persistence of several large species of carnivorans. In that time several cold species showed their last occurrence before the turnover of the LGM. *Ursus spelaeus* Rosenmüller, 1794, is generally frequent in the central European sites (Kempe and Döppes, 2009; Diedrich, 2006) and northern Italy (i.e. Grotta del Broion in the Verona province, Sala 1980; Bon et al., 1991), becoming rare during the MIS3 and completely extinct at around 24 ky ago from the Alps (Pacher and Stuart, 2008). *Crocuta crocuta spelaea* (Goldfuss, 1823) became extinct approximately at the same time (Stuart and Lister, 2007) but the frequency of this scavenger animal is really high during the early MIS3 reaching also central and southern Italy, namely at Buca della Iena, near Equi (Pitti and Tozzi, 1971), Tana delle Iene near Bari (Giaccio and Coppola, 2000), but also at Grotta S. Teodoro in Sicily (Bonfiglio et al., 2008; Mangano, 2011). Like hyenas, *Panthera leo spelaea* was spread in Europe and Italy from the Galerian, but it disappeared just before the LGM, at about 20 ky (Stuart and Lister, 2011). It frequently inhabited caves, as well as hyenas and bears and together represent the major part of the carnivore assemblage in cave deposits at the end of Aurelian.

Smaller species, such as *Lynx lynx*, *Felis silvestris*, *Canis lupus* and *Vulpes vulpes*, continued to characterize the faunal deposits also after the LGM, showing a similar phylogeographic history (Kutschera et al., 2013) but, while the two canids increase their frequency in many Italian sites, the two smallest felids are always represented by a small number of remains. At Equi, for example, the lynx is represented by only one third phalanx (*Lynx* cf. *lynx*) and a humeral fragment, as well as wild cat which was represented also by one right astragalus (Del Campana, 1954). The ranges and chronological variability of *P. pardus* and *Cuon* *alpinus* are more doubt, representing two quite weak protagonists in the Late Pleistocene scenario.

After the MIS2, the huge number of hunters decreased and the sole *Ursus arctos* (recorded for the first time, in Italy, in the Fontana Ranuccio FU; Sardella et al., 2006) continue to survive in Europe among large carnivorans.

3. Materials and Methods

3.1. Materials

In this thesis I describe the results of my studies on the fossils from the historical excavations carried out between 1910 and 1917 by Carlo De Stefani at Equi. Today, all the fossils from those ancient excavations are kept in the Geology and Palaeontology section of the Museum of Natural History of the University of Florence (De Stefani collection) and are partially shown there within the permanent exhibition. The whole data set about cranial and appendicular fossils of leopards and dholes was analyzed in detail, while the labels of the other species were considered only for the reconstruction of the distribution of fossil assemblage within the stratigraphic sequence.

I also focused my attention to the direct analysis of fossil crania of lions from Late Pleistocene European sites (see Chapter 6.1), namely Zoolithen Cave (the holotype; Dietrich, 1968), Igric Cave (Kormos, 1914) and Pocala Cave (Battaglia, 1922) (Table 1).

Zoolithen Cave is also known (since 1774) as Gailenreuth Cave (Bavaria, southern Germany). The stratigraphic record had been polluted and only an approximate age could be inferred dating basal speleothems, between the MIS3 and MIS8 (Rosendahl & Kempe, 2004). Diedrich (2008) rediscovered the holotype of the European lion (MB.Ma.50948) from this cave and described it as a large adult male; two other skulls were considered from the same cave (MB.Ma.48115 and MB.Ma.50947). All the specimens are housed in the Naturkunde Museum of Berlin (Rosenmüller collection). The same cave is the type locality for the holotypes of *Ursus spelaeus* Rosenmüller, 1794 and *Crocuta crocuta spelaea* Goldfuss, 1823 (Kempe and Döppes, 2009).

Igric Cave is a typical Late Pleistocene cave. The assemblage includes *Crocuta crocuta spelaea*, *Panthera leo spelaea* and *Ursus spelaeus* (Kormos, 1914; Hankó, 2007). The two almost complete specimens V.60.1785 and Ob-2978 are housed in the Hungarian Natural History Museum and the Hungarian Geophysics and Geological Institute in Budapest, respectively.

Finally, I considered the two crania from Pocala Cave are part of the permanent exhibition of the Geological and Paleontological Museum of the University of Padua. The specimens were determined as a large lion male, MGP-PD25260, and a smaller female, MGP-PD25262. The Cave, dating back to the Late Pleistocene (Bon et al., 1991), was signalled for the first time in 1893 and excavated in different seasons, until very recent times, by the Museum of Natural History of Trieste (Lazzaro and Tremul, 2003).

inv. n.	**Species**	**Location**	**Sex**	**Age**
DA-AMU 02	*P. leo*			a
DBE H73/38	*P. leo*			a
DBV 807	*P. leo*			a
MZ-PD M153	*P. leo*			a
MZS 490	*P. leo*	Barbary	m	a
MZS 8459	*P. leo*		m	a
MZS 1910	*P. leo*	Beles Cogani, Somalia	f	a
MZS 1911	*P. leo*	Bardera, Somalia	m	y
MZS 2131	*P. leo*	Bur Acaba, Somalia	m	a
MZS 2132	*P. leo*	Chisimaio, Basassa, Somalia	f	y
MZS 3394	*P. leo*	Giohar, Somalia	m	y
MZS 3522	*P. leo*	Gelib, Somalia		a
BNM MB.Ma.50948	*P. leo spelaea*	Zoolithen Cave		a
BNM MB.Ma.48115	*P. leo spelaea*	Zoolithen Cave		a
BNM MB.Ma.50947	*P. leo spelaea*	Zoolithen Cave		a
HNM V.60.1785	*P. leo spelaea*	Igric Cave		a
HNM Ob-2978	*P. leo spelaea*	Igric Cave		a/o
MGP-PD 25260	*P. leo spelaea*	Pocala Cave		a
MGP-PD 25262	*P. leo spelaea*	Pocala Cave		a
DA-AMU 01	*P. tigris*			a
MZ-PD M156	*P. tigris*			a
MZS 8460	*P. tigris*			a

Table 1: Specimens of large Felidae used for the taxonomical revaluation of European lions.

The specimens of lynxes from Valdemino Cave were also considered in this work, since they represents the oldest and best-preserved collection of *Lynx spelaeus*. The cave is located near Savona (Liguria, western Italy) and was discovered in the mid-twentieth century. A nice sample of relatively well preserved remains of such a small lynx was found in the lower layer, generally referred to the Middle Pleistocene (corresponding to the Isernia FU, in the western European Biochronological subdivision). Today, the fossils are temporarily housed in the Department of Earth Science at the University of Florence.

All the considered specimens are recorded in a dedicated database whose rationale is detailed further on in this chapter and provided in a printed version in the Appendix (Chapter 9).

3.2 Comparative materials

More than 450 sites have been recorded in my database for comparative purposes, from 23 European countries. Each single find has been recorded associated with information about the specimen, site, chronology and bibliographic reference (if any) (see next paragraphs).

For the detailed comparison of the fossils considered within the present work, I basically have used direct observation (for collections in Italy, Germany and Hungary), but also measurements of fossils and modern skeletons from other publications have been used for dimensional analysis.

In particular reference papers for my studies have been: Kotsakis and Palombo (1979), Spassov and Raychev (1997), Nagel (1999), Hemmer et al. (2001), Meijaard (2004), Cardoso and Regala (2006), Madurell-Malapeira et al. (2010), Marciszak et al. (2011), Baryshnikov (2011), Cherin et al. (2013b), Diedrich (2013), and Saoqué et al. (2013, 2014a,b), Stimpson et al. (2014) for the study about leopards; Bona (2006), Argant (1988) for lion cranial morphology; Bonifay (1971), Testu (2006), Cipullo (2010), and Cherin et al. (2013a) for dental and postcranial analysis of lynxes.

For this research project, I compared leopards from Equi with materials from the Early Pleistocene site of Stráská Skála, the early Middle Pleistocene site of Mauer (Schütt, 1969), the Middle Pleistocene sites of Soave Sentiero (Pasa, 1947), Cerè Cave (Ghezzo et al., 2014), and Upponyi (Hankó, 2007), and the Late Pleistocene of Fumane Cave (Cassoli et al. 1991), Lambrecht Cave (Janossy, 1986), Niederlehme (Fischer, 2000), Baumann's Cave (Diedrich, 2013), Vraona Cave (Nagel, 1999). The site of Vraona Cave and Los Rincones (Saoqué et al. 2013, 2014a, 2014b) represented a considerable source for comparison. The latter was recently descovered (2005) and attributed to the Late Pleistocene on the basis of its faunal assemblage. Leopards from this cave was included to *Panthera pardus spelaea* variability; meanwhile, Nagel (1999) studyed the older Vraona leopard collection creating a new subspecies, *P. pardus vraonensis,* for the massive autopodials. Both these collections seem to underline the similitude (evolutive convergene) between the European leopard and snow leopard, *P. uncia*, and in my thesis I evaluate the variability of leopard from Equi in order to clarify this point. A third analysis conducted by Spassov and Raychev (1997) was considered with the purpose of comparing the specimens from Equi to the dental morphology of leopards from Triagalnata Cave.

All these collections are stored in several Italian and foreign museums: in Italy the Museum of Natural History of the University of Florence (Paleontological Section), the Museum of Geology and Paleontology of the University of Padua, the Civic Museum of Natural History of Verona, Civic Museum of Natural History of Trieste; in Germany, Berlin Museum für Naturkunde, Munchen Paläontologisches Museum; in Hungary the Magyar Természettudományi Múzeum in Budapest.

The determination of *Cuon alpinus* was done using direct comparison with University osteological collections (Florence and Ferrara Universities; Civic Museum of Natural History of Venice). It was dimensionally compared with wolves from the same site of Equi and other sites (i.e. Cava Filo, Bologna, MIS3) and foxes from Cerè Cave (Veneto).

Lynx remains were compared to *Lynx issiodorensis valdarnensis* housed in the Natural History Museum (Geology and Paleontology Section) of the University of Florence and bibliographic sources. In addition, modern osteological collections represented the main comparative materials from Italy: the osteological collection of the Archaeozoology laboratory (University of Florence); Museum of Natural History (Zoology Section "La Specola"), Florence; Museum of Natural History of Venice; Department of Biology and Agriculture and Department of Biology "A. Vallisneri", and the Museum of Zoology of the University of Padua; Archeozoology Laboratory of the University of Siena; the Vertebrate Paleontology Laboratory of the University of Ferrara.

3.3 Methods

Recording of paleontological data – The cornerstone of paleontological research consists in the possibility to neatly organize objective data about the stratigraphic record and all the possible details (taphonomical and paleontological) of the fossil under examination.

To maximize the data availability and management, this thesis is organized on a thematic and opensource database in order to avoid expenses and management and to guarantee the best data accessibility. The graphic user interface for information recording is pgAdmin version 1.16.1 (2013) and is a PostgeSQL Tool.

Therefore, data are being inserted into three core tables cross-related with binary constraints (Chen, 1977), which were associated to other attribute-tables, regarding additional information. The core records essential information used by paleontologists, namely SITE, FIND and PUBLICATIONS (Figure 2). Other sub-tables linked to it, record collateral information. Therefore the tables about museums (MUSEUM), collections (COLLECTION), in addition to information regarding the fossil itself (SPECIES), were added to the system. Moreover, the reference site is often associated with information about the excavation (DIG DATA), the chronology (CHRONOLOGY) and the age (DATING). All these tables are cross connected as, for example, when a collection is stored in one or more museum warehouses, a site chronology could refer to more dating, etc.

Finally, the FAUNAL_LIST table was added to contextualize information about a specimen recorded in FIND. The faunal list provides information on relative chronology and on species frequency in the site.

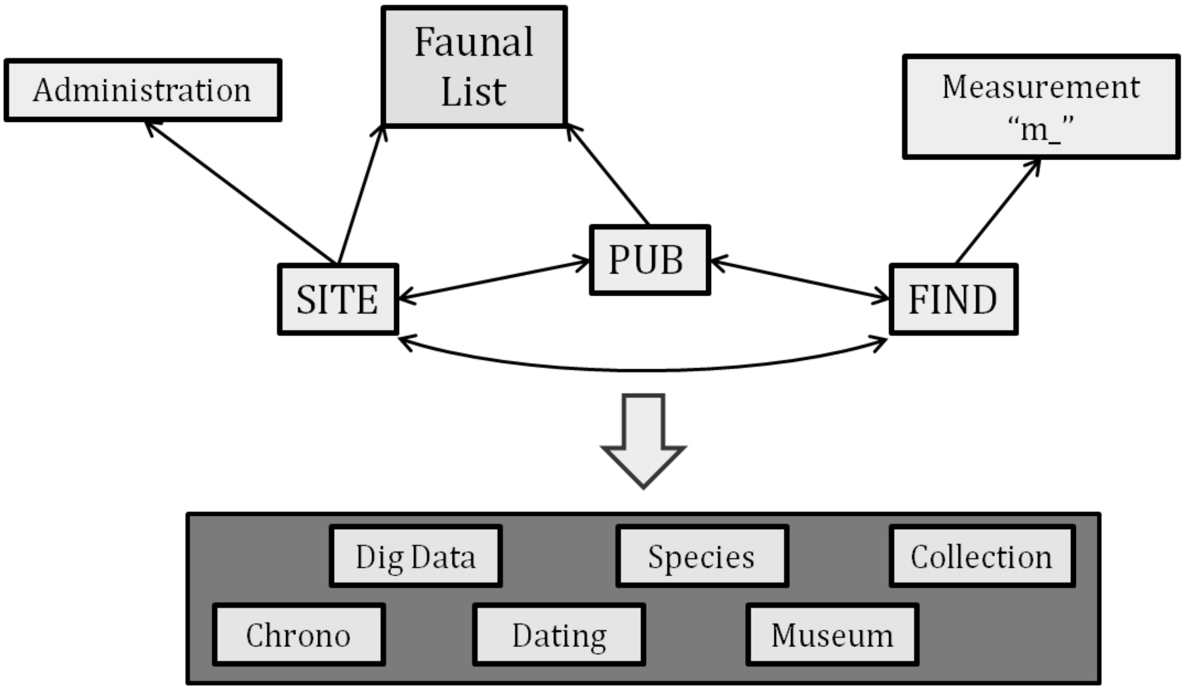

Figure 2: graphic overview of the database organization. The three tables in the middle are the core of the db, namely SITE, PUB (publications) and FIND. Together were linked to specific tables, recording all the correlated information. The measurements of each singular specimen have been recorded in tables named with the prefix "m_" (Measurement in figure). For more details see the text and Chapter 9.

All the remains analyzed during the three year of research were archived into the FIND table, obtaining a matrix of 1793 remains of the Felidae family. Each specimen was measured and numbered were stored in independent tables for each attribute (ten tables named with prefix "m_"). The SITE table contains information about a paleontological site such as map localization (city, province, region), geo-localization (with geo-referencing WGS84) and site chronological dating. The former is fundamental in order to draw graphics of the paleontological record contained in the databases (see the next Chapter).

Finally, the information supplier was recorded into the table PUBLICATIONS which contains scientific publications, book and other sources of information both historic and current (e.g. web site). These information sources could be related either to the site or the remains. As of today the PULICATION table contains 1048 records.

Concerning the content and status of correlate attributes, it is necessary that the database could manage many kind of information, and unfortunately often these data are not comparable to each other. An example of easy understanding is that relative dating is not comparable with radiometric (absolute) dating because the chronological ranges are not the same. Or, it is not possible to exactly identify a fossil using binomial Linnean naming (Linneus, 1758) and the determined ranks (genre, species, common name) creates a cloud of unrelated information: the different denominations create sets that increase in size but lose details.

Following some examples, the medium Pleistocene contains the Galerian Age and Aurelian Age (Gliozzi et al., 1997), which differ in terms of many faunal aspects, like species and weather. Therefore, two dating such as 200Ky and 800Ky mean important differences that will be lost if the biochronological name that contains both is used.

As we will see hereinafter (Chapter 6.1), the specific determination of the European lion changed over the years. Since the first original description of Goldfuss in 1810, the lion fossil was named in the beginning as *Leo spelaea*, which changed afterward and took the name of *Panthera spelaea* (Sotnikova and Nikolskiy, 2006), *Panthera leo spelaea* (Schütt, 1969a), *Panthera tigris spelaea* (Groiss, 1996), *Panthera* (*Leo*) *spelaea* (Sotnikova and Foronova, 2014). If there are doubts about naming, it is possible to use only the genus *Panthera* sp., or of similarity with other species, *Panthera* cf. *spelaea*. These attributions always identify the same conceptual set of "a big cat who lived in Europe during the medium-upper and upper Pleistocene". The only way to correctly manage such kinds of information is to choosing a-priori how to name this set of animals and identify the chronological range.

This problem is adressed and solved using the most suitable name that synonymized the species. It is also necessary, for species and chronologies, to produce different research projects that consider the different increasing grouping levels.

Georeferencing of sites - Georeferencing the paleontological sites consists in locating a site in the space and then picking up its coordinates in relation to a prefixed reference system. In this thesis, WGS84 has been used as standard reference system (which is used, among others, by Google Maps and GPS).

The graphic performance for the GIS maps has been possible using the QuantumGIS software (QGIS) version 2.2.0-Valmiera, linked to the PostgreSQL database by the PostGIS extensor. The latter has made it possible for me to extend the recorded coordinates into a new spatial format, manageable within the QGIS platform.

At present, this branch of studies is one of the main types of research currently growing in importance in palaeontology, mostly due to implementation of different faunas and the deeper analysis about animal migrations, including the genus *Homo* (Field et al., 2007; Carto et al., 2009).

During my thesis, the chronic loss of precise information about the sites has been represented as one of the main problems (particularly for the historical collections, but not only), both for intrasite and intersite analysis. Precisely located information in the territory is essential when a regional comparison among sites is carried out (intersite analysis). Unfortunately, the site investigated in historical times recorded only superficially of incompletely identified locations so some kinds of analysis cannot be done for geo-palaeontology.

When the database and the software for the management of coordinates are linked together, it is possible to manage all the data obtaining, in this case, initial graphic feedback, i.e. the pointed-distribution of fossils in Europe, recorded in the database in any of the tables related to the SITE matrix (which recorded the coordinates - Figure 2).

For example, Figure 37 represents the distribution of *Cuon alpinus* in Europe, while Figure 3 shows the lion and leopard distribution recorded in the table FAUNAL-LIST for the Italian Peninsula. Lion sites are divided into the two sets with the subspecies *P. leo fossilis* (Isernia and the complex of sites near the town of Soave – yellow square) and *P. leo spelaea* (including the site of Equi – green diamonds). This simple map reveals only the presence of lion and leopard in the different sites, without any information about the amount of fossils or about the relationship among these sites (i.e. differences of altitude, the presence/absence of coeval sites, etc.).

The distributional study of felids lies beyond the purposes of this thesis, but undoubtedly the recovering of paleontological information as computer data allows me to create a solid instrument that, with future implementations, will operate as a source for new research.

Tools for the dimensional and morphological analysis

Cranial and postcranial osteological nomenclatures follow Barone (2003a).

Dental morphology follows Barone (2003b) and Hillson (1996). Deciduous teeth were described following the terminology of Butler (1948) and Rawn-Schatzinger (1983).

For the estimation of dental emersion in leopards, I cross-checked data about extant animals (Broom, 1949; Slaughter et al., 1974; Crowe, 1975; Rawn-Schatzinger 1983; Stander, 1997; Férnandez et al. 2002).

The epiphysis ossification was evaluated for relative aging of the fossils.

Measurements (taken with a digital calliper with accuracy at the nearest 0.05 mm) followed von den Driesch (1976) or are differently cited in the follow paragraphs.

Fossils were photographed using a reflex camera (Nikon camera D40X and Nikkor-lens 18–55 and 105 micro). PAST 3.02a software was used for the cluster analysis (Hammer et al. 2001); digital images were modified using GIMP 2.8.2 and Inkscape 0.48, softwares for image processing.

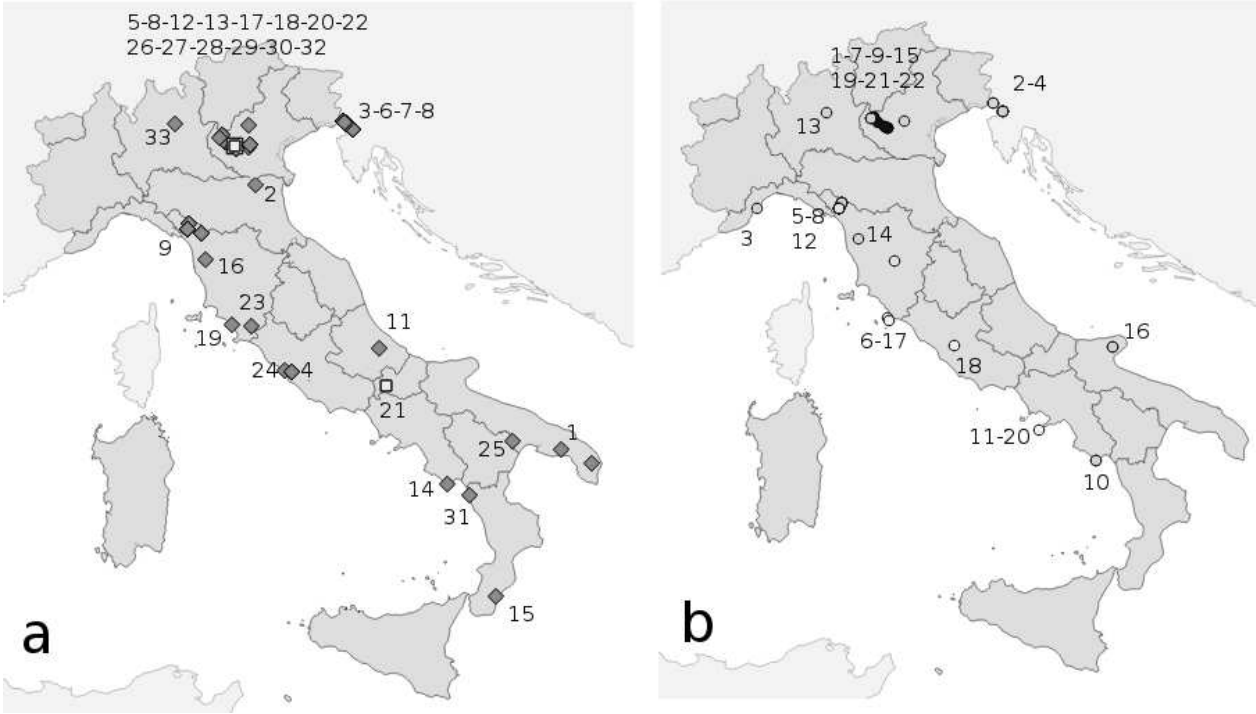

Figure 3: distribution of lion (a) and leopard (b) in the Italian Peninsula: *P. leo fossilis* (yellow square); *P. leo spelaea* (green diamond); Middle Pleistocene leoprads (blue circles); Late Pleistocene leopards (green circles); leopard reported without chronology (gray circles). For references of sites see Chapter 9.

Abbreviation

inv. n.: inventory number

MNI = Minimal Number of Individuals

FU = Faunal Unit

<u>Cranium and teeth</u>:

C-M1: total length of the canine and cheek teeth

d = deciduous tooth

L = length

LP4: total length of the upper carnassial

m1L: total length of the lower carnassial

p-m: total length of lower dental cheek series

<u>Postcranium</u>:

B = breadth

GL = greatest length

SD = minimum diameter of the diaphysis

Bp = proximal breadth

Dp = proximal depth

Bd = distal breadth

btr: width of the trochlea

Dd = distal depth

Mc = metacarpus

Mt = metatarsus

<u>Ages</u>:

a: adult

y: young

o: old

<u>Institutions:</u>

MZS = Natural History Museum of the University of Florence

DBE = Department of Biology and Evolution, University of Ferrara

MZ-PD = Museum of Zoology, University of Padua;

MGP-PD = Museum of Geology and Palaeontology, University of Padua

DBV = Department of Biology “A. Vallisneri”, University of Padua

DA-AMU = Department of Biology and Agricolture, University of Padua

HNM = Hungarian Natural History Museum, Budapest

BNM = Natural History Museum, Berlin

4. The Late Pleistocene site of Equi[1]

4.1. Early studies

The Equi Cave is named after the nearby hamlet “Equi Terme” located in the northern side of the “Parco Regionale delle Alpi Apuane” (Massa-Carrara, Tuscany). The Equi “baths” are known since Roman times because of the occurrence of sulphurous hot springs (Tonini, 1907). The entire area is also known for the occurrence of an extensive karstic complex with different structures and cavities. The palaeontological site, a karst cavity located at 257 m amsl, produced thousands of vertebrate remains, as well as lithic industries and artefacts. Equi is an important prehistoric archaeological site in Italy, referred to as an example of the lithic industry referred to the final stages of the Mousterian (a peculiar facies of the Mousterian defined as Alpine Mousterian). As paleontological site, Equi cave is celebrated for its outstanding record of carnivorans (Del Campana, 1923, 1954), including an unusually rich sample of fossil leopard, and a spectacular record of cave bear remains which represent one of the southernmost cave bear occurrences in the Italian peninsula.

The Equi site faces the Fagli valley (WGS84: 44.150, 10.167), which is a narrow, deep, V-shaped valley containing a mountain stream (Figure 4). The site consists of two primary areas of excavation: a shelter (locally known as the “Tecchia”), exposed to the south and a cave discovered one year later the beginning of the excavation. There are few evidences of glaciations events in the area of Equi. Deeper analyses about the Apuan Alps were made by Braschi et al. (1986) and Giraudi (2004, 2011), but they couldn’t recognise clear geological evidences of glaciations datable to the MIS3.

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[1] modified from GHEZZO E., PALCHETTI A. & ROOK L., 2014. Recovering data from historical collections: stratigraphic and spatial reconstruction of the carnivoran record from the Late Pleistocene Equi cave (Apuane Alps, Italy). *Quaternary Science Reviews*, 96: 168-179.

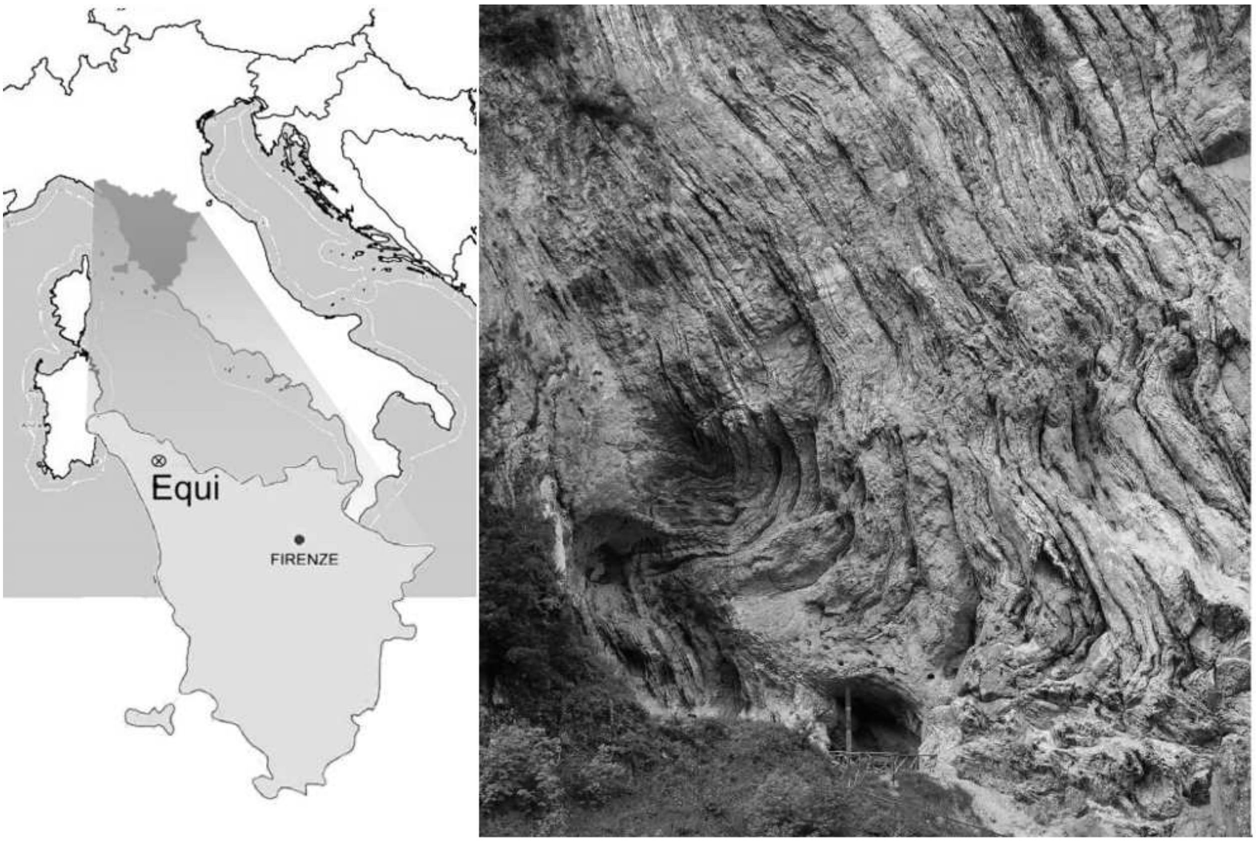
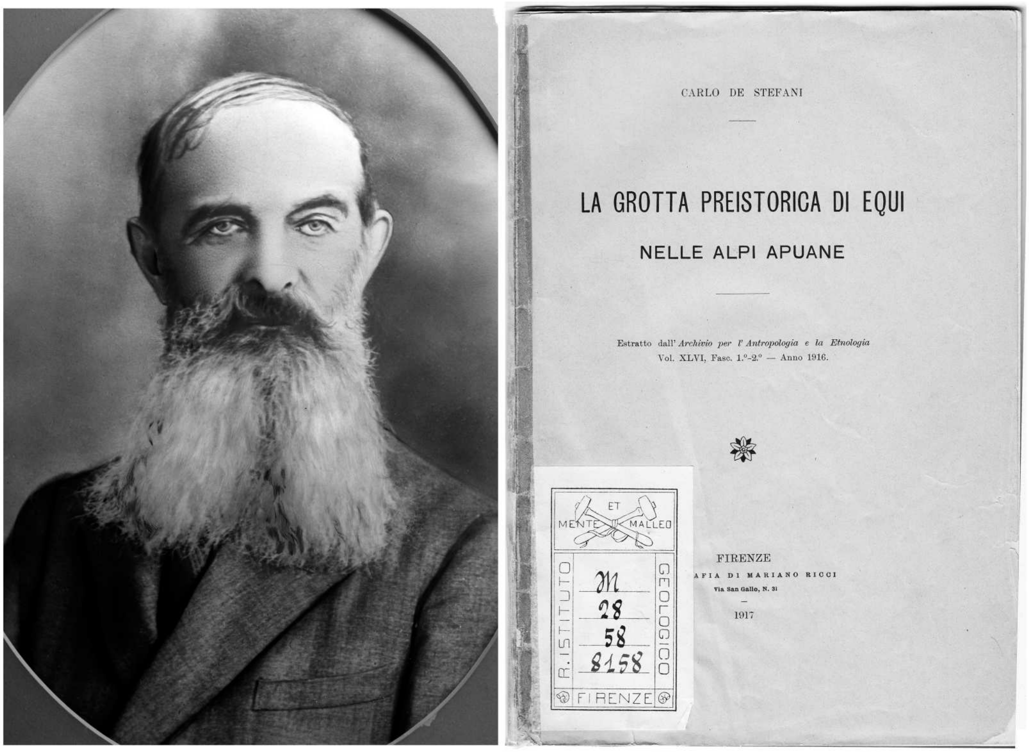


Figure 4: Location Map and general view of Equi shelter from the Lucido valley (Photo by P. Nannini, Soprintendenza per i Beni Archeologici della Toscana).

The excavations at the Equi site were begun in 1909 by G. Poderzana, who was active at the Museo Civico of La Spezia and investigated the outside deposit under the shelter. After this first explorative excavation, the site was studied under the direction of C. De Stefani (Figure 5), chair of Geology and Physical Geography at the Florence "Regio Istituto di Studi Superiori". De Stefani continued investigating the site with the goal of improving the collections of the Florence Museum. Regularly from 1910 to 1917 (and occasionally until 1920) he directed excavations at the site, and recovered thousands of fossil specimens. In addition to bats, birds, herpetofauna and fish, the faunal assemblage from Equi cave includes cave bear (*Ursus spelaeus*), gray wolf (*Canis lupus*), red fox (*Vulpes vulpes*), dhole (*Cuon alpinus*), cave lion (*Panthera leo spelaea*), leopard (*Panthera pardus*), Eurasian lynx

(*Lynx lynx*), wild cat (*Felis silvestris*), weasel (*Mustela nivalis*), polecat (*Mustela putorius*), pine marten (*Martes martes*), beech marten (*Martes foina*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), chamois (*Rupicapra rupicapra*), ibex (*Capra ibex*), wild goat (*Capra hircus*), hare (*Lepus* sp.), Alpine marmot (*Marmota marmota*), European beaver (*Castor fiber*; one tooth only), edible dormouse (*Glis glis*), garden dormouse (*Eliomys quercinus*), water vole (*Arvicola amphibius*), snow vole (*Microtus nivalis*) (De Stefani, 1917; Del Campana, 1923, 1954).

The vertebrate fauna were preliminarily examined by Regalia (1911). Subsequently, Pieragnoli (1919) and Fracassi (1920) described the cave bear remains, while Del Campana (1923) published a short note on weasel and dhole, a description of the avian fauna (Del Campana, 1924), and, later on, a detailed report on the carnivorans (Del Campana, 1954). The "Equi" fauna, though not re-examined in detail in recent times, is generally correlated (Caloi and Palombo, 1994) with the middle of MIS 3 (thus approximately in the range of 24-56 ka; cfr. Siddall et al., 2008).



CARLO DE STEFANI

LA GROTTA PREISTORICA DI EQUI
NELLE ALPI APUANE

Estratto dall' *Archivio per l' Antropologia e la Etnologia*
Vol. XLVI, Fasc. 1.°-2.° — Anno 1916.

FIRENZE
AFIA DI MARIANO RICCI
Via San Gallo, N. 31
—
1917

Figure 5: Graduated in law at the University of Pisa in 1870, the Paduan Carlo De Stefani had a vocation for Geology, and holds the Chair of Geology and Physical Geography at the Florence "Regio Istituto di Studi Superiori" from 1885 until 1924.

De Stefani approached the excavation of Equi cave not just as an opportunity to enhance the Florence museum collections with thousands of bones, but with the goal of recording the stratigraphic information using precise methods as much as possible.

In 1911 the De Stefani's team discovered the entrance of the cave on the right side of the shelter. He described the cave as a relatively large chamber, 18.3 m long and 7 m wide. The shelter floor was originally explored via a trench 8-9 m long extending from the wall to the outer margin of the shelter. A first planimetry of the site was given by Tonelli (1855-1929) (Figure 6), the engineer who firstly upraised the thermal town of Equi. De Stefani team dug the two areas, the shelter and the cave, from the upper surface (as left by the previous excavation of La Spezia Civic Museum), to a depth of approximately 6 meters.

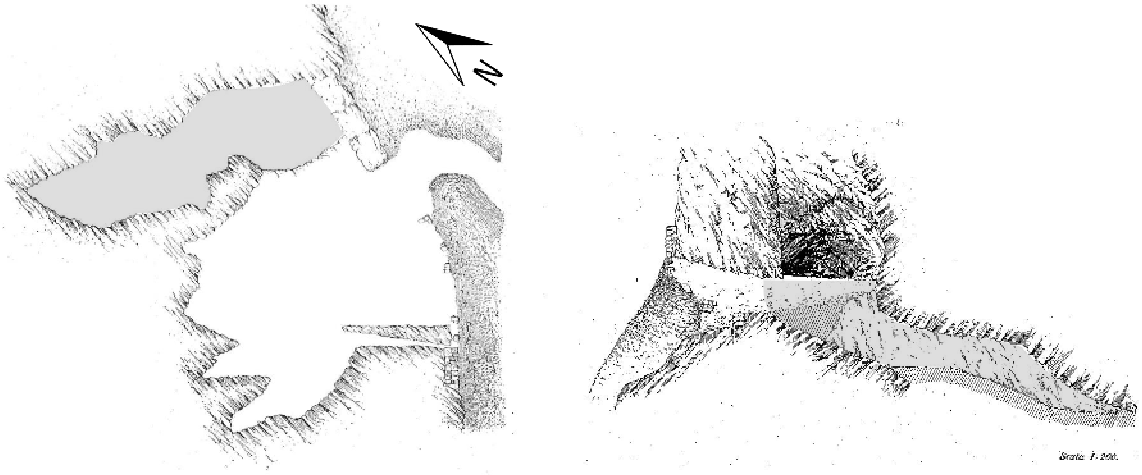


Figure 6: investigated area by De Stefani and his team. The cave, was descovered in 1911 under 1.35 meters under the surface, in the right (northern) part of the shelter (modified from De Stefani, 1917).

These excavations resulted in an enormous number of fossil bones, associated with stone tools, pottery and two different hearths. The first hearth, found during the 1914-1915 field work, was at a depth of 3.80 m from the surface, on the left side of the cave, near the entrance. The second hearth was found further 1.70 m deeper than the first (Figure 7). In 1921, according to the Italian law (L.364/1909), the site of Equi was declared a site of paleontological importance, under the responsibility of the local Soprintendenza Archeologica.

The evidence of least two distinct phases of human presence (ceramics and Palaeolithic artefacts) induced a lengthy harsh scientific debate between the highest authorities in the field (Mochi, 1916, 1920, 1929; Rellini, 1917, 1929, 1924) which was resolved only fifteen years later when an excavation by the Italian Institute of Human Palaeontology (Graziosi, 1934; Rellini, 1935) confirmed the absence of ceramics within Palaeolithic levels. The first analytical description of the Palaeolithic Equi artefacts was by Branchini (1928) who published the only available analysis of all of the archaeological artefacts from the cave. The analysis confirmed the presence of a lithic industry with clear Mousterian characters, which were assigned to the final stages of the Mousterian. Later, the characters of the Palaeolithic tools and the presence of so-called "bone Mousterian fibulae" (Giacobini, 1982) prompted the identification of a peculiar facies of the Mousterian known as the Alpine Mousterian (Battaglia, 1932; Graziosi, 1934; Rellini, 1935, 1937).

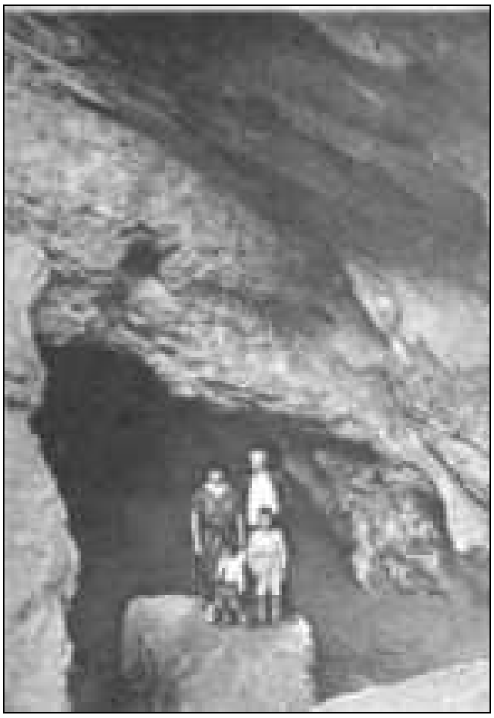


Figure 7: family photos. The family is on the geological testimony (unpreserved today) left by De Stefani at the entrance of the Cave (Iardella et al., 2009).

After the extensive excavations by De Stefani, the deposit was not systematically and coherently excavated again. Although, in addition to the work by the Italian Institute of Human Paleontology in Rome, small excavations were undertaken by various researchers in the late 1960s to early 1970s (Ambrosi and Fabbri, 1975) and late 1970s (Guerri, 1980, 1982).

4.2. New research

In 1996 the Equi site was included again in the areas of special planning and control for archaeological and landscape importance (Paribeni et al., 2009; Iardella et al., 2011). Thirteen years later, in 2009, under an agreement among the Soprintendenza per i Beni Archeologici della Toscana, the Municipality of Fivizzano and the Apuane Alps Regional Park, a new project began with the aim of validating the site with new excavations. In accordance with an Italian law regarding cultural heritage, the Equi site has been included in the areas of special planning and control for archaeological and landscape importance (Paribeni et al., 2009; Iardella et al., 2011). These new studies (directed by E. Paribeni, Soprintendenza per i Beni Archeologici della Toscana) led to the identification of a new layer in the shelter area containing Mousterian stone tools. An initial radiometric date (on charcoals) indicated an age older than 50 ky (Bigagli et al., 2013). At the same time, a new excavation survey of the cave confirmed the presence of in situ archaeological deposits with radiometric ages consistent with the biochronological interpretation (radiocarbon ages of 43,700_1900 and 44,000_2200 BP; Bigagli et al., 2013). The new finds from the Equi cave fit coherently into a framework of Palaeolithic human settlement dynamics in the Apuane Alps region, thereby documenting a phase of Neanderthal presence during the middle of MIS3.

Also, new dating was made using historical De Stefani's collection. Three bone samples were selected with registered stratigraphic provenance. They were sent to the Beta Analytic Inc. (Miami, Florida, Usa) for radiometric dating (Accelerator Mass Spectrometry, AMS, analysis) and all the three remains contained sufficient collagen and we obtained valid dating (Table 2). Even though the *Panthera pardus* specimen (sample #360175) tentatively referred to layer HB seems to indicate an age inversion from a layer stratigraphycally superimposed to that of samples #370173 and #360176, the degree of uncertainty due to possible bias in the data available for the historical collections (samples were excavated in 1911-1917), do not allow us to exclude the provenance of the specimen from an older layer (Ghezzo et al., in press).

Beta sample	Type of sample	Layer	Measured Age	13C/12C	Conventional age	2 Sigma Calibration
360175	*Panthera pardus* ilium fragment	HB?	32910±260 BP	-19.6 0/00	33000±260 BP	Cal BC 36630 - 34840 Cal BP 38570 - 36800
360173	*Rupicapra rupicapra* bone fragment (diaphysys)	F	26960±140 BP	-20,9 0/00	27030±140 BP	Cal BC 29480 - 29240 Cal BP 31430 - 31190
360176	*Rupicapra rupicapra* femur fragment (diaphysys)	B	27560±160 BP	-20.5 0/00	27630±160 BP	Cal BC 30030 - 29480 Cal BP 31980 - 31430

Table 2: New datings using the De Stefani's historical collection.

Despite this uncertainty, the overall information furnished by the radiometric dating of these three samples from historical collections allow me to chronologically place the Equi historical collection record within the middle to latest portion of the MIS3, a time span characterised in Mediterranean Europe (noticeably France, Italy, Greece and Turkey) by significant cold phases (Hugues and Woodward, 2008) and by climate-driven changes in the vegetation (Harrison & Prentice, 2003; Fletcher et al., 2010). It is noticeable that the Equi sample testifies the survival of several carnivorans until a period of severe climate, with mean temperatures progressively diminishing towards the Last Glacial Maximum (Mangereud et al, 2004).

4.3. Stratigraphical analysis of De Stefani's historical collection

The re-opening of Equi excavation in 2009 (Paribeni et al., 2009; Iardella et al., 2011) was an important occasion in our attempt to restore and recreate the hypothetical scenario of the older excavations and to compare the various levels and faunal associations with the new findings.

Although De Stefani's Equi diaries were lost, most of the labels that are associated with each specimen provide information on the position of the bone (in relation to either the entrance, or the right or left wall of the cave, and the depth from the original surface and/or from the hearths), and the date of recovery. Matching this information with the reports of the excavations, I could analyse the stratigraphic distribution and certain taphonomic aspects, and even develop conclusions regarding the ecology of certain species. Until the last 30-40 years, paleontological excavations were usually characterised by the lack of standardised methodologies. In many cases, the sediments were subdivided into single cuts or the field workers just collected fossils, ignoring information regarding the exact locations of findings, the context and/or many other characteristics of the deposit (for examples see Bon et al., 1991). An exception in the Italian scenario was De Stefani's methodology. During the excavation, he trained his collaborators to take notes of the position of each finding, and later in his publication (De Stefani, 1917) he described analytically the Equi site, recognising the importance of the general context and the stratigraphic setting of the deposits (e.g., the inclination of the layers). Due to the detailed description by De Stefani and the pictures of the site and excavations available in his paper, it was possible to recognise and locate certain historical reference points in the site during field surveys at Equi in 2012. I easily identified certain structures on the rock surface (Figure 8), i.e. the two holes above the entrance of the cave and a cavity in the southern part of the shelter (visible in De Stefani's pictures). Differences in the colours of the rock surfaces gave me the exact indication of the original surface of the deposits before the first excavations. Having established these reference points, I had the opportunity of derive further indirect data regarding the surface, the original (relative) zero-layer (Figure 8c-d) and to calculate that the De Stefani team most likely excavated more than 1000 m^3 of sediments during their 6 years of activity.

At the time of De Stefani's excavations, European bone caves had been studied for several decades, with interest already reaching overseas (cfr. Petraglia and Pots, 2004). It is widely recognised that the exploration and study of bone caves was prompted by the publication of W. Buckland's treatise Reliquiae Diluvianae (1823) in which the Professor of Mineralogy and Geology at the University of Oxford noted several instances (at least eight) in which human remains were found in cave strata apparently in association with bones of extinct mammals.

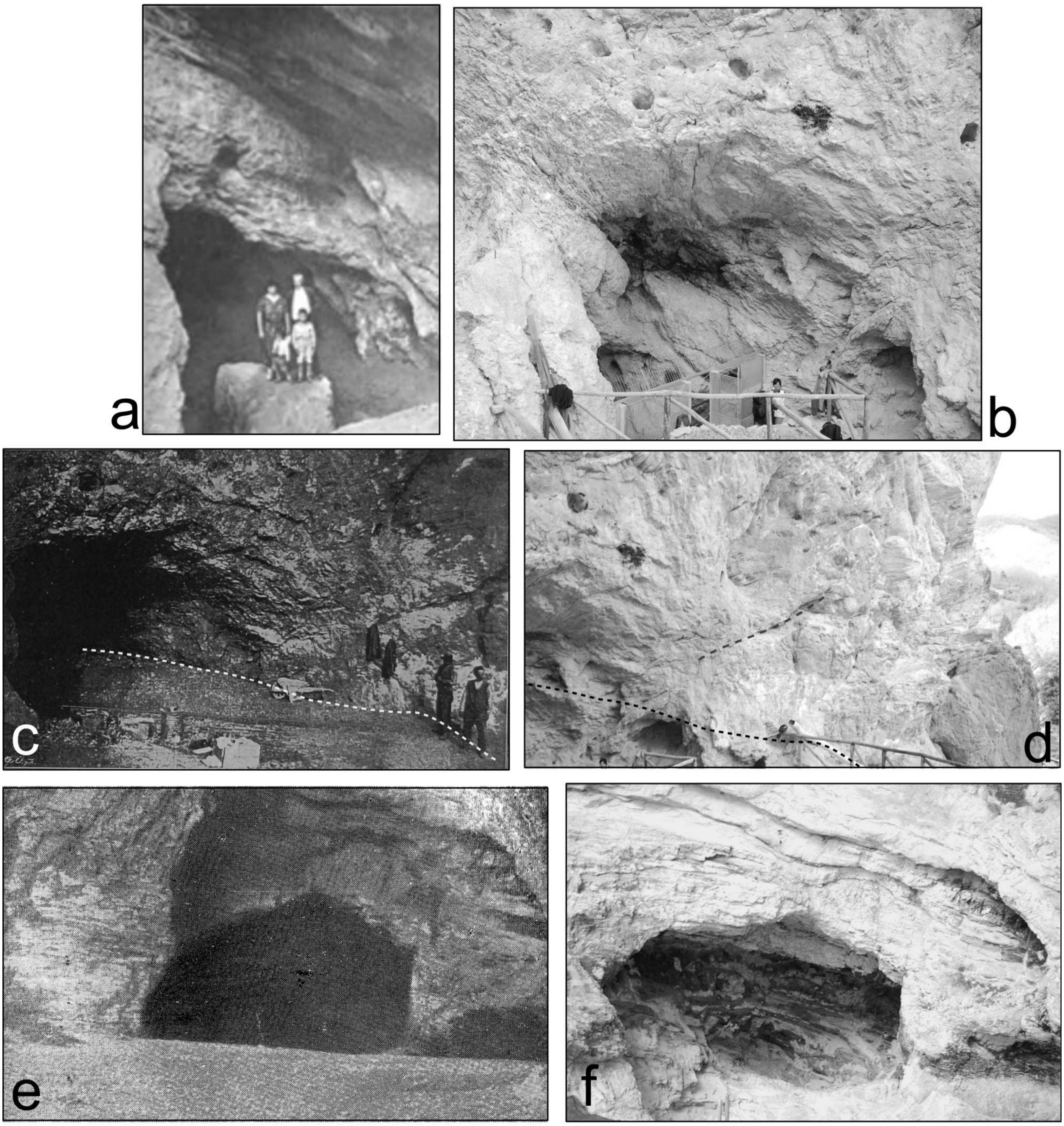


Figure 8: comparison of De Stefani (on the left) and 2012 view (on the right) of Equi. a-d: view of the entrance of the cave; e-f detail of the southern wall of the shelter. In all the photos, the black surface of the rock wall was exposed before De Stefani excavations; the structures evident in De Stefani photo-c (included the relative original surface) are underlined in the correspective modern photo, being still recognizable on the site.

Such findings questioned the prevailing Natural Theology based on Biblical scripture and led those in the emergent fields of geology and archaeology to conduct excavations intended to address the controversial issue of the coexistence of human artefacts and extinct mammals (Rudwick, 2008). Geologists in charge of these excavations were thus forced to develop operative working systems enabling them to find corroborating evidence of coeval humans and extinct animals against counterarguments that digging or other recent anthropic human activity had compromised the stratigraphic records. The British geologist W. Pengelly was a pioneer in establishing the basis for archaeological excavation methods. He established a prototype excavation method at Brixham Bone Cave in 1858, which enabled him to keep track of the three dimensional provenance of each find (McFarlane et al., 2010). Pengelly modified his method during the excavation of Kents Cavern, a site that had already yielded collections of tens of thousands of paleontological and archaeological remains, thanks to the earlier excavations by J. MacEnery between 1825 and 1829. Pengelly excavated at Kents Cavern between 1858 and 1880 and employed an innovative system allowing the locations of specimens to be recorded precisely in three dimensions within the cave (Mihai et al., 2010). Another geologist, R. Tiddeman, who from 1874 to 1878 directed the excavations at Victoria Cave, instead used a three-dimensional grid system based on a numbered series of parallels, recording the coordinates of findings in the excavation records and directly on the bones (Lord et al., 2007). Victoria cave was initially explored beginning in the late 1830s, but large-scale excavations commenced in 1870, primarily focused on relating the cave deposits to the abundant evidence of glaciation (cfr. Hansen, 1970).

In Italy, the late 19th century to earliest 20th century exploration of caves was primarily aimed at the search for, and collection of, well-preserved cave bear fossils and late Palaeolithic artefacts or figurative cave art (Guidi, 2008). Only two discoveries of Neanderthal remains or middle Palaeolithic artefacts had been made in Italian caves: (i) the first documented evidence of Italian Neanderthals was from Caverna delle Fate (Savona, Liguria), where A. Amerano collected Neanderthal remains in 1887-88. Since the mid 1870s the cave was known to be rich in cave bears and other extinct mammals (De Pascale, 2008), but no systematic excavation was performed until the 1980s (Giacobini et al., 1984). (ii) A rich fossil fauna comprising cave bears and other extinct mammals associated with Palaeolithic stone tools was recovered by K. Moser in 1893 and 1904-05 at Caverna Pocala (Trieste, Friuli-Venezia Giulia). The deposit was successively surveyed by C. Marchesetti (1908) and E. Neumann (1910-14) and finally excavated (though with issues regarding the stratigraphic record) by R. Battaglia in 1926-29 (Boschian, 2003).

The present spatial analysis is based on 356 fossil remains limited to the non-ursid carnivorans. They were determined as *P. leo spelaea* (sensu Burger et al., 2004) (number of identified specimens NISP = 25), *P. pardus* (NISP = 85), *C. lupus* (NISP = 142), *Vulpes vulpes* (NISP = 40), *Cuon alpinus* (NISP = 12) and mustelids (NISP = 52). We decided to not include cave bear records at this stage because the available record (entries with IGF catalogue number) does not represent the entire excavated collections, and their inclusion would have obliterated the signal of the remaining carnivorans (some thousand bear specimen are still not entered in the IGF catalogue and are undergoing revision). We also did not include archaeological artefacts, due to the restricted amount of associated detailed label information. In the case of artefacts, it appears that the early researchers were more interested in recording their location in relation to other findings rather than their position in a stratigraphic context. In this study we emphasize the presence of a great number of specimens identified as *P. pardus* (more than 220 specimens, although unfortunately only 85 have good stratigraphic information and could be included in the analysis)

The distribution of fossil remains was studied and the possible reconstruction of the site was created using a database of the historical information from the original labels and early papers, and a grid of the possible distribution of features superimposed on the original drawing and sketch of the cave by De Stefani (1917).

Metods - The deductive method described below was used for reconstruct the relative distribution of the fossils in the historical stratigraphic record of Equi.

In his descriptions, De Stefani (1917) recorded the various characteristics of the statigraphic record (Figure 9). He divided the floor into various layers and described the different area of excavation for each year, from 1911 to 1915, and consequently I divided the cave into five primary squares and the shelter in a singular external trench (Figure 10). The entire cave surface was cleaned in last year (1915), and I allocated the bone probability within the squares following the descriptions on the specimen labels.

Depth (m)	Description by De Stefani (1917)	Layer
1.15-1.35	large blocks of stones without soil. This layer, more consolidated in respect to the superficial colluvium, represents the base of a recent human newborn burial. De Stefani included in this layer all the upper sediment (colluvium), that was just outside of the cave	n
1.35-2.55	breccia layer at the base of the shelter which continue into the	l
2.55	travertine breach concretion of about 20 cm with a few stones	i
2.55-3.80	no description	hb
3.80	first fireplace discovered in 1914, located on the left side of the entrance of the cave	h
3.80-4.28	soil and gravel with small ruminant bones	g
4.28-4.43	soil with abundant and well preserved fossils of bear	f
4.43-4.45	gravel	e
4.45-4.80	soil with bear bones and flint artifacts	d
4.80-5.00	gravel and bones	c
5.00-5.90	soil and bones with few small gravel	b
5.30	second fireplace	ab
5.90-6.10	lower part of the deposit consisting in yellow soil	a-a0

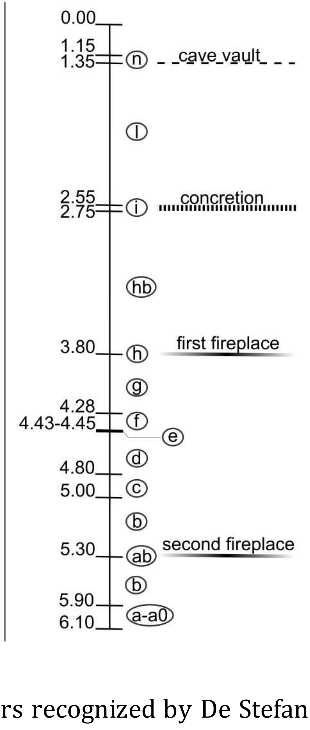


Figure 9: Depth, original description and new denomination of the different layers recognized by De Stefani (1917).

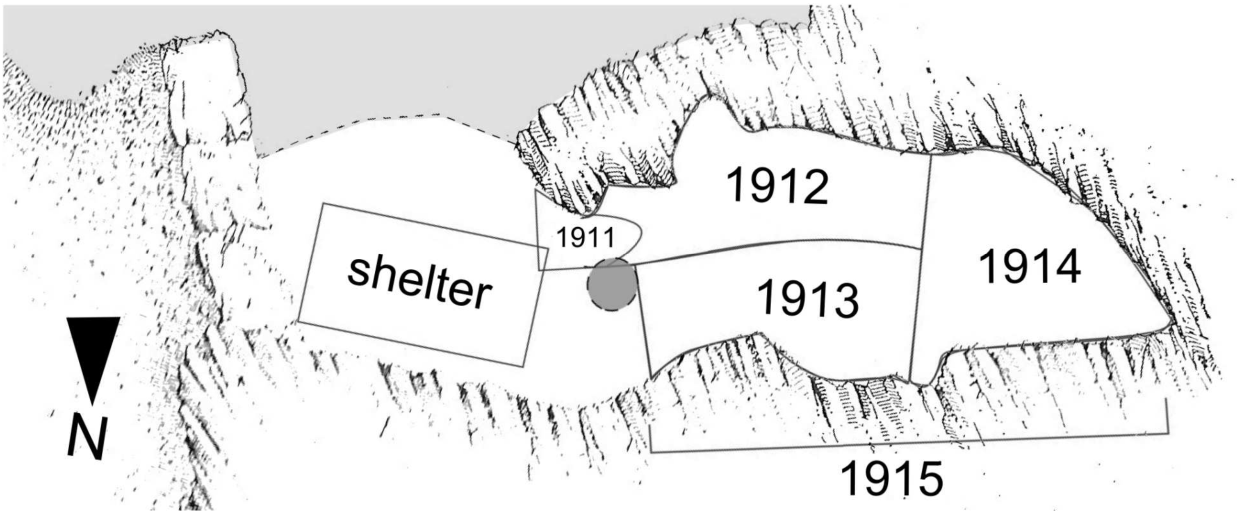


Figure 10: Redrawn from De Stefani 1911: Plain view of the two side of the Equi site. Shown are the main Equi shelter (in gray, partially omitted), the trench in front of the cave entrance, and the cave (from the bottleneck of the rock to the left side) outline planimetry with various areas of each year of excavation (from 1911 to 1915). The wavy orange dot represents the position of the upper hearth (layer "h").

Despite a definition of the excavation perimeters with permanent references points are lacking, I approximated to such limits (using the summary description in the De Stefani manuscript) and I assumed that each area of excavation (which differed from year to year) could be placed into a square in a Cartesian system. Such matrix was made by ordinate (y) as a proximal, central or distal point and the abscissa (x) as a left, central or right point. The depth (z) allowed us to insert the find in the correct layer of the square (Figure 11). When a label had no layer indication, the z-data were unavailable, and the specimen could not be considered in the spatial reconstruction.

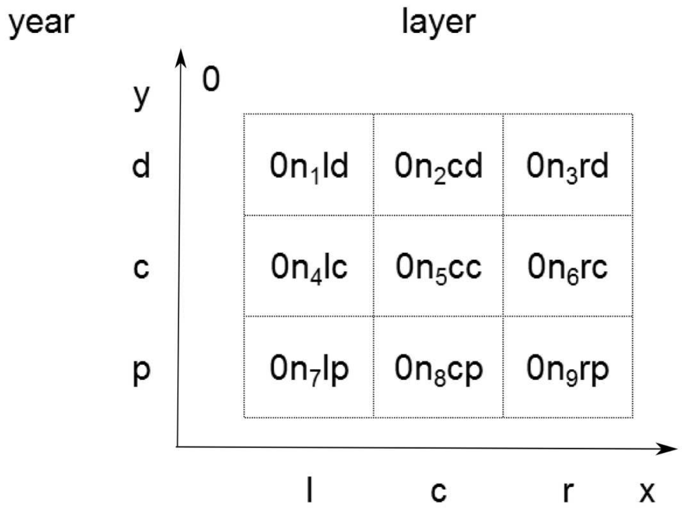


Figure 11: Square division used for estimation of fossil distribution. The abscissa (x) is divided into a left (l), central (c) and right (r) portions; the ordinate (y) is also subdivided into a proximal (p), central (c), and distal (d) portions. Each factor (l, c, r, and p, c, d) is equivalent to 1/3 of the referred sample for each square in the matrix. Specimens lacking additional information except for the year of recovery were also recorded in the square (0) and are 1/9 of the total number of samples with only this information for each square. Finally, nn value is the sum of all the specimens with information about year of excavation and relative location in the site, and the probability for that square is 1 for each single specimen.

Depending on the information available in each label, I organised the data into three levels of accuracy in terms of the probability of placing each fossil within the nine sub-squares. In the case of labels with just the year of excavation, the probability is 1/9 in each sub-square. When the label contained the year and the x or y data, the probability was equal to 1/3 for the corresponding column/ row but 0 in the other six sub-squares. When the label contained the year and the x and y data, the probability was 1 in its sub-square and zero in the other eight (entire location information available).

Then, the different probabilities were summed in order to provide a distributional index of the fossils in the site (see below).

In some cases, the label reported the location in relation to the first or the second hearth (respectively 3.8 m and 5.30 m). In such cases the positions were obtained with an empirical sum, assuming the hearth depth from De Stefani (1917): in this case I know that the z-data in the trench were taken from the ground surface, and the depth in the cave was obtained from the vault of the cave, which was originally buried 1.35 m under the surface of the shelter. As a first step, I catalogued the distribution of the different finds in each layer and square, both in the cave and in the shelter trench, and I correlated the probability of the partial distribution to the total number of finds discovered in all of the layers.

Finally, I stretched each square to the dimensions described by De Stefani both for each year of excavation and for each layer, the output resulting into a colour-based distribution.

Results - The results provided a map of the fossil carnivorans spatial position of each fossil in the cave and shelter for each year of excavation (Figure 12a) identified as *P. leo spelaea*, *P. pardus*, *C. lupus*, *Vulpes vulpes*, *Cuon alpinus* and mustelids (for a totality of 356 finds) and details for the leopard (85 finds) (Figure 12b).

Although incomplete, these maps display the hypothetical distribution probability of the finds at the Equi site. Forty-eight percent of the finds (174 specimens) were from the cave, whereas the remaining finds were from the shelter (186 specimens). The distribution maps show that these species were found throughout the layers, although a higher percentage of finds were apparently from the upper layers, and certain layers are barren of the taxa considered here (such as “e” to “b”, between depths of 4.43 and 5.30 m). In the cave deposits, the majority of the specimens apparently came from the inner portion and from the left/southern side. A smaller number of finds came from the right/northern side of the cave. De Stefani (1917) noted that the majority of the samples came from near the wall, and it is difficult to say whether this distribution reflects taphonomic agents or if it is the result of a bias in the collection and data acquisition. In the shelter trench, 1915 yielded the majority of the findings from layer “hb”, and from the upper two layers “l” and “n” from 3.80 m up to the surface (above the first hearth).

Approximately 50% of the findings in each layer are represented by Canidae (with the species *C. lupus*, *V. vulpes* and *C. alpinus*), the best represented family in the site. The percentage of wolves is the most stable throughout the Equi succession, and wolves are the most abundant non-ursid species in the Equi collection. The record of leopards was provided with very thorough label information for 85 specimens. *P. pardus* findings were slightly more numerous in the cave than in the trench (45 versus 40 specimens, respectively) and were especially concentrated in layer “hb” in the cave, and layers “l” and “n” in the shelter. The 1917 fieldwork yielded several leopard specimens, but unfortunately we could only rely on data from the collections labels, and no information was available concerning the area of discovery (i.e. this accounts for 1/3 of the leopards without location data; this field work season occurred after the publication of De Stefani’s pivotal 1917 paper). I could also observe the distribution of the various species in the Equi record derived from the evaluation of the numbers of each species in the layers (Figure 13). Excluding the layers with less than ten specimens and the barren layers “e” and “d”, *P. pardus* and *C. lupus* (and to a lesser degree, *P. leo spelaea*) are well distributed throughout the entire record and they represent the 60-90% of the entire fossil collection.

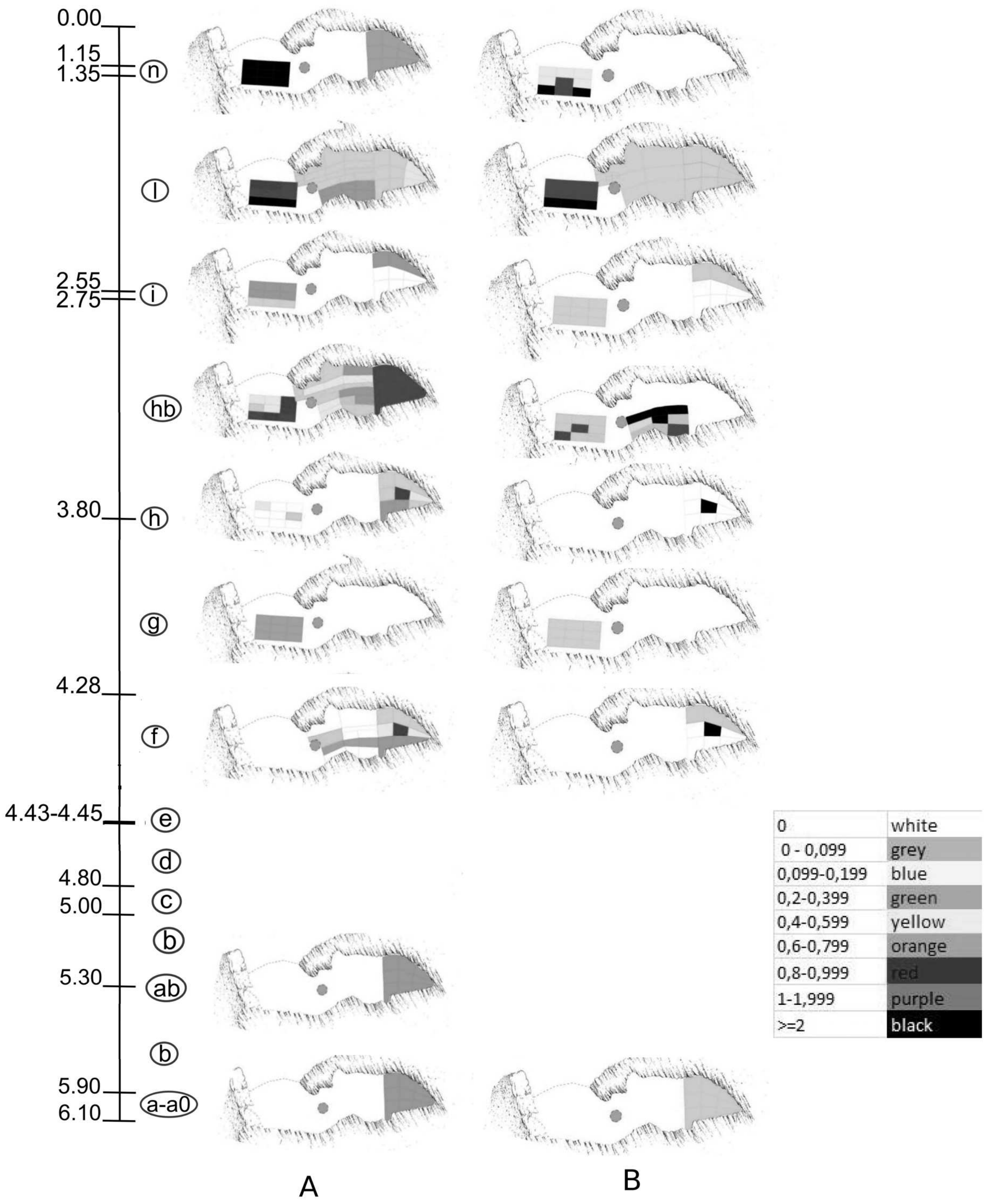


Figure 12: Maps of the entire record of carnivorans under consideration (A) and the record limited to *Panthera pardus* (B). Corresponding layers and depth are indicated on the left. The colour scale indicates the estimated range of probability

	lion	leopard	wolf	fox	dhole	mustelid	amount per layer
n	4	11	32	8		25	80
l	14	26	31	12	6	4	93
i*		2			1		3
hb	1	22	41	15	3	16	98
h	2	2	7	3	1		15
g*		2	3	1		1	7
f	2	3	5	1		4	15
e							0
d							0
c*		2	2				4
ab	2	7	15		1		25
b		6	4			1	11
a a0*		2	2			1	5
amount per species	25	85	142	40	12	52	356

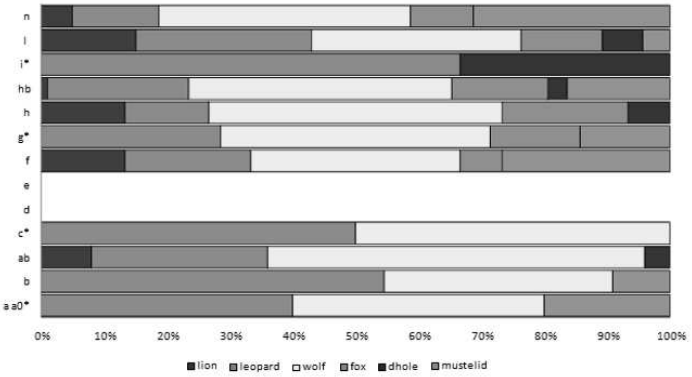


Figure 13: bar chart of vertical distribution of canivorans species across the stratigraphic succession of De Stefani (1917) layers. Asterisk (*) indicates layer with fewer than 10 specimens. Layers “e” and “d” are sterile.

As shown in Figure 12b, leopard bones were especially abundant in layers “hb” and “l”. The lion is represented by a small number of specimens (two phalanx, one metapodial, two teeth and two tarsal bones) in the deeper layers until the layer “hb” (the thicker and, unfortunately, the only un-described layer) and increases in abundance in the younger layer “l”, with a maximum of 14 specimens. Leopard and wolves show a different trend, with a constant distribution throughout the stratigraphic record except for a notable increase between depths of 3.80 and 2.55 m (layer “hb”) and in the upper layers. In the most recent layer (“n”) all of the percentages of the larger species decrease in favour of mustelids. This was also the case in layer “f”. The dhole is first present in layer “ab”, with a single finding (III Mc), near to the first hearth. Most of the dhole remains are recorded in higher layers, between depths of 3.80 m (“h”) and 1.35 m (“l”). The third canid species, *V. vulpes*, appears above a depth of 4.43 m and its percentage remains stable up to the youngest deposits.

Discussion - Almost all of the fossils considered provided data regarding their original locations. Moreover, the focused analysis of leopards was chosen among the fauna for their abundance in this deposit. Leopard finds in Europe from the Middle and Late Pleistocene consist of a few (fragmentary) specimens from European mainland (southern latitudes). A general overview of the species in the European fossil record has been recently offered by Diedrich (2013), revealing that Equi represents the most important assemblage from the Late Pleistocene for its exquisite preservation of the fossils and for the number of anatomical elements represented (see Chapter 5.2.1).

Only a few skeletal elements are missing, such as cervical (with the exception of two atlases) and thoracic vertebrae and the third phalanxes.

Based on this analysis, I am also able to discuss certain taphonomic processes. No signs of human involvement were found on the bone surfaces, although a few specimens display taphonomic marks, such as weathering, gnawing and bite marks (sensu Lyman, 1994), and evidence of pathology (see also Pieragnoli, 1919, for pathologies on bear bones). No indications of the discovery of entire articulated skeletons was reported in De Stefani (1917), although a few articulated specimens were found, consisting mostly of appendicular bones of bear and lion (the relocation of these samples in their stratigraphical context is not possible due to the lack of detailed excavation data). Although a bias by selective collection cannot be excluded, the presence of abundant microfaunal remains (i.e., rodents, birds, herpetofauna) in the Florence collection indicates that a detailed investigation of the sediments was conducted by De Stefani, and that the original paleontological associations are likely to be well represented. The relocation of specimens allowed me to demonstrate the similar accumulation percentage of the species in both the cave and trench and the distribution of the species among the various layers. Frequencies of findings increase in succession from the lower to upper layers, mostly in the two primary represented species, i.e., wolves and leopards. The number of species in the upper layers is also enriched by the appearance of a few remains of foxes and dholes.

All of the species are represented in nearly all of the layers, and there is no evidence of differentiation of the faunal assemblages, which is interpreted as evidence of a relative short time of accumulation and rapid sedimentary deposition. I can interpret this accumulation as reflecting nearly stable climatic conditions during the cold phases of the middle of MIS3, a chronology reinforced by the recent new radiometric dating of the lower levels in the cave re-excavations beginning in 2009 (Bigagli et al., 2013) and dating of three specimens from historical collection.

The faunally richest layer is between depths of 3.80 and 2.75 m. However, I lacked a description of the soil type (colour, structure, texture), and we are unable to evaluate the sedimentation agent (e.g., clay, exfoliation of the vault). The upper layers ("l" and "n") also display a higher number of specimens and are composed of unrefined stones and breach rocks related to the seasonal disaggregation of the vault.

For a better understanding of the context, we compared the Equi fauna with those of two other caves located not far from the Equi site in the Apuane Alps area: the Grotta del Capriolo and Buca della Iena (Pitti and Tozzi, 1971). Both yielded Mousterian artefacts associated with mammal fauna, and their deposits are considered age-equivalent to the lower layers of the Equi cave. The first, Grotta del Capriolo, has a lower percentage of carnivores than herbivores, with a predominance of *Capreolus capreolus* (followed by *S. scrofa*, *C. elaphus*) and few remains of *P. pardus* and *Felis silvestris* (respectively 4 and 2 remains). Buca della Iena contains a richer faunal assemblage, with 23 species of large mammals and *Crocuta crocuta spelaea* as the best represented species (with bones and coprolite evidence), followed by *U. spelaeus*, *Equus caballus* and *C. elaphus*. The Equi assemblage differs from both of those sites by way of its great predominance (more than

90%) of carnivorans over the herbivorous component, for the total number of species, total number of remains, and lack of evidence of hyaena accumulations.

Relatively next and coeval to the Equi site, Buca della Iena layer D represent a typical hyena den accumulation and, together with Grotta del Capriolo, differ in terms or their climatic conditions, with lower humidity and insolation rates in the area of Equi (cfr. Maracchi, 2008). I conjecture that these same differences may have been present in the past and we can suggest that during the middle of MIS3, Equi was probably an occasional refuge for various types of carnivores and humans, as indicated by the small set of lithic tools, and not a den or long-term shelter during hunts. Furthermore, the accumulation at Equi does not seem to be related to human activity because I observed no evidence of cut marks on the bone surfaces. More likely the assemblage is a natural one mediated by natural agents and limited transport of the samples, i.e., deaths during colder seasons and animal competition.

Distributional analysis seems to indicate considerable post-mortem redistribution of the remains both in the cave and shelter. The taphonomic explanation for this sparse deposition of fossils is not clear, and I can consider the coexistence of various agents. The abundance of bear remains, probably related to hibernation, would certainly have influenced the accumulation.

Lions are scarcely represented at Equi and show a discontinuous distribution among the layers. Heithaus (2001) and Steinmetz et al. (2013) demonstrated that the largest predators, such as lions, are distributed in relation to the richness of prey and the optimal environment. In contrast, smaller carnivores select their range to avoid competition with stronger animals and eventually spread to regions with less food availability. This seems to be the case in the Equi assemblage, judging from the ratio of lions to smaller carnivorans.

The dhole was not so common (for the complete description see Chapter 5.3.1). During the Pleistocene, it spreads into Eurasia, reaching central and Western Europe at the beginning of the Middle Pleistocene and into North America in the Late Pleistocene (Tedford et al., 2009). Dhole fossil remains are relatively rare but are sufficient to attest to a wide distribution, being observed at several Middle-Late Pleistocene sites in Eurasia (Petrucci et al., 2012). At Equi, its presence is indicated by two teeth (first and second lower molars) and the exceptional preservation of few postcranial remains. There is no general consensus regarding the environmental significance of dhole fossils and the Equi geographical and physiographical location generally matches the habitat of the extant dhole (Durbin et al., 2004).

Finally, I note the taxon absent at the Equi site, the hyaena. The hyena most likely never occupied the Equi cave, whether as a primary den or a hunting site. The absence of direct evidence is associated with the lack of animal remains with hyaena tooth marks, digested bones (compatible with this large carnivore), or coprolites. A comparable situation has been recently reported at the Middle-Late Galerian site of Cerè (Ghezzo et al., 2014), where a rich canivoran species assemblage (*Ursus deningeri*, *Canis mosbachensis*, *Vulpes vulpes*, *P. leo spelaea* and *P. pardus*) also lacks remains of the expected hyaenid *Crocuta crocuta spelaea*. Such a peculiar feature may be possibly explained by the comparable altitude or exposure of both sites or the relatively short time of accumulation and occupancy of the cave by other large carnivoran species.

5. Carnivorans from Equi

5.1. The carnivore guild

As previously mentioned, the complete mammal assemblage from Equi was determined by De Stefani (1917) and Del Campana (1923,1954) and includes *Ursus spelaeus, Canis lupus*, *Vulpes vulpes*, *Cuon alpinus, Panthera leo spelaea, Panthera pardus, Lynx lynx, Felis silvestris, Mustela nivalis, Mustela putorius*, *Martes martes, Martes foina, Cervus elaphus, Sus scrofa, Rupicapra rupicapra, Capra ibex, Capra hircus, Lepus* sp., *Marmota marmota, Castor fiber* (only one tooth), *Glis glis*, *Eliomys quercinus*, *Arvicola amphibiusa* and *Microtus nivalis*. Aves were studied by Del Campana (1924) while the herpetofauna was recently partially revaluated by Bartolini et al. (2014).

In this study I focused my attention on selected species of carnivorans from Equi, mainly *P. pardus* and *C. alpinus,* and their description and discussion about evolutionary and paleobiologic aspects are given in the next paragraphs. Lions and lynxes are discussed in the following Chapter 6, and here I just briefly offer account for the other carnivorans occurrence, namely bears, canids and mustelids.

At Equi, the dominant taxon (represented by hundreds of quite complete crania postcranial specimens) is the cave bear (De Stefani, 1917), and two more complete skulls were dug out during the recent excavation seasons (2012-2014). The skulls of *Ursus spelaeus* are well recognizable based on the large dimension and the typical depression at the frontal-nasals junction. *Ursus spelaeus* appeared at the beginning of the Aurelian (Hänni et al., 1994). For long time, it was sympatric with the extant brown bear and their range was overlapping without heavy effects for the more vegetarian diet of the former. The cave bears disappear at about 20 ky ago, probably as a consequence of the climatic deterioration. Its presences at

Equi testify the survival several animals in the Apuane Alps, just before the complete extinction of the species (Pacher and Stuart, 2008; Martini et al., 2014).

Foxes and wolves are represented at Equi with several remains. Modern *Canis lupus* and *Vulpes vulpes* reached Europe in the Aurelian (late Middle Pleistocene), at about 300 ky ago (Petronio et al., 2006; Palombo et al., 2008; Kutschera, 2013; Sardella et al., 2014). Red fox in Italy was firstly reported at Bristie (Trieste; Bon et al., 1991; Lugli and Sala, 2000) and Malagrotta (Rome; Capasso Barbato and Minieri, 1987), and colonized high latitudes during the middle and late MIS3 (Sommer and Benecke, 2004; Kutschera et al., 2013).

The bone morphologies and genetic analysis on wolves have been revealed a quite homogeneous population almost from 44 ky ago to the Holocene (Pilot et al., 2010), thus representing a singolar European clade, even thought the presence of a particular haplogrup (related to a specific wolf ecomorph) (Leonard et al., 2007) shows a decreasing at the end of the Late Pleistocene in Europe and a complete disappearance from North America.

Mustelids are represented at Equi both with teeth and postcranial remains. Little is known about the ancient divergence within the clade, but genetic research has recently pointed out the late speciation of the family from Musteloidea, in the Early -Middle Miocene (Marmi et al., 2004; Sato et al, 2012). In the Middle Pliocene, mustelids were recorded in Spain with the genus *Meles* (Madurell-Malapeira et al., 2009; Madurell-Malapeira et al., 2011) and in Italy the oldest occurrence of the genus *Lutra* was recorded from the Upper Valdarno Basin (Early Pleistocene; Cherin and Rook, 2014). The genera *Mustela* and *Martes* are less studied and the taxonomical identification turns out much more doubtful due to their morphological similarities in the postcranials and the cranial intraspecific variability (Reig, 1992). A complete distributional analysis for mustelids in Europe was proposed only for the post-LGM, when the family progressively increased in the continent (Sommer and Benecke, 2004), becoming one of the most typical record in the extant fauna.

5.2. Family Felidae Fischer Von Waldheim, 1817

Today, the family Felidae includes several species, about thirty-six up to forty depending from the scholars, divided in fifteen genus and eight recognised genetic lineages (Wozencraft, 2005; Werdelin and Peigné, 2010; Sunquist and Sunquist, 2002). Among these species, only seven are large felids, namely lion, tiger, giaguar, leopard, snow leopard, cougar and cheetah (Sanderson and Watson, 2011). With the exception of tigers and snow leopards, which evolved quite late in the Late Pleistocene, all were part of the European fauna in specific times.

Felidae firstly evolved in Africa during the Early Miocene (Werdelin and Peigné, 2010) and here the group diverged through the last 7-15 My (Testu, 2006; Johnson et al., 2006), reaching all the main continents and size-variation, maintaining approximately the same basic morphological features (Turner and Anton, 2007). It means that there were little variation among the species and, with few exceptions i.e. Machairodontinae and the genus *Acinonyx*, clear skeletal morphological differences were not developed.

Despite the first occurrence of cat-like species in Europe is reported in a French Oligocene site with a member of the extinct family of Nimravidae, *Proailurus lemanensis* (Kemp, 2005; Turner and Anton, 2007), the true Felidae reached Eurasia at about 10 My, just after the first appearance in Africa, with the genus *Machairodus* (Augustí and Antón, 2002).

The genera *Panthera* and *Lynx*, examined in detail in this thesis, evolved later and reached the European in the Late Pliocene (Augustí and Antón, 2002; Werdelin and Peigné, 2010), shortly after their appearance in Africa. In the Middle and Late Pleistocene, they putatively occupied all the European territories from the flat valleys up to the mountain regions.

Subfamily Felinae Fischer Von Waldheim, 1817

Genus *Panthera* Oken, 1816

Panthera pardus (Linnaeus, 1758)

Today *Panthera pardus* is the largest spotted cat in Africa and Asia, with several recognized subspecies. It is a relatively common, solitary, and opportunistic predator in the wild (Sunquist and Sunquist, 2002; Miththapala et al., 1996; Uphyrkina et al., 2001). It shows a great variability in size within its range: generally speaking, in open country with a large variability in food habits the animals are larger than in the forest, from 20-30 kg up to 90 Kg (Hayward et al., 2006; Stein and Hayssen, 2013). It can live in a wide range of habitats, most commonly associated with cover forests and mountain terrain, from sea level up to over than 5.000 meters (Sunquist and Sunquist, 2002). At present the species is critically endangered in some parts of its range, listed as Near Threatened in the IUCN Red Data Book (Henschel et al., 2008; Sunquist and Sunquist, 2002; Gavashelishvili and Lukarevskiy, 2008).

A general revision of European Pleistocene leopards has been recently provided by Fischer (2000), Saoqué and Cuenca-Bescós (2013), and Diedrich (2013): *Panthera pardus* was firstly determined in Europe in late Early Pleistocene at Vallonnet Cave (Moulle et al., 2005), and Mauer (Schütt, 1969b) at about 600ky. It was quite common across the continent during the Middle and Late Pleistocene (Diedrich, 2013) with a Late Pleistocene northern limit of the range at the site of Niederlehme-Rixdorfer Horizont in Berlin (Fischer, 2000). In Europe leopards disappeared during the Late Pleistocene, with a strong decrease at about the LGM, probably surviving only in Eastern Europe until historical times (Spassov and Raychev, 1997; Baryshnikov, 2011).

Molecular phylogenies indicate that African leopards are the most primitive ones, those from Western and central Asia evolved later from African ancestors, and those of northern and Eastern Asia shows the youngest genome sequence (Miththapala et al., 1996; Uphyrkina et al., 2001, 2002). Uphyrkina et al. (2001) inferred leopards' origins of African and Asian subspecies should be dated around 0.47-0.825 Ma and 0.17-0.30 Ma respectively, even though these data are completely in disagreement with paleontological evidence (O'Regan and Menter, 2009). On the other hand, Lei et al. (2011) estimate *Panthera pardus* origins at about 4.35 Ma ago, a time older than the first sure fossil evidence of the species in Africa at ca. 2.0 Ma (Werdelin and Peigné, 2010). As a matter of fact the question about European leopard older appearance and differentiation is still far from being resolved.

5.2.1. The remarkable *Panthera Pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology[2]

Leopard remains are rare in the European fossil record, probably a consequence of its solitary and elusive habits. Equi represents a rich and outstanding exception with a total of 224 finds discovered by the historical excavations (for 85 specimens were possible to obtain their relocation into the stratigraphical record; see Chapter 4.3).

Even though many authors attempt to recognize fossil subspecies from morphological analysis (Kotsakis and Palombo, 1979; Spassov and Raychev, 1997; Diedrich, 2013; Schütt, 1969b), I have proven that, till today, leopard occurrences are too scarce (and morphologically variable) to allow for firm conclusions, and specimens are classified into different sub-groups without a bold cladistical and/or genetic analysis. Boule (1906) recognized *Panthera pardus fossilis* characterized by more massive dental features and an elongated lower carnassial in comparison to the p4 (Bonifay, 1971). Similar characters are differently notable both in other fossils and extant subspecies and are not so precisely identified by the author. We emphasize that if intraspecific variability was taken into account, also the Diedrich (2013) hypothesis of successive migration waves from Africa would not be justified, and the four subspecies *Panthera pardus begoueni* (Fraipont, 1923), *Panthera pardus sickenbergi* (Schütt, 1969), *Panthera pardus antiqua* (Cuvier, 1835), and *Panthera pardus spelaeus* (Bächler, 1936) should be better considered as a single chronospecies *Panthera pardus* Linnaeus, 1758 (instead of different subspecies characteristics of Early, Middle, and Late Pleistocene).

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[2] modified from GHEZZO E. & ROOK L., in press. The remarkable *Panthera pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology. *Quaternary Science Reviews.*

Following this species-reductional trend, Hemmer (1972) synonymized *Felis* (*Panthera?*) *lunellensis* Bonifay, 1971 and *Panthera pardus begoueni* (Fraipont, 1923) to *P. pardus*, previously erected on the basis of the absence of the upper second premolar. We agree with the sentence reinforcing it observing that P2 is quite variable in the crania from Equi.

The role of leopards in the Pleistocene carnivore guild is related to the interaction with other carnivores and with prey, and, according to Saoqué et al. (2014) and de Ruiter and Berger (2001), the leopard presence can influence the mammal assemblage structure, rebalancing the species occurrences. For this reason, understanding its behaviour in comparison to other predators (including humans) is crucial.

Anatomical description - The site of Equi returned five well preserved leopard crania (Figure 14 and Figure 15). Three of them (IGF10036V, IGF15110V, and IGF15111V/1) are almost intact. The neurocranial and splancnocranial sides are preserved as well as the zygomatic arcs, muzzles and teeth. .

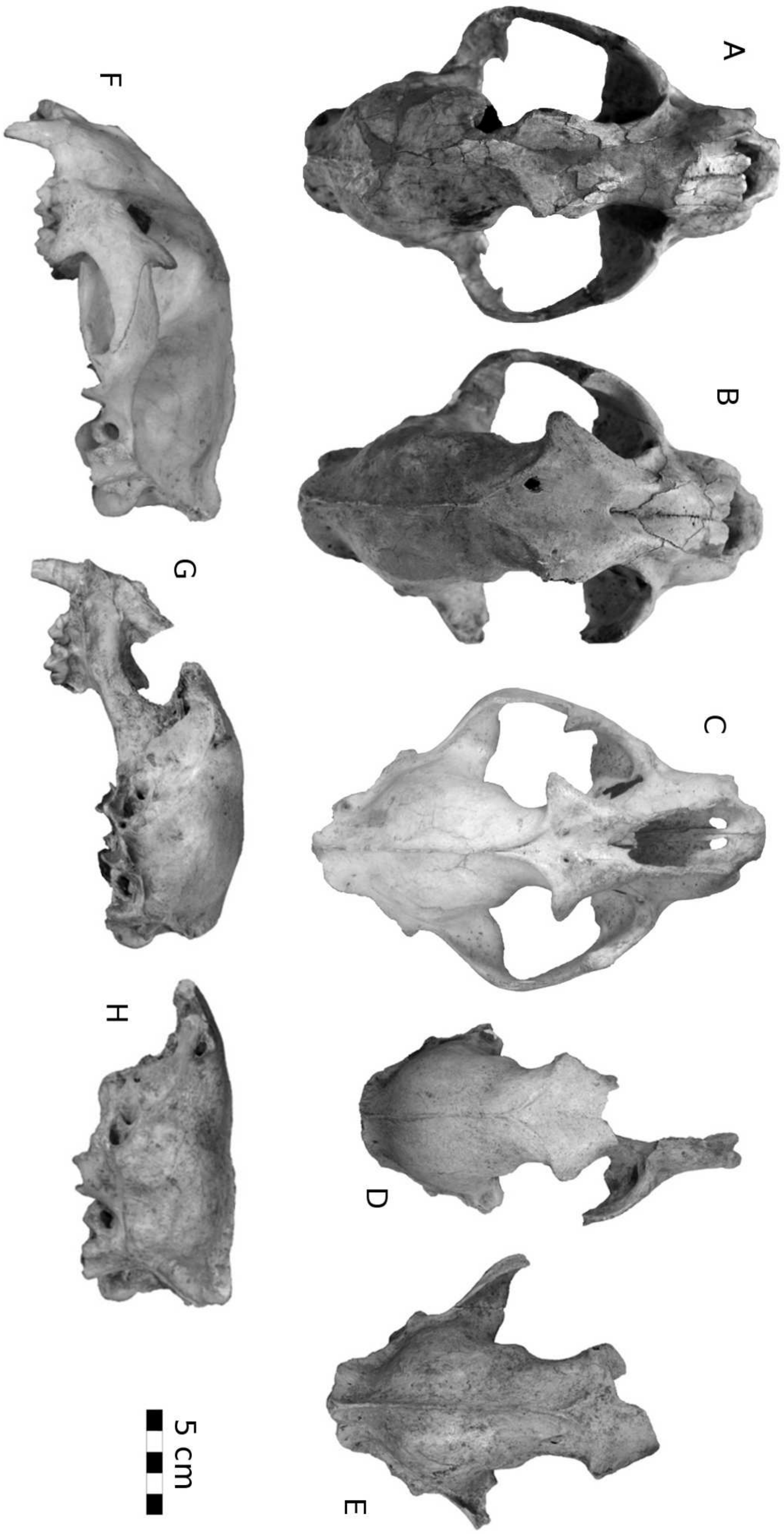


Figure 14: Cranial leopard remains from Equi in top view: IGF15111V/1 (A); IGF15110V (B); IGF10036V (C); IGF185V/1 (D); IGF184V (E). IGF10036V, IGF182V, IGF185V/1, and IGF184V are also represented in lateral views (F, G, H, respectively)

IGF10036V (Figure 14c, f and Figure 15a-e) is the largest and most massive, compared to the other samples from the same site. On the contrary, IGF15111V/1 (Figure 14a, Figure 15f-g) is the smallest and most slightly built cranium, and also the most damaged one (probably ruined during the excavation). IGF15111V/1 slightness is a feature not related to a young individual because all sutures are almost ossified and the tooth wear is at an advanced stage.

In lateral view, the crania have a straight sagittal crest. Compared with the cranium of extant leopards it is not projecting so far upward. With the exception of IGF185V/1, this crest sticks out slightly over the occipital surface.

Dorsal outline of the muzzle is convex, shorter than the neurocranial portion, with the nasal bones frontally sloped. The fronto-nasal suture is slightly sunken-in, and produces a deep depression (especially evident in IGF10036V and IGF15110V). The canine roots produce a swelling of the maxillar bones, ending above the infraorbital foramen. IGF10036V is the only specimen showing the maxillary suture. This line follows the orbital edge and ends close to the fronto-nasal suture. In ventral view, the three complete crania (IGF10036V, IGF15110V, and IGF15111V/1) show a wide palate, with the choanae opened between the canines.

The post orbital constriction is not marked in IGF185V/1, IGF10036V and IGF15110V, while is well pronounced in IGF184V and IGF15111V/1. The braincases are elongated, elliptical (barrel-like) or spherical (globe-like) (Table 3).

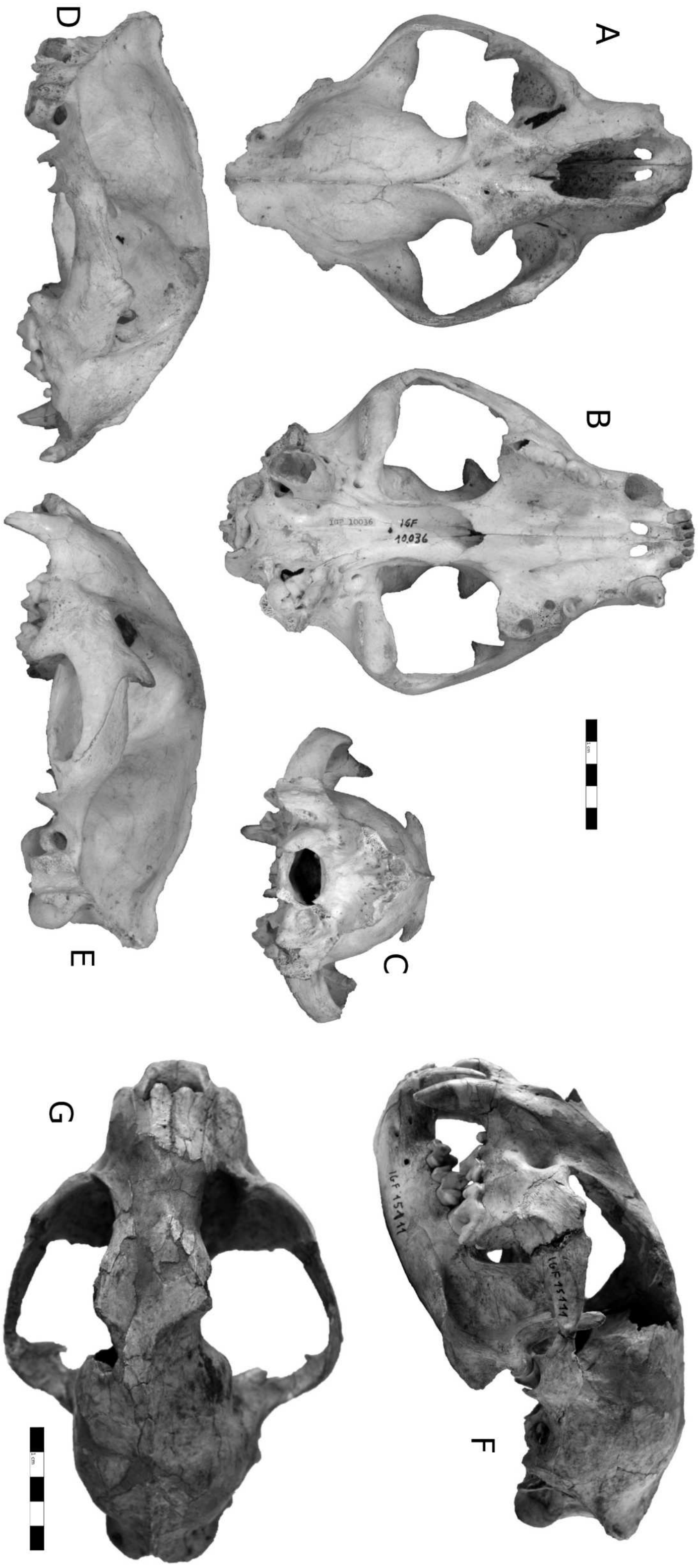


Figure 15: IGF10036V and IGF15111V/1 in detail. IGF10036V on dorsal (A), ventral (B), caudal (C), left (D) and right (E) views. Cranium IGF15111V/1 in dorsal view (G) and with mandible IGF15111V/2 in left side view (F).

	fronto-nasal suture is slightly sunken-in	**post-orbital constrinction**	**upper diastema**	**neurocranium feature**	**P2 r/l**
IGF15110V	yes	large	short	barrel	0/0
IGF15111V/1	-	narrow	short	globe	0/1
IGF10036V	yes	narrow	no	barrel	1/1
IGF185V/1	-	narrow	short	barrel	0/-
IGF184V	-	narrow	-	barrel	-/-
Manga Larga	no	large	no	barrel	1/1
Monte Sacro	no	large	no	barrel	1/1 (?)
8748 (OC-FI)	no	large	no	globe	0/1
8439 (OC-FI)	yes (small)	large	-	barrel	-/-

Table 3: Morphological characters of the specimens of *P. pardus* from Equi compared to other Pleistocene and Holocene skulls. OC-FI: osteological collection of the Natural History Museum of the University of Florence

Skull IGF15110 shows two large holes throughout the temporal bone (Figure 16). They pierce the skull from side to side. The edge of the right one is hollow, while the opposite one is larger and broken in recent times. On the bone surface there are no more evidences of bite, chew or gnawing or ever other kind of injuries, even thought the broken right supraorbital process could be related to such evidences.

Upper incisives series is preserved only in IGF185V/2 (Figure 17). The I1 and I2 are frontally flat and their lingual outline curves forming an enlarged crown surface. There is a short diastema between incisives and canines.

The presence of P2 is variable. IGF15111V/1 bears it only on the left side. IGF10036V has P2 on both sides, while IGF15110V has no P2s at all (even the alveoli). Del Campana (1954) reported that the first premolars of IGF15110V were lost during the lifetime and the alveolus was obliterated from the re-growth of the maxillar. In our opinion, in this skull the P2 never erupted because there is no sign of bone remodelling on the maxillary bone.

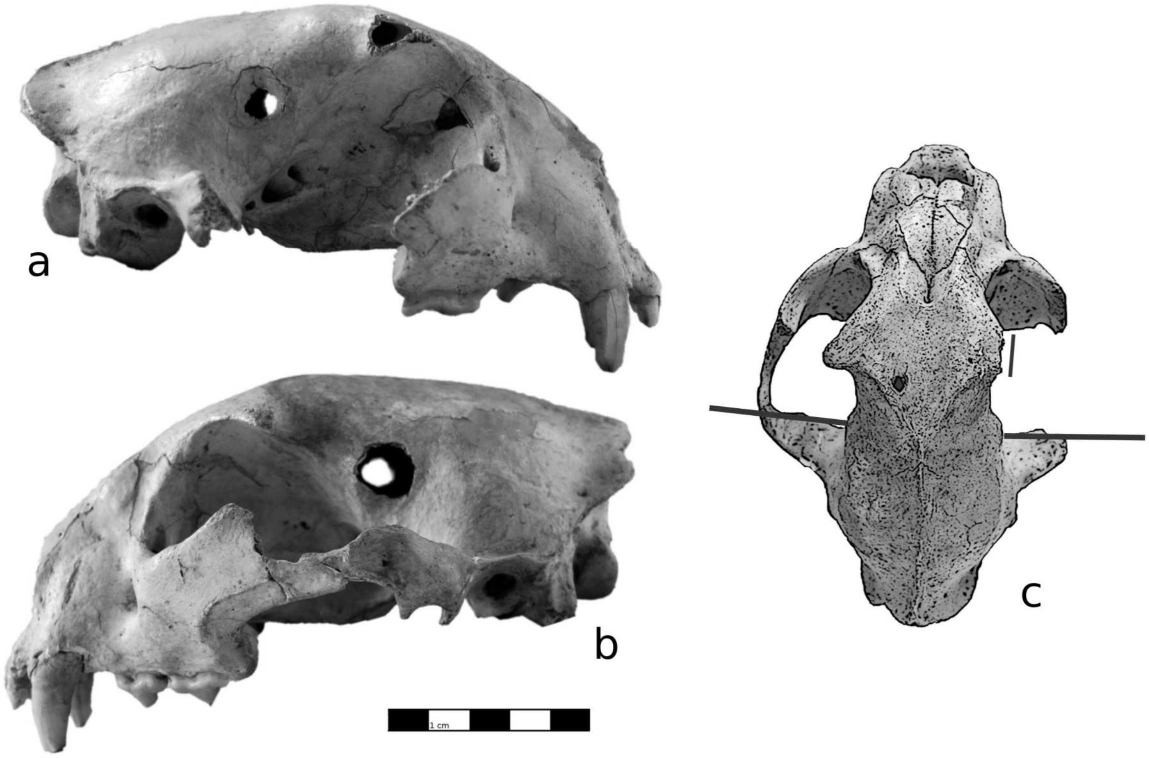


Figure 16: IGF15110V on right (a) and left (b) views. The schema on the right (c) shows the main symmetry of the probable bite and the right suvra-orbital process broken

The third premolars are worn in all specimens. IGF15111V/1 shows an unusual wear of distal side of paracone, probably due to a wrong occlusion of the maxillary and mandibular dental margins.

The carnassials are massive, deeply worn and morphologically variable among the specimens. IGF10036V do not bear the left carnassial (probably lost for post-depositional events). The best preserved is the left P4 of IGF15111V/1, which has a slightly bi-lobed metacone (similar to IGF185V/1). The latter is smaller than the paracone tip (a characteristic that does not seem related to the wear stage). The distal lobe is stretched posteriorly. Protocone is transversally developed on the palatal surface and do not create a constriction between paracone and metacone.

Figure 17: Premaxillar IGF185V/2 with incisive serie in frontal (A) ventral (B) and dorsal (C) views

The M1 alveolus is preserved in all the crania, and is still present only on the left side of IGF15111V/1.

All the mandibles have a rectilinear horizontal branch (Figure 18). The synphysis is long and inclined. No lower incisives and second premolars (or their alveoli) are found in our specimens.

Lower incisive alveoli are small, showing only a slight dimensional increase from i1 to i3. Cheek teeth are short and embricated. Canines are elongated, with the typical feline middle grooves on the labial side of the crown. There is no diastema between incisives and canines, and a short diastema separates the canine from the third premolar. The p3 is a small tooth; mesial and distal ends of paraconid bear one small tip.

The p4 is larger: the protoconid mesial edge is inclined, long and straight, while the distal one is shorter and curved. As a result, the cuspid ends before the midpoint of the tooth.

The m1 is similar in length to the p4. A short valley separates protoconid and paraconid. The latter is higher and occupies more than half of the tooth-blade length. Distally, a small tip, when present, never creates a real metaconid.

Deciduous teeth are smaller and slender than the permanent dentition. The canines do not show the typical features of feline, namely the longitudinal grooves on the lingual side and all deciduous post-canine teeth show supernumerary small cusps.

On the upper jaw, IGF6120V (Figure 26a-c) shows the small canine, the alveolus of dP3 (with only one small alveolus) and the dP4. The latter is a shearing tooth and has two similarly developed tips, the preparastyle and parastyle, a slender and high paracone, and a bilobed metacone. The protocone protrudes from the palatal side of the paracone. The enamel is developed on the palatal surface and forms a short bulge without a real tip. Under the metacone of dP4, the carnassial paracone is pushing out the tooth. Both the P4 and definitive C emerged on the palatal side these teeth, the permanent carnassial and canine are both in eruption. IGF6136V show the dM1 (Figure 19a-c).

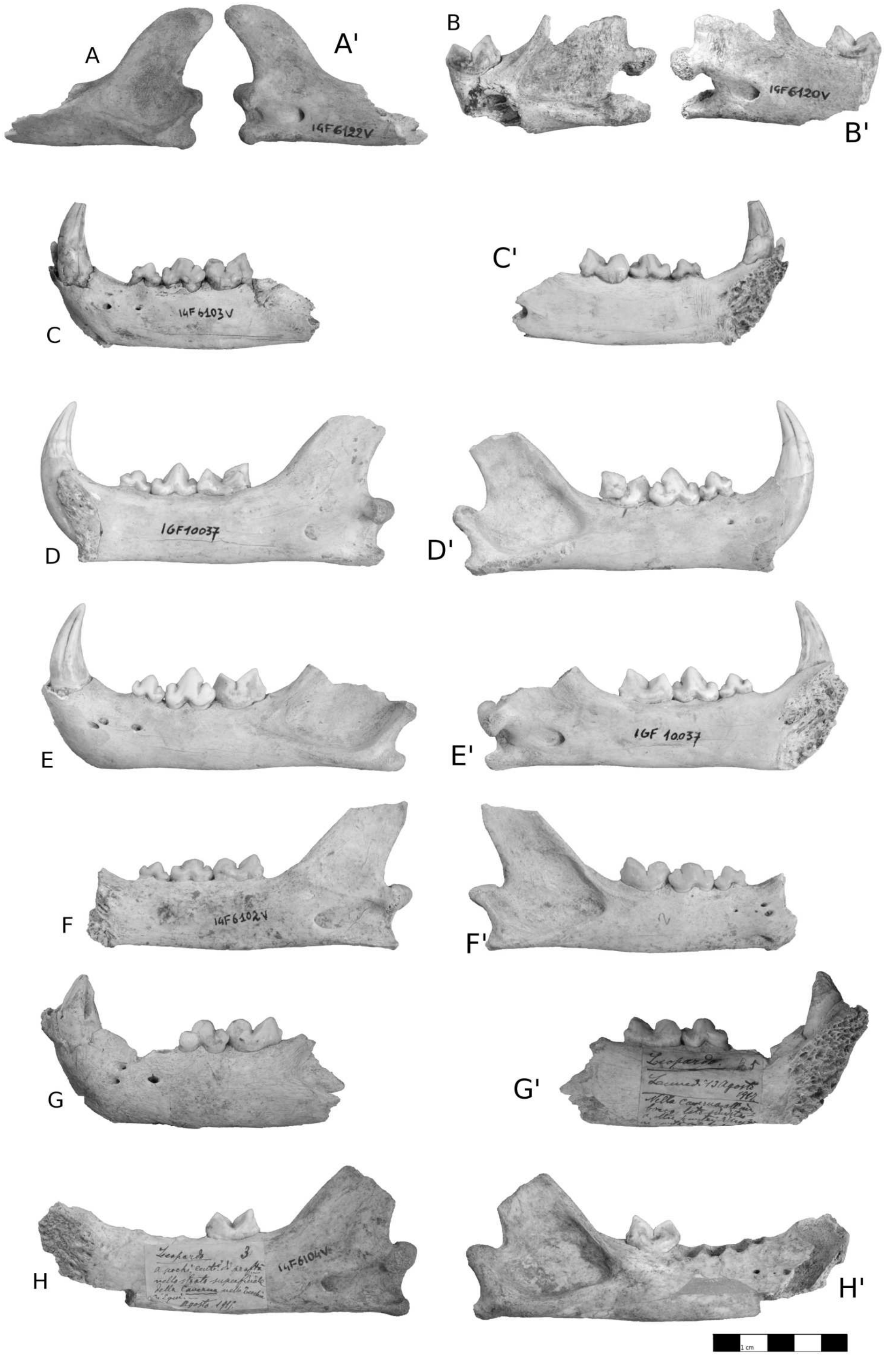


Figure 18: Leopard mandibles from Equi: IGF6122V, IGF6120V, and IGF6103V in labial (A, B, and C) and lingual (A’, B’, and C’, respectively) views; IGF10037V/1 in lingual (D) and labial (D’) views; IGF10037V/2 in labial (E) and lingual (E’) views; IGF6102V in lingual (F) and labial (F’) views; IGF185V/4 in labial (G) and lingual (G’) views; IGF6104V in lingual (H) and labial (H’) views.

The tooth is prone and has two developed and divergent roots, and the enamel is formed by one proximal and one distal little cusps and a mesial bulge directed to the medial plane, similarly to the dP4 one. The dental gem (enamel cap) of carnassial develops behind the last deciduous and starts to destroy the inner mandibular bone for to emerge.

The third and second permanent premolars are not still visible in both the juvenile maxillars.

The maxillar bone of IGF6120V is shorter than on adult (61 mm in front of an average of about 70 mm). The infra-orbital *fossae* is located above the mesial root of second premolar in both the specimens and the adult ones, but in the younger bones the appearance of the muzzle is strongly shorter.

In the best preserved juvenile mandible, IGF6123V (Figure 19d-f) there is a short diastema (11 millimeters) and the chin bone is massive in comparison to the articular side of the mandible. The lower permanent canine is still emerging but the dC was already missing after the die of the animal (because the bone does not show a remodeling of the bone).

The dp3 has a mesial parastylid and the higher and thinner paraconid is posteriorly oriented. Distally, a metastilid is present with a distal enlargement of the posterior neck of the tooth. The deciduous carnassial, dp4, is preserved in specimen, IGF6125V (Figure 19g-i) and IGF6119V (Figure 19l-m), and is characterized by a larger metaconid in comparison to the paraconid, and by one distal smaller cuspid, directly developed on the lingual side of the metaconid. A clear bulge is visible on the distal collar of the tooth, extended over the distal root.

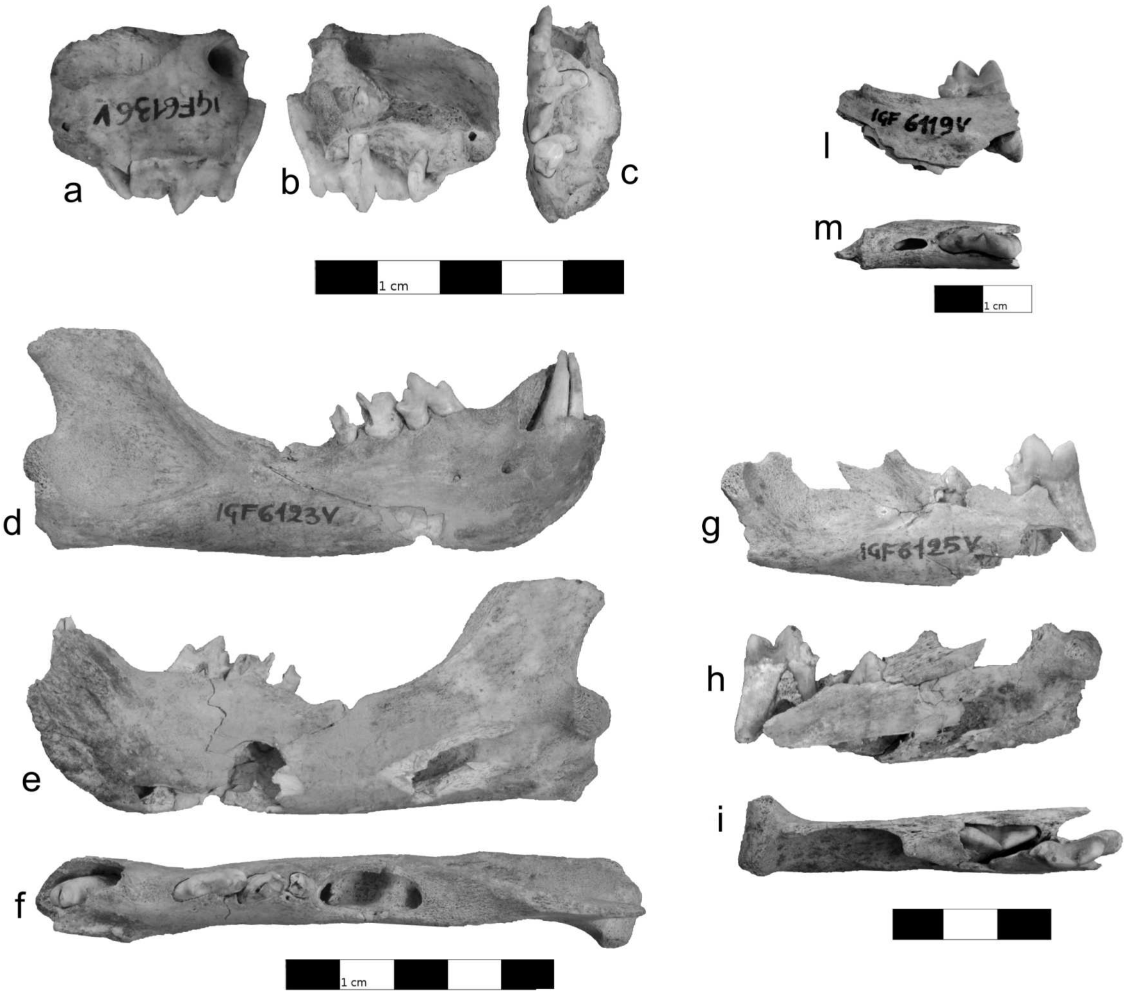


Figure 19: cranial and mandibular cub remains from Equi. Maxillar IGF6136V on labial (a), lingual (b) and ventral (c) views. Right mandible IGF6123V on lateral (d), medial (e) and dorsal (f) views; right mandible IGF6125V on lateral (g), medial (h) and dorsal (i) views; left mandible IGF6119V on medial (l) and dorsal (m) views.

In both the young mandible, the permanent carnassials were emerging on the gingival bone but, in IGF6123V, this tooth was quite come out and lost.

As previously mentioned, appendicular bones are well preserver. The eleven humeri are long and don't show a marked rotation of the diaphysis. IGF5342V is complete and its diaphysis shows evidence of *pectoralis* muscle stress (Figure 20a). IGF5352V and IGF5351V are significantly smaller, due to the ontogenetic growth.

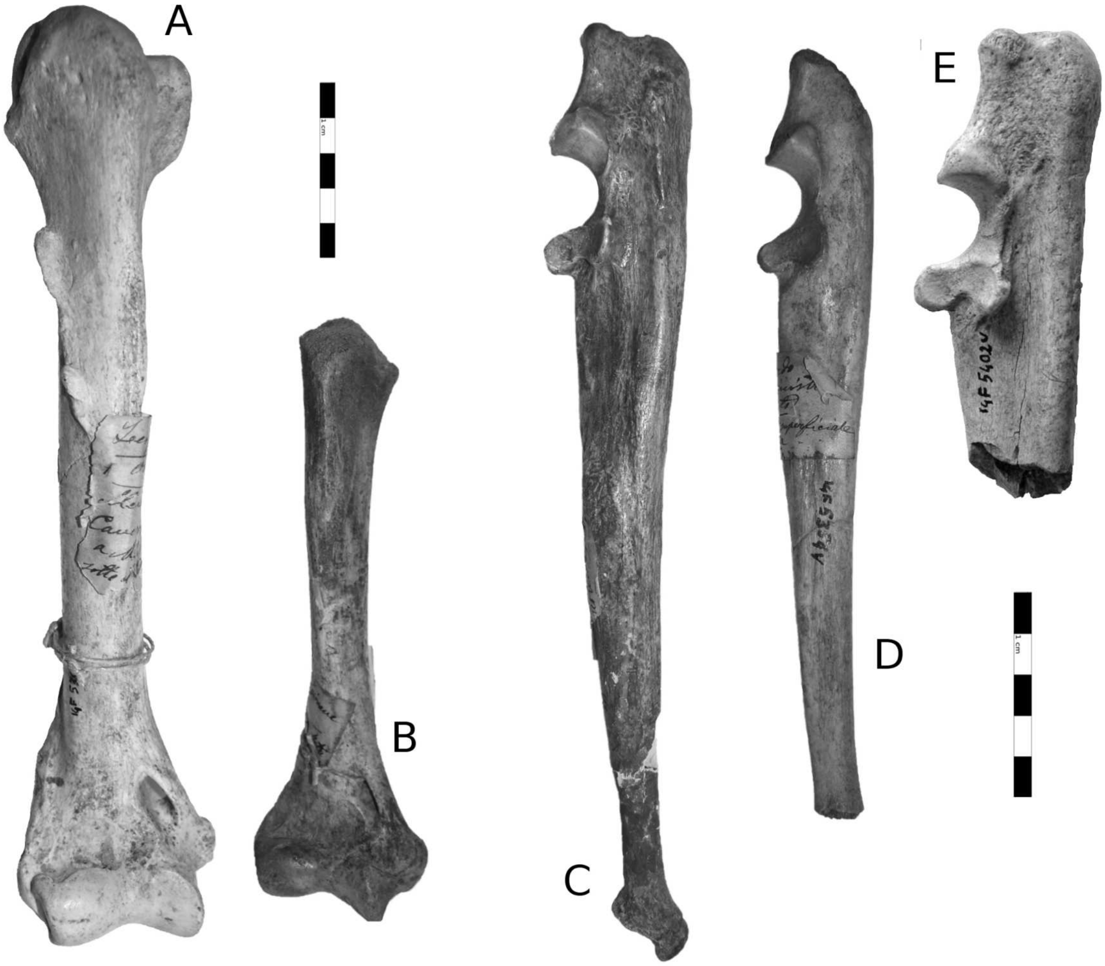


Figure 20: postcranial fossils of leopard: right humerus (IGF5342V) with evidence of *pectoralis* muscle stress on the proximal diaphysis; B) young right humerus (IGF5341V); left ulna in lateral view: from an adult animal (IGF5355V) (C) and a cub (IGF5354V) without the proximal and distal epiphysis (D); specimen IGF5402V (E) is massive and probably from a male or old animal.

The distal sovracondilar foramen is elongated to the distal end and its process is massive. The trochanter ventral outline is rounded and curves from the lateral to the medial side. IGF5341V (Figure 20b) is from a very young animal and does not preserve the proximal epiphysis (un-ossified); the same specimen instead preserves the distal epiphysis showing the ossification line at the contact with the diaphysis.

Ulnae in the sample are represented by six specimens. Only two are complete (Figure 20c), with the both the extremities ossified. Ulnae show a great size variability. The articular concavity of IGF5402V (Figure 20e) is similar to the homologous in IGF5354V (Figure 20d), but the former is larger and has a greater outline.

The diaphysis of the radius (eight discovered in the whole collection) is not compressed and is transversally elliptical. The tuberosity is large and produces a hump just under the proximal epiphysis on the latero-distal surface. IGF5337V is the slender radius specimen in the sample belonging to an adult animal (Figure 21).

Figure 21: radious of leopards: IGF5337V is from a left paw of an adult animal (A) and IGF5340V is a left radious from a younger one (B).

The McII (Figure 22 a-c) has a sub-rectilinear diaphysis. Frontally, there is a small bulge at the proximal medial margin. The articular surface with the trapezoid is unique and has a triangular shape. There is a concavity on the middle side of the surface. It ends before the distal convex elongation, which is curved behind and medially directed. On the lateral view, there is an elongated frontal socket just under the epiphysis, where the McIII is joined; above this concavity, on the antero-lateral corner there is a horizontal convexity. The proximal-lateral edge of McIII is sub-rectangular and flat (Figure 22d-f): it curves and forms a sizeable convexity directed to the medial surface. Medially, the articular surface is divided into two sides: frontally, the first one is horizontally elongated, stretching out and sloping to the medial plane. Behind, there is a flat and short limit of the surface. Laterally and frontally, there is only one concavity for the location of the McIV, similar to that described on the previous bone. The diaphysis width slightly increases from the proximal to the distal end. Comparing to the other metacarpals, the McIV is slender (Figure 22g-i), with the exception of IGF5297V, which has a massive and enlarged diaphysis. There is a tuberosity above the distal side of the diaphysis, at the radial flexor muscle insertion. The lateral side of the proximal end is rectilinear or slightly convex. Behind, there is a deep convexity. The articular surface is sloping and convex, rectangular in shape, ending frontally with a curved large edge. Medially, there is an articular protrusion, with a sinuous trend (concave and convex). On the plantar side, the proximal articulation ends whit horizontal steps. For the junction with McIII there is a sloping surface.

We note the differences in dimensions and robustness for the three McV (Figure 22l-n). IGF5309V is longer and larger than the other two McV. The proximal epiphysis is deeply convex and the anterior limit ends with an acute angle. Laterally, it develops a bulge and forms a semilunar convex surface. The diaphysis has a rectangular transversal section.

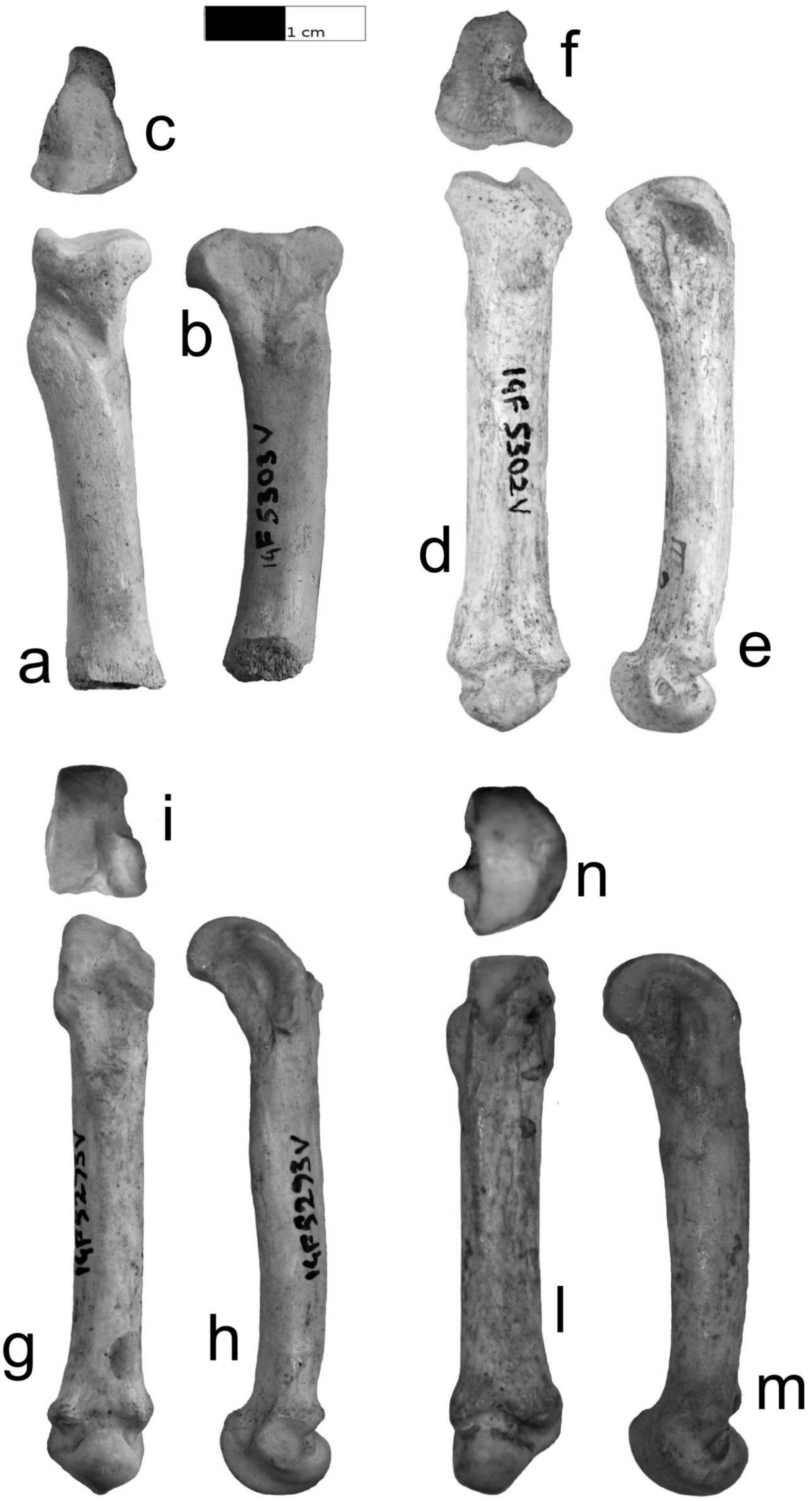


Figure 22: left McII (IGF5303V) in dorsal (a), proximal (c – not in scale), and medial (b) views; right McIII (IGF5302V) in dorsal (d), proximal (f– not in scale), and lateral (e) views; right McIV (IGF5293V) in dorsal (g), proximal (i– not in scale), and lateral (h) views; left McV (IGF5309V) in dorsal (l), proximal (n– not in scale), and medial (m) views.

Only one femur from an adult animal is kept within the historical excavations collections (IGF5347V, found in 1918). This bone is broken along the diaphysis and the broken edge was smoothed after the deposition. Nine more femurs in the collection from Equi belong to young or sub-young individuals (Figure 23a-c).

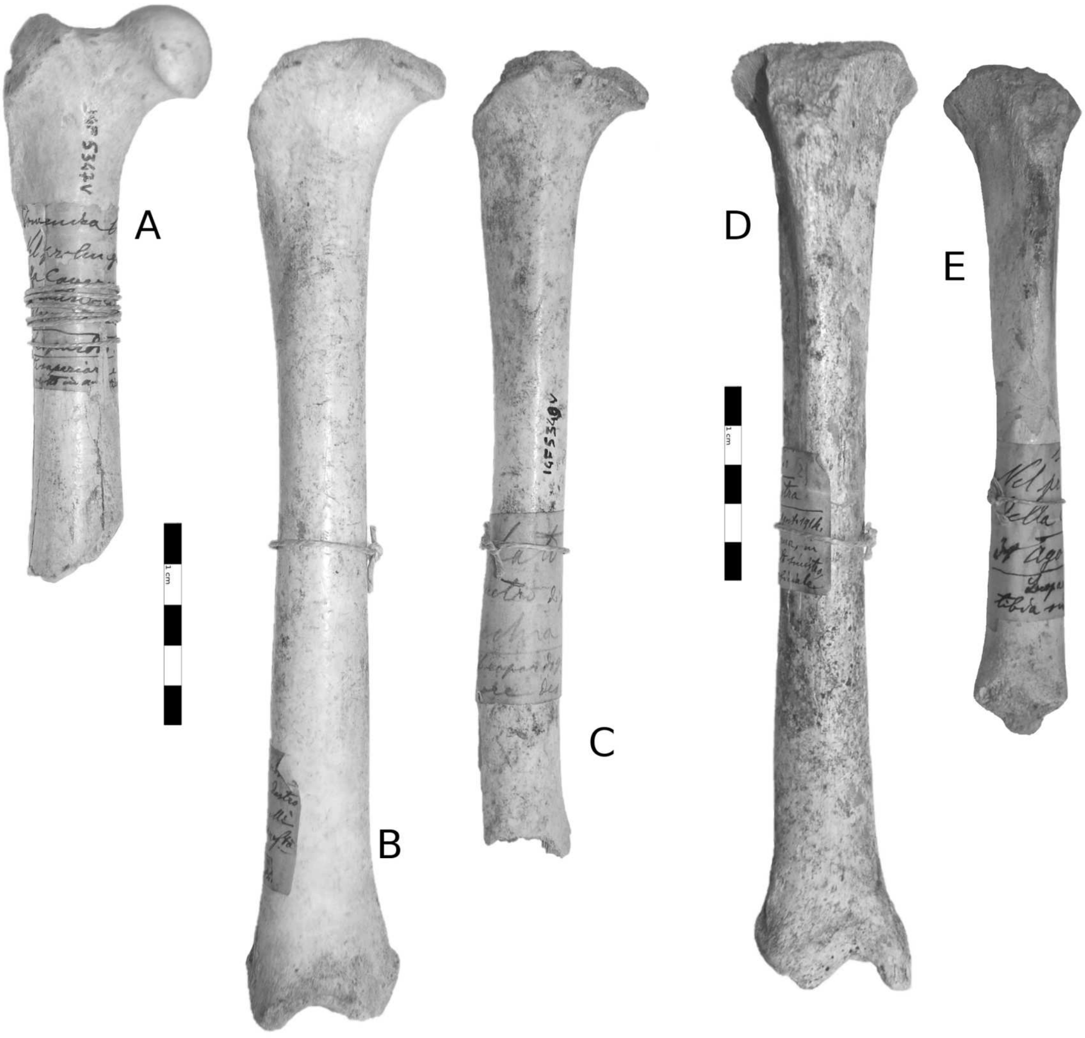


Figure 23: Hindlimb bones of leopards from Equi in frontal views: right femurs from adult (IGF5347V) (A) and juvenile (B: IGF5350V; C: IGF5349V) animals; right tibia of sub-adult (D - IGF5346V) and left tibia from a young animal (E - IGF5344V)

No found of tibias (nor fibulae) from adult animals are kept within the Equi historical collection with the exception of the specimen in exposition (numbered as nn46 in Appendix). IGF5346V (Figure 23d-e) has a sub-rectangular distal diaphysis in transversal section and a developed medial malleolus.

IGF5311V is a MtII (Figure 24 a-c). The proximal end is thinner than the distal one, and its massive diaphysis forms a medial concavity. The proximal articulation is formed by a medial concavity that is frontally bulged and posteriorly directed to the medial side. Laterally, there are two well marked surfaces, both concave and joined to the MtIII.

The MtIII (Figure 24 d-f) has a massive and curved diaphysis. It is fronto-distally flattened and rectilinear. The proximal articulation is joined to the middle cuneiform bone. Frontally, it is enlarged and curved. Medially, it forms a brief constriction and a distal bulge.

The MtIV (Figure 24 g-i) has a less curved diaphysis. The proximal end is clearly directed toward the caudal side. The articular area for the lateral cuboid is convex, slightly higher on the distal edge, and frontally tilted. Like for the McIV, it has a marked convexity for the junction with the last metatarsus. MtV is well represented by IGF5318V (Figure 24 l-n). Two are probably from the same very young animal (IGF5325V and IGF5324V): proximal and distal epiphysis are unfused (and consequently smaller size and a different kind of fossilization and colour). The MtV diaphysis has a triangular section and the proximal epiphysis show a lateral bi-lobed edge. From these two lobes, the articular surface is medially inclined. The lateral junction to MtIV is formed by an enlarged frontal structure and a distal plane.

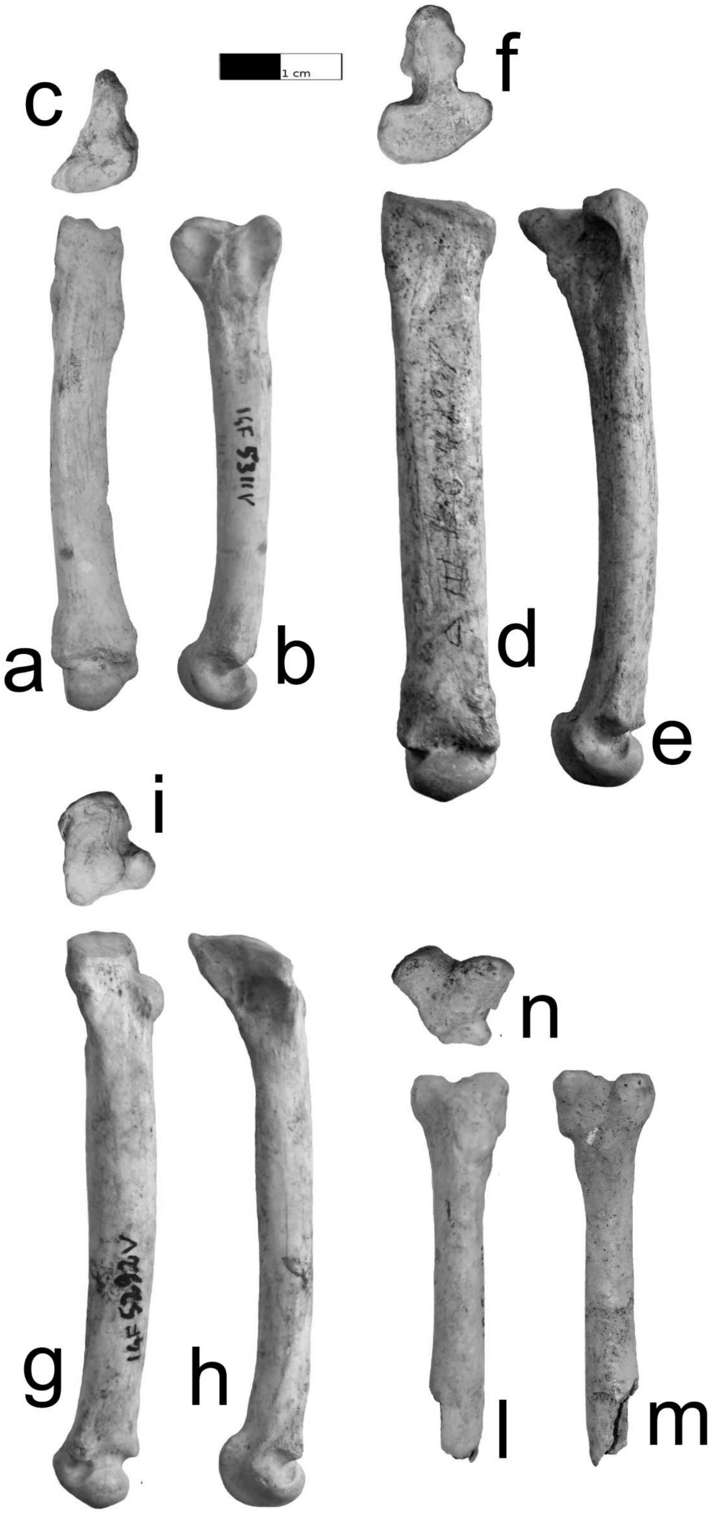


Figure 24: right MtII (IGF5311V) in dorsal (a), proximal (c– not in scale), and lateral (b) views; right MtIII (IGF5313V) in dorsal (d), proximal (f– not in scale), and lateral (e) views; right MtIV (IGF5292V) in dorsal (g), proximal (i– not in scale), and lateral (h) views; right MtV (IGF5318V) in medial (l), proximal (n– not in scale), and lateral (m) views (distal end is broken by gnawing).

Taphonomy- With a total number of 224 determined finds, Equi currently represents the most abundant collection of leopards across Europe, far exceeding the Late Pleistocene sites of Wildkirchli Cave (Switzerland), Baumann's Cave (Germany), the assemblage from Cueva de Los Rincones (Spain), and Caune de l'Arago and Hortus (France) (Testu, 2006; Diedrich, 2013; Saoqué et al., 2014).

Adults are dominant (60% of the whole collection), followed by young-adult animals (17%) (Figure 25a). Adult age-stages are also predominant among different anatomical regions (Figure 25b). As observed by Del Campana (1954), all the anatomical regions of leopards were sampled, with the exception of ribs, vertebrae and third phalanxes that are very under-represented (Figure 25d), both for young and adult animals. Autopodials are the most frequent elements in the collection, with a total number of 46 determined metapodials (Figure 25c).

The Minimum Number of Individuals (MNI), calculated considering humeri and Mt within the stratigraphic distribution (see Chapter 4.3), is 6 for the humeri (one for each layer a-a0, ab, hb, and i, and two right humeri in the layer l) or the Mt frequencies (one for each layer a-a0, ab, c, g, hb, and l), but this approximation is probably underestimated. The MNI calculated using right tibias of litters (IGF5343V, IGF5345V, IGF5346V, IGF6160V) is 4.

Evidences of peridepositional larval damage of periostium are on IGF6141V (Figure 26d), characterized by twelve pinholes on the diaphysis (about 2.5 mm of diameter each one) never reaching the spongy *lumen* of the bone. Similar occurrences were observed in several fossils but have just recently been analyzed by Fejfar et al. (2005), Harris and Timm (2013), and Holden et al. (2013).

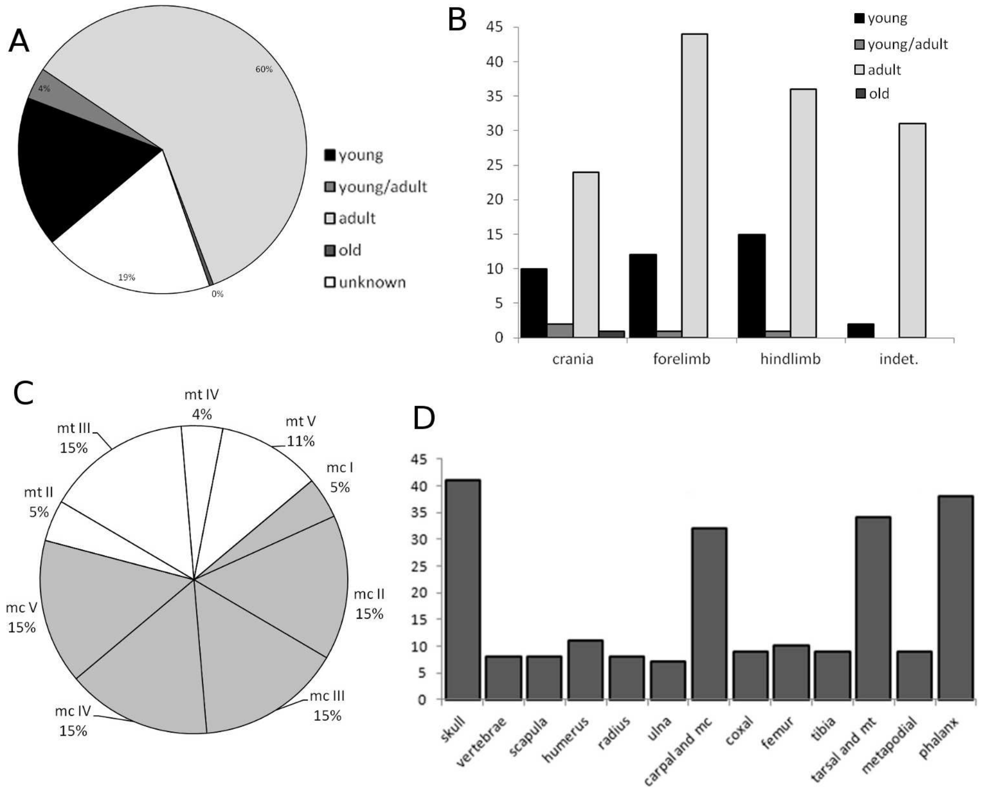


Figure 25: Pie chart of leopard bones' age-stage (A), and age-stage frequencies for anatomical regions (B). Pie chart describing metapodial leopard remains (C) and general representation of leopard specimens from the site (D).

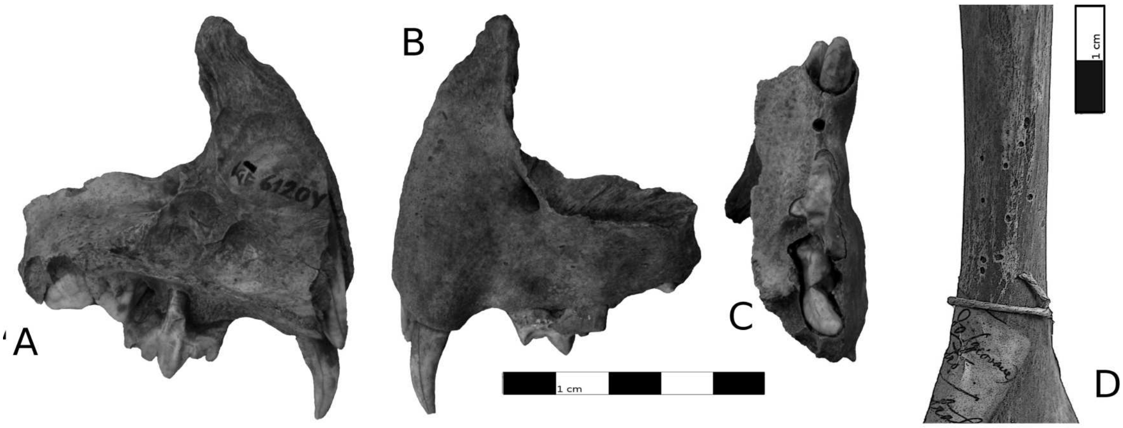


Figure 26: Fossil of leopard cub IGF6120V in lingual (A), labial (B) and ventral (C) views. D: putative larval holes on diaphysis surface of a young humerus (IGF6141V)

On the basis of the available information from original labels in the Florence museum collection I proved that there are not very remarkable differences in the distribution of large carnivores' anatomical elements through the stratigraphic record (Chapter 4.3). Wolves and leopards were the most numerous animals in the site (not considering bear remains) and their distribution increases in the uppermost layers. The occurrence of the same species throughout the sequence is probably related to climatic conditions within the middle to later part of the MIS3.

The lack of axial skeleton and autopodial ends in the collection seems not to be due to scavenging, but, most likely, it could be related to the effects of excavators' selection rather than to taphonomic agents (even though such consideration is partially in disagreement with the presence of well preserved small bones in the Equi collection, implying a favourable depositional environment and careful recovery work during the field work in early times).

Few peculiar features of the leopard bones from Equi testify the occurrence of disease and consumption, not related to a precise type of carnivores. There are rare examples of gnawing and fluitation (*sensu* Fisher, 1995; Lyman, 1994) within the entire assemblage, most on the proximal and distal ends of long bones. However, there are no digested leopard bones. Usually, bone consumption is related to hyena activity, but there is no evidence, at Equi, of hyena frequentation. Examples of different predator carcasses being sorted by hyenas when scavenging is recorded at several open air sites (Bottrop, Perick and Keppler Cave; Diedrich, 2009b, 2012), and at the site of Gran Dolina (level TD10-1), lion remains were sorted due to human action (Blasco et al., 2010). These sites were characterized by a common preservation pattern for bone accumulations, with large predators carcasses damaged most at fore and hind limbs (as a consequence, vertebrae are not destroyed and are usually preserved). The preservation pattern is the opposite at Equi, where entire skull, and fore and hind limbs are well preserved, meanwhile, the axial skeleton is almost completely missing.

Not so far from the Equi deposit, faunal guild from Buca della Iena was described and dated back to the MIS3 (about 41 ky) by Pitti and Tozzi (1971). Layer D of the cave represents a typical hyena den site with the high frequency of the predator in association to several large preys (horses, deers, and aurochs) and few other carnivores, such as *Ursus spelaeus* and *Meles meles*. As mentioned above (Chapter 4.3), in the Equi assemblage the differences are notable, both for specific occurrences and frequencies; few herbivorous are represented and several species of carnivores are recorded, such as lions, wolves, foxes, dholes, and mustelids.

Recently, many studies about leopards as bone collector were made in comparison to hyenas, and their role as scavengers seem to have been underestimated (de Ruiter and Berger, 2001; Carlson and Pickering, 2003; Pickering and Carlson, 2004; O'Regan and Menter 2009; Pickering et al., 2011; Saoqué et al., 2014), as for dholes and wolves (Mallye et al. 2012; Fosse et al. 2012; Fourvel et al. 2014), even though extant leopards use caves where trees are rare, just avoiding food-competitors and never as a durable den (Ruiter and Berger, 2001 and references therein). The herbivores are scarcely represented at Equi, and there is little evidence of gnawing on leopard bones surface. As a consequence, the co-presence of adult and perinatal and young cubs (less than three years, see below), and the contemporary absence of real preys can be interpreted as an evidence for the use of the cave as a den for birth and rest, more than just as a hunting site (implying a different and characteristic behaviour of this population). Up to now, the frequency of young leopards in the cave is unusual for this species and a real exception in European record, where adults are always the largest part of the collection for this species (Diedrich, 2013, and references therein; Sauqué et al., 2014) with only few evidences of decidual teeth at Hortus in France (Testu, 2006), in the Cave of Jou Puerta in Spain (*Panthera* cf. *pardus*; Álvarez-Lao, 2014), Vraona Cave in Greece (Nagel, 1999) and in the entrance area of Baumann's Cave in Germany (Diedrich, 2013).

However, the sites with several carnivorans species are not infrequent during the Pleistocene. Argant et al. (2007) found *P. onca gombaszoegensis* and *Panthera spelaea fossilis* in association to *Ursus deningeri* and *Canis mosbachensis* in the site of Château Breccia (France). Diedrich (2013) described the younger association in the Wildkirchli Cave (Switzerland) and Baumann's Cave (Germany), where *P. leo spelaea*, *Ursus spelaeus*, *Panthera pardus spelaea* and *Cuon alpinus fossilis* were found with Neanderthal evidences. Similar to Equi, the interesting site of Los Rincones (Spain) recorded several evidences of leopards in association to *Ursus arctos*, *Canis lupus*, *Lynx* sp., but with also many herbivores with taphonomical signs, which allowed the authors to conclude that the cave probably represents a leopard hunting den.

In the case of Equi, the presence of many fossils of leopards in opposition to the rare top predator (lion) could imply a borderline environment. According to several authors (Balme et al., 2007; Bhattarai and Kindlmann, 2012; Steinmetz et al., 2013), the largest predators (i.e. lions in Africa and tigers in Asia) occupy the best areas to maximize their hunting and fitness success, where the prey availability represents the mainstay for the range selection (Lovari et al., 2014). The subordinate predators' ranges (leopards, wolves, and the smaller dholes and foxes) are the results of avoiding the largest carnivorans, and balancing the disadvantages of prey availability with less selective habits, their agility and (not for the former) pack organization. Also, the steep valley of Fagli was probably considered by leopards in order to avoid other predators (such as hyenas), and bears for hibernation. A last hypothetical scenario for explain a so high frequency of leopard in the site of Equi was already depicted by Diedrich (2012, 2013) for other European Pleistocene sites, with the opportunity of scavenge bears remains.

Bites – On the skull IGF185V I have noted the damage of both temporal bones. This kind of injury seems to be related to a singular bite and I have excluded a recent damage of the skull, almost for the right side, because the broken edge shows the same color and fossilization-stage of the entire skull. The fresh bone better respond to the bite pressure compared to dry ones (Kim et al. 2004) and, in this skull, the relative elasticity of the bone avoided to leave the broken boundary of the right injury. In fact, the surface of the right temporal is recessed and the hole results concave, with a clear entry wound.

All carnivores ever show a competitive approach to the prey and the reconnaissance of some mark origins are usually difficult due to this similar approach and slaughtering of the carcass. In few cases, the differentiation can be made by the dimensional analysis of injuries or peculiar kind of bite and chew meats and bones; for example, Diedrich (2009a, 2011; 2012), among others, demonstrated that European hyena principally chews epiphysis and the ends of bones, while other carnivores, such as wolves and dholes show different strategies (Haynes 1983; Fosse et al., 2012; Mallye et al., 2012; Fourvel et al., 2014).

Hyenas' chews insist on occipital side of the skulls, probably for brain consumption, destroying the braincases (Diedrich 2012). This was not the case for the damaged skull from Equi, where the occipital region is totally well preserved.

I rejected the hypothesis that the two holes were made by humans, because typical lithic artifacts, such as arrows or assegais, leave elliptical injury on the bone surfaces (Bachechi et al. 1997; Smith et al. 2007; Letourneux and Pétillon 2008).

Among carnivorans, leopard seems to be unable to create simile large damage on skulls, and today the animal prefers to concentrate the interest and attacks on the neck of the victims (Nabi et al. 2009). Moreover, taphonomical studies reveals that the animal in general leave only small pits on the long bone surface (Pickering et al. 2004).

The bite from a bigger carnivore, such as lion or bear, is considered here more probable, for the diameter of the holes (about 1 centimeter for the right pit) and the opening of the mouth of the guilty (more than a decimeter). Modern lions usually kill their prey attacking hindquarter and the muzzle, provoking a death for suffocation, whereas killing method of bears imply focused injuries on skull, face or neck (Roka et al. 2012; Nabi et al. 2009).

Also, the bite force is related to the body mass and Grandal-d'Anglade (2010) calculated that the bite force of skulls of *Ursus spelaeus* from MIS3-2 was more crushing than extant bears and as aggressive as lions.

As conclusion, according to the few evidences of lions from Equi and probable examples of fight between leopard and bears in Vjetrenica Cave (Dinarid Mountains, Bosnia Herzegovina) (Diedrich, 2013), the latter is here considered the most probable guilty for this unique taphonomical evidence.

Sex determination- Frequently, cranial morphology reveals general characteristic allowing sex recognition of individuals. This is also the case, since leopards from Equi show a similar trend of features, with massive crania interpreted as male, and thinner ones determined as female. Pocock (1930, Plate IV) analysed the variability of "panthers" through Asia, determining the differences between male and female cranial morphologies in different regions of the "United Provinces" (he was active during English Colonial time). Even though he couldn't recognize any constant evidence of local races ("*I have failed to establish the existence of any constant differences between the skulls of the local races of panthers, admitted in this paper, except in the matter of size*": Pocock, 1930), he noted that males have larger teeth and a less rounded cranial portion, with a high medial and a prominent occipital crest, deeper post-orbital constriction, and the braincase is longer and narrower than in females. The right and left temporal lines are joined to each other from the post-orbital process on male and further on females (Figure 27). In the latter, all crests are less developed and the sagittal one does not begin from the post-orbital process but from a position situated further back.

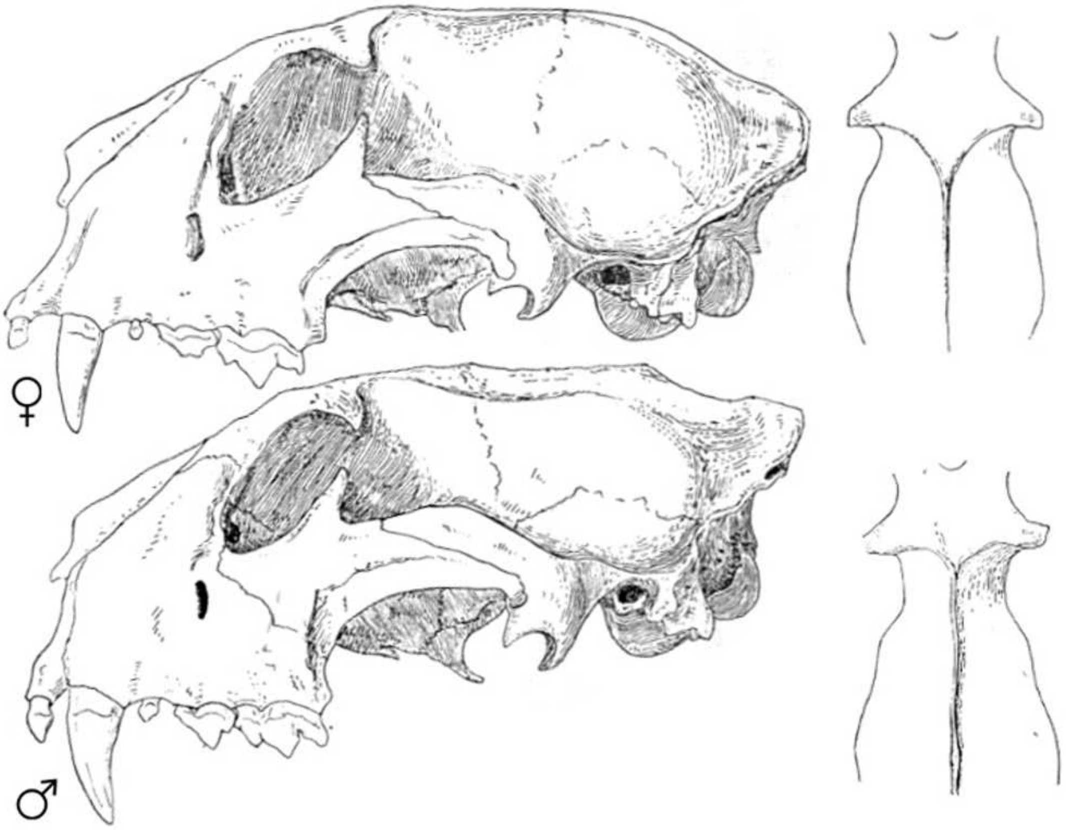


Figure 27: female and male comparative morphologies of leopard crania (from Pocock, 1930; modified): major differences are on temporal lines junctions, the development of the sagittal crest, the feature of the braincase, more or less evident postorbital constriction.

These differences are not so marked in juvenile animals where, sometimes, intermediate morphologies are shown. Finally, Pocock supposes that the skulls of both sexes tend to flatten along the top as age advances, becoming lower and longer than in young-adult individuals. Sunquist and Sunquist (2002) add that, in general, males' are larger than females' of the same regions, often reaching a 30-50% heavier body mass.

On the basis of Pocock's (1930) analysis, a sex determination is possible for the Equi fossil material. Crania IGF10036V and IGF184V have masculine features, while the frailer (with under developed sagittal crests) IGF15111V/1 and IGF185V/1 seem to be better attributable to female individuals. IGF15110V cranium has sub-spherical outline of the neurocranium, undeveloped sagittal crest and long temporal lines, but the bone appears massive as a male, so we cannot rule out that this specimen represents a very old female.

Diedrich (2013) tried to infer the two genders from the size of their crania. A similar conclusion was possible for lions (Turner, 1984) and could be considered true within a well-defined population, but it is not possible to compare cranial remains from far territories and long geological times, without considering climatic oscillations and the typical morphological and size flexibility of this species. In the previous study of carnivorans from Equi, Del Campana (1954) reported that total lengths of males and females of modern leopards from different regions (South Africa, Congo, eastern Africa, and central India), respectively 178-247 and 205-218 mm, showing a clearly overlapped range. The shorter skulls from Equi, IGF15111V/1 and 15110 are within the small male size range, and IGF185V/1 is the most massive and largest skull, besides the upper limit of length for modern leopards: a result exactly opposite to the morphological conclusion.

We conclude that the general rule that males are larger than females could be considered valid, but the range and size variability of these animals don’t allow inferring the genders, and their morphology should be preferable to size analysis for sex determination (Figure 28).

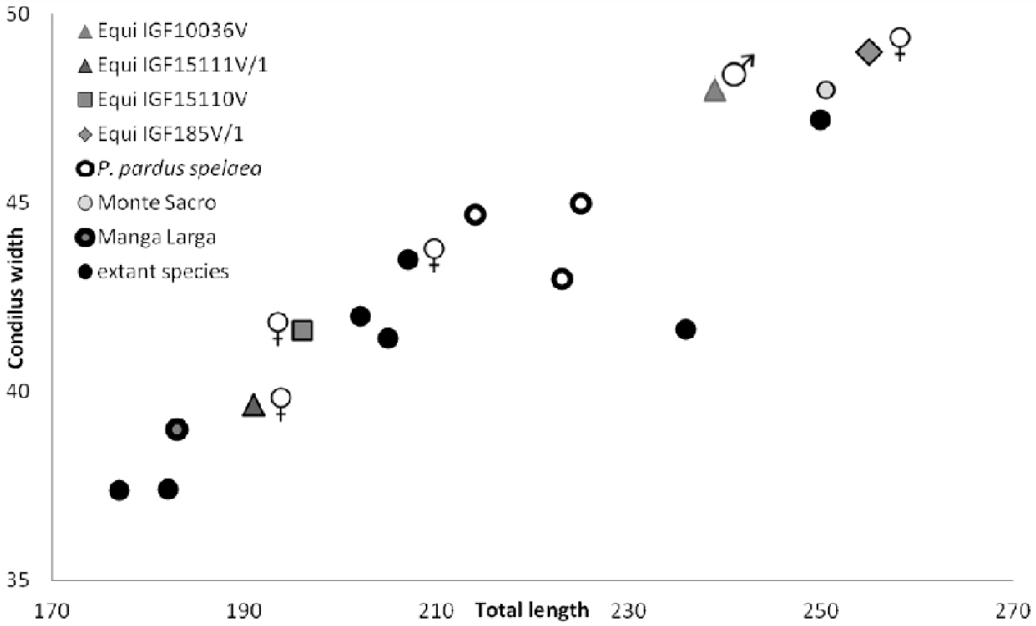
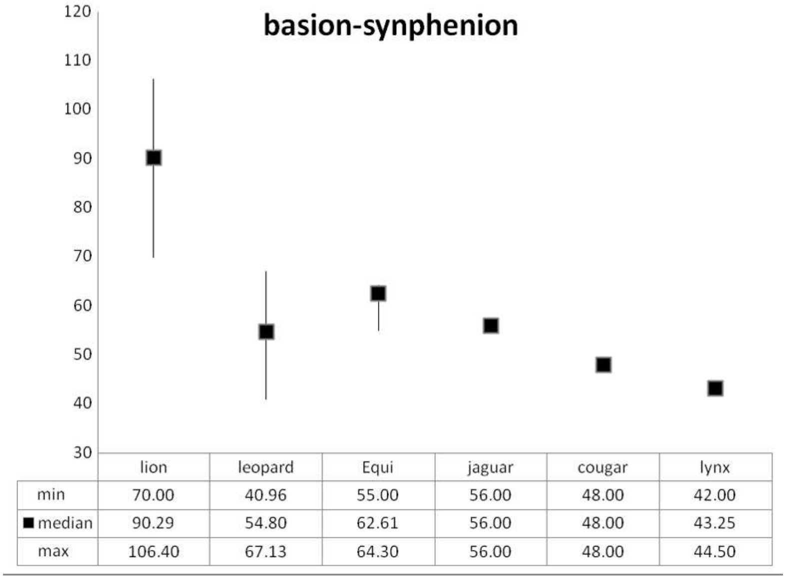


Figure 28: total length vs. condilus width scatter diagram of fossils and extant species: black dots are from extant animals from different regions (a single specimen has a declared gender); the gray dot is the Monte Sacro Middle Pleistocene cranium (M.P.U.R./V.1191: Kotsakis and Palombo 1979); the gray-black dot is the cranium from Algar do Manga Larga (Cardoso and Regala, 2006); white dots are fossils crania described by Diedrich (2013); square, triangle and diamond represent the crania from Equi. Genders were defined on the basis of morphological characters.

Body size – Dimensionally speaking, the crania from Equi fall within the range of extant leopards (Figure 29). They are generally massive, and all larger than extant subspecies for the palatal and neurocranium width (Figure 30). Jaguars (*Panthera onca*) and cougars (*Puma concolor*) are intermediate in size among *Panthera pardus* and lions, and within the leopard-lynx lower limit respectively. Leopards from Equi are quite larger than the conspecific extant animals. It is also notable that all leopard crania from Equi had a shorter muzzle in comparison to extant relatives, even though the check teeth are always 2.8 times longer (in average) than the carnassial for both the species.



	lion	leopard	Equi	jaguar	cougar	lynx
min	70.00	40.96	55.00	56.00	48.00	42.00
■ median	90.29	54.80	62.61	56.00	48.00	43.25
max	106.40	67.13	64.30	56.00	48.00	44.50

Figure 29: cranial length maximun-minimun ranges of different species of big cats.

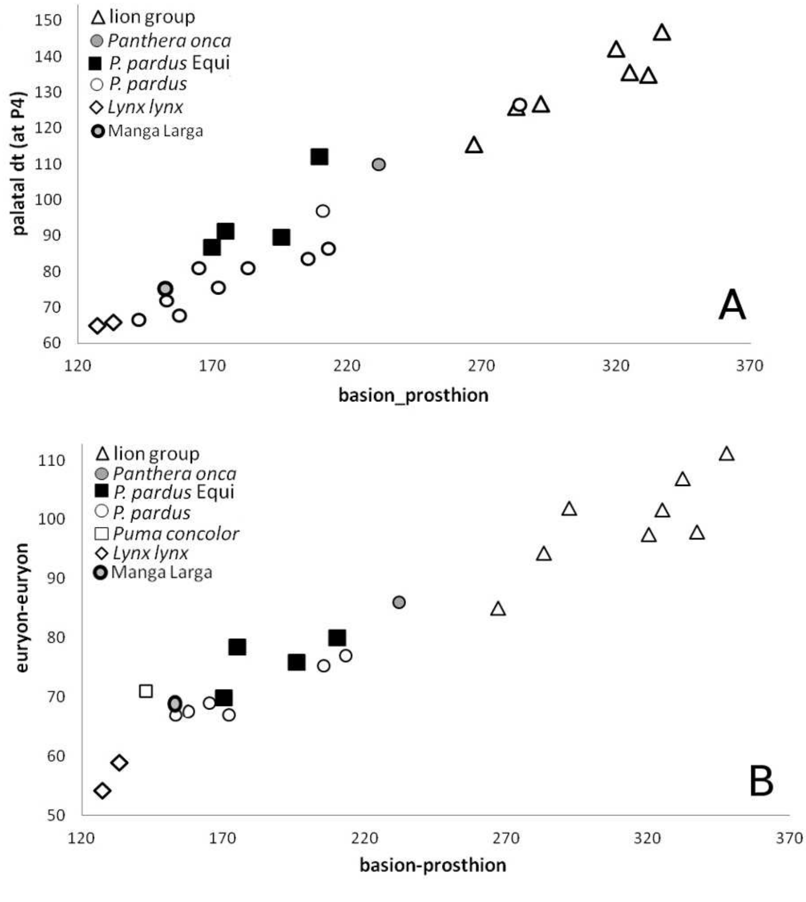


Figure 30: basion-prostion vs. palatal weigth (A) and euryon-euryon (B). In comparison to extant leopards, the fossils from Equi are larger, stoutly built and massive, and clearly distinct from other species of felids.

As mentioned above for leopards, a strongest overlapping of condilobasal lengths in the two genders can be appreciated also in the similar middle-sized felids *Puma concolor*, varying between about 110 and less than 200 (Giannini et al., 2010). The skulls of American and European cougars are shorter than leopards, being rounded both in the braincase and splancnocranial regions.

Upper teeth reveal a clear separation of leopards from lynx in the LP4/C-M1 ratio (Figure 31a).

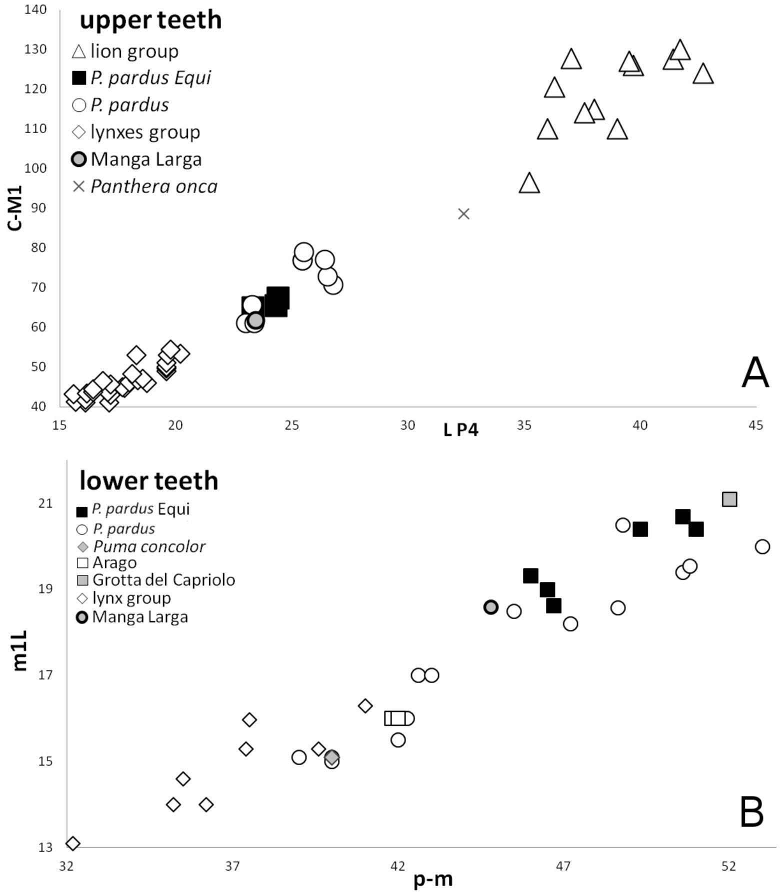


Figure 31: Dental comparison among upper (A) and lower (B) teeth of leopards from Equi (black squares), extant (white circles) and extinct leopards (Arago – white squares, unpublished data; Grotta del Capriolo – gray square, Pitti and Tozzi 1971; Manga Larga – gray-black circle, Cardoso and Regala 2006), extant and extinct lions (white triangles) and lynxes (white rhombus), and cougar (gray diamonds).

The specimens from Equi are set on the lower limit of variability and match with the leopard from Portugal from the Late Pleistocene and with *P. pardus* from Angola (specimen 8748 from Natural History Museum of Florence). As consequence, the muzzles of the leopard from Equi can be considered quite short. The split is so evident also for lower teeth following the same pattern: the extant leopard set is partially overlying the lynx's, while specimens from Equi are larger and close to the coeval leopard tooth from Grotta del Capriolo (Pitti and Zorzi, 1971) (Figure 31b).

The sizes of upper carnassials from Equi are within the leopard's range. The Villafranchian European cougar shows a smaller upper carnassial, includes between 20 and 23.2 mm (Cherin et al., 2013), and shorter lower check teeth (Figure 31b), meanwhile jaguars are larger and placed far from leopards and closer to lions size.

Unfortunately, information about the original position of each cranium in the stratigraphy of Equi is completely missing. Instead, the lower m1 distribution seems to have a distributional pattern. IGF10037V/1, IGF6104V, and IGF10037V/2 are larger than IGF6102V, IGF6103V and IGF15111V/2 and both are well grouped in two sets. Anyway, this distribution is not justified by the stratigraphic distribution: the information was reported only for IGF6104V, IGF6102V, which were found just below the surface in the shelter and cave respectively, and for IGF6103V, which is older (layer hb in Chapter 4.3).

The m1L/m1B ratio diagram (Figure 32) show that the three most representative sites of Los Rincones, Vraona and Equi, have parallel trendlines but the latter has clearly smaller teeth. This evidence must be considered with the shorter muzzles and large palate of Equi leopards, concluding a local variability of the population. At the same time, *P. concolor* is well defined by its shorter and slender lower carnassial and *P. onca gombaszoegensis* is quite larger than Late Pleistocene leopards.

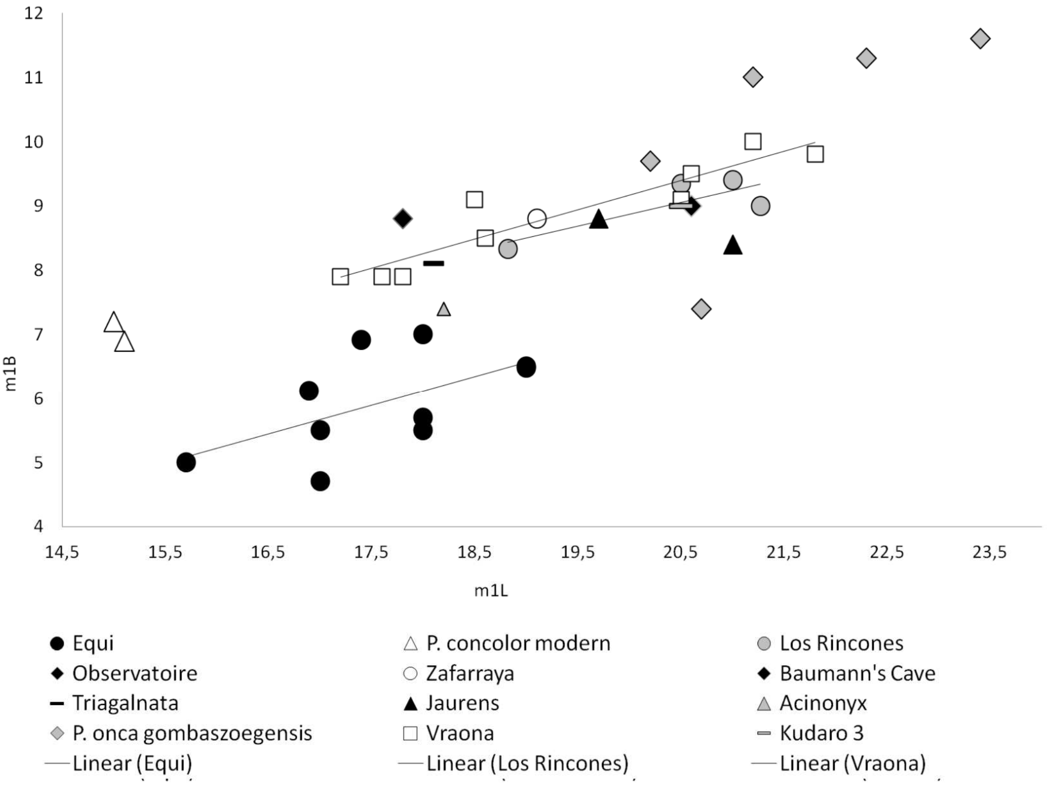


Figure 32: length and breadth of lower carnassials and respective trendlines of the main leopard collections, namely Equi, Los Rincones and Vraona Cave. The lines are quite parallel to each other and precisely specify for the shape of leopards m1s.

Postcranial bones are more fragmented and there are only one entire humerus and radius (Figure 20 and Figure 21). The bones are well discerned from lions and the humerus is included into the extant leopard variability for the trochlear width (Figure 33a).

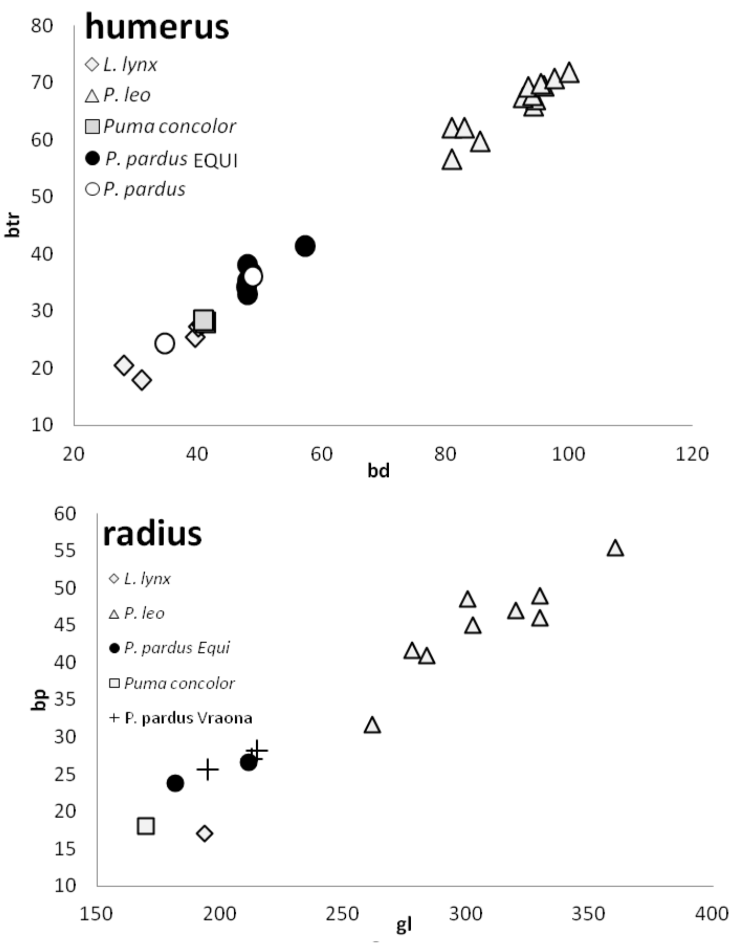


Figure 33: Postcranial comparison among different species of Felidae. A: humerus (IGF5342V) B: radius (IGF5339V); total length (Gl) and distal breadth (Bd) ratios

The largest humerus, IGF5342V, is also the older one (layer b, just above the second hearth; cfr. Chapter 4.3) and its size is better explainable with sex dimorphism or wide intraspecific variability. As we can see in Figure 21, the size of radius varies in relation to ontogeny and intraspecific variability: it is an individual-related character. The length patterns of metacarpals and metatarsals for the species of big cats allow us to well-define the limit between lions and leopards, for extant and for the fossil materials too. Lynxes metapodials tend to be longer than leopards ones, but the weight of diaphysis is larger for the latter in comparison to the slenderer lynx and consequently they cannot be confused (Figure 34).

There are not a trend among leopards from Middle to Late Pleistocene and extant animals, and an overlap between this species and cougar (both *P. concolor* and *P. pardoides*) can be observed at least for the McIV.

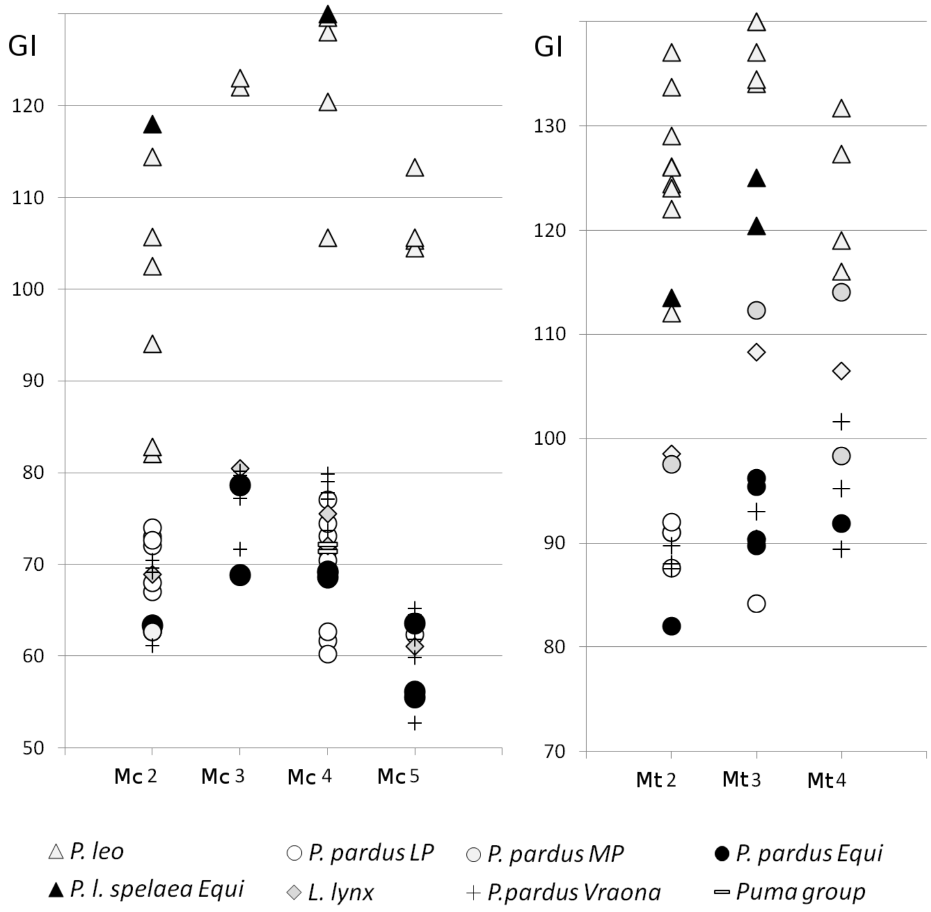


Figure 34: metacarpals (A) and metatarsal (B). Comparative dimensional range of Gl in Holocene and Late Pleistocene big cats.

Nagel (1999) noted a particularly robustness of feet bones of leopard from Vraona Cave. Compared to Equi, the specimens seem effectively larger, but the absolute ranges have not a statistical significance (the variance between the two collections is about 1-2 mm both for metapodial min and max SD).

The morphological features are quite variable in all the specimens from Equi (Table 3) and the dimensional analysis must be used together for a definitive determination.

Leopards are even smaller than lions and the teeth are slender. Compared to *P. pardus*, the mandibles of *P. onca gombaszoegensis* are higher and the canine is larger. The lower carnassial is also massive and the two tips are closer to each other (Spassov and Raychev, 1997; Hemmer et al. 2001). Leopards are quite larger than *Lynx lynx*, and in this case both the morphology and dimension allow the bones to be correctly determined.

Spassov and Raychev (1997), Nagel (1999), Diedrich (2013) and Saoqué et al. (2014b) described the morphological affinities of the Late Pleistocene leopards to *Panthera uncia*. I have excluded the snow leopard for determining the specimens from Equi because the crania clearly diverge both for size and morphology from *P. uncia*. The most visible difference between the extant snow leopard and African leopard is the very concave dorsal edge of the short splancnocranium in the former. In the mandible, the symphysis is quite vertical and the diastema shorter. The shortness of snow leopard diastema doesn't fit with modern leopard and the specimens from Equi are within the variability of the latter (Figure 35). The same trend is shown for almost all the Middle and Late Pleistocene specimens include in this analysis. On the contrary, the diastema of the mandible from Stràskà Skàlà is very short and was firstly determined as snow leopard by Thenius (1969) and included to *P. pardus* by Hemmer (1971).

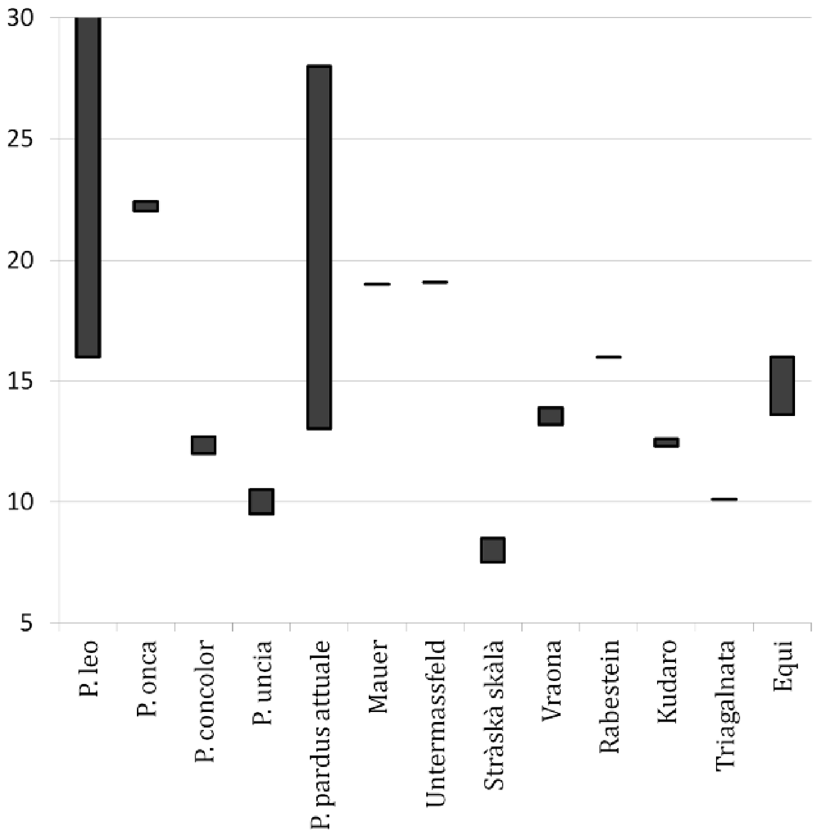


Figure 35: diastema length of different species of Felidae. Modern leopards are partially included to lion's variability but are well-divided to *P. uncia*. The same is generally for the leopard fossils with the exception of the short mandible of Triagalnata and the problematic Stràskà Skàla specimen.

Diedrich (2013) resumed the evolutive trends of European leopards indentifying the most ancient animal with elongated skulls, medium-wide frontals and low-crowned P4. The youngest animals assumed and a progressive change of these characters, with a short and enlarged skull and developed cusps of P4.

The features of individual variability offered by the leopard cranial record from Equi allow me to point out a different scenario, given that the variability observed in literature can be easily explain with intraspecific (intrapopulational) variability. The cranial length is variable as much as the frontal widths, and P4 crown height varies in relation to the wearing stage. IGF15110V is very similar to the cranium from Algar da Manga Larga Cave (Portugal) (Cardoso and Regala, 2006) with a quite short muzzle, a barrel-like braincase and a large postorbital constriction. They differ for the sunken-in feature of the dorsal end of the nasals. This last character seems to be specific for the leopards from Equi but it is represented by a plesiomorphic feature, being visible also in lions (see Chapter 6.1). Otherwise, the skull from Monte Sacro (Rome) has long splancno and neurocranium and a developed sagittal crest (Kotsakis and Palombo, 1979). IGF10036V is similar to such skull, showing a comparable development of neurocranial side and sagittal crest, but the splancnocranium is verticalized and the muzzle results shorter (Figure 15). In this specimen, the postorbital constriction is narrowed (as probably in the restored cranium IGF15111V), showing more affinities to the modern specimen from the Horn of Africa (from the Venice Museum of Natural History) but unlike the presumed trend for Late Pleistocene European leopards.

As mentioned above, the presence of P2 is quite variable in the skulls from Equi, while they are present at the cave of L'Observatoire and Monte Sacro, lacking instead in the specimens from Lunel-Viel (Bonifay, 1971; Kotsakis and Palombo, 1979) (Table 2).

Two dental morphotypes were recognized by Spassov and Raychev (1997) for the lower p4-m1 and we not that the leopards from Equi are ascribable to the "gracile type" (Figure 36) with a concave lingual edge of the carnassial and especially for the mesio-distal symmetry of p4. The mesial side of these teeth are equally developed than the distal one, giving a rectangular shape to the tooth.

The modern comparative specimens from Angola (MZF 8748) show a triangular p3 and a narrow m1, implying a not definitive differentiation between the two groups in modern animals. The authors identified the robust type belong to archaic animals and the gracile one to the Late Pleistocene leopards. In fact, the mandible from Mauer, identified as *P. pardus sickenbergi* by Schütt (1969b) has a clear triangular p3 and a shorter and rectilinear lingual edge of the m1.

Figure 36: comparison between the types recognized by Spassov and Raychev (1997) and the p4-m1 from Equi. 1) robust type; 2) gracile type. Equi teeth: IGF185V/3 (A); mirrored IGF6102V (B); IGF6103V (C); mirrored IGF10037V/1 (D); IGF10037V/2 (E). Black lines show the differences between the two types.

Lower teeth are embricated, the horizontal *ramus* is high, both under the third premolar as well as the last molar, and the lower edge is linear and straight. Madurell-Malapeira et al. (2010) and Testu et al. (2011) stated that usually there are two mental fossae in leopards and three in *P. uncia* and *P. concolor*. In the specimens from Equi, IGF10037V/1 (and perhaps the broken IGF6104V) has two foramina. All the other ones have three nervous insertions, like the mandible of *P. pardus* from Aragó (Testu et al., 2011) and *P. pardus* from Los Rincones (Ri10/C1/2010) (Sauqué and Cuenca-Bescós, 2013).

The m1B/m1L ratio for the specimens from Equi is between 28 and 40, really under the ratio expressed for the other Late Pleistocene European leopards (Vraona and Los Rincones), and interpreted as a local variation of the species.

Postcranial bones of leopards are rare in the fossil record. The specimens from Equi are quite well preserved but most are from juveniles, with the diaphysis unfused. Nagel (1999) noted the robustness of leopard feet bone from Vraona Cave and determined the whole collection as *Panthera pardus vraonensis*, aiming to emphasize the differences of this particular population, waiting for more exhaustive comparisons. As mentioned above, the comparison between these specimens and Equi reveals a massive feature for the former, but the Gl/SD ratio for postcranial is quite similar in both the collections. In this case, it should be useful a large and more complete comparison among fossils and modern species before to infer conclusions about a real differentiation.

To conclude, as proven for other large felidae taxa, such as *Homotherium latidens* (Galobart et al., 2003) and cave lion (Burger et al. 2004, Sotnikova and Nikolskiy, 2006), specific and subspecific determination are often a consequence of the rarity of finds, the distance among sites and chronology, or are due to different authors' points of view, more than being a real and realistic divergence among two or more evolutive branches.

Cubs –One third of the whole leopard collection from Equi includes juvenile specimens. As described for adults, they are mostly from cranial and appendicular regions.

There are no information about when the postcranial junction ossified in leopards, and the comparative material include only far related species (i.e. dogs or large herbivores).

Already Stander (1997) admitted that a standard criteria for age determination is lacking for leopards. Some information are available about the dental eruption, both for leopards and other felids, allowing Rawn-Schatzinger (1983) to infer the growing stages of *Homotherium serum* from Friesenhahn Cave (Bexar County, Texas), as a real examples of multidisciplinary approach of paleontological questions.

The eruption sequences from deciduous teeth to the permanent dentition changed from the first mammals toward the specialized taxa. The ancient warm-blood animals engaged a front-to-back sequence, inheritance of the reptilinean teeth and this standard changed overturned with the eruption of a singular dentition for the mesial premolars in carnivorans (first and second one) and the early appearance of molars. The specific evolutive change had a functional significance, probably related to the change of tooth structure (molarization).

While mustelids and viverrids partially lost the deciduous teeth before the complete eruption (and function) of molars, canids and felids need to contemporary change the deciduous upper and lower carnassials for guarantee the efficiently of the bite and the cutting function.

Felidae are also the only carnivores with a long diastema, emphasizing the role of carnassials and last premolar, and the emersion trend is clearly aims to take advantage of the early appearance of the cutting teeth. Decidual carnassials (dP4/dp4) are hold till the P4 and m1 are ready to use and permanent p4 emerge just after the complete eruption of m1, followed by the third premolars (Slaughter et al. 1974) (Table 4).

Felidae:		
Felis concolor	P2/M1-P4-P3	m1-p4-p3
Lynx rufus	M1-P4-P3	m1-p4-p3
Panthera leo	P2/M1-P4-P3	m1-p4-p3
Acinonyx jubatus	P2/M1-P4-P3	m1-p4-p3

Table 4: tooth emergence in different species of felids. The virgule imply a contemporary complete eruption (Slaughter et al. 1974)

The ontogenesis of upper teeth entail that carnassial growing occupies the position of dP4, and the elongation of maxillar results as a consequence of permanent canine eruption, giving space for the premolars emersion. In both the arches, the permanent carnassials emerge when the other deciduous teeth are still well integrated in the alveolus, shedding them out with the paracones (Rawn-Schatzinger, 1983).

Leopards have 24(+2) decidual teeth, as follow:

Upper teeth: 3dI - 1dC - 1(+1)dP - 1dM = 6(+1)

Lower teeth: 3di - 1dc - 2dp = 6

and 28(+2) permanent teeth:

Upper teeth: 3I - 1C - 2(+1)P - 1M = 7(+1)

Lower teeth: 3i - 1c - 2p – 1m = 7

As previously demonstrated for the upper jaw, the presence of P2 is not so foregone (the alveouls of tiny premolar compare in IGF6120V). The complete replacement of deciduous teeth occurs after two years from birth, approximately at the same time to the complete independence of the animals from the mother (Henschel et al, 2008). The first deciduous cheek teeth appear at about 34-42 days after birth, after emersion of deciduous incisives and canines (Broom, 1949). Litters start to follow the mother at about three months, when the permanent teeth are not yet formed. The follow dentition begins at about 8 months with the emersion of incisives and at about one year the substitution is complete, except for the permanent later canine.

This sequence is very similar to large felids, such as lions (Crowe, 1975) where the first appearance of deciduous teeth after 20 days from birth and the permanent cheek teeth and carnassial emersion at about 7 and 14 months, respectively but, for example, is shorter in cheetah (Broom, 1949). In lions the substitution of deciduous teeth is reached almost 6 months later than leopards.

Small felids show a short period for replace the two dentitions (Férnandez et al., 2002). For example, deciduous teeth begin to emerge at about 7 days after birth in Canadian lynxes and in the 12th day in the Iberian lynx. The former substitutes the dentition from 4 months after born (Van Zyll de Jong, 1963; Fernández et al. 2002).

For the juvenile specimens from Equi an evaluation of the age has been possible:

IGF6136V	complete eruption of upper dP3 and dM1	2-3 months
IGF6119	complete closure of dp4 (molariform) and fissuration of mandibular bone by the m1	<8-10 months
IGF6125V	same stage of IGF6119V but little later	<8-10 months
IGF6123V	emersion of m1 behind the dp4. Distal cuspids of the latter shows heavy weared. Definitive canine starts to erupt.	12 months
IGF6120V	P4 emerging and pushing the dP4. Canine is quite inside the maxillar	12 months

Unfortunately, the heat time for leopards has not a specific or periodical season but depends on food availability and clime (Sunquist and Sunquist, Even though it is premature to conclude a periodicity for the use of the Equi shelter and cave for leopards, Seidensticker (1977) did a study about Nepal leopard litters, reporti). As consequence, the presence of litters cannot be used for estimate a time of frequentation.

5.3. Family Canidae G. Fischer de Waldheim, 1817

Even thought evidences of dog ancestors were discovered in the Oligocene, the clade definitely emerge from the paleocarnivora during the Miocene in North America, with several genera (Matthew, 1930). They reached Eurasia only in the latest Miocene. In Europe, the arrival of the family is represented by the genus *Eucyon*. The most represented genus *Canis* definitely expands its range in western Europe only in the late Pliocene (Late Villafranchian), with the so called "Wolf event" (Azzaroli, 1983, Rook and Torre, 1996; Sardella and Palombo, 2007; Sotnikova and Rook, 2010) as a consequence of the environmental changes that brought the developing of open air habitats. The Early and Middle Pleistocene are characterized by the presence of several taxa and species, but the diversity of the family drastically decrease in Europe in the late Middle Pleistocene and the survival, in Italy, of few modern taxa, i.e. *Canis lupus*, *Canis aureus*, *Vulpes vulpes*, *Alopex lagopus* and *Cuon alpinus*.

The evolutionary trends within Canidae lie outside of the main goal of this thesis, so the following paragraph is limited to the description about the evolution and European spread of the genus *Cuon*[3].

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[3] modified from GHEZZO E. & ROOK L., 2014. *Cuon alpinus* (Pallas, 1811) (Mammalia, Carnivora) from Equi (Late Pleistocene, Massa-Carrara, Italy): anatomical analysis and paleoethological contextualisation. *Rendiconti Lincei*, 25: 491-504

Genus *Cuon* Hodgson, 1838

Cuon alpinus (Pallas, 1811)

In Europe, the occurrence of dhole remains is spread over the continent and ranges chronologically from the early Middle Pleistocene to the Holocene.

Today, *Cuon alpinus* (Pallas, 1811) (also known as ‘‘dhole’’ or ‘‘Asiatic wild dog’’) is a hypercarnivore middle-sized Canidae living in southeastern Asia (Durbin et al. 2008). The extant *Cuon alpinus* is characterised by a length (head– body without the tail) of about 80–110 cm, a shoulder height of 40–50 cm and a body mass of about 10–20 kg (Cohen 1978; Kawanishi and Sunquist 2004). The dhole, if compared with other dogs, is a less selective animal with respect to social and territorial behaviours. For example, packs consist of a maximum of a few dozen individuals, are more open, lack a strict hierarchical organisation and are less territorial when compared to wolf groups. Numerous females can also use a common den for weaning the cubs (Zhang and Chen, 2011). They are diurnal and opportunistic animals and can prey numerous different species of ungulates and bovids of different sizes, among others axis deer (*Axis axis*), mouse deer (*Tragulus kanchil*) and muntjac deer (*Muntiacus*) or sambar deer (*Rusa unicolor*), and other carnivore remains in dhole scats are not so infrequent (Kawanishi and Sunquist, 2004; Kamler et al., 2012; Ullas Karath and Sunquist, 2000).

Several studies have been carried out to define feeding and habits of this specialised carnivore. The species ranges in Southern Asia and since 2004 it is reported in the Red List of Threatened Species as Endangered with about 2,500 adult individuals (Durbin et al., 2008) in different kinds of habitat, such as tropical deciduous and thorn forests, grassland with patchy forests, and the alpine steppe above 3,000 m (Zhang and Chen, 2011).

Some authors suggest the existence of different subspecies of dhole based mostly on fur features (Iyengar et al., 2005). The American Society of Mammalogists also defines two subspecies of dhole: *C. a. alpinus* and *C. a. hesperius* (Cohen, 1978), but no evidence exists in their genome to justify this differentiation (Iyengar et al., 2005). Iyengar et al. (2005) identified two main phylogeographical groupings from their DNA–mitochondrial analysis, and tried to explain this differentiation with the effects of a glaciation scenario during the Pleistocene.

Cuon alpinus is the unique species within the genus *Cuon* and diverged from the *Canis* lineage about 5–7 My ago, after the first branch of the genus *Nyctereutes* and *Vulpes* (Zhang and Chen, 2011). During the Pleistocene, it spread into Eurasia, reaching central and Western Europe at the beginning of the Middle Pleistocene and into North America in the Late Pleistocene (Tedford et al., 2009). In the Middle and Late Pleistocene, the dhole was well represented, albeit rare, throughout the European mainland.

Its range extended into Europe from Asia during the Middle Pleistocene with the species *Cuon priscus* (Thenius 1954) and was then reduced into Asia during the Upper Palaeolithic (Pérez-Ripoll et al. 2010; Petrucci et al. 2012) (Figure 37). However, genetic analysis (Zhang and Chen 2011; Iyengar et al. 2005) seems to indicate the disappearance of the dhole from Europe at about 12,000–18,000 BP.

The first record of *Cuon alpinus* in Europe is from the Middle–Late Pleistocene sites of the Mars Cave, France, (Petrucci et al. 2012). It also quickly appeared in Western Europe, in Spain, for the first time in Trincera-Galerìa (Atapuerca, Burgos) (Pérez-Ripoll et al. 2010) so its range was widely distributed. Brugal and Boudadi-Maligne (2011) named *Cuon priscus* as a chronospecies with a decreasing size trend of lower teeth to the Late Pleistocene group (called *Cuon fossilis*/*europaeus*), while Adam (1959) stated that there was a *C. priscus*–*C. fossilis*–*C. europaeus* species succession. Bonifay (1971) hypothesised a wide differentiation of the group, with several numbers of species and subspecies. A parsimonious analysis should consider the scarcity of remains and intraspecific variability, and the occurrence of this species in Europe is not sufficiently frequent to allow a clear overview of their evolutionary trends.

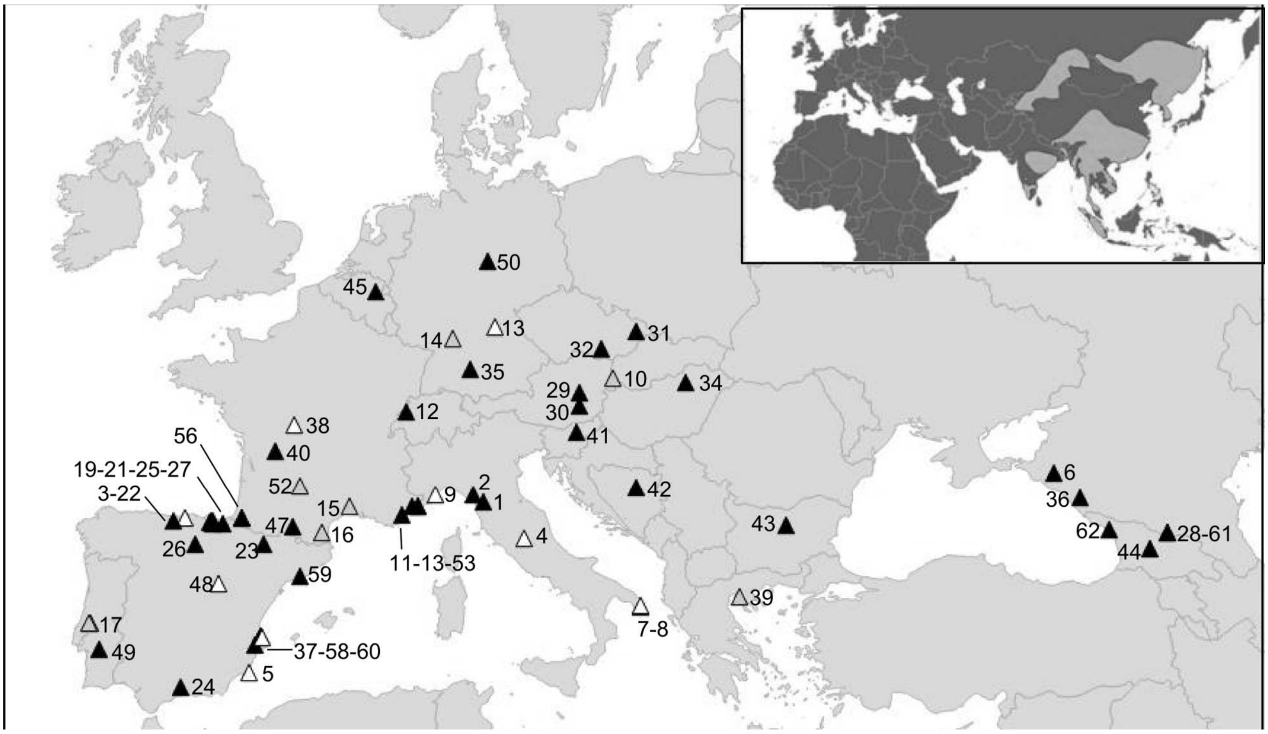


Figure 37: distribution of the extant dhole (on the upright corner) and dhole occurrence in Europe during the Pleistocene. Different markers indicate the species *Cuon priscus* (gray triangles), *Cuon alpinus* (black triangles), and *Cuon* sp. (white triangles). The sites are numbered as follow: Austria: Hundsheim-Hole (10), Ofenbergerhohle (29), Repolust-Hohle (30); Belgium: Chokier (45); Bosnia and Herzegovina: Crvene Stijena (42); Bulgaria: Bacho Kiro (43); Czech Republic: Slipka (31), Certova dira (32); France: Lunel-Viel (15), Caune de l'Arago (16), Mars Cave (18), Rosiers (38), Fontechevade (40), Isturits (56), Malarnaud (47), Coudoulous1 (52), Pe`cheurs (53); Georgia: Kudaro 1 and 3 Cave (61, 28), Tsona (44), Kepshinskaya Cave (62); Germany: Zoolithenhohle (13), Mosbach (14), Gutenberger Höhle-Heppenloch (35), Baumann's Cave (50); Greeck: Petralona Cave (39); Hungary: Subalyuk (34); Italy: Melpignano (8), San Sidero (7), Buca del Tasso (1), Equi (2), Valserra (4),Grotta degli Armorari (9); Principality of Monaco: Grotte de l'Osservatoire (11); Portugal: Galeria Pesada (17), Gruta di Escoural (49); Republic of Russia: Matuzka (36), Ilskaya1 (6); Slovenia: Apnarjeva jama (41); Spain: Rascaño (3), Cueva de Obarreta (19), Parpallò (58), Duranguesado (21), La Riera (22), Gabasa (23), Boquete de Zaraggaya (24), Amalda VII (25), Trinchera Galeria (26), Bolinkoba (27), Cova Negra (37), Los Casares (48), Gegant (59), Santa Maria (60), Cueva Victoria (5); Switzerland: Gruta de Cotencher (12).

Data from Del Campana (1923, 1954), Thenius (1954), Baryshnikov (1996), Brugal and Valente (2004), Pérez-Ripoll et al. (2010), Brugal and Boudadi-Maligne (2011), Iurino et al. (2013), Petrucci et al. (2012), Bacon et al. (2011).

The main osteological features for identifying skeletal remains of this species is the smaller dimension in comparison to wolves, the lack of the lower third molar, and the reduction of the talonid on the lower carnassial to a single hypoconid tip (Del Campana, 1923, 1954; Petrucci et al., 2012; Zhang and Chen, 2011). The oldest dhole species, *Cuon priscus*, apparently never crossed the Alps, expanding its range in Italy and being recorded in Greece, Germany, Austria, France and Portugal (Figure 37) (Petrucci et al., 2012; Brugal and Valente, 2004).

Cuon alpinus finds are more common in Europe and Italy, and the species ranges across the European continent up to the 51th parallel (actually, their Asian upper range limit is around the 56th parallel, down to the Russian lowland; Durbin et al., 2008). Our conclusion has been confirmed by Mallye et al. (2012) recording the northern European find at Chokier (Belgium; 50° lat N). The southern limit of the dhole range in Europe was inevitably the Mediterranean coastline, about down to the 37th parallel with the Spanish site of Boquete de Zafarraya (Pérez-Ripoll et al. 2010). Eastern Europe apparently is out of *Cuon alpinus* range (with the exception of Bacho Kiro in Bulgaria and few other sites; see Mallye et al., 2012), but it is realistic to presume that this is more related to a lack of documentation rather than an effective absence of findings. The latest occurrence of *Cuon alpinus* is recorded at two sites: Riparo Fredian in Italy (Cilli et al., 1998) and Les Coves de Santa Maira in Spain (Pérez-Ripoll et al., 2010). These samples have been recovered from Holocene levels dated between 8,500 and 9,000 years BP and about 11–14 ky, respectively. Despite this determination in the faunal assemblage of Riparo Fredian (Cilli et al., 1998), we realised that the species was identified based on a very limited set of fragments: a left scapholunate and a small sized lower incisor. The first one, despite its small size, as discussed for the Equi carpals finds, cannot be indicative of the species since this bone varies in size according to the age of the individual. Therefore, we cannot consider its small dimensions as sufficient to be indicative for the species. The tooth (lower incisor) is also very small, and it could be better attributed to a fox rather than to a dhole. On the other hand, the Spanish find is a neurocranium and a canine identified as *Cuon alpinus* and to the genus (cf. *Cuon*), respectively. Therefore, the survival of this species in the later Pleistocene and Holocene should be reconsidered also for its interaction within a Neolithic context.

The role of this species in the palaeoecological environment is still debated. In fact, *Cuon alpinus* shows hypercarnivore habits (Van Valkenburgh, 1991), with morphological adaptations of the lower carnassial and the lack of the last lower molar, implying a high antagonism with the other large predators.

5.3.1. *Cuon alpinus* (Pallas, 1811) (Mammalia, Carnivora): anatomical analysis and palaeoethological contextualisation

The dhole remains from Equi were preliminarily determined as *C. lupus* and *C. aureus* by De Stefani (as reported in his pivotal 1917 paper, and documented by the handwritten original labels). The recognition of the dhole occurrence among the Equi material is due to Del Campana (1923), who subsequently (1954) analysed these finds in a revision of all carnivores from Equi.

Anatomical description - IGF6467V is a fragment of the left maxillary bone with carnassial (Figure 38a, b). It preserves a small piece of the maxillary bone with the preorbital foramen, located just above the P3 distal alveolus. P4 bears three roots. The paracone is damaged on its apex, probably as a consequence of post-depositional history, and also has the enamel partially abraded. The base of the tooth is inflated, markedly on the lingual side of the metacone. Lingual side of the tooth is very flat and perpendicular to the palatal surface. Mesially, along the paracone, a weak crest runs until the base of the tooth and forms, on the lingual side, a slightly pronounced groove. The tooth is relatively small (L = 22.0 mm; W = 10.7 mm).

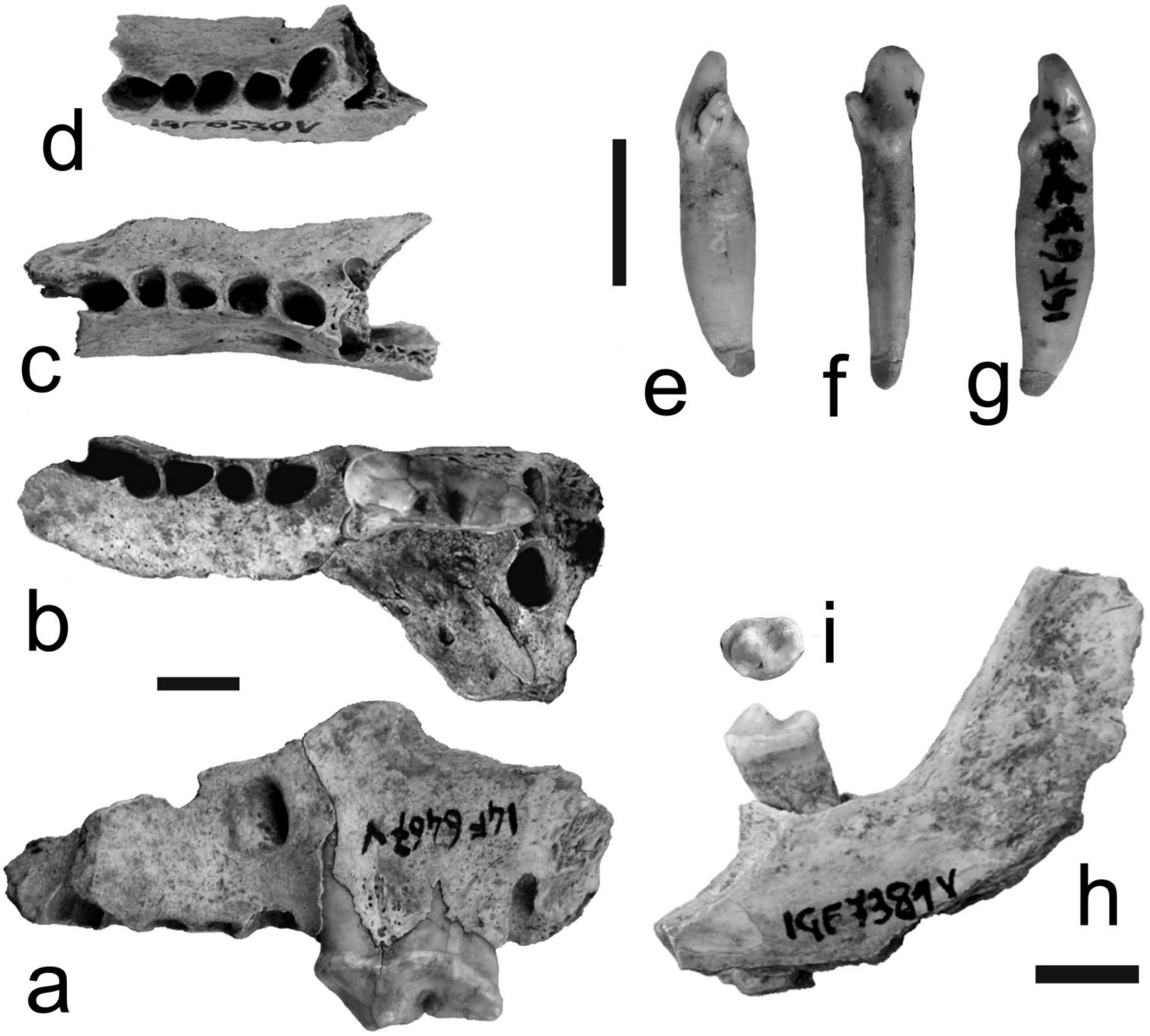
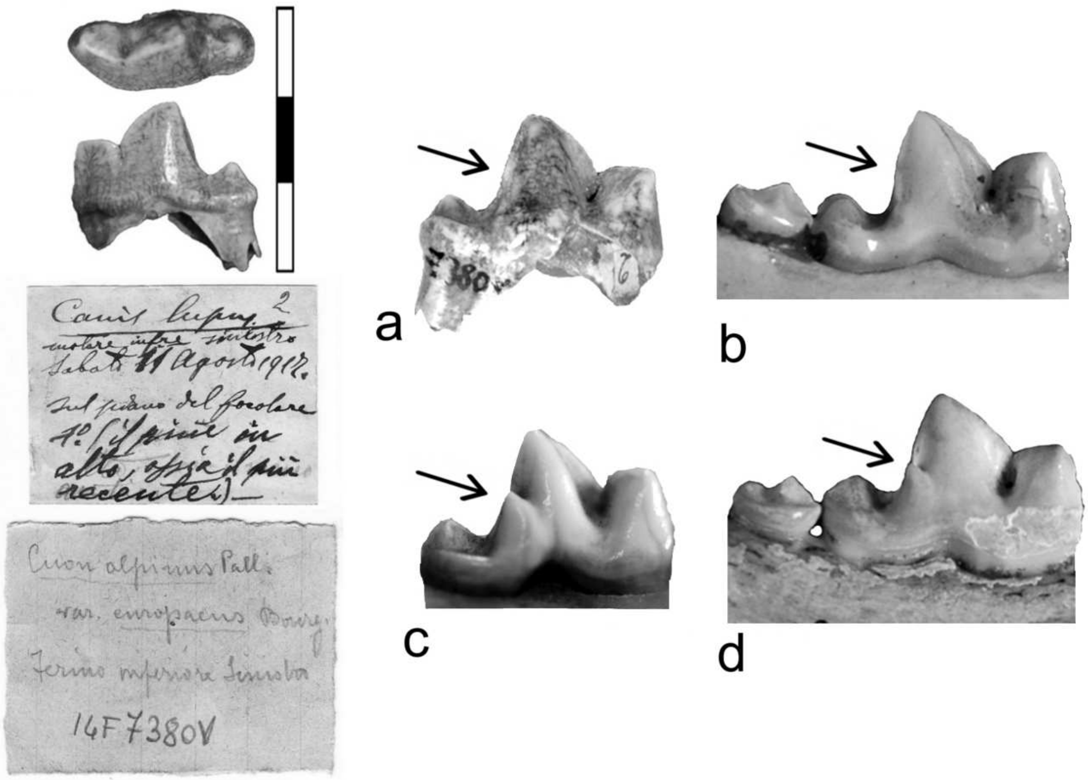


Figure 38: cranial and dental remains of *Cuon alpinus* from Equi: left maxillary bone (IGF6467V) in labial (a) and occlusal view (b); left (c) and right (d) edentulous maxillary bones (IGF6530V) in occlusal view; left i2 (IGF6375V) in lateral (e) distal (f) and mesial (g) view; fragment of right mandible with m2 (IGF7381V) in lingual view (h), and occlusal view of m2 (i). Scale bars equal 1 cm.

IGF6530V/1 and IGF6530V/2 are the left and right fragments of maxillary bone (Figure 38c, d). Both fragments are toothless and preserve the alveoli of the jugal teeth (P3 and P2). They were determined as *Canis aureus* during a previous cataloguing. Both right and left preorbital foramens are located above P3 distal alveoli. These two specimens do not show any peculiar features. Dimensionally, they are much smaller than those of the wolf, and are here considered as *Cuon*, being comparable in size with IGF6467V.

The left lower second incisive (IGF6375V; Figure 38e–g) is complete and well preserved. It was recorded as *Canis* sp. by historical determination. It has a developed lobe on the lateral outline and its dimensions (L: 5.6 mm; W: 5.3 mm) are smaller than those of a wolf but larger in comparison to the fox teeth, so it could be putatively determined as a dhole.

The left lower carnassial (IGF7380V; Figure 39) is generally more trenchant than the wolf lower carnassial for the presence of the unicuspid talonid. This feature allowed Del Campana (1923) to identify it as belonging to the genus *Cuon*. The specimen lacks the roots, and only the crown enamel is present, without evidence of the dentine. The paraconid is about half the height of the protoconid. Both these cuspids have a convex edge diverging from each other to the tips. The talonid shows a noticeable and enlarged cingulum with a single central cusp (hypoconid). The distal wall of the paraconid is flat and has a crest joining the edge to the hypoconid, and just above, it branches with another smaller crest directed to the lingual-basal margin of the tooth. The trigonid lacks the lingual cusp, the metaconid, a feature already noticed by Del Campana (1954). This morphological feature is peculiar, since the dhole carnassial usually bears a well-recognisable metaconid. This cusp is always present as typical characteristic in most of the Canidae, such as in the wolf (*Canis lupus*) and jackals (e.g. *Canis aureus* and *Canis mesomelas*); however, according to Van Valkenburgh (1991), it is not always present in the hypercarnivorous forms. In the extant *Cuon alpinus*, this feature is variable, with individuals showing lower carnassials with small metaconids, while the metaconid is totally absent in others (Figure 39b–d). The structure of this tooth, with just the external enamel without dentine, allows us to deduce here that IGF7380V was a lower carnassial in the crypt.



Canis lupus 2
molare infer. sinistro
Sabato 11 Agosto 1912.
Sul piano del focolare
4° (il più in
alto, ossia il più
recente)—

Cuon alpinus Pall.
var. europaeus Bourg.
Ferino inferiore sinistro
IGF7380V

Figure 39: IGF7380V. Left upper and labial views with the original labels (bar scale is 3 cm). The figure also offers a lingual view of IGF7380V (a), compared with extant *Cuon alpinus* carnassials from the NMHN (b C.G.2007-473; d C.G.1930-228) and the osteological collection of the University of Florence (c #130). Note (black arrows) the individual variability for metaconid presence/absence in extant dhole (a–d not to scale).

The morphology and dimension (Figure 40a) of IGF7380V agree with the identification of the species *Cuon alpinus*. In fact, the tooth is within the dholes' range of variability and well discerned from the wolf. In this figure, we included *Canis aureus* (the golden jackal) teeth which are well grouped in the smaller dimensional range of the diagram, and allow concluding that the size of the lower carnassials, over the general morphologies and the occurrence of the third molar, prevents the assignment of the Florence specimens within the genus *Canis*.

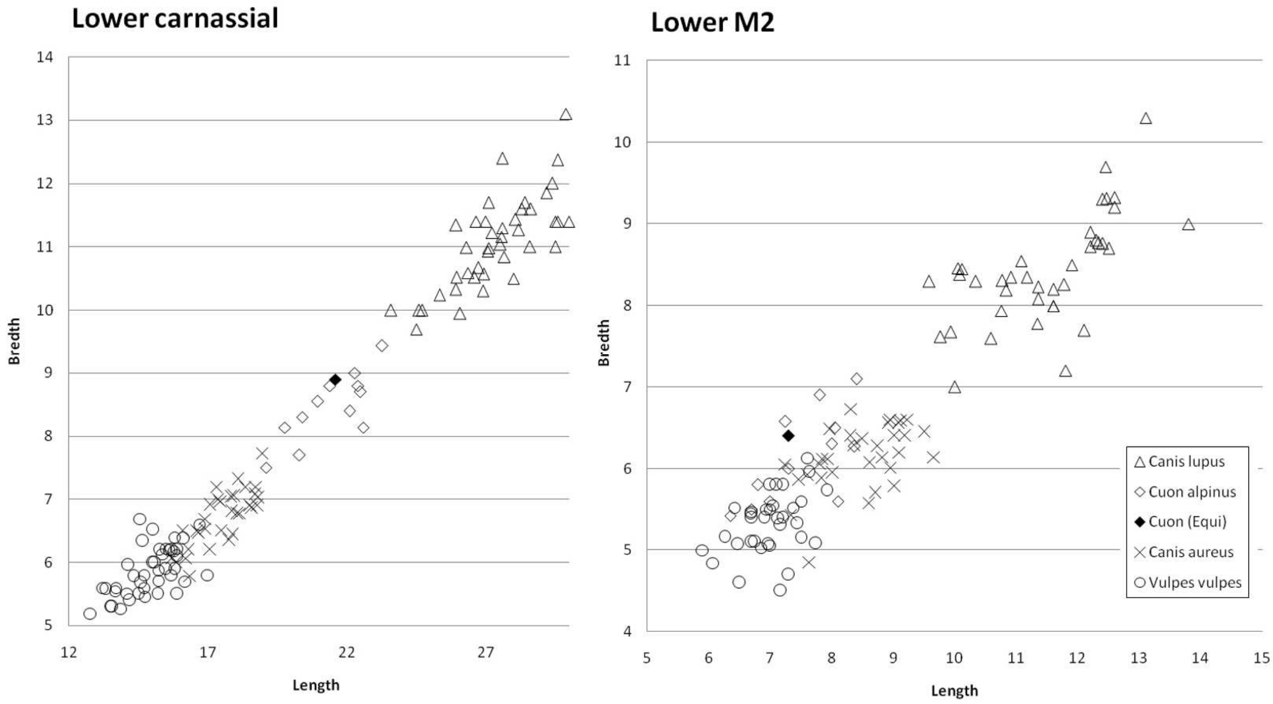


Figure 40: *Scatter diagram* of breadth/length for lower m1 (a) and m2 (b).

IGF7381V is a fragment of right mandible with m2 (Figure 38h, i). This specimen consists of a fragment of the ascending ramus with the coronoid process, partial masseter muscle fossa, and a small portion of the horizontal ramus under the m2, until the distal alveolus of the carnassial. There is no evidence of an m3 alveolus in the mandible. The occlusal outline of the m2 is oval shaped and mesially enlarged. The single small mesial cusp has two lingual crests directed mesio-lingually and transversal to the medial surface. The two crests end at the neck. Distally, another small crest joins the mesial cusp with the distal apex. Roots are fused but we still can appreciate that the distal was larger than the mesial one. This tooth is very similar to the second molar of extant *Cuon alpinus*, while is quite different from the wolf tooth. In wolves, it has a more complex morphology, with a medial cusp lingually elongated by a crest and an accessory cusp on the tooth neck. The larger cusp is located somewhat labially, and is associated with a smaller distolabial tip. The wolf typically bears an m3, which is relatively small and very simple in morphology, with a single central tip. Dimensional analysis (Figure 40b) is not as conclusive as the evaluation of the carnassial tooth. The scatter diagram shows a partial overlap of *Vulpes vulpes*, *Canis aureus* and *Cuon alpinus* teeth. In this case, it seems that morphology should be the unique method for clearly identifying dhole remains.

Based on the morphology, the cervical vertebra (IGF6468V; Figure 41a, b) is probably the fifth vertebra of the neck. The body and the proximal and distal articular surfaces, perfectly welded, are oblique and the general dimensions (proximal breadth at articular surface = 12.7 mm; height proximal articular surface = 12.8 mm; length of corpus vertebralis = 24.2 mm) are smaller than in the wolf. Therefore, we can indicate that this specimen is a small Canidae, most probably a dhole.

Carpals are represented by two scapholunates (IGF6531V; Figure 41c, f). Del Campana (1954) identified these bones as *Cuon europaeus* [recte *alpinus*] for their smaller size compared to an adult wolf. Actually, these bones do not show specific characters, even if the three distal articular surfaces are slender than the homologue structure of wolves. They are considered as belonging to *Cuon alpinus* based only on their size (maximum breadth of about 19.0 mm for Equi specimens and 25.0 mm for extant wolf).

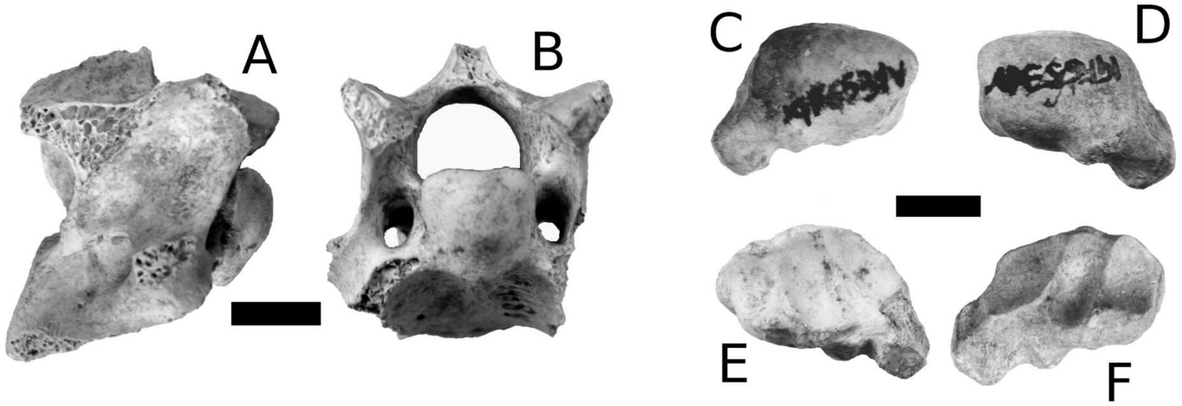


Figure 41: Cervical vertebra (IGF6468V) in lateral (a) and proximal (b) views; right and left scapholunars (IGF6531V) in proximal (c, d) and distal (e, f) views. Scale bar is 1 cm.

IGF6463V and IGF7378V are two McIII (Figure 42): The diaphysis has a circular section, distally enlarged. It becomes more prismatic towards the proximal end. The proximal articular portion is subtriangular. Centrally, it bears a marked concavity for the articulation of the capitate bone. In medial view, two small articular surfaces are present, the rostral one with a triangular to lobated edge, while the latter shows a semilunar outline. Laterally, a continuous surface runs from the caudal side to the anterior one. This surface markedly enlarges at the rostral angle, forming a distally directed stripe. If compared to the third metacarpal of *Canis lupus*, either extant or Late Pleistocene from the same site (IGF951V), both McIIIs appear definitely slender and weak. In the wolf McIII, the antero-lateral surface of the diaphysis forms a sharp angular margin, a feature almost not developed and more elusive in *Cuon alpinus*. Dorsally, the caudal terminal aspect of this element in dhole is large, while in wolf it is more curved and pointed. This morphology influences the medial half-moon surface, which seems less defined in the wolf. In *Canis lupus*, the proximal-lateral surface has a characteristic morphology: the rostral portion is strongly convex with a small eminence. In comparison, the dhole shows an anterior small surface, flat or concave, and never so developed or convex.

The diaphysis of the McIV (IGF6464V and IGF7377V; Figure 43) tends to enlarge towards the distal epiphysis. On superior view, the epiphysis is rounded and has a proximal articulation made up of a rectangular outline, antero-distally enlarged. The lateral margin has a continue surface that runs posteriorly to the rostral side, and then deviates to the distal side with a marked angle. The medial articular side has a long surface, with a tip forming a medial obtuse angle at the midpoint. Laterally, the rostral surface forms a very small process and, beneath it, a concavity.

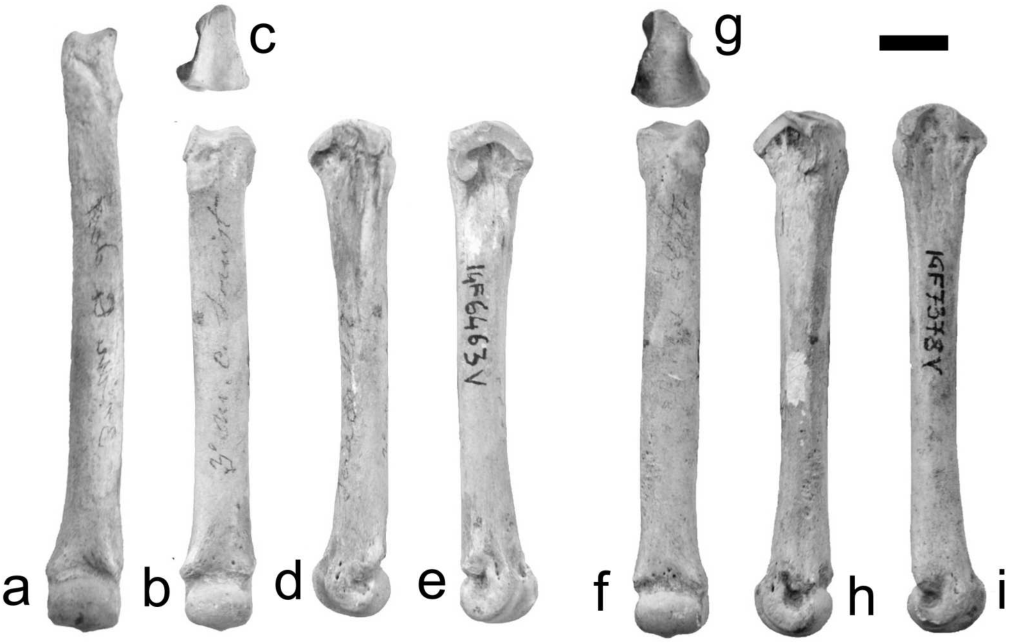


Figure 42: McIII: comparison among *C. lupus* IGF951V (a, right mirrored, in frontal view), left (IGF6463V) and right (IGF7378V) McIII of *C. alpinus* in frontal (b, f), proximal (c, g), medial (d, i) and lateral (e, h) views. Scale bar is 1 cm.

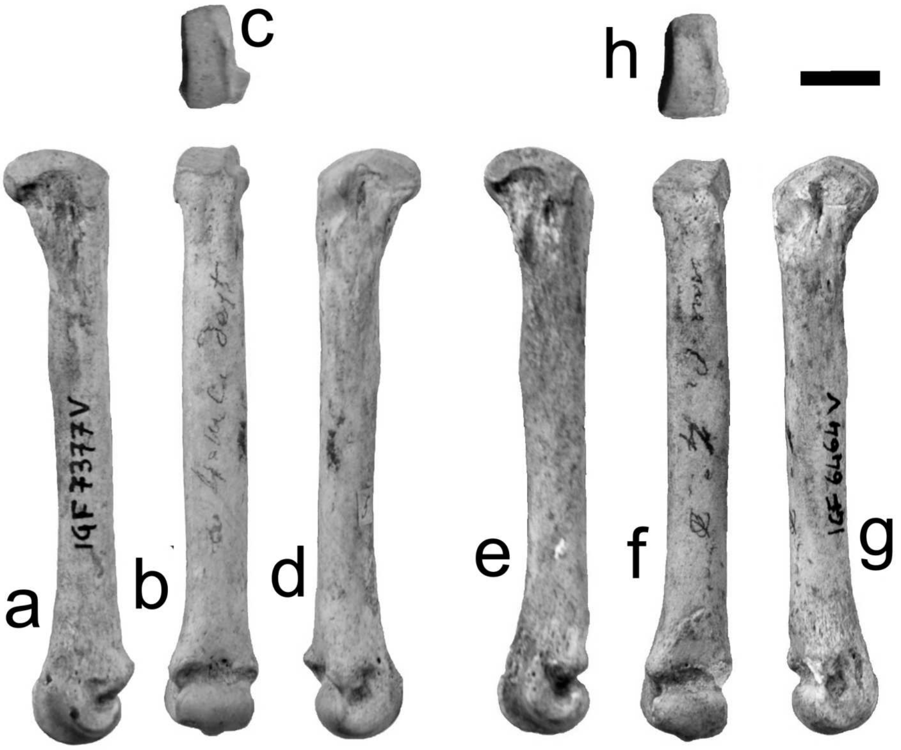


Figure 43: McIV (IGF7377V and IGF6464V): right metacarpals in lateral (a, e), frontal (b, f), proximal (d, h) and medial (c,g) views. Scale bar is 1 cm.

IGF6466V and IGF7379V (Figure 44) are two McVs. This metacarpal is rather short, with a section of the diaphysis transversally flattened. The medial outline of the diaphysis is sub-rectilinear, while it is clearly concave along the lateral margin. The proximal epiphysis has a convex surface, rostrally inclining and ending into a pyramidal structure that is the articulation for the fourth metacarpal. The medial view shows a posterior articular surface and another one following the proximal surface outline. Except for size and robustness, no noticeable morphologies allow a distinction of the V metacarpal of the dhole from that of the wolf.

Figure 44: McV: comparison between the last metacarpus of C. lupus (a, in frontal view) and dhole. The latter is represented by left (IGF6466V) and right (IGF7379V) specimens in frontal (b, f), proximal (e, i), lateral (c, h) and medial (d, g) views. Scale bar is 1 cm.

IGF6465V is a distal fragment of a metapodial. The specimen does not preserve the proximal epiphysis, and following Del Campana (1954), its attribution to *Cuon* is mostly based on its relatively small size, which allows us to exclude it from *Canis lupus*.

In terms of size, when compared to wolf, dhole metapodials are smaller and generally more slender (Figure 45; Table 5).

One right and one left femur (IGF6366V/1, IGF 6366V/2; Figure 46), and a tibia (IGF6366V/3; Figure 47) were recorded as jackals in the historical data labels. They are smaller compared to the corresponding bones of wolves. Each has a taphonomical sign, such as gnawing and pits along the broken margins, and gives them smoothed features. In more detail, IGF6366V/1 loses the greater trochanter and the distal epiphysis. The head of the femur, which in dogs becomes ossified at 9–12 months, allows recognition of this find as an adult individual (Barone 2003).

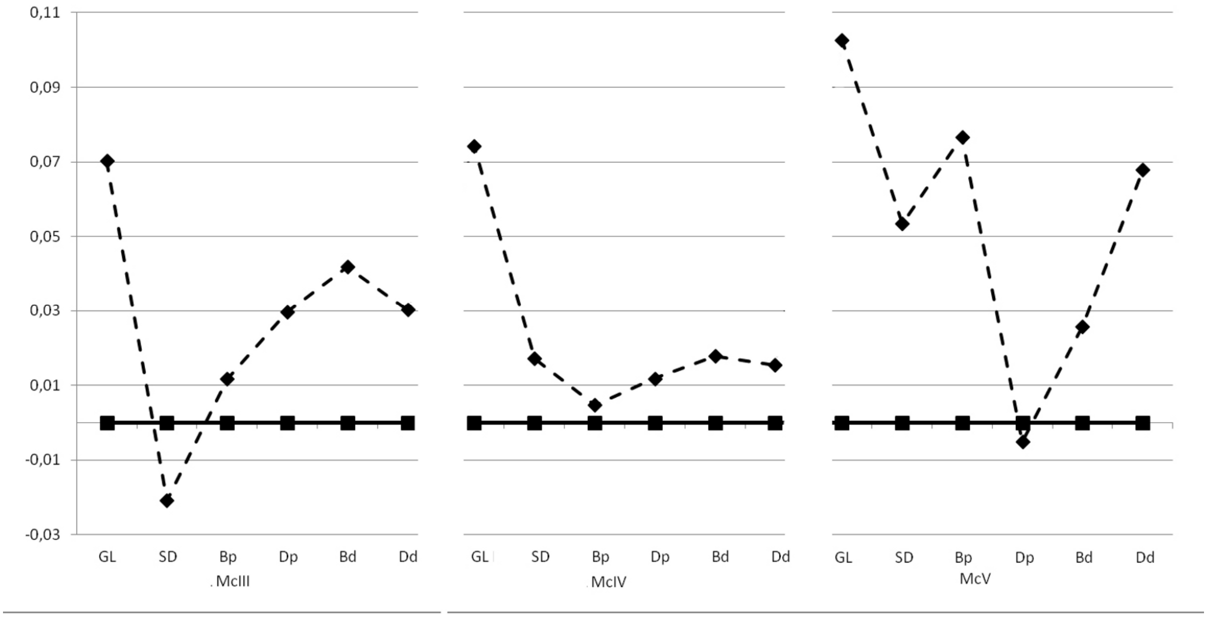


Figure 45: comparing *C. alpinus* McIII, MCIV, and McV from Equi (diamonds), versus *C. lupus* (solid square) using Simpson's diagram (wolf is represented by the mean value of extant and fossil sample). Dohle is characterised by a general slenderness and markedly smaller Gl values.

	species	inventory number	**GL**	**SD**	**Bp**	**Dp**	**Bd**	**Dd**
McII	*C. alpinus*	IGF6463V	73.4	8	10.5	12.5	11	11.6
	C. lupus	IGF952V	80.3	9.8	8.8	14.9	13	12.2
	C. lupus	extant species	77.7-82.6	7.6-9.4	9.7-11.1	13-14.2	11.7-12.7	10.10.7
McIII	*C. alpinus*	IGF7378V	75	8	10.5	13.6	11.2	11.3
	C. alpinus	Paris	65	5.84				
	C. lupus	Cava Filo	91.2	8	12.4	14.5	12.3	13.7
	C. lupus	IGF951V	91.2	8	12.4	14.5	12.3	13.7
	C. lupus	IGF6362V	90.9	8.2	8.4	13.6	1.6	13.2
	C. lupus	extant species	8.6-93.5	6.8-8	10.2-12.6	13.2-15.6	11.5-12.6	11.6-12.5
McIV	*C. alpinus*	IGF6464V	71.5	7.4	8.6	13.3	10.7	11.3
	C. alpinus	IGF7377V	73.8	7.5	9.4	13	11.3	11.4
	C. alpinus	Paris	62.53	5.78				
	C. lupus	IGF5444V		8.2	9.4	13.2		
	C. lupus	extant species	81.3-93	6.9-8.2	8.4-10.4	12.6-15	11.2-12.3	11.6-12
McV	*C. alpinus*	IGF6466V	58.5	8.6	12	13.6	12	9.5
	C. alpinus	IGF7379V	59	8.5	12	13	12.5	10.4
	C. alpinus	Paris	51.1	5.6				
	C. lupus	IGF5439V	71.7	9.4	13.7	12.4	12.7	11.5
	C. lupus	Cava Filo	74	10.6	15.8	14.7	14.6	13
	C. lupus	extant species	70.4-78.8	8.9-10.6	12.5-14.4	12.2-13.4	11.3-13.3	10.8-11.3

cervical vertebra V(?)	**bredth of proximal articular surface**	**height proximal articular surface**	**bredth of distal articular surface**	**height distal articular surface**	**height of vertebral corpus**	**lenght of vertebral corpus**
IGF6468V	12.7	12.8	15.2	12.3	12	24.2

Table 5: measurements (in mm) of postcranial bones of *C. alpinus* from Equi and the compared specimens. IGF elements are all from Equi..

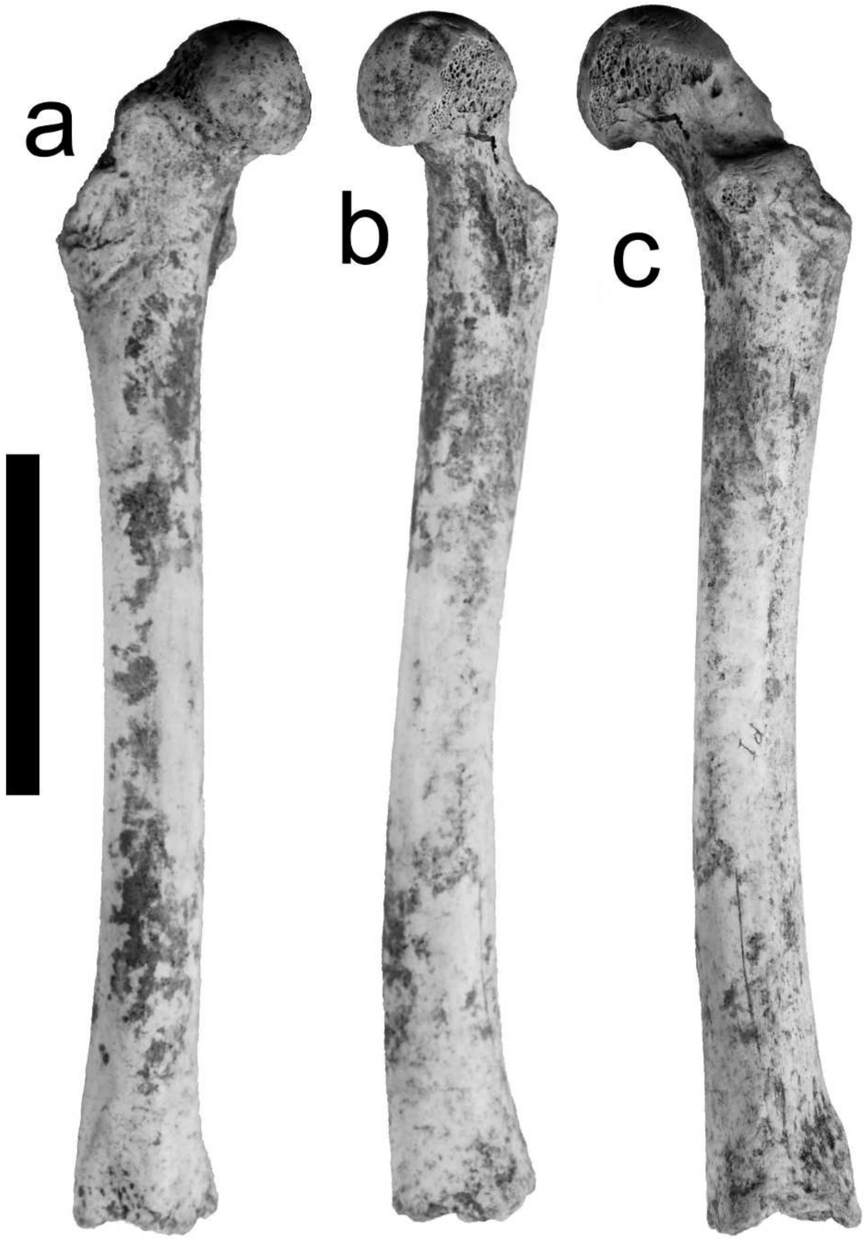


Figure 46: IGF6366V, *C. alpinus* right femur in frontal (a), medial (b), and caudal (c) views. Scale bar is 5 cm.

The tibia lacks the proximal portion while the distal epiphysis is fused. The diaphysis was broken and successively restored. A probable bite mark is evident on the distal portion, just above the epiphysis, observable as two deep and small pits on the opposite surface of the bone (a diameter of about half a centimetre).

Figure 47: size comparison between the tibia of *Canis lupus* from Equi IFG6381V (a, in frontal view') and *C. alpinus* (IGF6366V) represented in frontal (b), medial (c) and lateral (d) views. Scale bar is 5 cm.

The dhole within the carnivore guild - The relation among tigers (*Panthera tigris*), leopards (*Panthera pardus*) and dholes has been well studied. Kawanishi and Sunquist (2008) recorded the occurrence in Malaysia of the latter in association with the small leopard cat

(*Prionailurus bengalensis*) and the bear (*Helarctos malayanus*). Unfortunately, our knowledge about interactions with these other carnivore is too poor for a comparison with the faunal association from Equi. The body mass of tigers and leopards, respectively, 180–245 and 45–65 kg in Thailand, is much larger than that of dholes (10–21 kg). Even if aggression by the largest predator occurs, the killing of dholes is uncommon; furthermore, a large pack of dholes can cope with a tiger (Steinmetz et al. 2013 and the references therein). Today, in Thailand, ranges of tigers and dholes are divergent; this means that when the top predator is frequent—where larger prey such as wild pig are available, as well as a suitable habitat—the presence of dhole is unlikely and vice versa (Steinmetz et al. 2013). Comparing this situation to the Equi site, the few remains of dhole (NMI = 2) are not surprising in a cave with a high frequency of other large predators, such as bears, lions and leopards (Figure 48). Kawanishi and Sunquist (2004) postulated that the range today influences the optimisation of the number of members in a clan. Covered forests support smaller packs because large prey animals are scarce, the vegetation favours stalk and ambush hunting and the competition for food is high, even if this context improves the possibility of avoiding other predators.

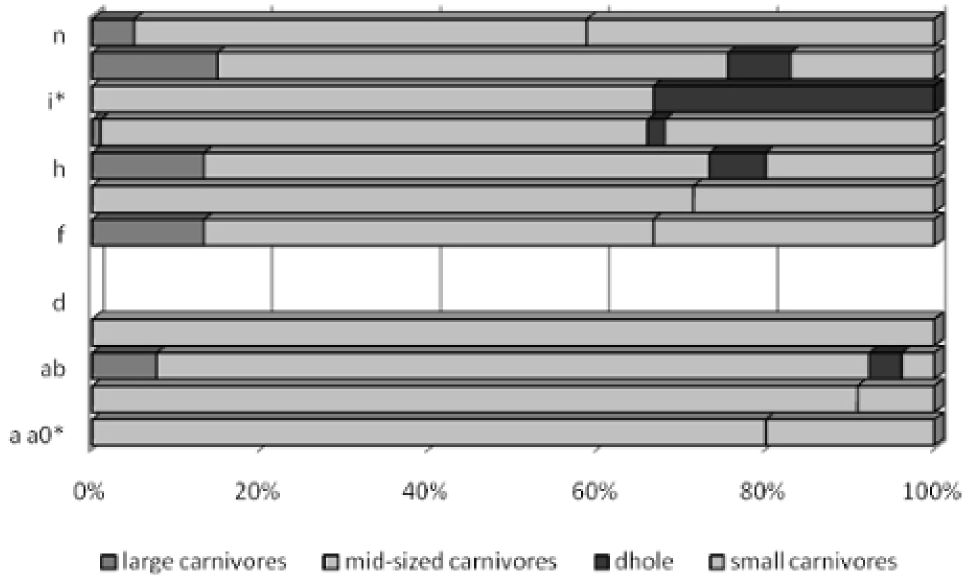


Figure 48: the comparison of dhole occurrence versus other carnivore distribution, asterisk indicates layer with less than 10 specimens (see also Figure 13).

The Equi site may also have an ''intra-guild predation ratio'', where the largest predators are spread in relation to food availability and the other predators must take into account both the food availability and their own safety (Heithaus 2001; Steinmetz et al. 2013). In addition, dholes are diurnal predators, while leopards and tigers are more nocturnal or crepuscular hunters (Kawanishi and Sunquist 2004); therefore, de facto, they are mutual avoiding behaviourally. This ethological and behavioural evidence can be considered when interpreting the Equi fossil record. The abundance of each species from Equi, in fact, seems to indicate that these different animals probably were behaving under the same (or strictly comparable) ethological model in their choices of prey, hunting time and their own protection.

Concluding remarks - The taxonomy of the *Cuon* lineage has been debated and different authors are frequently in disagreement. Petrucci et al. (2012) summarised the different opinions of researchers over time, especially concerning the specific and sub-specific identification. In general, *C. priscus* seems to be the first species to appear on the European mainland during the Middle Pleistocene but it never clearly reached the Italian Peninsula. Later, it was replaced by *C. alpinus*, a species that became extinct during the later Late Pleistocene, such as Middle Palaeolithic (late Musterian) in Italy and Late Palaeolithic in Spain. The two possible exceptions — regions in Central Italy and Southern Spain — must be reconsidered and are partially rejected here, at least for Riparo Fredian. Moreover, the current scarcity of European remains, in addition to the intraspecific variability, does not allow a sub-specific determination. Therefore, more complete studies and new finds are necessary to improve our knowledge about *C. alpinus* dispersal events and taxonomic status. The dhole fossil remains from Equi attest to the occurrence of this species in northern Tuscany during MIS3; this evidence is reinforced by the occurrence of the same taxon at the nearby site of Buca del Tasso (Fabiani 1923; Manzi 2004).

The morphologies of the dhole metacarpal and tooth remains from Equi allow recognition of particular features for determining this species, such as the absence of the m3 and hypercarnivorous dental structure, and, for the postcranial, the proximal-lateral articulation surface of the third metacarpal.

I analysed the variable occurrence of the metaconid at the m1. As demonstrated by Baryshnikov (1996), the variations in size and occurrence of this structure are not related to chronology or geographical range, but are due to phenotypic pattern.

Dimensional analysis reveals that *C. alpinus* could be well separated from other canids, such as wolves, jackals and smaller foxes based on the lower carnassial measurements. The size of the lower molar from the site falls within the variability of Late Pleistocene and extant dholes (c.f. Brugal and Boudadi-Maligne 2011). The distribution and extinction of the dhole in Europe could be related to the human presence across the continent as well as the drastic climatic change at the MIS 2–3 boundary. Not surprisingly, two of the latest occurrences of the dhole in Italy are from sites (Buca del Tasso and Equi) with a contemporaneous or sometimes later Neanderthal frequentation (Longo et al. 2012).

At present, the fossil record confirms that the dhole is not recognised in northern Italy and the Alps (Bon et al. 1991). Its fossil record in Italy is punctuated, with numerous gaps. The first records occur in Apulia and Latium (late Middle Pleistocene), with some evidence later on in the Late Pleistocene (Valserra, Equi, Buca del Tasso and San Sidero). The revision of the canid material from Equi, with the identification of additional dhole materials within the historical collection, demonstrates that the scanty fossil record of this taxon could be an artefact due to the lack of proper determination. Quite possibly, a number of *Cuon* remains (especially parts of the postcranial skeleton) are currently in museum collections but have been identified as Canidae or *Canis* sp. (or even unidentified). An extensive revision of Italian (and European) fossil remains of midsized Canidae remains from the Middle to Late Pleistocene would be mandatory for a better picture of the dhole fossil record.

6. Focused studies on Felids

Subfamily Felinae Fischer Von Waldheim, 1817

Genus *Panthera* Oken, 1816

Panthera leo spelaea (Goldfuss 1810)

Lion spreads into Europe during the Middle Galerian (Middle Pleistocene). Its oldest occurrence is from the lower Middle Pleistocene deposits of Mauer (Mis 15-14) and Mosbach (Germany) (Schütt, 1969; Hemmer, 1974, 2011; Wagner et al., 2011) with the subspecies *Panthera leo fossilis* von Reichenau, 1906. At MIS 9, it was recognized at TD10-1 of Gran Dolina (Atapuerca, Spain) (Blasco et al., 2010), recording evidences of anthropic exploitation. Other few fossils of *P. leo fossilis* were recognized (apart Italy, see below) at the Middle Pleistocene sites of Vértesszőlős II, Solymar, and Paks in Hungary (Hankó, 2007). Argant et al. (2007) report ancient lion finds in the early-mid Middle Pleistocene site of Château Breccia (Saône-et-Loire, Burgundy, France). Recently, Sotnikova and Foronova (2014) recognized the first mandible of *P.* (*Leo*) *fossilis* in Asia (dated back to the late Early Pleistocene), while the occurrence of *P. leo fossilis* at Petralona Cave (Greece) (Kurtén and Poulianos, 1977) was recently rejected by Baryshnikov and Tsoukala (2010). The latter authors dubitatively referred the Petralona lion to the late Middle Pleistocene (ca. 400-350 ky) faunal assemblage of the cave, and newly determined it as *Panthera leo spelaea*.

P. leo spelaea was firstly radiocarbon dated with confidence at about 50 ky ago in the Gamssulzen Cave (Cal median 52.042 years ago; Austria), Zoolithen Cave (Cal median 48.877 years ago; Germany), Siegsdorf (Cal median 48.557 years ago; Germany), and in the quite coeval deposit Sibyllen Cave (> 48.100 years ago; Germany) (Rosendahl and Darga, 2004; Barnett et al., 2009; Diedrich 2010, 2012; Stuart and Lister, 2011). The frequencies of this top predator reached its maximum up to the MIS3, when it was quite common in the whole Europe (among others Kurtén, 1968; Bonifay, 1971; Piccoli, 1979; Bon et al., 1991; Kurtén, 1985; Janossi, 1986; Guzvica, 1988; Lewis, 2010; Stuart and Lister, 2011) and drastically decrease during and after the LGM (Stuart and Lister, 2011), probably as a consequence of a new climatic change towards strongly colder temperatures and, probably, the increasing stress due to the competition with the human expansion in Europe (Rosendahl and Darga, 2004; Rabal-Garcés et al., 2011). The richest deposits of the younger species are from the Late Pleistocene sites of Hermann's and Zoolithen caves in Germany (Diedrich, 2008), Abîmes sur la Fage and Cave of Jaurens in France (Ballesio, 1980; Turner, 1984), Grotta Pocala and Grotta del Brojon, in Italy (see below), and Igric Cave in Hungary (Hankó, 2007). The European lions became completely extinct at about 12 ky in northern Europe and few before in the lower latitudes (Stuart and Lister, 2011).

In Italy, lion was determined for the first time at Isernia La Pineta with a single P4, as *P. leo fossilis* (Sala, 1990). Bona and Sardella (2012) refer postcranial samples from Brecce di Soave (Vicenza) as *Panthera* cf. *P. leo fossilis*. Up to today, no more specimens of lions are recognized in Italy for this larger subspecies, and it was suddenly replaced by the more common *Panthera leo spelaea*. This lion is well represented in the whole peninsula, especially in the pre-Alps sites of Pocala Cave and Broion Cave, both dated back to the Late Pleistocene (Sala, 1980; Bon et al., 1991; Masseti and Salari, 2012), and seems to be completely lacking in the highest Apennines. In Italy, *P. leo spelaea* is definitively absent at about 20 ky, with its last occurrences at the Paleolithic sites of Paglicci Cave (at about18 ky; Boschin and Boscato, 2012) and the indirect proof of its occurrence at Riparo Tagliente, with an engraving draw of a lion on a stone surface (Mezzena, 1964; Bartolomei et al., 1974).

6.1. Critical overview about cranial variability of European and African lions (*Panthera leo*)[4]

This chapter is focused on the concept of species and subspecies within the genus *Panthera*, particularly for the Middle-Late Pleistocene European lions.

Far from a complete compendium about the problem, I want to point out that for many years palaeontologists determining fossil lions followed a "lumping" tendency, which since Sotnikova and Nikolskiy (2006) published their precise comparison among lion crania, seems surpassed by a "splitting" approach (Mallet, 2007).

The divergence between African and European lions was dating back to the early Middle Pleistocene (later than 600 ky. García García, 2001; Burger, 2004), and the relatively recent speciation of the family Felidae probably entailed an incomplete reproductive barrier among the species. Even though the fur pattern and behaviour can be very specialized for each environment (Sunquist and Sunquist, 2002; Pocock, 1930), the feline skeleton can be considered as a standard model with different sizes for every single species, with few specific and much derived characters (Turner and Antón, 1997). The uncompleted separation of the group is evident in extant species: the interbreeding between bobcat (*Lynx rufus*) and canadian lynx (*Lynx canadensis*) (Homyack et al., 2008; Schwartz et al., 2004; Libby, 2004), or domestic cat (*Felis catus*) with serval (*Leptailurus serval*) (Markula et al., 2009) and wild cat (*Felis silvestris*) (Pierpaoli et al., 2003). Also the Asian and African larger felids are interfertile in peculiar circumstances (i.e. in zoological gardens), with the birth of liger cubs (from a male of lion and a female tiger) or tigons (tiger male and lioness).

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[4] modified from GHEZZO E. & BERGAMO A., submitted. Critical overview about cranial variability of European and African lions (*Panthera leo* ssp.). *Annales de Paléontologie*

Today, the concept of species and subspecies is of interest for zoologists, and for palaeontologists as well, for several reasons, from wildlife legal protection and conservation of endangered species, to evaluation about paleoecosystems and evolution (Minelli, 1999, 2003; Tautz et al., 2003; Agapow et al., 2004). The main question concerns the intraspecific and interspecific boundary (both in extant and extinct species) for phylogenetic affinities. Unfortunately, morphology and genetic are generally considered separately, whereas their reliability should be considered case-by-case. In fact, the incomplete separation between species is not so uncommon in zoological studies, where different genotypes are not related to phenotypical divergences and *vice-versa* (i.e. Cronin, 1992; Cronin et al., 1991).

In palaeontology, the problem is amplified and emphasized because the variability in chronospecies morphology and the fragmentary and smaller sequences of mtDNA (so that genetics should be always critically considered).

For Mayr (1982) a subspecies is: "*a taxonomic category below the species level that recognizes geographic and temporal subdivisions*". O'Brien and Mayr (1991) stated that a member of a subspecies would "*share a unique geographic locate, a set of phylogenetically concordant phenotypic characters, and a unique natural history relative to other subdivisions of the species*". It doesn't mean that they are reproductively isolated, but they usually are allopatric and they have recognizable phylogenetic partitioning with independent genetically based traits (Avise and Ball, 1990). Darwin (1874) already had the same approach, using the term 'species' to identify two forms separated by the absence of varieties linking their ranges. At the same time, he admitted that geographical distribution do not give any information about the taxonomical ranks. With the beginning of trinomial nomenclature for subspecies (1850s), determined as groups connected by intergradation (Mallet, 2007), the problem of basal common features in two o more groups was solved.

Beyond the occurrence of interfertile individuals, a quite similar approach is often used for taxonomical ranks. Could one character be considered enough for a specific determination? Unlike his predecessors, Cracraft (1989) stated that a single fixed character should justify a separate species, probably to obtain better invasive and effective species' conservation purposes. The consequence of his determinations is ideally the precipitous increasing of the number of species, particularly alarming when the concept is transported into the paleontological scene, where missing features are usually more frequent than the comparable evidences.

Jánossy (1986) well resumed the paleontological problem in his book about Hungarian Pleistocene faunas: "*The different opinion among certain palaeontologists as regards the nomenclature of mammalian species osteologically slightly (mainly statistically) different, or not different at all. Some palaeontologists apply names of contemporary species to these forms, others recognize subspecific differences, whereas others consider these species distinct from extinct forms*".

Bernardi and Minelli (2011) made an overview of the concept of species in palaeontology. They described the inconformity and constantly changing significance of the word species in times and in different scientific branches, wishing for a biological and geological solution to the problem, with a unitary interdisciplinary work (monotetic concept).

A solution is far from being solved and palaeontologists must critically evaluate the term, considering the specific and subspecific determinations, variation in osteology gross anatomy, and the importance of geologic time and scattered (in time and space) findings.

Different scholars for the European lion - Schütt (1969a) defined and described the characteristic of European lions at subspecific level. According to him, several authors (among others Piccoli et al., 1979; Burger et al., 2004; Rosendahl and Darga, 2004; Sommer and Benecke, 2006; Diedrich, 2008; Hankó, 2007; Baryshnikov and Tsoukala, 2010; Davis et al., 2010; Blasco et al., 2010; Stuart and Lister, 2011) considered the lion fossils as a subspecies of the current lion *P. leo* and, consequently, determined the Pleistocene lions as *Panthera leo fossilis* and *Panthera leo spelaea*.

On the other hand, Riedel (1982), Turner (1984), and Mazza et al. (2005) preferred a more cautious solution because of the scarcity of the available material, referring all fossil specimens as “lion” or *Panthera leo*. Instead, Capasso Barbato and Minieri (1987), Argant (1988), Capasso Barbato and Gliozzi (1995), Turner (1997), and Guzvica (1998), consider the Pleistocene lion as a separate species (*Panthera spelaea*) on the basis of size (larger than extant animals), time, ecology and environment. In their view, all these characteristics would make it difficult to consider the extinct lion as a living lion's subspecies. A chronological approach was followed by Argant et al. (2007) in their study about large felids from Château Breccia, determining the *Panthera spelaea fossilis* and *Panthera spelaea spealaea* as chronosubspecies. Ballesio (1975) described the new subspecies *Panthera (Leo) spelaea* by few mandibular and postcranial remains from Abîmes de la Fage and, according to Dietrich (1968), Sotnikova and Foronova (2014) followed the same sub-genus determination for a fossil Asian lion.

Baryshnikov and Boeskorov (2001) morphologically analysed Middle and Late Pleistocene lions from Russia, Alaska, and Canada, concluding that the European and American records represent separate species, and that the Berigian smaller form should be classified as *Panthera spelaea vereshchagini*.

Contrary to all previous mentioned authors, Groiss (1996) defines the Pleistocene lion as a subspecies of the extant tiger, namely *Panthera tigris spelaea*, for its large similarity to modern tigers' external cranial features and hypophysial side on the brain.

Most recent authors (Turner, 1997; Yamaguchi et al., 2004; Torregrosa et al., 2010; Meloro, 2011) agree in classifying *P. leo spelaea*, and considering the North American form as an independent species (*P. atrox*), since it differs in size and has a separate geographic position (effect of allopatric speciation).

Finally, the comparative analysis of Sotnikova e Nikolskiy (2006) can be considered as the milestone of the question. They carefully studied the three groups of lions from Europe and America, naming them *P. fossilis, P. spelaea*, and *P. atrox* respectively. Furthermore, they listed the morphological differences between extant lions and tigers.

Recent molecular studies offer an important contribution to better decipher fossil taxonomic and phyletic relationships of European lions within Pantheridae. Burger et al. (2004) analysed the phylogenesis of Late Pleistocene European lions, comparing their citocrome *b* gene to the extant one. The analysis reveals that the two European populations were probably completely isolated. Albeit with some doubt, they concluded that lions could be set within sub-specific variability, and named the cave lion as *Panthera leo spelaea*. They inferred the same determination for Middle Pleistocene lions, calling them *Panthera leo fossilis*. Later, Davis et al. (2010) found a clear supported monophyly of lions and leopards with the supermatrix and BEST analyses. Barnett et al. (2009) assumed the existence of three distinct genetic lion lineages: extant *P. leo*, *atrox*, and *spelaea* without naming the latter two as a species or subspecies. Using molecular clock, the authors determined that the divergence among the two Late Pleistocene species occurred about 337 ky ago (Figure 49).

Authors	year	*P. leo spelaea*	*P. leo fossilis*	*P. spelaea*	*P. spelaea spelaea*	*P. spelaea fossilis*	*P. spelaea vereshchagini*	*P. fossilis*	*P. tigris spelaea*	*P. tigris fossilis*
Schütt	1969	x	x							
Piccoli et al.	1979	x	x							
Capasso Barbato and Minieri	1987			x						
Argant	1988			x				x		
Sala	1990	x	x							
Gross	1992	x								
Capasso Barbato and Gliozzi	1995			x						
Groiss	1996								x	x
Turner	1997			x						
Guzvica	1998			x						
Baryshnikov and Boeskorov	2001			x	x	x	x			
Palombo and Valli	2003	x	x							
Von Koenigswald	2003	x								
Burger et al.	2004	x	x							
Rosendahl and Darga	2004	x								
Yamaguchi et al.	2004	x								
Alvarez-Lao and Garcìa-	2006	x	x							
Sommer and Benecke	2006	x								
Sotnikova and Nikolskiy	2006			x				x		
Bona	2006	x								
Argant et al.	2007					x				
Diedrich	2007	x								
Hankó	2007	x	x							
Diedrich	2009	x								
Baryshnikov and Tsoukala	2010	x	x							
Davis et al.	2010	x								
Blasco et al.	2010		x							
Marciszak and Stefaniak	2010				x	x				
Diedrich	2010	x								
Torregrosa et al.	2010	x								
Diedrich	2011 a-d	x								
Stuart and Lister	2011			x						
Meloro	2011	x								
Diedrich	2012	x								
Rothschild and Diedrich	2012	x								
Ghezzo et al.	2014	x								
Marciszak et al.	2014			x	x	x				

Figure 49: list of the authors and year of the publication dealing with lions, reporting the specific or subspecific attribution.

General overview - The intraspecific variability within lions was previously noted by several authors (Kurtén, 1968; Schütt, 1969; Sotnikova and Nikolskiy, 2006; Bona, 2006; Hankó, 2007; Marciszak et al., 2014), pointing out the differences between Middle and Late Pleistocene species, the *fossilis* and *spelaea* group, namely the greater size, the narrow and long rostrum and temporal regions, the almost flat frontal region, the V-shaped posterior end of the palate, the less inflated bullae, the smaller incisors and low paracone of P3 and paraconid of p3 and p4, the lacking of preparastyle on P4, the major height and shorter length of the paraconid of the lower carnassial, and the smaller orbits of the former (Sotnikova and Nikolskiy, 2006; Marciszak et al., 2014). These characteristics were usually related to primitive or progressive features, in a quite linear evolutive trend from the Middle to Late Pleistocene lions. The advanced features seem to be related to a southwestern Asia expansion (Sabol, 2011) and effectively the fossil from Petralona Cave (Hemmer, 1974; Baryshnikov and Tsoukala, 2010) and Azé Cave (Argant, 1988, 2010) are previously interpreted as intermediate forms.

The small preparastyle on P4 was described as typical of living lions (Sotnikova and Nikolskiy, 2006). In our analysis it appears only in few *Panthera tigris* specimens, namely MZS8460 and AMU01, and also in some *Panthera leo* crania, such as MZS1911, MZS1910, and MZS2131. Actually, it appears also as a small tip in some of the fossils of lions, namely MB.Ma.50947 and MGP-PD25262.

The carnassial protocone is quite reduced in all studied *Panthera leo* specimens without a real cusp, sometimes to just a small bulge. The timpanic bullae are subcircular in *Panthera tigris* and elongated (elliptical) in all *Panthera leo*. In studied European lions, timpanic bullae are quite smaller than in extant specimens.

Unlike the other members of the genus, lions have post-orbital and frontals bones placed more backwards (Torre, 1967; Ficcarelli and Torre, 1968), and this feature is ever notable in both the extant and the extinct species.

The comparison among different specimens of lion and tiger (Figure 50) reveals that the two species have a different cranial structure, already noticed by Sotnikova and Nikolskiy (2006): on the lateral view, the lion's cranium is weakly curved between the sovraorbital processes, whereas the tiger's has a convex surface. Furthermore, in *P. leo* the nasal opening is rounder and wider at the base, the intra-orbital *foramina* is larger and less elliptic, the zygomatic frontal process and the zygomatic processes of the frontals are more rounded compared to *P. tigris*. Further differences between the two species concern the frontal-maxillary suture, which in lions forms a sharper angle; instead, in tigers it forms an obtuse line. The nasal-frontal suture is more rounded in lions, while in tigers it looks sharper and more sunken-in.

The lion's nasal-maxillary suture is straighter and less sinuous compared to the tiger's. On the dorsal view, the lion's cranium has an emphasized sagittal crest and is extended beyond the *acrocranion*. The inter-temporal area and the post-orbital constriction of the lion's skull are narrow.

In the modern *Panthera leo,* all the studied specimens bears elongated tympanic bullae (while in tigers they are subcircular). Specimens MZS490 and MZS8459 have a rather enlarged nasal opening, dorsally sunken-in, and the ascendant process of the zygomatic and the descendant of the frontal are rounded. Both the sutures between the frontals with nasals and maxillars are curved. The nasal-maxillar suture is rectilinear, and the post-orbital constriction is narrow. The lions MZS3522 and MZS2131 are similar to the tigers' for the line of the nasal-frontal suture (which forms an acute angle). In half of observed skulls, the maxillary-frontal sutures are truncated and the preparastyle is lacking in half of the extant lions.

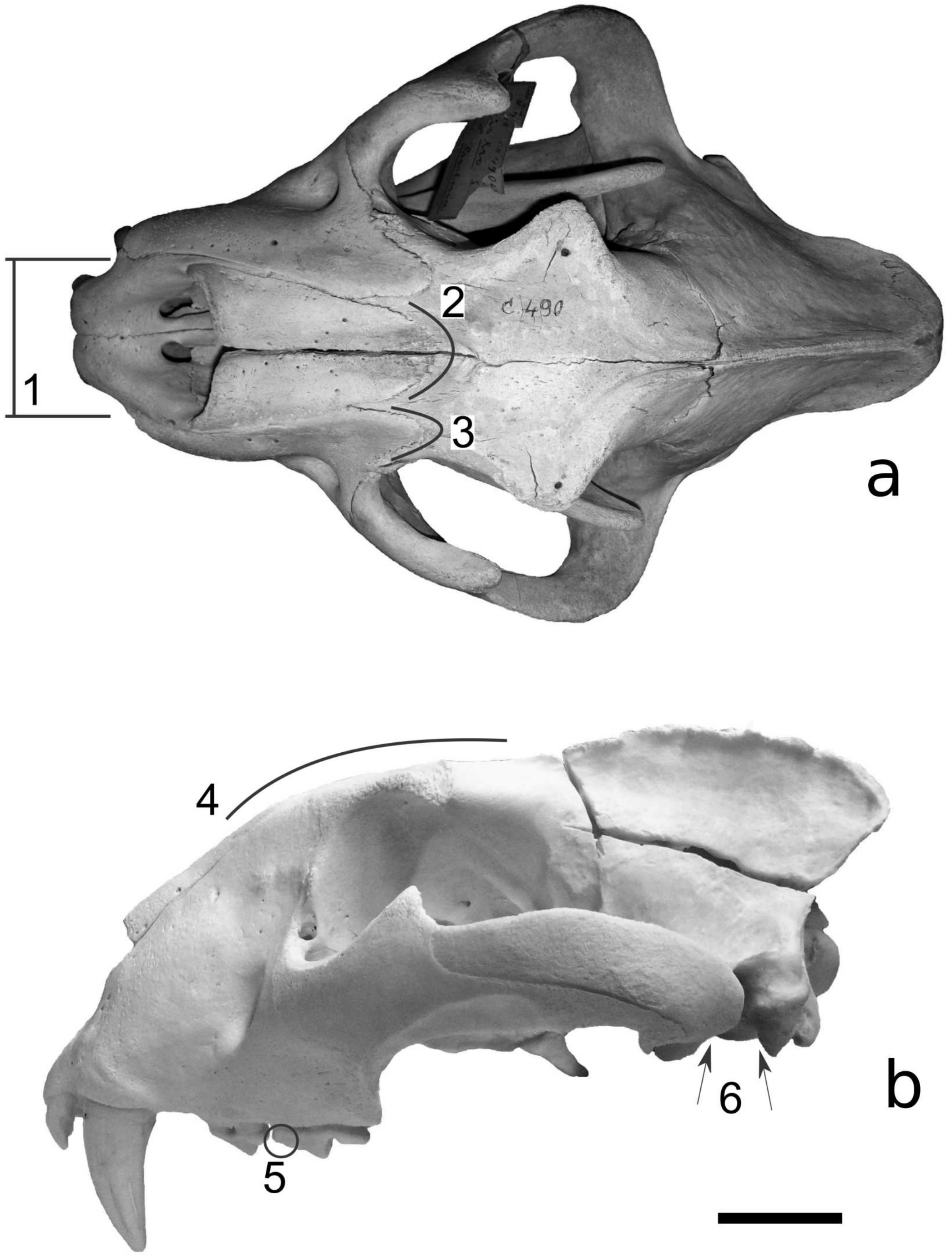

Figure 50: main differences observed between *Panthera leo* and *Panthera tigris* crania: outline of the nasal aperture (1); frontal-nasal suture (2); frontal-maxillar suture (3); dorsal profile of the cranium (4); presence/absence of the preparastyle on P4 (5); development of the tympanic bullae (6). Scale bar 5 cm.

Cranial description - The nasal bones of the holotype MB.Ma.50948 are joined to the frontal ones with an obtuse line. On the lateral view, cranium and muzzle are elongated and the dorsal profile is flattened. The tympanic bullae are not so prominent. MB.Ma.48115 and MB.Ma.50947 are similar to the previous one, but the former has a shorter muzzle and the nasal-frontal junction forms an obtuse angle in the latter. In MB.Ma.48115 the maxillar bone forms a V-junction with the frontal. The sagittal crest is noticeable. MB.Ma.50947 has a narrow braincase and a larger postorbital constriction, and the sagittal crest is quite developed.

The nasal opening of MGP-PD25260 is wide and the corresponding bones form a slightly sunken-in reciprocal joint. The nasal-frontal suture is sharp and the maxillary-frontal one is quite rounded. The dorsal side of the cranium forms an evident concavity between the sovra-orbital processes. The intra-orbital *foramina* have an elliptic outline with greater axis on the vertical. The zygomatic arches are very wide and the nasal-maxillary suture has a rectilinear and regular edge. The sagittal crest is accentuated.

In MGP-PD25262 differs from extant tigers the sagittal crest is developed and the tympanic bullae are enlarged. The nasal opening is wide. The nasal-frontal suture is sharp, the maxillary-frontal suture is only slightly rounded, and the temporal bones are less massive than MGP-PD25260. The intra-orbital *foramina* are elliptic. The two processes of the orbit are sharper than those of the extant lions. The sagittal crest and the tympanic bullae are very well developed.

V.60.1785 and Ob-2978 from Hungary are quite well preserved. The postorbital constriction is narrow, and the bullae are very small. In both the crania, the nasal-frontal junction is large and the latter bone forms a U-shaped suture with the maxillar one. On Ob-2978 all the sutures are almost completely ossified, probably representing an old individual. The nasal overture is large and the infraorbital foramina are oval. The zygomatic process of the temporal bone is massive and high.

Results **-** Sotnikova e Nikolskiy (2006) did not considered juveniles and female individuals in their comparative analysis. In my study I considered both sex individuals as well as juvenile ones, evaluating the sexual variability within the sample. According to Turner (1984), I used the length-breadth ratios of canines to infer the sex of my collection and Figure 51shows that there is an evident separation between females and males. With the exception of the two crania from Pocala Cave, which didn't conserve their own canines (Figure 52c), the European lions fall within the range of males (from 25 to 31 mm of length). The specimen Ob-2978 (Figure 52a-b) is at the boundary of the two size groups; it seems a large female individual. The specimen Ob-2978 bears most of the lion-like characteristics and I included it in this study.

Even though entire crania are quite rare in Europe, few well preserved specimens were precisely described. Argant (1988) depicted the entire skull from the Azé Cave; the profile of this find and the sutures agree with the typical lion's morphology. Also the palatal posterior edge of this specimen (staphylion region) has exactly the same feature of MB.Ma.50947, while in the other fossils here described this characteristic is not preserved. In the extant lions from the MZS and MZ, this edge is bilobed (as represented by Argant, 1988 - fig. 2 – for *Panthera leo*), and the tiger MSZ8460 has a rectilinear edge, similarly to *Panthera spelaea* (Argant, 1988 – fig. 2). Bona (2006) described another *Panthera leo* cranium from Zandobbio (Bergamo).

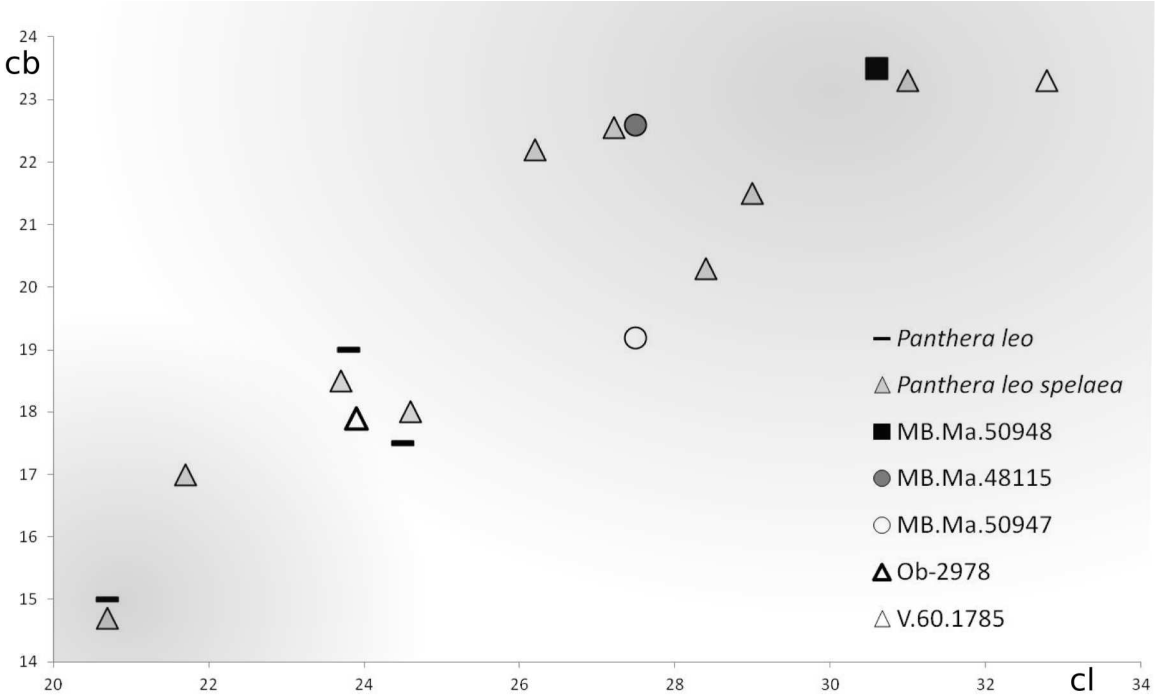

Figure 51: cranial sexual dimorphism, as evidenced according Turner (1984)

Such fossil reveals the same morphological and dimensional patterns of our collection, most in the splancnocranium. Haas et al. (2005) resumed the characteristics of modern species. In such description, the lion shows again the typical curved junction between frontals and nasals, the lacking of preparastyle on both P4s. The dorsal profile of this skull is interestingly curved, more similar to MGP-PD25262 than the other lions.

For the cluster analysis, I considered six defined features (Figure 50), namely: the presence/absence of the preparastyle on P4, the outline of nasal opening, the sutures between frontal and nasals and frontal and maxillar, the dorsal cranial edge and the main feature of the timpanic bullae (Figure 53). In general, I agree with the morphological features chosen by Sotnikova and Nikolskiy (2006), but I have not considered the neurocranium sutures and the braincase features, because they tend to disappear with age or are too subjective. At the same time, the suture between the maxillar and zygomatic bones is rectilinear for all our specimens, and varies just on extant lions.

Finally, Pocock (1930) stated that the shapes of infraorbital foramina are too variable both within tigers and lions and I note the same pattern on the crania used in this study.

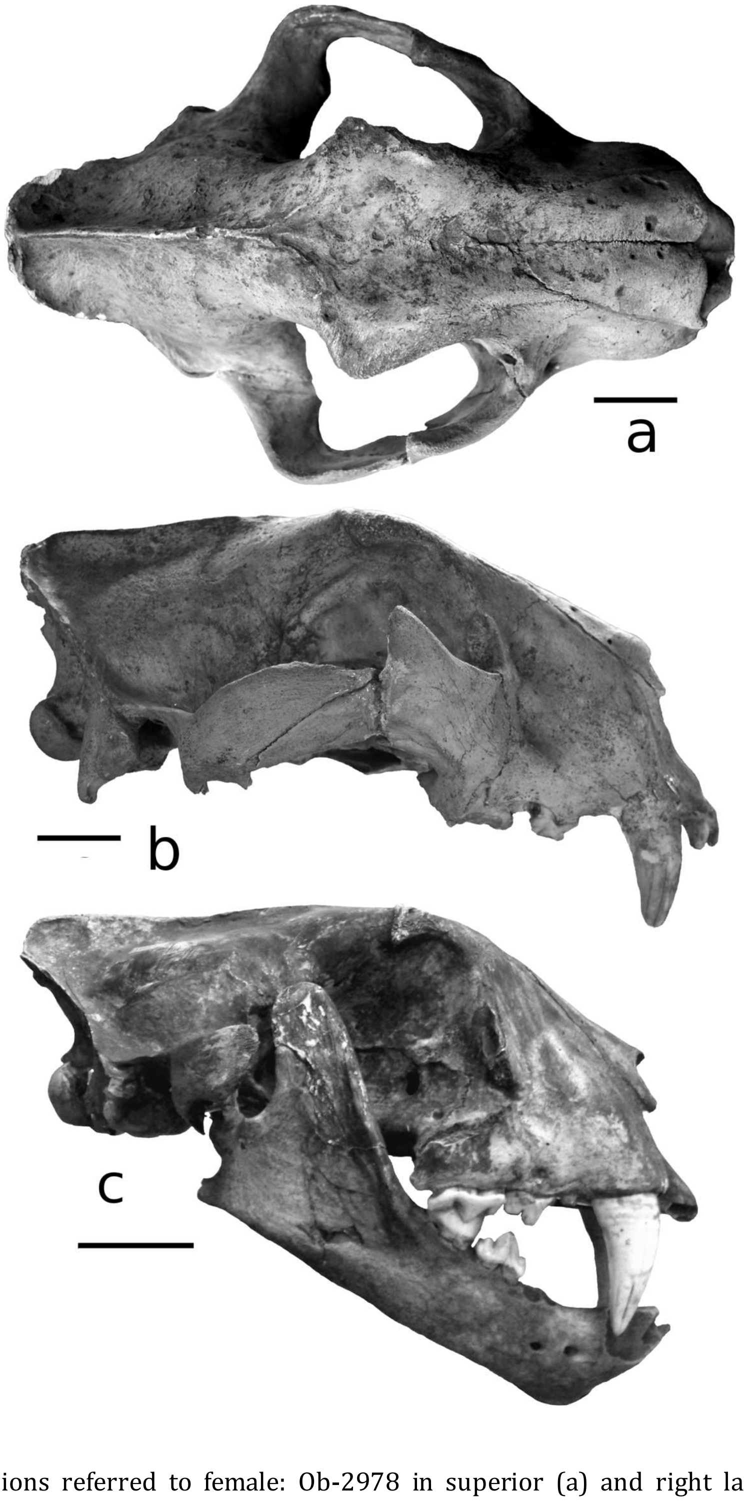

Figure 52: crania of lions referred to female: Ob-2978 in superior (a) and right lateral (b) view; MGP-PD25262 in right lateral view (c). The canine of the latter belongs to a different individual (smaller than the alveolus, and was probably re-placed for exposition purposes).

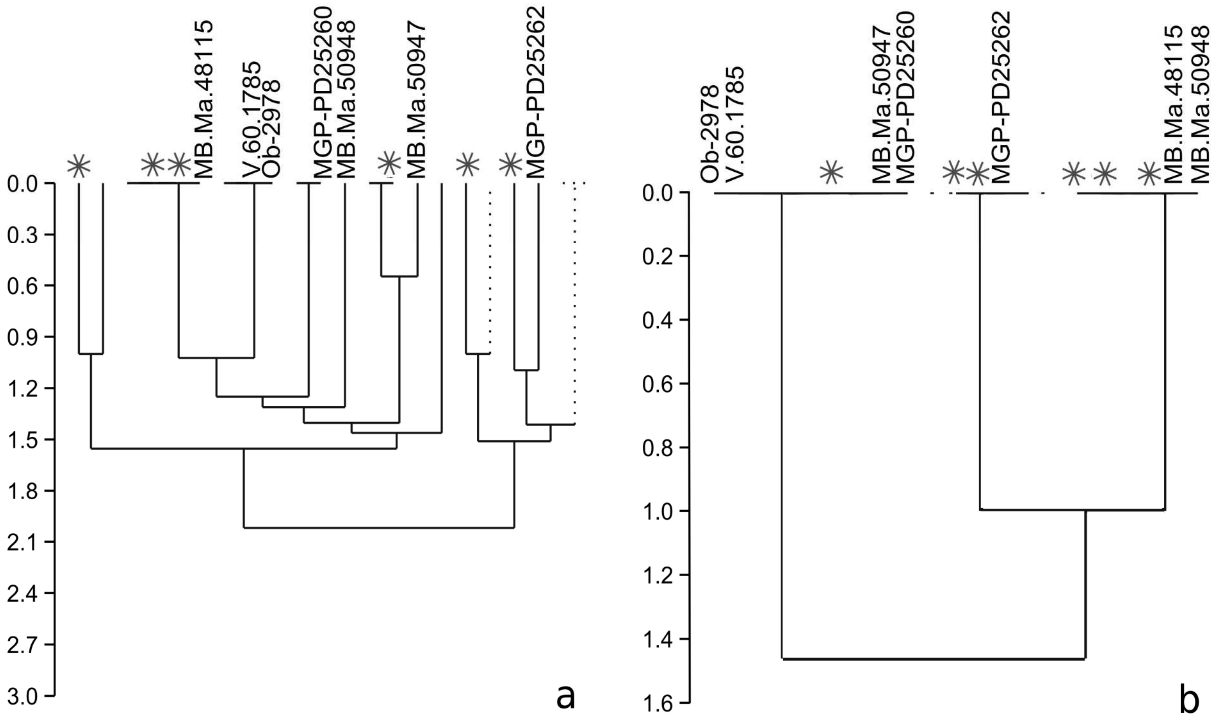

Figure 53: cluster analysis of the six features explained in fig. 51: simple Cluster tree (a) and k-means Cluster (b). Stars are lions from Somalia and hatching branches are tiger.

The tree cluster analysis using the Euclidean similarity index (Figure 53a) allows us to enhance that, while *Panthera leo* and *Panthera tigris* individuals are quite recognizable, fossils and extant lions are distributed in both the different branches. In particular, the smaller Italian specimen (MGP-PD 25262, probably a female due to its size) is closer to *Panthera tigris* than other specimens, since the specimen has a arched dorsal profile on lateral view and an acute nasal-frontal suture. The Pleistocene north European lions fall within the extant *Panthera leo* variability, like the larger cranium from Pocala Cave, being separated into different branches.

I tried to group crania starting from the hypothesis that they could be subdivided into three main groups, namely, *Panthera leo*, *Panthera tigris*, and extinct lions (Figure 53b). The k-means analysis might have divided them into clusters that are as distinct as possible, and I expected to obtain crania separated into the respective branches, with extant and extinct lions close to each other and far from tigers. Indeed, again, there is not a clear differentiation, and even the tigers are intermediate between the two lions' branches, with fossil specimens positioned within all the branches. The two probable females (MGP-PD25262 and Ob-2978) show the same variable features than other subgroups. It is noteworthy that a similar pattern exists also in the extant lions from Somalia, implying a generalized intraspecific variability even among extant lions. The two specimens from Igric Cave are more similar to each other, while the crania from Zoolithen Cave do not fall within the same group.

Referring these results to the taxonomical identification, Wilson and Brown (1953) argued that multiple characteristics could rarely or never justify subspecific determinations, because interbreeding prevented divergence. With the cluster approach I proved that fossils and extant lions are grouped in the same unseparated branches, while tigers split into a separated group. The intraspecific variability is clearly linked to the range (latitude and longitude, but also altitude), but there is not a definite morphological pattern among the considered specimens, as evidenced by the case of the six *Panthera leo* specimens from Somalia.

The common features between *Panthera leo* and *Panthera tigris* seem to be related to plesiomorphic characteristics of the group. Instead, the more stable characteristics that enable differentiation between tigers and lions are the more rounded tympanic bullae of *Panthera tigris* and, of course, the obtuse suture between nasals and frontals and the flattened cranial profile in *Panthera leo*. *Panthera tigris* has a shorter and vertical muzzle (more perpendicular to the ventral plane) than *Panthera leo*, and fossils seem to stress this differentiation, showing an elongated splancnocranium and a clear concave surface between frontals (except for the smaller cranium from Pocala Cave and the one from Zandobbio; Bona, 2006).

It is generally known that sizes of lions decreased from the first occurrences to the smaller animal of Late Pleistocene, but the decreasing trend is actually not so visible. Argant (1988) states that it would be naive to consider a steady decrease in size during the Pleistocene, and Marciszak et al. (2014) concluded that effectively a decreasing size occurred, but the biochronological meaning is missing. According to Marciszak et al. (2014) all the considered specimens never exceed 400 mm of length (they are between 267 mm to 345 mm) and well fit with the size of Late Pleistocene lion's skulls. The smaller male cranium is represented by MGP-PD25260, with a total length of 320 mm, and the postcranial elements of lions from the same cave (unpublished data) are in fact really small.

Among the large felids, lions are clearly larger than leopards and jaguars. Ficcarelli and Torre (1968) stated the main difference between lions on one side, and tigers, jaguars, and leopards on the other one, is the major distance between the post-orbital processes of the frontals and the upper molar, due to a more posterior position of such processes in the former. Once again, those features emphasize a flattened profile of lions on lateral view.

A clear size differentiation among extinct Late Pleistocene lions, extant lions, and tigers is completely lacking for the pollution caused by the climatic fluctuations and possible regional specializations (Gross, 1992; Diedrich, 2007; Lewis et al., 2010; Marciszak et al., 2014). As expected, the PCA analysis also confirms the similarity among the large carnivorans, and the first component is mostly conditioned by the condilobasal length, then by the splancnocranial size (due to several measurements), and less by the *foramen magnum* transversal diameter and premolar and molar size (Figure 54). The single older skull from Mauer is set out from the lions' variability most for the largest P3 and P4.

Summarizing, the morphological and dimensional analysis of cranial remains confirm the recognition of *Panthera tigris* and *Panthera leo* as districted species, but it is nearly unreliable for a differentiation among extant and fossil lions.

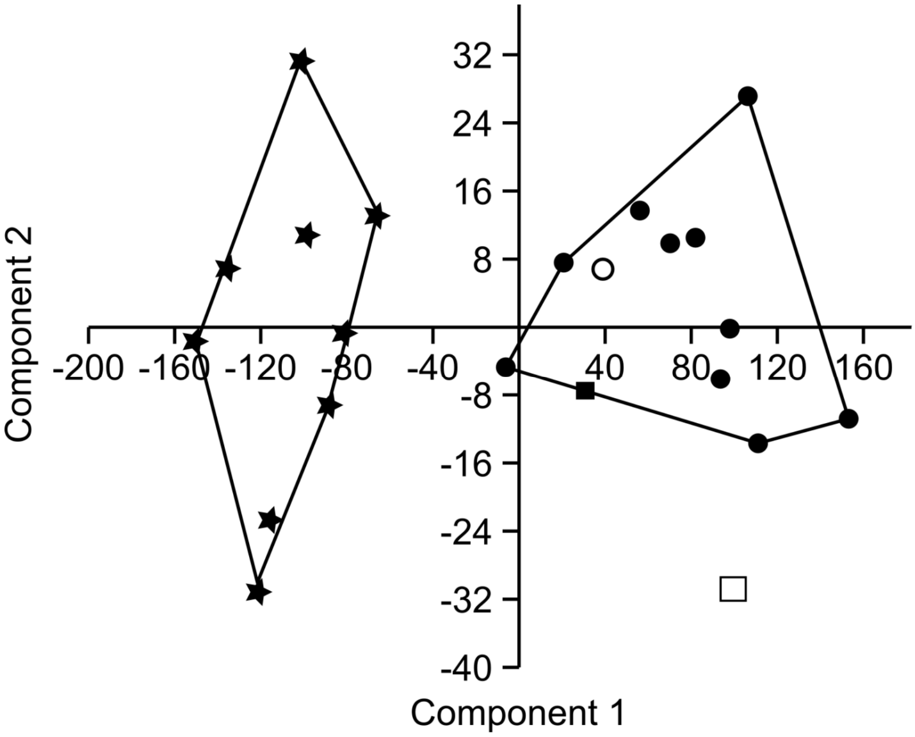

Figure 54: PCA analysis of European fossil 659 lions (black dots), *Panthera leo fossilis* from Mauer (white square), and other large felines, such as tiger (black square), extant lion (white dot) and leopards (black stars).

6.2. Lynx remains from the Pleistocene of Valdemino Cave (Savona, Northwestern Italy), and the best preserved occurrence of *Lynx spelaeus* (Carnivora, Felidae)[5]

Fossil remains ascribable to the genus *Lynx* are quite common in the Plio-Pleistocene sites of Europe, being a quite ubiquitous presence in the faunal lists of the related deposits (Werdelin, 1981; Lorfèvre, 2009; Cipullo, 2010). However, many aspects of their evolutionary history remain unclear, starting from their own in-group phylogeny (Kurtén, 1968, 1978; Werdelin, 1981; Palombo et al., 2008; Boscaini, 2014). This is ascribable to many causes, proposed in the past by many authors, namely: the scarcity of well-preserved fossils, the recent and quick divergence of the extant lineages (Johnson et al., 2004 and references therein), their extreme adaptability and ''plasticity'' of their body size, difficulties in defining reliable morphological diagnostic features (and observable in the fossil record) and dubious taxonomic attributions (Bonifay, 1971; Olive, 2006; Testu, 2006; Palombo et al., 2008). In recent times, a special attention has been directed on this group of felids, in the effort of clarifying these obscure points, specifically, in the last decade many studies on extant and fossil lynxes have been conducted on South-western European material (Testu, 2006; Lorfèvre, 2009; Cipullo, 2010; Cherin et al., 2013; Boscaini, 2014). Part of this problem relies on the taxonomic attribution of several Middle and Late Pleistocene remains, mainly from caves in Southern France and Northern Italy and putatively belonging to the species *Lynx spelaeus* or *Lynx pardinus spelaeus*, surely the most controversial fossil species of the genus (Testu, 2006; Palombo et al., 2008; Boscaini, 2014).

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[5] modified from GHEZZO E., BOSCAINI, A., MADURELL-MALAPEIRA J., ROOK L, (in press). *Lynx* remains from the Pleistocene of Valdemino Cave (Savona, Northwestern Italy), and the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae). *Rendiconti Lincei* doi: 10.1007/s12210-014-0363-4

The origin of the disagreement on the taxonomic attribution of this species must be tracked down in its first description by Boule (1919), when the author erected the subspecies *Felis* (*Lynx*) *pardina* race spelaea, now *Lynx pardinus spelaeus*. The specimens analyzed by Boule (1919) come from the Late Pleistocene Grotte du Prince and Grottes de Grimaldi (Grimaldi, North-West Italy) and immediately Boule notes typical intermediate characters between the living *Lynx lynx* and *Lynx pardinus*, stating that ''il est difficile è identifier á l'une des espèces actuelles'' (Boule and de Villeneuve, 1927). A summary of the historical ambiguous attribution of these remains is available in Bonifay (1971). Nowadays, the divergent evolution between *L. pardinus* in Europe and *L. lynx* in Asia from the common ancestor *L. issiodorensis* is generally accepted by several authors; tempo and mode of extant European lynxes appearance are however a still open debate (cfr. Rodriguez et al., 2011; Cherin et al., 2013; and references therein). Even if the majority of the scientific community still considers *L. spelaeus* as a subspecies (and direct ancestor) of the living Iberian species with a some kind of anagenetic evolution beginning with the Villafranchian *L. issiodorensis*, throughout *L. pardinus spelaeus* and finishing in the living *L. pardinus* (Werdelin, 1981; Kurtén and Granqvist, 1987; García and Arsuaga, 1998; among others), in other publications like Bonifay (1971), Testu (2006) and Lorfèvre (2009) a specific classification (*L. spelaeus*) of the cave lynx is preferred, considering that the last species are not in the phylogenetic lineage of extant *L. pardinus*.

I consider *Lynx spelaeus* as the typical lynx species from the Galerian and Aurelian faunal assemblages of Southern France and Northern Italy, in accordance with Bonifay (1971), Testu (2006), Sala et al. (1992) and Rustioni et al. (1995). This specific attribution is preferred while the phylogenetic relationships with the extant species *Lynx pardinus* still remain undisclosed (Boscaini, 2014). Another obscure aspect of the evolutionary history of *Lynx spelaeus* is the evolutionary relationship with the other extant species *Lynx lynx*

(Rustioni et al., 1995; Testu, 2006). While it is generally accepted that the Eurasian lynx reaches Europe from Asia in the Eemian period (Middle-Late Pleistocene boundary) (Werdelin, 1981), in the Italian Peninsula, it should be conducted a deep revision of the lynxes' fossil record of this time interval, to set accurately the arrival of this felid to the Alpine and Apennine ranges (Rustioni et al., 1995).

The Valdemino Cave - The Valdemino cave is situated close the Borgio town (Savona Province, Northwestern Italy; WGS84: 44.1600 8.3045; Figure 55a). It is a touristic karst cavity part of a larger karst complex discovered in the 1950s (the largest room of the cave is named ''Cranwell cavern'' in honor of the RAF soldier that first entered in the inner part of the cave; Lamboglia, 1955). In the early 1960s during the constructing works associated with the touristic guided tours, a vertical gallery was found which was filled with Pleistocene sediments (Fornasiero, 1989).

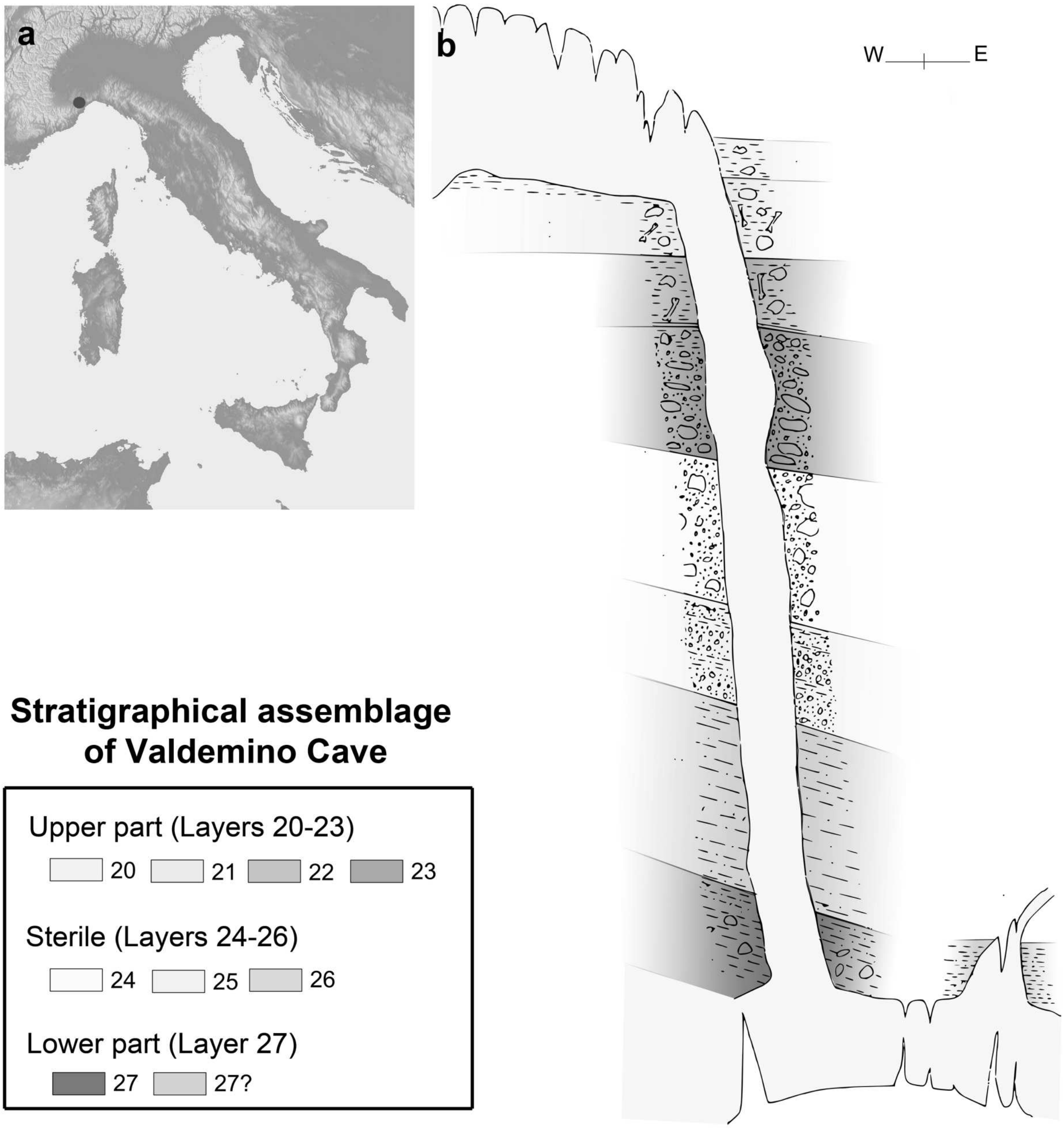

Figure 55: a) location map of the Valdemino cave site within Italy. b) stratigraphic sketch of the Valdemino cave. Dimensions are not to scale (modified from Fornasiero, 1989).

Similarly to Equi and in accordance with Italian law regarding cultural heritage, the Valdemino cave in 1962 has been declared a site of paleontological and speleological importance, under responsibility of the local Soprintendenza Archeologica.

The gallery was firstly excavated at the end of the 1960s by E. Torgiorgi and C. Tozzi (University of Pisa). A brief note on the fauna (Tozzi, 1969) also reported the occurrence of two discontinuous fossiliferous assemblages (called Upper and Lower Part), separated by a thick sterile layer. The excavation of the site was resumed by B. Sala (University of Ferrara) with two field surveys in 1989 and 1991 (Sala et al., 1992; Nocchi and Sala, 1997a). These excavations allowed the recognition of several layers corresponding to the Upper Part (layers 20–23) and the Lower Part (layer 27) separated by a sterile complex (Fornasiero, 1989; Nocchi and Sala, 1997a; Figure 55b). The following species customarily attributed to Middle Galerian assemblages have been recognized in the Lower Part (layer 27) (Tozzi, 1969; Sala et al., 1992; Sardella et al., 2006; Sala and Masini, 2007): *Microtus* (*Iberomys*) *breccensis*, *Apodemus* sp., *Allocricetus bursae*, *Miodes* sp., *Pliomys episcopalis*, *Microtus* (*Terricola*) sp., *Mammuthus armeniacus* (= *trogontherii*), *Stephanorhinus* cf. *kichbergensis*, Cervidae indet., *Sus scrofa*, *Bos primigenius*, *Macaca sylvanus*, *Ursus* sp., *Canis mosbachensis*, *Panthera pardus*, *Felis* (*Lynx*) gr. *spelaeus* and *Homotherium* sp.

Sala and Masini (2007) include the Lower Part of the Valdemino cave in the Isernia Faunal Unit (ca. 0.6 Ma) on the basis of the record of *Allocricetus bursae*, *Pliomys episcoplais*, small-sized *Microtus brecciensis* and *Oryctolagus burgii*. The inclusion of the layer 27 of the Valdemino cave in the Isernia Faunal Unit was supported by most of the scholars (see Palombo, 2014 and references therein for discussion).

On the other side, in the Upper Part (layers 20–23), a typical Late Pleistocene mammal assemblage has been identified (Nocchi and Sala, 1997b; Sardella et al., 2006; Sala and Masini, 2007) with the presence of *Erinaceus europaeus*, *Myoxus glis*, *Arvicola terrestris*, *Microtus agrestis*, *Microtus* (*Terricola*) sp., *Apodemus* sp., *Oryctolagus burgi*, *Canis lupus*, *Vulpes vulpes*, *Sus scrofa*, *Mustela putorius*, *Panthera pardus*, *Crocuta crocuta spelaeus*, *Cervus* sp., *Cervus elaphus*, *Bos primigenius* (Nocchi and Sala, 1997a, b). Until today, from the about 4.000 remains recovered from this cave, only very few taxa have been studied in detail: the mandible of a macaque *Macaca sylvanus*, the almost complete skeleton of red deer *Cervus elaphus*, the leporid remains *Oryctolagus burgi*, and the vole *Microtus* (*Iberomys*) *breccensis* (Tozzi, 1969; Nocchi and Sala, 1997a, b; Davì, 1994).

Taphonomical remarks - The specimens from Valdemino are basically well preserved. Few remains are entire, mostly from the Lower Part. All the specimens from the Upper Part are partly encrusted by a strong thin reddish concretion. There are no signs of root etching, trampling, and abrasion or burning, but there are evidences of weathering, mostly for the bones from Upper Part. The 22 Lynx remains are equally divided in the upper and lower layers, with a total MNI (Minimal Number of Individual) of four animals, two from each assemblage (MNI calculated on radius frequencies). The complete dental eruption, the limited tooth wear, the maxillary sutures (zygomatic-maxillary almost visible; maxillary–premaxillary completely fused), allow to consider cranial elements as belonging to young adults, with an estimated age of death older than 8 months. According to Canadian Lynx postcranial growth pattern data (Tumlison, 1987), joined epiphysis allows estimating age at death older than 32 months.

Description –

Lynx spelaeus (Boule, 1919)

Two maxillar fragments were recovered from layer 27 (015/01 and 015/02), probably corresponding to the same individual (Figure 56). Both specimens preserve the alveoli of I2 and I3, C1 and P3–P4. P3 displays high and sharp (buccal-lingually compressed) paracone, well-developed metastyle with a slightly developed distal cingulum. The protocone on P4 is proportionally small and diagonally oriented with respect to the mesial plane. No trace of ectoparastyle was observed on the well-developed parastyle. Paracone and metacone are sharp (buccal-lingually compressed); both cusps are more or less of the same mesiodistal length.

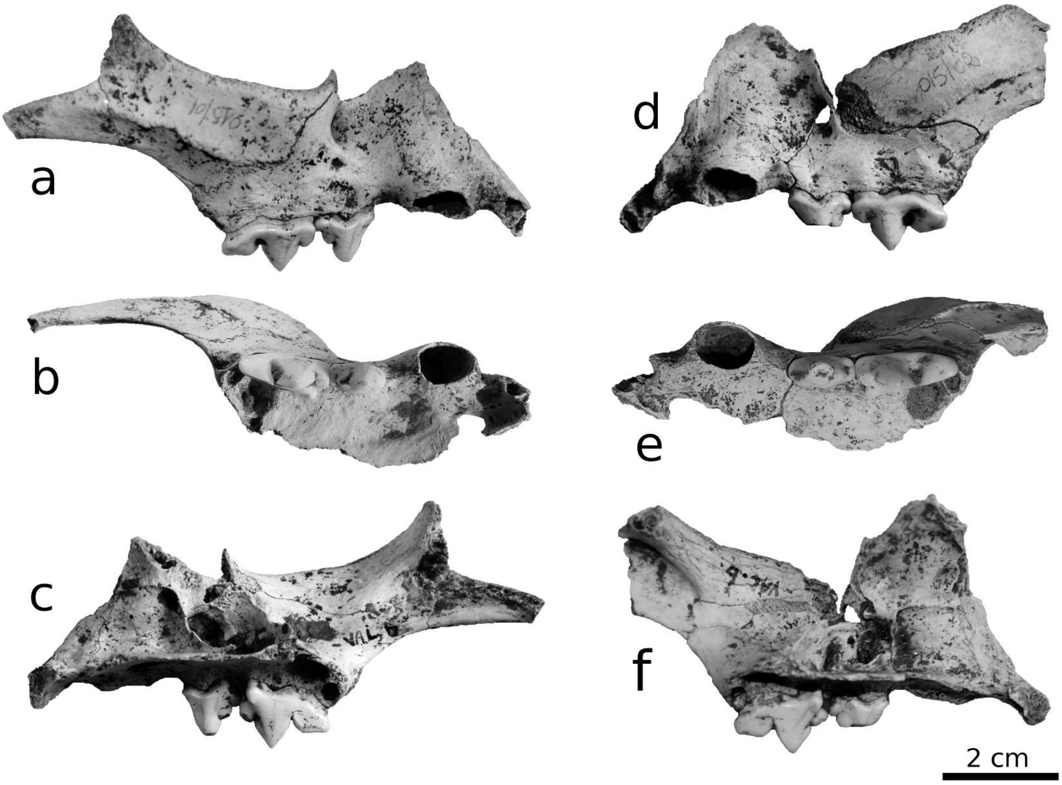

Figure 56: maxillar specimens of *Lynx spelaeus* from the layer 27 of Valdemino cave. Right maxillar 015/01 with P3–P4 in a buccal, b occlusal and c lingual views. Left maxillar 015/02 with P3–P4 in d buccal, e occlusal and f lingual views.

A left mandibular corpus (015/07) was recovered from layer 27 (Figure 57). The corpus preserves c1, p4-m1 and the alveoli of p3; the latter is slender with a short diastema and a slightly concave ventral profile. p4 has a symmetrical protoconid in lateral view with two well-developed accessory cusps (mesial and distal) and a marked distal cingulum. p4 and m1 as in the upper premolars are buccolingually compressed post-canine elements. m1 bears two cusps, paraconid and protoconid, without any trace of talonid or metaconid.

One distal fragment of left humerus was recovered from the lower layers (015/04).

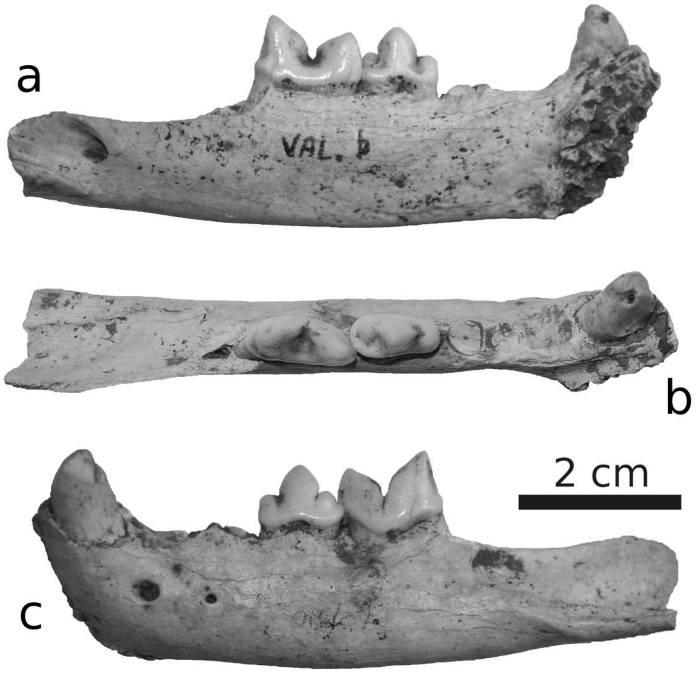

Figure 57: Left hemi-mandibular corpus 015/07 of *Lynx spelaeus* from the layer 27 of Valdemino cave in a lingual, b occlusal and c buccal views.

The morphology of the distal epiphysis, with supracondylar foramen, reduced epicondyles and a deep articular surface is characteristic of the genus *Lynx* (Figure 58e, f). The complete left radius (015/03) displays an anteroposteriorly flattened diaphysis, with a proximodistally enlarged radial tuberosity and reduced insertions for *m. brachioradialis* and *m. pronator quadratus* and a reduced articular surface for the distal ulnar facet (Figure 58a, b). The forth (007/01) and fifth metatarsals (015/05) show slender rectilinear diaphysis with a slightly dorsopalmar torsion (Figure 58d– i). The articular facet for the unciform in the proximal epiphysis of the forth metacarpal displays a slightly convex morphology.

Figure 58: postcranial specimens of the genus *Lynx* from the Valdemino cave. Left radius of *Lynx spelaeus* (015/03) from layer 27 in a anterior and b posterior views. Distal fragment of right humerus of *Lynx* sp. (017/02) from the upper part in c anterior and d posterior views. Distal epiphysis of left humerus of *Lynx spelaeus* (015/04) from layer 27 in e anterior and f posterior views. The pictures in gray behind the studied specimens correspond to living *Lynx lynx.*

Lynx sp.

A left maxillar fragment was recovered from the upper layers (017/06), it preserves P3 and P4 showing the same morphology of the previously described specimens only with an appreciable small ectoparastyle on the P4.

Two distal fragments of humerus were recovered from the upper layers (017/01 and 017/02); these specimens display in general the same morphology but larger biometrical dimensions when compared with the specimens from the lower layers (015/03) (Figure 58c-d). The radius (008/03) is a medial fragment of diaphysis with a flatted anterior surface and posteriorly convex. The proximal fragment of ulna (017/06) only conserves the olecranon process and fossae, being only observable a curved anconeus process. The proximal femur fragment (017/04) displays a rounded and slightly flattened head without fovea capitis and a proportionally reduced *m. vastus lateralis* when compared with *L. lynx*. The third metatarsal (009/01) displays a slender, rectilinear and slightly dorsopalmary torsioned diaphysis (Figure 59a–c).

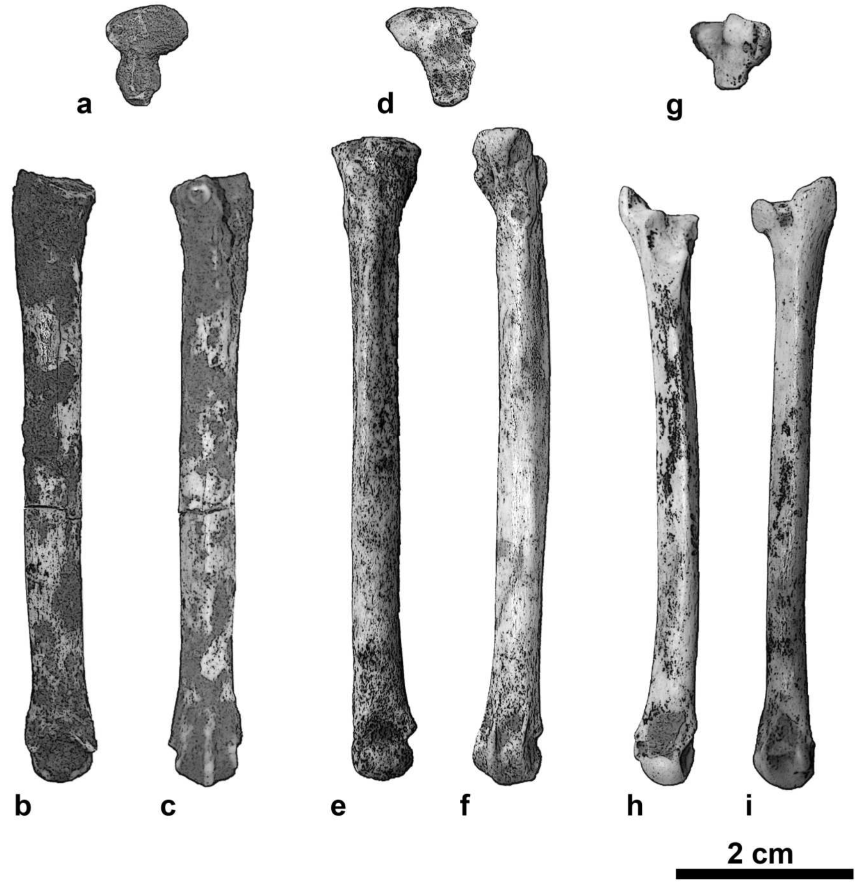

Figure 59: metatarsals of lynxes from Valdemino cave. Right third metatarsal of *Lynx* sp (009/01) from the Upper Part in a proximal and b anterior and c posterior views. Left forth metatarsal of *Lynx spelaeus* (015/06) from the layer 27 in d proximal e anterior and f posterior views. Right fifth metatarsal of *Lynx spelaeus* (015/05) from layer 27 in g proximal, h anterior and i posterior views.

Discussion - The material from the Lower Part (Layer 27) described above, is consistent both in features and measurements, with the fossil lynx material coming from the Middle and Late Pleistocene French localities of L'Escale, Lunel-Viel and Aragó Cave and attributed to the species *Lynx spelaeus* (Bonifay, 1971; Olive, 2006; Testu, 2006; Palombo et al., 2008). Some evident features, mainly in the lower dentition, allow a comparison with these Pleistocene lynxes. The main common characteristic is the presence of a small but detached cingulum in the distal margin of p4 (Bonifay, 1971; Testu, 2006). This distinctive character is also present in the species *Lynx issiodorensis*, its putative ancestor, and less marked (or even absent) in extant *Lynx pardinus*.

However, the material from the Valdemino cave slightly disagrees with the other Galerian remains in another feature: the corpus fragment 015/07 completely lacks the metaconid in the distal margin of m1. The presence/absence of the metaconid is a variable feature, whose ‘‘unfixed’’ occurrence has already been stressed by Viret (1954), Kurtén (1963), Bonifay (1971) and Testu (2006). Many authors evaluate this feature in percentages among the available sample: while it is almost ubiquitous in the latest Villafranchian lynxes (i.e., *Lynx issiodorensis valdarnensis*) (Garrido, 2008) and very rare in extant *Lynx pardinus* (García-Perea et al., 1985). The Galerian–Aurelian lynxes show a gradual decreasing of this structure through time. In L'Escale, it is present in 7 over 8 lower carnassials, in Lunel-Viel 2 over 4 and in the Grimaldi cave 3 over 7 (Bonifay, 1971). Also the material from the Aragó Cave, Orgnac 3, Portel-Ouest, Hortus, La Crouzade and Aldène presents similar proportions (Testu, 2006). In the past Bonifay (1971) and Testu (2006) suggested that the gradual decreasing of this feature is related with the achievement of a progressively more cutting/trenchant dentition. The studied specimens are too scanty to allow any kind of conjecture; in any case, it is remarkable the complete lack of this structure in sediments of this age. This does not affect the taxonomic attribution, given that also in L'Escale, 1 over 8 lower carnassials of *Lynx spelaeus* completely lacks the metaconid. Also the presence/absence of the ectoparastyle on P4 seems to be another variable character with scanty diagnostic value, being absent on Lower Part layer specimens (015/01 and 015/02) and present on the only recovered maxilla from the Upper Part layers (017/06). Even if it tends to be more common in large-sized lynxes *L. issiodorensis* and *L. lynx* (Kurtén, 1978), it can occur with some low percentages also in *Lynx rufus* and *Lynx canadensis* (Boscaini, 2014).

When looking at measurements, it appears that they are consistent with the range established for *Lynx spelaeus*, more precisely with the smallest representatives of the interval. They are also smaller in size than the Villafranchian *Lynx issiodorensis* and the extant *Lynx lynx*, but sensibly larger than extant *Lynx pardinus* (Figure 60).

The material recovered from the Upper Part layers is indeed more difficult to determine, as it lacks the main dentognatic diagnostic features. As I said above the presence of ectoparastyle in the P4 of the 017/06 maxilla is a taxonomic character without diagnostic value. Concerning measurements from both dentognathic and postcranial specimens, these fossils appear larger than the lower layers ones but of surely smaller size than in the extant *Lynx lynx*. For this reason, they have been parsimoniously classified as *Lynx* sp.

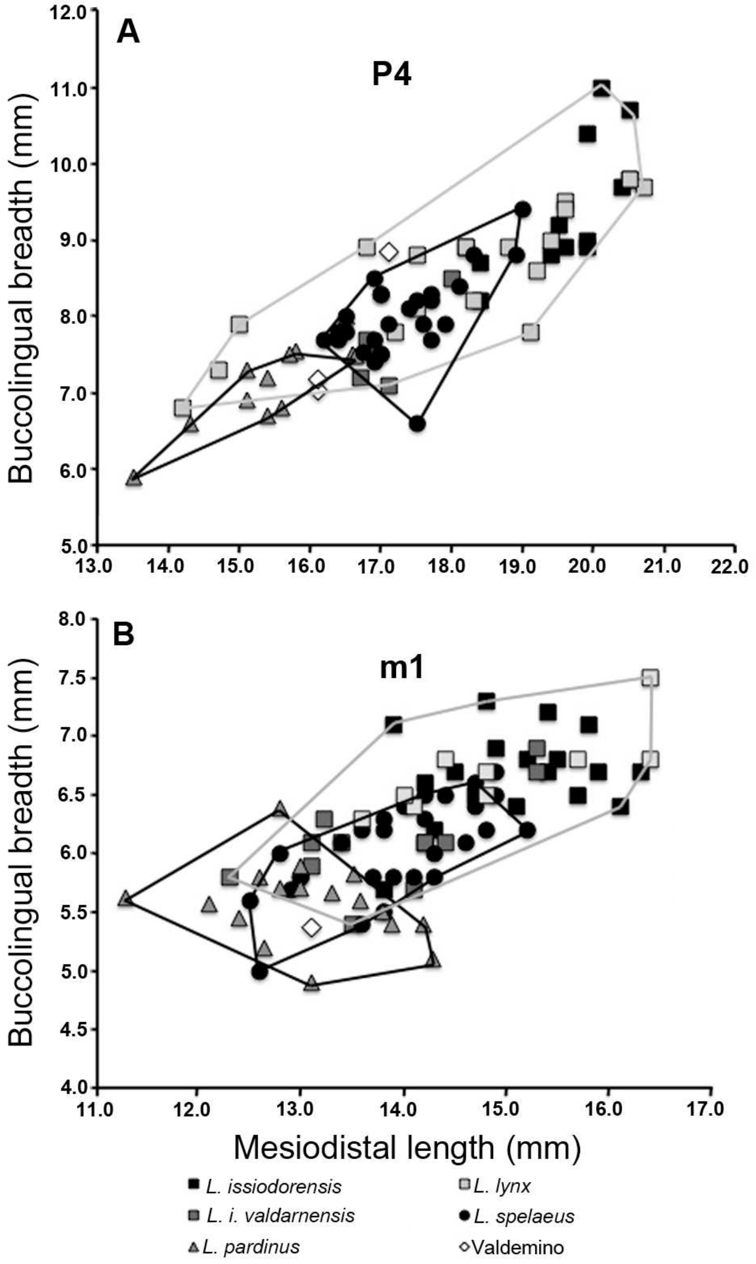

Figure 60: dental proportions of the cheek teeth in different living and extinct species of the genus *Lynx* compared with the specimens from Valdemino cave. Hand-drawn polygons link the most extreme values of each forms, to ease visualization of metrical differences among them, black polygons represent the small-sized lynx species and the gray polygons the large-sized. a P4 and b m1

Evolutionary implications - According to the provided data, the lynx remains from the Lower Part layer of Valdemino cave can be one of the earliest occurrences of *L. spelaeus* in the fossil record, for sure the most ancient recovered in the Italian Peninsula (Sardella et al., 2006) and probably the best preserved one. The Valdemino deposits are slightly older than the ones of the French localities of L'Escale (ca. 0.6–0.5 Ma; Bonifay, 1971) and Aragó Cave (ca. 0.55 Ma; MIS14; Moigne et al., 2006), the oldest well-known records of this species. Older deposits with putatively remains of *Lynx spelaeus* are La Sartanette and Le Vallonnet, again in France, respectively, 1.3 and 1.0 Ma in age. Anyway these lynxes are only known by scanty, not diagnostic, or unpublished remains (Palombo and Valli, 2003; Moulle, 1992). For the last reasons, the record of *Lynx spelaeus* from the Lower Part of Valdemino cave can be considered, to date, the most ancient well-documented material of this species. The obtained results show that the small size and the absence of m1 metaconid (derived features in the *Lynx* genus) were already present at least at 0.6 Ma, accordingly with the tendency pointed by many authors of progressive size reduction, gradual loss of m1 metaconid and acquisition of trenchant dentition throughout the Pleistocene in the *Lynx* genus (Bonifay, 1971; Testu, 2006; Cipullo, 2010).

The Valdemino Lynx record offers new evidences on *Lynx* evolutive trends. The slender craniodental features of Valdemino older remains (Lower Part, layer 27) are consistent with specific characters of *L. spelaeus*, and the postcranial features also retrace the skull characters with slender fore- and hindlimbs. Taking into account the evolutionary trend of *L. pardinus* in Spain (and the similar latitudinal range), I could infer that circum-Mediterranean populations may represent the result of a genetic bottleneck or allopatric effect (as demonstrated for the Iberian species by Rodriguez et al., 2011), and convergent evolution to a smaller size with trenchant teeth under similar geographic barriers and climatic variability throughout the Middle–Late Galerian and Aurelian Mammal Ages.

Finally, according to the former evidence, the described lynx material from Valdemino layer 27 (Isernia Faunal Unit, Middle Galerian) can be considered the earliest well-documented and preserved occurrence of this taxon close to the Early–Middle Pleistocene boundary. The obtained results also reinforce the idea of a progressive size reduction and gradual acquisition of trenchant dentition in the European lineages (*L. pardinus* and *L. spelaeus*) of the genus *Lynx*.

7. Summary and conclusions

This study focuses on two species of carnivorans, generally rare in the fossil record, *Panthera pardus* and *Cuon alpinus*, from the fossil fauna of Equi.

These findings, recovered between 1910 and 1917, with some additional discoveries until 1920, give new paleobiological and evolutive indications, thanks to the detailed information recorded during the excavation under the direction of Carlo De Stefani, chair of Geology and Physical geography at the Regio Istituto di Studi Superiori of Florence.

The evaluation of the rare lithic industry from the site attributed it to the "alpine musterian". New dating on coal fragments discovered in the basal layer of the cave (collected in 2009-2014), have confirmed the chronological attribution. During my thesis, new dating on three osteological fragments from the historical excavation revealed an age of 27-33 ky for the specimens considered in this study. These results define the Equi site as one of the last records for cave bears and leopards in Italy and classify the entire collection as part of the decreasing climatic conditions of the latest MIS3.

The study of the Felidae family, particularly frequent at Equi, has considered two more species, *Panthera leo* and *Lynx spelaea* from other Middle and Late Pleistocene European sites.

In particular, it should be emphasized that *Lynx spelaea* is represented by few European fossils, and that the specimens from the lower layer of Valdemino Cave are, at the moment, the most complete and best preserved proof of this small animal during the Middle Galerian in Italy.

The Equi Cave and Shelter: reconstruction of historical excavations and relocation of the fossils in the stratigraphic record.

The stratigraphic relocation of the fossils from De Stefani's collection has been made possible thanks to the detailed field work. De Stefani applied a geological approach to the excavation, recording the sediment changes and their arrangement, and the relative or absolute positions of the fossils in the layers. Such an approach was rather unusual at the beginning of the twentieth century, in a research context in which most previous fossil research had not involved the reporting of detailed information from findings.

Linking the description of De Stefani (1917) to those from the fossil labels, it has been possible to establish a probable distribution of the specimens in the site.

The most important result in this study concerns the fixed predominance of wolves and leopards in all the layers. Such carnivorans are quite different both in terms of trophism and ecology (social organization, hunting, etc.), but both are also subordinate species with respect to the larger lion. The former is represented, at Equi, by several findings (about fifty of fossils, of which – unfortunately – only half report the stratigraphic reference) but in any case it is an almost rare species at Equi and in other Apuan Alps sites (Del Campana, 1954; Massetti e Salari, 2012).

The fox and *Cuon alpinus*, as lions, are significantly frequently recorded only above the layer "f" (indicatively younger than 27 ky) and seem to characterize the later layers up to the surface.

Differently than was previously known, the fossil distribution in the stratigraphy, even though relative and with a margin of error, has allowed me to compare the historical excavations with the modern ones, observing a drastic reduction of fossils in the latter (since 2009 up to today, two more skulls of *Ursus spelaeus* have been discovered, in addition to a few other remains). Moreover, the co-occurrence of different species of middle and carnivorans larger than bears show the structured ecological and trophic network at Equi during the later Aurelian, and illustrate how these animals had certainly carried out a kind of reciprocal avoiding of each other as regards the frequentation of the site.

Panthera pardus (Linnaeus, 1758)

The outstanding preservation of leopard fossils allowed a popolational study about this elusive species to be performed for the first time.

Actually, leopard fossils are particularly rare. In Europe, the found bone material usually consists of only a few fragmented findings or teeth, preventing a comparison within the European population. As mentioned above, Equi represent one of the youngest records of this felid in Italy, discovered also in the quite coeval assemblage of Cala Cave at about 26 ky (Boscato et al., 1997) and in the post-LGM deposit of the Arene Candide Cave at about 23-20 ky (Cassoli and Tagliacozzo, 1994).

Today, the Pleistocene leopard taxonomical classification is based on some dental and cranial features. Following this approach and cranial features, Diedrich (2013) has tentatively retraced the evolutive trend of this species recognizing four subspecies of leopard from the Middle to Late Pleistocene.

The outstanding leopard collection from Equi allowed me to shed some light on the European leopard variability, revealing that the p4-m1 morphologies from Equi completely correspond to Spassov and Raychev's (1997) conclusions about Late Pleistocene leopards and their differentiation from the Middle Pleistocene specimens. Also, it allowed me to establish that cranial features are not taxonomically diagnostic per-sé. Instead, the neurocranium is clearly related to the typical pronounced sexual dimorphism of the European species as well as the extant species, as previously noted by Pocock in 1930s.

Speaking of the upper carnassial crown height, it is subject to progressive wearing resulting in it being too variable as the animal gets older to be considered as the sole diagnostic characteristic between two subspecies.

For all these reasons, the subspecies *P. pardus spelaea* recognized by Diedrich (2013) is here considered as a chronospecies, while *P. pardus sickenbergi* is accepted as valid for the diagnostic p4-m1 morphology. It is plausible that the latter was represented also by the skull from Monte Sacro, and I accepted the Diedrich redetermination. The evolutive and taxonomical position of *P. pardus vraonensis* (Niegel, 1999) and *P. pardus antiqua* remains unclear, and seems to be related to a relative local variability or return to the chronospecific determination.

At present, the Equi collection represents the best fossil record of leopards for Europe. As well as the large collection of *Homotherium latidens* from Incarcal (Spain; Galobard et al., 2003), the Equi leopards prove the wide intraspecific variability of European leopards. As a consequence, the different characteristics of the Late Pleistocene fossils from different sites are all seen in the observed features of the fossils from Equi.

Moreover, the historical collection allowed me to recognize a rather high frequency of young leopards, almost one third of the total. This relatively high percentage of young individuals (17%) is also the highest for Europe, and the comparative analysis with the extant similar sized specied allowed me to estimate the time when the animals died. All the juvenile cranial remains have an estimated age between three months and one year. Owen et al. (2010) estimated that 1.6 out of three cubs (in average for each litter) die before weaning (at about one year; Seidensticker, 1977) according to similar results obtained by Balme et al. (2012). Studying post-natal *L. pardinus* habits, Fernandéz et al. (2002) noted that in the case of death of one cub in the den, the mother moves the survival litters to a new one, leaving the dead body there (it is not, for example, removed from the den so that they can continue to use the same place). Similarly, the presence of leopard cubs at Equi can be interpreted as the first clear evidence of the use of caves for birth and development and not for hunting or for sporadic frequentation, proven also by the lack of real prey.

Finally, the direct competition between leopards and, probably, bears or one other large carnivorans is testified by the bite sign on the skull IGF15110V.

Cuon alpinus (Pallas, 1811)

At present, the dhole is one of the most endangered species in the world. Even though the animals are organized in packs and are less selective for ecological and trophic habits compared to wolves, the species is more vulnerable to climatic changes and competition with other carnivorans and humans.

The genus *Cuon* is particularly rare also in the Pleistocene fossil record. In Europe, the taxon appears for the first time in the Middle Pleistocene sites of Hundsheim and Lunel-Viel (central Europe) with the species *Cuon priscus*. During this first migration, the species seemed to not enlarge its range into the Italian Peninsula and was recognized only as a genus at Fontana Ranuccio and Colle Avarone (central Italy). The *C. alpinus* remains from Equi were determined and studied by Del Campana (1954) and re-evaluated and described in this study within an enlarged context.

The dental differences on the first and second lower molars allow for specific recognition; both these teeth show a simplification and a reduction of the cuspids. *Canis lupus* and *Vulpes vulpes,* both determined at Equi, and other Canidae such as *Canis aureus* and *Canis mesomelas* (Walton and Jolys, 2003), show a well-discerned dental morphology. The first and second molars are more complex, with more cuspids and a developed m3.

Generally, the postcranial morphology of canids has low diagnostic significance. Despite this similarity among species, the appendicular bones of the dholes from Equi are smaller than the wolves', as regards both the fossils and the modern specimens and, above all, the metacarpals here described have much more massive diaphysis in relation to the total length (Gl), which allows me to include these postcranial evidence whitin the morphology of the stocky dhole.

The revaluation of these canids in the Italian paleontological record pointed out the lack of the species in areas putatively suitable for its survival, such as the north-eastern side of the peninsula, and the inappropriate determination of the Holocene fossils from Riparo Fredian, underlining the necessity of a precise evaluation of similar sized fossils.

Panthera leo spelaeaus (Boule, 1810)

The European lion was a constant occupier of caves during the Late Pleistocene (Pocala Cave and Broion Cave, for cite only two Italian sites). Even though lions are rather well represented at Equi with several fossils, entire crania are completely missing. The general morphology and the small size completely agree with the recent specimens of this species.

In this thesis, the taxonomy of the Pleistocene lion was analyzed starting from Sotnikova and Nikolskiy's study (2006). The authors concluded that the variability in skulls of lions should be considered sufficient to support a specific determination of earlier Middle Pleistocene *P. fossilis* and the later Middle and Late Pleistocene *P. spelaea*.

I analyzed seven fossil skulls of lions with twelve modern crania of the same species and three crania of tiger, also including the description for the modern animal published by Haas et al. (2005) and the depictions of the fossils from Zandobbio (Bona 2006) and Grotte d'Azé (Argant, 1988). All these specimens have allowed me to more deeply analyze the typical characteristics of the European species, considering the six most objective cranial features and concluding that the differentiation between lion and tiger, in the modern species, can be clearly observed on skulls: in lions the suture between frontals and nasals is curved and rarely sub-acute, while the lateral profile is flat. In tigers, the latter is curved with a shorter muzzle. Moreover, tigers frequently show a preparastyle on the mesio-labial side of the upper carnassial and this characteristic is quite unusual in fossils and modern lions.

Within the lion group, a clear morphological differentiation between Late Pleistocene and modern animals was not seen. The cluster analysis revealed that, surprising, the six crania from the same African region (considered more similar to each other than the other specimens) are spread into different branches, showing the un-constancy of cranial features in different times.

To conclude, the substantial similitude between modern lions and the European large fossils is proved by my analysis, allowing for a preference for the subspecific determination, i.e. *P. leo spelaea*; meanwhile, the older lion's remains, attributable to the *fossilis* group, show major dimensional differences.

Lynx spelaeaus (Boule 1919)

At Equi, *Lynx lynx* is represented by two singular findings, a distal humeral fragment determined by Del Campana in 1954 and a third phalanx exposed to the Paleontological museum of the Natural History Museum of the University of Florence (IGF6696V).

While the idea about the evolution of Eurasian lynx from African *L. issiodorensis* is generally accepted, the taxonomical position of the autochthonous European species is more widely debated.

L. issiodorensis appeared for the first time in the Late Pleistocene site of Etouaires, France (Kurtén, 1978; Werdelin, 1981) and rapidly spreads in the whole central-meridional Europe (Cherin et al., 2013). During the Galerian, the species evolve in *L. pardinus* and *L. spelaea* and the particular conformation and clime of Iberian Peninsula hurried the shift and speciation of the former (Boscaini, 2013-2014). Indeed, the origin, the range and cranial and postcranial morphology of *Lynx spelaeus* is more unsure, compared for the first time at Aragó Cave (Middle Galerian; Moigne et al., 2006).

In the Valdemino Cave two fossil associations were found. The earliest, attributed to the Late Pleistocene, include postcranial remains of *Lynx* sp. The fossils are small, but the missing neurocranium and lower teeth prevent the taxonomical identification of these bones.

Indeed, the lower layer was attributed to the Middle Galerian (FU Isernia) and gave better-preserved specimens. The lack of a metaconid in the lower carnassial and a little-developed distal cingulum in the last lower premolar allowed me to include the fossils in a progressive trend of simplification of teeth morphology typical of Middle Pleistocene European lynxes and to determine these specimens as *L. spelaeus*.

So far, these specimens represent the most ancient and best preserved fossil testimony for this species in Italy (Sardella et al., 2008).

Conclusions

This study points out how the critical comparisons among fossils and modern animal bones represent a basic method for a correct taxonomical interpretation of paleontological records.

Panthera leo spelaea and *Cuon alpinus* could be perfectly included in the morphological standards of the modern exponents, while the *L. spelaeus* differ both from the Eurasian lynx and the *L. issiodorensis* from the Villafranchian, validating the hypothesis of a local evolution for the Mediterranean area.

Today, the leopard collection rediscovered at Equi is the most important proof of the high frequency of this species in Europe. The morphological variability in adults confirms the heterogeneity affinity with the extant species, the general coherence of the European animals from the Late Pleistocene, and finally the divergence of the latter from the more ancient species.

Moreover, for the first time the morphology and ontogenesis of European leopards was studied, allowing me to confirm, at least in some cases, the cave as a den for birth and growth for litters.

Finally, the re-evaluation of the historical collection has been confirmed once again as one of the most important instruments for awareness and appreciation of the excavated sites, allowing for the increase in knowledge about the European Pleistocene complex.

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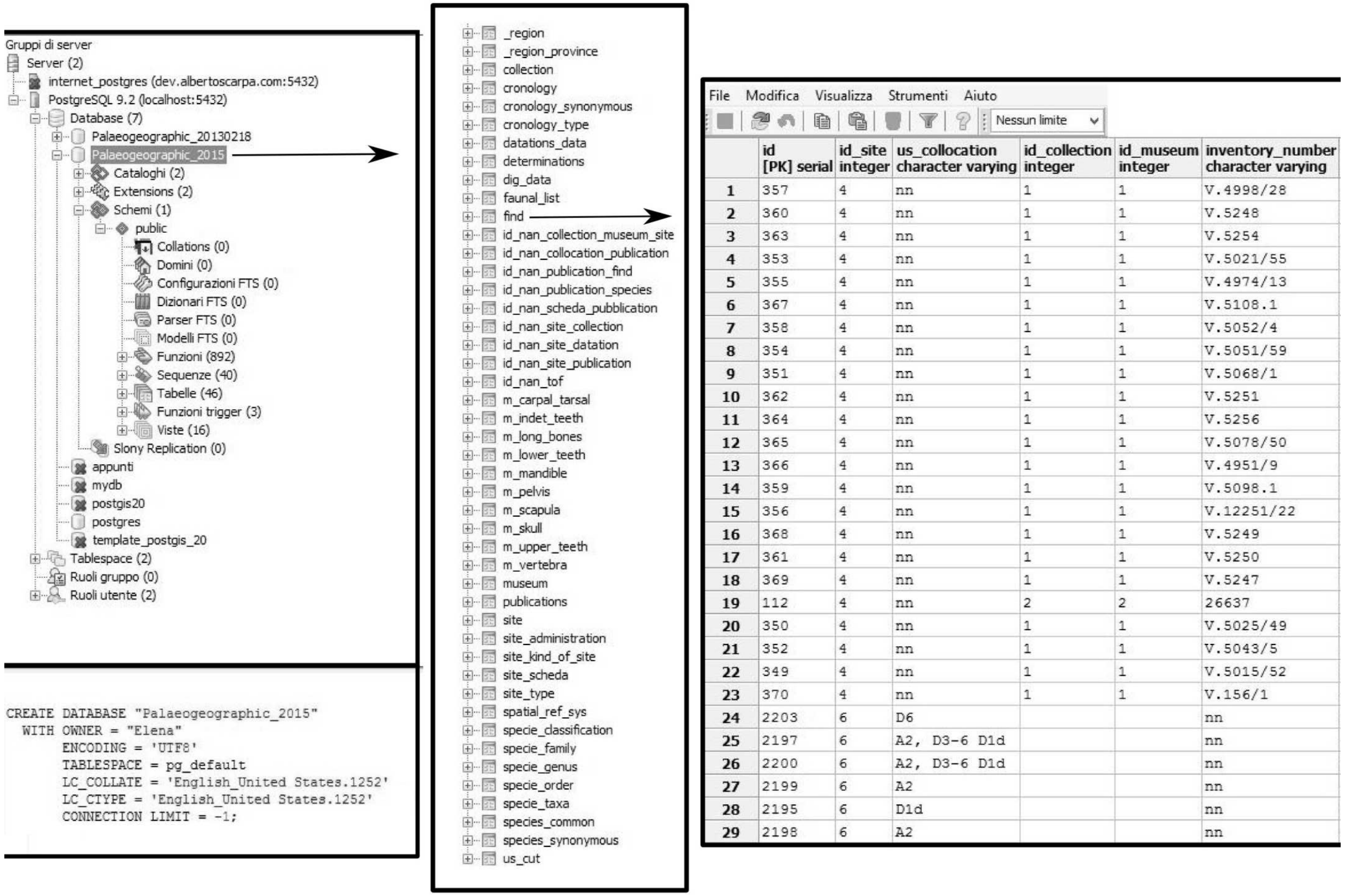
9. Appendix

Caption Figure 4a

	specie	site_name	state	cronology_name	publication_name
1	*Panthera leo*	AVETRANA	Italy	Pleistocene Late	Pandolfi et al. 2011
2	*Panthera leo spelaea*	BONDENO	Italy	MIS 3	Sala B. unpub
3	*Panthera leo*	BRISTIE	Italy	Glacial Wurm	Bon et al. 1991; this thesis
4	*Panthera (Leo) spelaea*	CASTEL DI GUIDO	Italy	Paleolithic Early	Mussi et al. 2001
5	*Panthera leo spelaea*	CASTELLO	Italy	Galerian	Bon et al. 1991
6	*Panthera leo spelaea*	CAVERNA DEGLI ORSI	Italy	Pleistocene Late	Berto et al. 2011
7	*Panthera leo spelaea*	CAVERNA POCALA	Italy	Pleistocene Late	this thesis
8	*Panthera leo spelaea*	COVOLI DI VELO VERONESE	Italy	Glacial Wurm	Bon et al. 1991
9	*Panthera leo spelaea*	EQUI	Italy	MIS 3	This thesis; De Stefani 1917; Del Campana, 1954; Masseti and Salari 2012
10	*Panthera leo spelaea*	GABROVIZZA	Italy	Unknow	Fabiani 1919
11	*Panthera leo*	GROTTA DEGLI ORSI VOLANTI	Italy	Musteriano	Mazza 2005
12	*Panthera leo spelaea*	GROTTA DEL BROION	Italy	Pleistocene	Bon et al. 1991; this thesis
13	*Panthera leo spelaea*	GROTTA DEL CERE'	Italy	Galerian	Bon et al. 1991; Ghezzo et al. 2014
14	*Panthera leo*	GROTTA DEL POGGIO	Italy	Pleistocene Late	Sala 1979
15	*Panthera leo*	GROTTA DEL SANTUARIO DELLA MADONNA	Italy	MIS 2	Masseti et al. 2012
16	*Panthera cf. leo*	GROTTA DI CUCIGLIANA	Italy	Pleistocene Late	Masseti et al. 2012
17	*Panthera leo*	GROTTA DI FUMANE	Italy	Pleistocene Late	Cassoli et al. 1991
18	*Panthera leo*	GROTTA DI PAINA	Italy	Pleistocene Late	Bon et al. 1991
19	*Panthera leo*	GROTTA LA FABBRICA	Italy	Pleistocene Late	Masseti et al. 2012
20	*Panthera leo spelaea*	GROTTA TILDE	Italy	Pleistocene	Fabiani 1919; Bon et al. 1991
21	*Panthera (Leo) fossilis*	ISERNIA LA PINETA	Italy	Galerian	Sala 190; Mussi et al. 2001
22	*Panthera leo spelaea*	MONTE ZOPPEGA I	Italy	Interglacial Mindel-Riss	Bon et al. 1991
23	*Panthera leo spleaea*	MONTEMERANO	Italy	Pleistocene	this thesis
24	*Panthera leo*	PALIDORO	Italy	MIS 2	Masseti et al. 2012
25	*Panthera leo spelaea*	RIPARO L'OSCURUSCIUTO	Italy	Paleolithic Middle	Boscato et al. 2009
26	*Panthera leo*	RIPARO TAGLIENTE	Italy	Pleistocene Late	Masseti et al. 2012
27	*Panthera cf. leo*	SAN SIDERO 3	Italy	Pleistocene Late	De Giuli 1983
28	*Panthera leo spelaea*	SENTIERO	Italy	Galerian	Bon et al. 1991
29	*Panthera leo spelaea*	SERBARO DI ROMAGNANO	Italy	Pleistocene Middle	Fabiani 1919; Bon et al. 1991
30	*Panthera leo spelaea*	SOAVE	Italy	Unknow	Fabiani 1919
31	*Panthera leo spelaea*	TORRE TALAO	Italy	Pleistocene Late	Mangano unpub
32	*Panthera leo spelaea*	VIATELLE	Italy	Glacial Mindel	Bon et al. 1991
33	*Panthera leo spelaea*	ZANDOBBIO	Italy	Eemian	Bona, 2006

Caption Figure 4b

	specie	site_name	state	cronology_name	publication_name
1	*Panthera pardus cf. antiqua*	CASTELLO	Italy	Galerian	Bon et al. 1991
2	*Panthera* cf. *pardus*	CAVERNA DEGLI ORSI	Italy	Pleistocene Late	Berto et al. 2011
3	*Panthera pardus*	CAVERNA DELLA ARENE CANDIDE	Italy	Pleistocene Late	Masseti et al. 2012
4	*Panthera pardus antiqua*	CAVERNA POCALA	Italy	Pleistocene Late	Bon et al. 1991; this thesis
5	*Panthera pardus*	EQUI	Italy	MIS 3	This thesis; De Stefani 1917; Del Campana, 1954; Masseti and Salari 2012
6	*Panthera pardus*	GROTTA DEI SANTI	Italy	Pleistocene	Lanfredini et al. 2008
7	*Panthera pardus antiqua*	GROTTA DEL BROION	Italy	Pleistocene	Bon et al. 1991
8	*Felis [recte Pantherat] pardus*	GROTTA DEL CAPRIOLO	Italy	MIS 3	Pitti and Tozzi 1971; Caloi et al. 1994
9	*Panthera pardus*	GROTTA DEL CERE'	Italy	Galerian	Bon et al. 1991; Ghezzo et al. 2014
10	*Panthera pardus*	GROTTA DEL POGGIO	Italy	Pleistocene Late	Sala 1979
11	*Panthera pardus*	GROTTA DELLA CALA	Italy	MIS 3	Masseti et al. 2012
12	*Felis [recte Panthera] pardus*	GROTTA DELLA IENA (Lucca)	Italy	Musteriano	Pitti and Tozzi 1971
13	*Panthera pardus*	GROTTA DELLE OSSA (BG)	Italy	Eemian	Bona 2006
14	*Panthera pardus*	GROTTA DI CUCIGLIANA	Italy	Pleistocene Late	Masseti et al. 2012
15	*Panthera pardus*	GROTTA DI FUMANE	Italy	Pleistocene Late	Cassoli et al. 1991; Tagliacozzo et al. 2013
16	*Panthera pardus*	INGARANO	Italy	Pleistocene Late	Petronio 1998; Petronio 2006
17	*Panthera pardus*	MONTE ARGENTARIO	Italy	Pleistocene	Martinez Navarro 2012
18	*Panthera pardus sickenbergi*	MONTE SACRO	Italy	Pleistocene	Kotsakis and Palombo 1979
19	*Panthera pardus*	MONTE TENDA	Italy	Interglacial Mindel-Riss	Bon et al. 1991
20	*Panthera pardus*	QUISISANA-CERTOSA	Italy	Pleistocene	Capasso Barbato et al. 1995
21	*Panthera pardus*	SENTIERO	Italy	Galerian	Bon et al. 1991
22	*Panthera pardus antiqua*	SERBARO DI ROMAGNANO	Italy	Pleistocene Middle	Bon et al. 1991
23	*Panthera pardus lunellensis*	ISERNIA	Italy	Pleistocene Middle	Sala 2006



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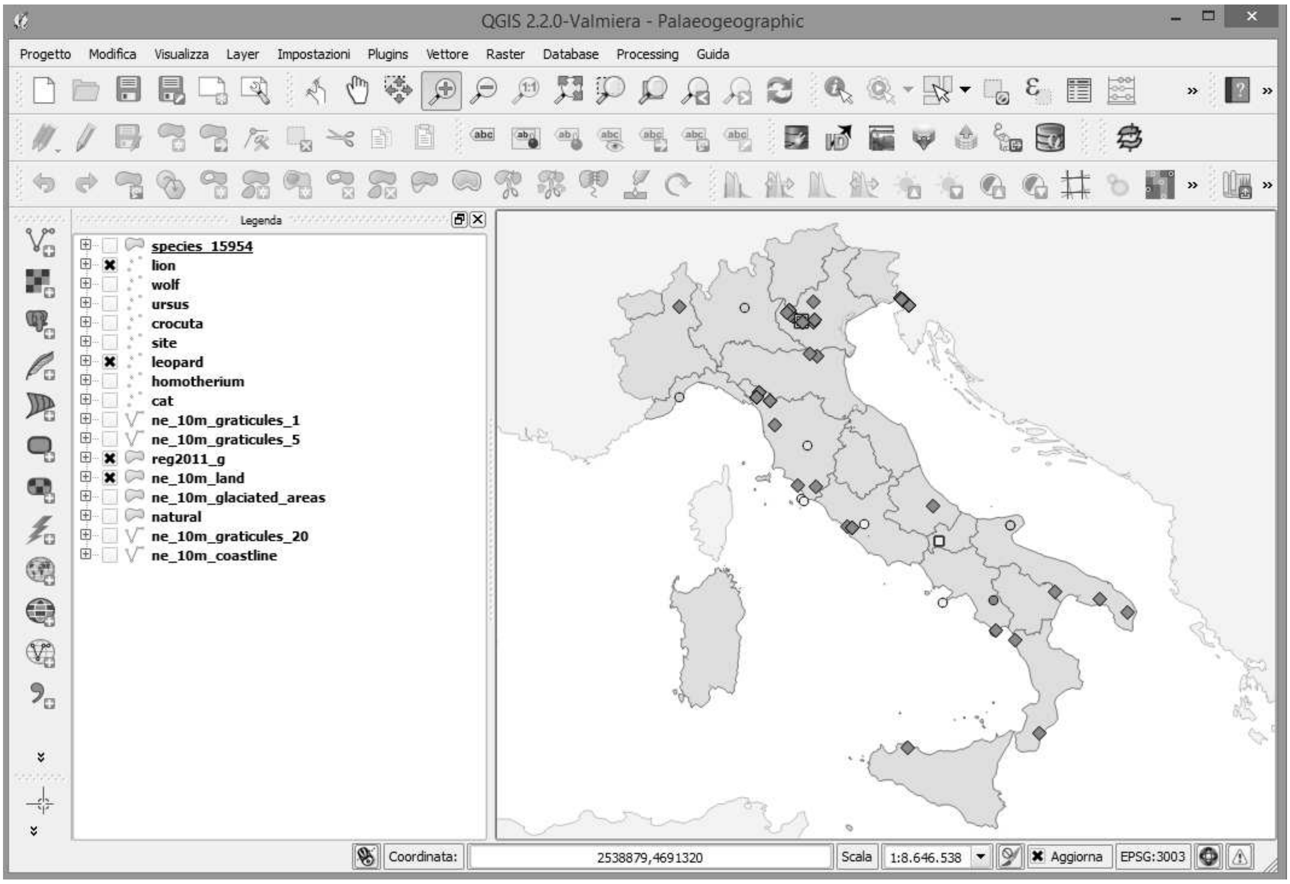
1	357	4	nn	1	1	V.4998/28
2	360	4	nn	1	1	V.5248
3	363	4	nn	1	1	V.5254
4	353	4	nn	1	1	V.5021/55
5	355	4	nn	1	1	V.4974/13
6	367	4	nn	1	1	V.5108.1
7	358	4	nn	1	1	V.5052/4
8	354	4	nn	1	1	V.5051/59
9	351	4	nn	1	1	V.5068/1
10	362	4	nn	1	1	V.5251
11	364	4	nn	1	1	V.5256
12	365	4	nn	1	1	V.5078/50
13	366	4	nn	1	1	V.4951/9
14	359	4	nn	1	1	V.5098.1
15	356	4	nn	1	1	V.12251/22
16	368	4	nn	1	1	V.5249
17	361	4	nn	1	1	V.5250
18	369	4	nn	1	1	V.5247
19	112	4	nn	2	2	26637
20	350	4	nn	1	1	V.5025/49
21	352	4	nn	1	1	V.5043/5
22	349	4	nn	1	1	V.5015/52
23	370	4	nn	1	1	V.156/1
24	2203	6	D6			nn
25	2197	6	A2, D3-6 D1d			nn
26	2200	6	A2, D3-6 D1d			nn
27	2199	6	A2			nn
28	2195	6	D1d			nn
29	2198	6	A2			nn

Scheme of the pgAdmin GUI (Graphical User Interface) for my DB. 46 tables constitute the DB Palaeogeographic 2015, which are classified, where required, with suffixes id_ (relation n-to-n), m_ (measurements), chronology, site and species. Partially completed table FIND is shown, with the standard codes of sites and collections and the specific catalog number (the entire figure can be better appreciated in the attached CD)



- ☐ species_15954
- ☒ lion
- ☐ wolf
- ☐ ursus
- ☐ crocuta
- ☐ site
- ☒ leopard
- ☐ homotherium
- ☐ cat
- ☐ ne_10m_graticules_1
- ☐ ne_10m_graticules_5
- ☒ reg2011_g
- ☒ ne_10m_land
- ☐ ne_10m_glaciated_areas
- ☐ natural
- ☐ ne_10m_graticules_20
- ☐ ne_10m_coastline

Coordinata: 2538879,4691320 Scala 1:8.646.538 ☒ Aggiorna EPSG:3003

QGIS 2.2.0 Valmiera, the GUI with the overlapped layers shown in fig. 4. As in other similar softwares, the upper part of this figure shows several tools, layers are on the left side and, on the right, there is the Italian graphic output. Scale and reference system (RS) are shown on the right-bottom.

In the next tables there are few examples of the complete DB available in the attached CD.

Sites:

id	complex	site_name	state	metresasl	latitude WGS84	longitude WGS84	Age	start dating	end dating	single dating
30		SLOUP CAVE	Austria		49.4	16.67				
143		HUNDSHEIM	Austria		48.1	16.9397				
353		OBSERVATOIRE CAVE	Austria				Eemian MIS 5e			
354		OCHSENTAL CAVE	Austria				Middle Wurmian/Weichselian			
340		HUNDSHEIM	Austria		48.1	16.9	Middle Pleistocene			
350		MERKENSTEIN CAVE	Austria		47.9	16.1	Late Pleistocene			
410		GAMSSULZEN CAVE	Austria				MIS3			49900
413		TISCHHOFER CAVE	Austria	598	47.5	12.1	MIS3			31890
133	ENGIHOUL CAVES	ENGIHOUL CAVES	Belgium		50.5	5.4				
307	GOYET CAVES	GOYET CAVES (generic)	Belgium		50.4	5.0	Pleistocene			
407		SCLADINA CAVE	Belgium		50.4	5.0				
372		VJETRENICA CAVE	Bosnia Herzegovina		43.1	17.9	Late Pleistocene 37300-31360			
131		TRIAGALNATA PESHTERA	Bulgaria		41.6	24.5		17550	15570	
55		SAN VINCENTI D'ISTRIA (VILLA BOCCORDI?)	Croatia		45.0	13.8				
237		TÜRMIZ	Czech Repubblic		50.8	14.0				
146		STANSKA SKALA	Czech Republic		49.1	16.6				
165		PRAHA-PODBABA	Czech Republic		50.1	14.3		65000	34000	
239		BUBASTIS	Egypt							
280	TORQUAY	TORBRYAN CAVE	England		50.4	-3.5	Pleistocene			
281	TORQUAY	BANRWELL CAVE	England		50.4	-3.5	Pleistocene			
335		GENISTA CAVE GIBRALTAR	England				Late Middle to Late Pleistocene			
367		TOWER ROCK SHELTER GIBRALTAR	England				Late Pleistocene			
323		BLEADON CAVE	England				Late Pleistocene			
119		MULHULI AMO	Eritrea		14.7	39.9				
120		WADI AALAD	Eritrea		14.8	39.8				
15	BALZI ROSSI	BALZI ROSSI	France		43.7	7.5				
465	CH√ÇTEAUX	BRECCIA 4	France							
463	CH√ÇTEAUX	BRECCIA 2	France							
97		ARAGO	France		42.7	2.8				
95		ABIMES de la FAGE	France		45.0	1.5				
71		CAUNE DE L'ARAGO	France		42.8	2.7	Middle Pleistocene OIS 14 TO 5			
136		GROTTE DU MARS	France		43.7	7.1				
134		GROTTE DI TROIS	France		43.0	1.2				
138		LUNEL-VIEL	France		43.6	4.0				
329		CROUZADE CAVE	France				Late Pleistocene			
324		BLANOT CAVE 2	France		46.4	4.7	Late Pleistocene			
322		CHAUDE CAVE (BDR)	France				Eemian, MIS 4, 54.100 BP)			
332		ÉTRIGNY	France		46.5	4.8	Late Pleistocene?			
345		LA NICHE CAVE MONTMAURIN	France				MIS 7			
359		PORTEL-WEST CAVE	France				Late pleistocene			
339		GROTTE DE L'HORTUS	France		43.7	3.8	MIS4			
348		LUNEL-VIEL	France		43.6	4.0	Middle middle Pleistocene			
370		VERCHIZEUIL CAVE	France		46.3	4.7	?Late pleistocene			
355		ORGNAC	France		44.3	4.4	Middle Pleistocene			
368		TROIS FR√àRES CAVE	France		43.0	1.2	Late pleistocene			
393		GROTTE D'AZE	France	275	46.4	4.7				
341		JAURENS	France				Late Middle to Late Pleistocene			
400		GROTTE DU JAURENS	France		45.0	1.5				
405		GROTTE COTENCHER	France		47.1	6.8				
404		PUECH MARGAL	France		44.1	4.6				
127		GROTTE DU LAZARET	France		43.6	7.2	MIS 5	220000	120000	
129	GREATER CAUCASUS	KUDARO 3	Georgia		42.5	43.6	early Late Pleistocene			
148	GREATER CAUCASUS	KUDARO	Georgia		42.5	43.6				
128	GREATER CAUCASUS	KUDARO 1	Georgia	1600	42.5	43.6	early Late Pleistocene			
121		DMANISI	Georgia		41.3	44.3				
264	BERLIN	KREUZBERG	Germany		52.5	13.3	Early Pleistocene			
243	BERLIN	LICHTERFELDE	Germany		52.8	11.8				

301	BERLIN	KÖPENICK	Germany		52.4	13.5	Early Pleistocene			
315	Modern Coll.	MONACO	Germany							
295	FRANKISCHEHOHLEN	GAILENREUTH CAVE	Germany		49.7	11.2	pleistocene			
267	FRANKISCHEHOHLEN	FRANKISCHEHOHLEN	Germany		49.0	11.0	Jungpleistozan			
262	GEISENTAL	BRAUNKOHLENTAGEBAU ELISE II	Germany		51.0	10.7	Mittepleistozan			
253	GEISENTAL	LAUCHSTÄDT	Germany		51.3	11.8	Pleistocene			
251	HARZ MOUNTAINS	QUEDLINBURG	Germany		51.7	11.1	Pleistocene			
276	HARZ MOUNTAINS	HERMANNS CAVE	Germany		51.7	10.8	Early Pleistocene			
277	HARZ MOUNTAINS	HARZ (generic)	Germany		51.8	10.2	Early Pleistocene			
270	HARZ MOUNTAINS	BALVE CAVE	Germany		51.3	7.3				
229	HARZ MOUNTAINS	BALVE-SANSSOUCI	Germany		51.3	7.3				
231	HARZ MOUNTAINS	BALVE-SANSSOUCI SUDL. HOHLE	Germany		51.3	7.3				
230	HARZ MOUNTAINS	BALVE-SANSSOUCI MITTL. HOHLE	Germany		51.3	7.3				
221	HARZ MOUNTAINS	GOSLAR (generic)	Germany		51.9	10.4				
292	ISERLHON	LETMATHE	Germany		51.3	7.6	Pleistocene			
248	ISERLOHN	DECHENHÖHLE	Germany		51.3	7.6	Pleistocene			
293	ISERLOHN	ISERLOHN (generic)	Germany		51.3	7.6				
291	PÖSSNECK	PÖSSNECK	Germany		50.6	11.7				
296	PÖSSNECK	KROELPA	Germany							
106		TORBIERE DI BRUNNDORF	Germany		40.5	15.3				
225		OHNE FUNDORTANGABE	Germany							
226		ROTER BERG	Germany		50.6	11.3	Early Pleistocene			
140		VOIGTSTEDT	Germany		51.3	11.3				
236		NANKENDORF CAVE	Germany		49.8	11.3				
142		WEIMAR	Germany		50.9	11.3				
139		MOSBACH	Germany		49.3	9.1	Middle middle Pleistocene			
202		GRABSCHÜTZ	Germany		51.5	12.3	Eemian			
206		TAUBACH	Germany		50.9	11.3	Eemian, Middle middle pleistocene			116000
200		LEHRINGEN	Germany		52.8	9.3	Eemian			
208		STUTTGART-UNTERTU*RKHEIM	Germany		48.7	9.2	Eemian			
203		NEUMARK-NORD	Germany		51.3	11.8	Saalian-Weichselian-Eemian			
204		RABUTZ	Germany		51.4	12.1	Eemian			
201		GRÖBERN	Germany		51.6	12.4	Eemian			
235		WALBECK	Germany							
205		SCHÖNFELD	Germany		51.3	13.7	Eemian E4-E5			
207		BURGTONNA	Germany		51.0	10.7	Eemian	111000	104000	
247		PHOEBEN	Germany		52.4	12.8				
289		HALLE-SAALE (generic)	Germany				Pleistocene			
266		KÖRBISKRUG	Germany		52.2	13.8	Pleistocene			
282		FRETTER	Germany		51.2	8.0	Pleistocene			
287		FLÖRSHEIM	Germany		50.0	8.4	Pleistozan Loss			
249		KOSTRITZ	Germany		50.9	12.0	Early Pleistocene			
285		MUGGENDORF	Germany		49.8	11.2	Early Pleistocene			
255		SENZIG	Germany		52.2	13.6	Early Pleistocene			
254		NIEDERLEHME	Germany		52.3	13.6	Early Pleistocene			
242		STEETEN	Germany		50.4	8.1				
263		OBERROBLINGEN	Germany		51.4	11.3	Pleistocene			
256		SEDDIN	Germany		52.2	13.0	Early Pleistocene			
265		BAD SALZUNGEN	Germany		50.8	10.2	Early Pleistocene			
274		ODERBERG-BRALITZ	Germany		52.8	14.0	Pleistocene			
227		PEGNITZ	Germany		49.7	11.5				
290		LINDENTHALER HÖHLE	Germany		50.8	12.0	Pleistocene			
252		WESTEREGELN	Germany		51.9	11.3				
232		BÖRSSUM	Germany		52.1	11.0				
286		POHLITZ	Germany		50.9	12.0	Pleistocene			
257		ZEMENTFABRIK	Germany		51.1	11.7	Mittepleistozan			
258		FREYBURG	Germany		51.2	11.7	Pleistocene			
288		WESTFALEN (generic)	Germany				Pleistocene			
279		RÖSENBECK	Germany		51.4	8.6	Pleistocene			
224		WILDSCHEUER	Germany		49.8	9.4				
246		KORBISDORF	Germany		51.3	11.8				
234		OBERFRANKEN (generic)	Germany		49.9	11.3				
278		PISEDE	Germany		53.7	12.7	Quartar			
275		GAMSENBERG CAVE	Germany		50.7	11.6	Pleistocene			
297		SUNDWIG	Germany				Pleistocene			
298		KIESGRUBE	Germany				Pleistocene			
196		ZOOLITHENHOHLE	Germany	452	49.7	11.1		29000	24000	
261		THIEDE	Germany		52.1	10.4	Jungpleistozan			
222		LIMMERER LOCH	Germany		52.3	9.6				

223		SCHNEIDERLOCH	Germany		50.6	12.7				
284		HEINRICHS CAVE	Germany		51.3	7.7	Early Pleistocene			
308		GROSSES SCHULERLOCH CAVE	Germany				Pleistocene			
313		WINTESHOF-WEST	Germany							
304		WEINBERGH CAVE	Germany				Late Pleistocene Wurm			
306		SCHAMBACH CAVE	Germany		48.9	11.3	Pleistocene			
147		RABENSTEIN	Germany		50.8	12.8				
326		BRÜHL	Germany				Late pleistocene			
302		HÖHLENHYÖNE	Germany		50.5	7.2	Pleistocene			
334		GEINSHEIM	Germany				Late Pleistocene			
336		GROSSROHRHEIM	Germany				Late Pleistocene			
346		LAMPERTHEIM	Germany				Late pleistocene			
357		PETERS CAVE	Germany				Late Pleistocene			
305		OFNET CAVE	Germany		48.7	9.2	Late Pleistocene			
309		SCHERNFELD	Germany		48.9	11.1	Late Pleistocene, spaltenfüll			
141		MAUER	Germany		49.3	8.8	Middle middle pleistocene			
376		BAUMANN'S CAVE	Germany		51.7	10.8	Late Pleistocene			
411		GREMSDORF	Germany		49.6	10.8	MIS3			47600
406		UNTERMASSFIELD	Germany				Epivillafranchian, Jaramillo			
412		SIBYLLEN HÖHLE	Germany				MIS3			48100
414		SIEGSDORF	Germany		47.8	12.6				
311		PIKERMI	Greece		38.0	23.9	Pliocene inferiore			
321		APIDIMA CAVE	Greece		36.6	22.3	Middle Pleistocene			
331		DRYOS CAVE	Greece				28.000 BP			
344		KLISOURA CAVE	Greece				Aurignacian, 34700-27200BP			
343		KITSELI POTHOLE	Greece				Late Pleistocene			
347		LOUTRA ARIEDAS CAVE, BEAR CAVE	Greece				Late pleistocene			
373		VRAONA CAVE	Greece				Latest late pleistocene 25.000-7000 BP			
358		PETRALONA CAVE	Greece		40.3	23.1	Late pleistocene			
466		VRAONA	Greece	12				24000	7000	
371		VETERNICA CAVE	Hungary				Late Pleistocene MIS 4-5			
441	LAMBRECHT	LAMBRECHT CAVE Holocene	Hungary		48.1	20.6	Holocene			
432	LAMBRECHT	LAMBRECHT K. CAVE Late Pleistocene	Hungary	410	48.1	20.6	Varbónian			
145		CSARNOTA	Hungary		45.8	18.2	Middle Middle Pleistocene			
415		SZALAY ÁGOSTON BARLANG	Hungary							
421		ÖLYVESKŐ	Hungary							
424		ÖLYVESKŐ. ZÖLDESSZÜRKE R.	Hungary							
433		KISKEVÉLYI CAVE	Hungary		48.2	20.4	Late Pleistocene			
422		MISKOLC SAJÓMEDER	Hungary		48.1	20.7				
428		TATA	Hungary		47.6	18.3		50000	33600	
435		SOLYMAR	Hungary		47.5	18.9				
420		BAJÓT	Hungary		47.7	18.5				
429		SÜTTŐ	Hungary	210	47.7	18.4	Süttőian			
430		PORLYUK	Hungary		48.4	20.5				
426		LENGYEL CAVE	Hungary		46.3	18.3	Wurm I			
417		VÁRHEGY MOSBACHIEN	Hungary		46.6	24.5				
425		PILISSZÁNTÓ II HUMUSZ.	Hungary		47.6	18.8				
434		UPPONYI I. KŐFÜLKE	Hungary		48.2	20.4	K. Pleistoszt.			
423		SÁRKÁNY LYUK	Hungary		47.7	18.4				
436		VÉRTESSZŐLŐS II	Hungary		47.6	18.3				
416		PESCŐ CAVE	Hungary		45.0	20.4				
419		ISTÁLLÓSKŐI CAVE	Hungary		48.0	20.4				
449		KISKŐOLDALI	Hungary		47.7	18.5				
450		DRACHENBRUNN.	Hungary		46.0	18.2				
448		BAITS CAVE	Hungary		47.7	18.5				
444		BIVAK CAVE	Hungary		47.7	18.9	Lower Wurm			
455		DI√ìSGYŐRI CAVE	Hungary		48.0	20.6				
442		DOROGI KŐF√úLKE	Hungary		47.7	18.8	Lower wurm			
453		HÁROMKÜTI CAVE	Hungary							
454		BERVAVÓLGYI SZIKLAÜREG	Hungary				Late Pleistocene			
462		BUDAPEST, 72-73 Öri utca	Hungary		47.5	19.0				
460		JANKOVICH CAVE	Hungary		47.7	18.5				
457		KŐLYUK	Hungary		48.1	20.6	Late Pleistocene			
459		KISLÁNG	Hungary		46.9	18.3	Early Pleistocene (Als√≥ Pleistoc√©n)			
446		HÁRVÖLGYI FÜLKE	Hungary		48.1	20.5				
456		SZELETA CAVE	Hungary	349	48.1	20.5				
447		SZELIM CAVE	Hungary		47.5	18.4				
443		TOKOD-NAGYBEREK	Hungary		47.7	18.6	Lower wurm			
439		SZUHOGY	Hungary		48.3	20.6				
451		MÉLYVÖLGYI KÖFÜLKE	Hungary		46.1	18.3				
427		CAVE in the stonemine in HEJŐCSABAI	Hungary		48.0	20.7				
445		REMETE CAVE	Hungary		47.5	18.9				

440		SUBALYUK	Hungary	300	47.9	20.5	Subalyukian stage			
461		MUSSOLINI CAVE	Hungary							
337		GOMBASZÖK CAVE	Hungary				middle Middle Pleistocene			
110	ARENE CANDIDE	CAVERNA DELLA ARENE CANDIDE	Italy		44.1	8.3	23470 +-320 23450+-220 BP	23470	23450	
50	ARGENTARIO	MONTEMERANO	Italy		42.6	11.4				
113	ARGENTARIO	MONTE ARGENTARIO	Italy		42.4	11.1				
151	ARGENTARIO	POLVERIERE CAVA 2	Italy							
161	ARGENTARIO	GROTTA DEI SANTI	Italy		42.3	11.1				
360	BALZI ROSSI	GROTTA DEL PRINCIPE	Italy				Late pleistocene			
9	BRECCE DI SOAVE	CASTELLO	Italy		45.4	11.2				
34	BRECCE DI SOAVE	SCIVOLONE	Italy		45.4	11.2	Early Middle Pleistocene			
31	BRECCE DI SOAVE	SENTIERO	Italy		45.4	11.2				
29	BRECCE DI SOAVE	VIATELLE	Italy		45.4	11.2				
73	BRECCE DI SOAVE	SOAVE	Italy		45.4	11.2				
32	BRECCE DI SOAVE	MONTE ZOPPEGA I	Italy		45.4	11.2				
33	BRECCE DI SOAVE	MONTE TENDA	Italy		45.4	11.1	Galerian			
123	CAPRI	QUISISANA-CERTOSA	Italy	100	40.5	14.2	Late or latest Middle Pleistocene			35000
53	CARSO TRIESTINO	BRISTIE I	Italy		45.7	13.7	Early Middle Pleistocene			
63	CARSO TRIESTINO	SLIVIA	Italy		45.7	13.6	Early Middle Pleistocene			
40	CARSO TRIESTINO	GROTTA DELL'ORSO, SAN PRIMO, GABROVIZZA	Italy		45.7	13.7				
99	CARSO TRIESTINO	CAVERNA DEGLI ORSI	Italy	360	45.6	13.8				
54	CARSO TRIESTINO	BRECCIA DI SLIVIA	Italy		45.7	13.7				
59	CARSO TRIESTINO	CAVERNA POCALA	Italy		45.7	13.6	Neolithic			
37	CARSO TRIESTINO	GROTTA POCALA	Italy	139	45.7	13.6				
107	CARSO TRIESTINO	BRISTIE	Italy		45.7	13.7				
58	CARSO TRIESTIO	PICCOLA POCALA	Italy		45.7	13.6				
158	COLLEZIONE ATTUALE	SIENA	Italy		43.3	11.3				
159	COLLEZIONE ATTUALE	FERRARA	Italy		44.8	11.6				
178	COLLEZIONE ATTUALE	PADOVA (Museo di Zoologia)	Italy		45.4	11.8				
182	COLLEZIONE ATTUALE	FIRENZE (Sala delle ossa)	Italy		43.7	11.2				
183	COLLEZIONE ATTUALE	PADOVA (Agraria)	Italy		45.3	11.9				
195	COLLEZIONE ATTUALE	PERUGIA Casalina	Italy		42.9	12.4				
62	EQUI	EQUI	Italy	356	44.1	10.1				
154	EQUI	TECCHIA DI EQUI	Italy		44.1	10.1				
153	EQUI	GROTTA DI EQUI	Italy		44.1	10.1				
5	GESSI BOLOGNESI	CAVA FILO	Italy	240	44.4	11.3		20000	11000	20000
100	GESSI BOLOGNESI	GROTTA SERAFINO CALINDRI	Italy		44.4	11.4				
69	GRANDE RACCORDO ANULARE	II km Raccordo	Italy		41.9	12.3				
169	GROTTE DI CASTELLANA	BUCA DELLA JENA (Bari)	Italy		40.8	17.1				
10	GROTTE DI VEJA	GROTTA DI VEJA A	Italy		45.6	10.9				
157	ISOLA D'ELBA	GROTTA DI REALE	Italy							
118	PIRRO	PIRRO 10	Italy		41.8	15.3				
126	PIRRO	CAVA PIRRO	Italy		41.8	15.3				
132	ROMA	MONTE SACRO	Italy		41.9	12.5		420000	160000	
176	ROMA	CASTEL DI GUIDO	Italy	73	41.9	12.2		327000	260000	
180	VENTAROLE	SAN SIDERO 3	Italy		40.1	18.3				
177	VENTAROLE	CAVA 5	Italy		40.1	18.2				
57		GROTTA DELL'ORSO	Italy							
67		RIPARO TAGLIENTE	Italy	226	45.5	11.0				
21		GROTTA DEL VAGO	Italy		45.6	11.0				
4		GROTTA DEL CERE'	Italy	816	45.6	10.9				
20		COVOLI DI VELO VERONESE	Italy		45.7	11.5				

18		BUCO DELLA STREGA	Italy		45.5	10.1				
98		GROTTA CANNITA	Italy		38.1	13.3				
27		TORBOLE	Italy		45.8	10.8				
51		ROSELLE	Italy		42.8	11.1				
8		ISERNIA LA PINETA	Italy		41.5	14.2		700000	450000	
23		PIZZOLANA	Italy		45.6	10.9				
12		GROTTA DEL BANDITO	Italy		44.2	7.4				
35		GROTTA DEL BROION	Italy	150	45.4	11.5	Middle Paleolithic			
13		RIPARO MEZZENA	Italy		45.4	10.9				
41		SELVAVECCHIA	Italy		45.6	10.9				
104		GROTTA DELL'ARDUINO	Italy							
25		TOMBOLA DI CEREA	Italy		45.1	11.2				
19		COLOMBARE	Italy		45.5	10.9				
49		VALDARNO SUPERIORE	Italy		43.4	11.8				
46		VELO VERONESE	Italy		45.6	11.0				
47		VALDARNO	Italy		43.4	11.8				
38		MONTE ZOPPEGA	Italy		45.4	11.2				
64		SERBARO DI ROMAGNANO	Italy		45.5	11.0				
16		GROTTA DELLA VOLPE	Italy		45.4	10.9				
28		VEREZZI	Italy		44.1	8.3				
78		PANTALLA	Italy		42.7	12.4	Olivola/Tasso FU	2E+06	2E+06	
80		VIGNA NUOVA	Italy		42.9	12.0				
26		TORBIERA CASACCE	Italy		45.3	10.6				
90		FORNACE FERRINI	Italy		43.0	12.4				
70		COMPLESSO SABATINO	Italy		42.1	12.3				
87		CASALE MONTECCHIO di CASALINA	Italy		42.9	12.3				
11		DOMEGLIARA-SELVA VECCHIA	Italy		45.5	10.8				
42		TORBIERE DI VAL LIONA	Italy		45.4	11.4				
81		TORRE PICCHIO	Italy		42.6	12.4				
36		GROTTA DEL BRUSCO	Italy		44.0	9.8				
84		COLLE S. ANDREA	Italy		42.7	12.5				
103		GROTTA DI CASTELCIVITA	Italy		40.4	15.2		35000	31000	
17		BARCHE DI SOLFERINO	Italy		45.3	10.5				
79		PARRANO-FRATTAGUIDA	Italy		42.8	12.1				
74		CONTRADA IANNI'	Italy	80	38.5	16.0				
39		VELIKA JAMA	Italy	372	46.1	13.5	Holocene			
92		MONTE PEGLIA	Italy	837	42.7	11.9				
85		ELLERA DI CORCIANO	Italy		43.1	12.2				
45		dintorni di PALERMO	Italy	220	38.0	13.4				
72		GABROVIZZA	Italy		45.7	13.7				
101		GROTTA DELLE OSSA (BG)	Italy		45.6	9.8				
102		GROTTA PETROSA	Italy	100	38.3	15.8				
14		GROTTA DEI PUNTALI	Italy		38.1	13.1				
93		COLLELUNGO-RAVIGLIANO	Italy		43.1	12.3				
82		CAVA CASTIGLIANO e CASALE VIOLINO	Italy		42.7	12.5				
83		CAVA SAN FAUSTINO	Italy		42.7	12.5				
114		COLLE CURTI	Italy		43.0	12.9				
76		GROTTA DI TORRE NAVE	Italy	8	44.8	8.8				
44		GROTTA DEI VIGANTI	Italy	540	46.2	13.2				
94		GROTTA DEI CERVI DI PORTO BADISCO	Italy	0	40.0	18.4	Late Pleistocene			
22		GROTTA PAGLICCI	Italy	590	41.6	15.5				18000
66		GROTTA MAGGIORE DI SAN BERNARDINO	Italy	132	45.4	11.5				
109		GROTTA DELLA CALA	Italy		40.0	15.3	26.880+-320	26880	26380	
116		INGARANO	Italy	270	41.7	15.8		40000	35000	
111		PALIDORO	Italy		41.9	12.1	Epigravettian 15900+-150 15520+-140 BP	15900	15520	
88		CIOTA CIARA	Italy	670	45.7	8.3	Musteriano, Mis 5c o 5a	80000	70000	
68		GROTTA DI PAINA	Italy	335	45.4	11.5				
125		GROTTA DEL ROMITO	Italy	296	39.9	15.9	Late Paleolithic			
52		BUCA DELLA IENA (Grosseto)	Italy	100	42.8	11.1				
112		GROTTA DEL SANTUARIO DELLA MADONNA	Italy		38.2	16.1	Epigravettian 12100+-150 BP			12100
117		TANA DELLE IENE	Italy		40.6	17.5		60000	40000	50000
77		AVETRANA	Italy		40.3	17.73				
61		GROTTA DEL SOLDO	Italy		45.7	13.7				
115		GROTTA DI VISOGLIANO	Italy	105	45.7	13.6	Middle Pleistocene	500000	350000	
75		TORRE TALAO	Italy	25	39.8	15.7				
170		GROTTA ROMANELLI	Italy	8	40.0	18.4				
163		STEGGIO	Italy		45.8	11.8				
152		CIOTTOLI DEL MASPINO	Italy					100000	10000	
124		GROTTA DEL CERVO	Italy		42.1	13.0				
48		GROTTA DELLE FINESTRE o DELLE GALLERIE	Italy		45.6	13.8				
156		BUCA DELLA IENA (Lucca)	Italy		44.2	10.1		41000	37000	51000
168		GROTTA DELLA IENA (Lucca)	Italy		44.2	10.1				
164		GROTTA DEGLI ORSI VOLANTI	Italy		42.2	14.1				
155		GROTTA DEL CAPRIOLO	Italy		44.2	10.1				
56		GROTTA TILDE	Italy		45.7	13.7				

162		RIPARO L'OSCURUSCIUTO	Italy	240	40.5	16.7				40000
175		BONDENO	Italy		44.8	11.4				
185		CAVA DELLA CROCE	Italy							
43		CASTELLON DEL BROSIMO	Italy		45.4	11.6				
179		BRISIGHELLA	Italy		44.2	11.7				
190		GROTTA ALL'ONDA	Italy				Musterian			
184		MONTIGNOSO	Italy		44.0	10.1	Middle-Late Pleistocene			
186		GROTTA DI CUCIGLIANA	Italy		43.6	10.5				
199		BUSE DE JASBINE	Italy				Aurelian			
210		GROTTA DI SAN TEODORO	Italy	145	38.0	14.5	32000+-4000 yr			
181		VISOGLIANO	Italy		45.7	13.7	MIS 13 MIS 10, 500+-350 Ka BP	500000		
209		CASAL SELCE	Italy		41.8	12.3	MIS 18			
65		GROTTA SAN LEONARDO	Italy		45.6	11.4				
192		GROTTA LA FABBRICA	Italy		42.6	11.0				
24		SCALUCCE	Italy		45.6	10.9				
187		GROTTA DI GOLINO	Italy		42.5	11.1	Late Paleolithic			
193		GROTTA DI GOSTO	Italy							
197		GROTTA DI VALDEMINO	Italy		44.1	8.3	Galerian			
283		JASOA POD KALAM	Italy				Pleistocene			
327		GROTTA DELLE CAMPAGNE	Italy				Late Pleistocene			
328		CAPRI	Italy				Late Pleistocene			
3		POGGIOROSSO	Italy		43.4	11.4				
386		CASAL DE' PAZZI	Italy		41.9	12.5				
338		GROTTA DI GRIMALDI	Italy				MIS 5e			
351		MONTE CUCCO	Italy				Late Pleistocene			
356		GROTTA DEL PASTORE	Italy				Late pleistocene			
362		GROTTA DI SANBUGHETTO VALSTRONA	Italy				Late Pleistocene			
363		GROTTA DI S. AGOSTINO DI GAETA	Italy				Late Pleistocnee			
375		ZANDOBBIO	Italy				Late pleistocene			
380		REDICICOLI	Italy							
381		CESI	Italy							
382		G.R.A. (Roma)	Italy							
384		BUCINE	Italy							
385		CAMPO VERDE	Italy							
387		PRATI FISCALI	Italy							
388		CARNELLO	Italy							
389		VALLE RADICE	Italy							
390		SAN DONA' DI LAMON	Italy							
379		FONTANA RANUCCIO	Italy		41.7	13.1				
6		GROTTA DI FUMANE	Italy	374	45.5	10.9		44000	15000	
394		GROTTA COLA	Italy		42.0	13.2	MIS 5-3			
395		GROTTA DEI CERVI DI PIETRASECCA	Italy				130000			
396		GROTTA MARITZA	Italy				Upper Paleolitic; 13.500-10.55	13500		10500
408		OLIVOLA	Italy		45.0	8.3	Late Villafranchian			
333		GROTTA DELLE FATE	Italy	220	44.1	8.3	Late pleistocene?			
191		BUCA DEL TASSO	Italy	415	43.9	10.3	Musterian			
198		FIRENZE (Collezione Mazza)	Italy		43.7	11.2				
383		TORREINPIETRA	Italy		41.9	12.2				
401		GROTTA DI ORTUCCHIO	Italy		41.9	13.6	Paleolitic	13000		12000
402		RIPARO MAURIZIO	Italy		41.9	13.6				
188		GROTTA ROSE MARY	Italy		42.4	11.2				
189		BUCA DELLA IENA	Italy		42.4	11.2	Musterian			
91		VILLA SPINOLA	Italy		43.0	12.4				
86		PIETRAFITTA	Italy		42.9	12.2				
89		vicinanze di PACIANO	Italy		43.0	12.0				
220		GROTTA DEL POGGIO	Italy		40.0	15.3				
194		RIPARO FREDIAN	Italy		44.0	10.4				
105		GROTTA MILANO	Italy	640						
241	COLLEZIONE ATTUALE	SUSWA	Kenia				recent			
238		TEGELEN	Nederland		51.3	6.1	Cromer			
272	CHRISTBURG	CHRISTBURG (generic)	Poland		53.9	19.3	Pleistocene			
268	CHRISTBURG	MENTHEN	Poland		53.9	19.3	Pleistocene			
130		BIŚNIK CAVE	Poland		53.4	19.6	Late Middle Pleistocene, MIS 11-10			
271		KITZELBERG (KAUFFUNG)	Poland		50.9	15.9	Pleistocene			
273		GROSS WAPLITZ	Poland		53.5	20.3	Pleistocene			
409		WIERCHOWSKA	Poland				MIS3			
213		GALERIA PESADA/BRECHA DAS LASCAS	Portugal		39.5	-8.6	241000+-30-22 in layer B2			241000
211		ALGOZ	Portugal		37.1	-8.3	upper Lower Pleistocene	1E+06		
214		CASAL DO TORQUATO	Portugal							
216		MEIRINHA	Portugal							
217		SANTO ANTAO	Portugal							34000
215		CARREGADO	Portugal							

212		MEALHADA	Portugal		40.3	-8.4	Middle Pleistocene	
218		GRUTA DO CALDEIRÃO	Portugal	120	39.6	-8.4	Paleolitico superiore iniziale, 27-22000 BP	
377		GRUTA DA FIGUEIRA BRAVA	Portugal		38.5	-8.9	Musterian	
378		GRUTA DA COLUMBEIRA	Portugal		39.2	-9.1	Musterian	
458		IGRIC CAVE	Romania		47.0	22.2	Late Pleistocene	
144		GOMBASZ√ñG	Slovakia		48.4	20.3	Early Pleistocene	
438		TARKŐ rock shelter	Slovakia		47.2	20.9	Varbónian	
418		TARKŐI-SZFÜLKE	Slovakia		47.2	20.9		
60		GROTTA DELLE OSSA (SLO)	Slovenia		45.7	13.8		
122		INCARCAL	Spain		42.1	2.5		
219		LAS VENTANAS CAVE	Spain					12780
319		ALLEKOAITZE CAVE	Spain				Late Pleistocene	
320		ARBREDA CAVE	Spain				Eemian MIS 5e	
325		BOQUETE DE ZAFARRAYA	Spain				Late Pleistocene (Middle Weichselian)	
361		ROMANI ABI	Spain				Late pleistocene, early-middle weichselian	
364		SIMA DE LAS PALOMAS KARST	Spain				Late middle to late pleistocene 130.000-60.000 BP	
366		TORREJONES CAVE	Spain				Late pleistocene	
369		VALDEGOBA CAVE	Spain				Late middle to late pleistocene MIS 6-3	
391		ATAPUERCA	Spain		42.3	-3.5		
403		LA PARTE	Spain		43.3	-5.6		150000
399		LOS RINCONES CAVE	Spain					
137		SCHNURENLOCH CAVE	Switzerland		46.6	7.4		
135		WILDKIRCHLI	Switzerland		47.2	9.4		
233		ROBENHAUSEN	Switzerland		47.3	8.7		
374		WILDKIRCHLI CAVE	Switzerland		47.2	9.4	Late Pleistocene	
240	COLLEZIONE ATTUALE	OLDUVAI (Attuale)	Tanzania				recent	
300	COLLEZIONE ATTUALE	OSTAFRICA	Tanzania					
244		GARUSSI	Tanzania					
294		OLDUVAI (Fossile)	Tanzania					
245	Modern Coll.	TIBET	Tibet				recente	
310		GARKIN	Turchy				Vallesium	
312		AKCAKÖY	Turchy				Vallesium	
314		YENI ESKIHISAR	Turchy				Vallesium	
342		KARAIN CAVE	Turchy				Eemian MIS 5e	
7		EMINE-BAIR-KHOSAR CAVE	Ukraine		44.8	34.2		42000
108	Unprecise	Undetermined	Unknown					
96	Unprecise	Unknown	Unknown					
250	Modern Coll.	WAHRSCHINL					recent	
259	Modern Coll.	nessun dato						
299	Modern Coll.	OSTAFRICA						

WGS84 coordinates are rounded off. For the complete references please refer to the attached CD

Finds:

site_name	**museum_name**	**collection_name**	**inventory number**	**find**	**find_type**	**rx_lx**	**age**	**fragment**	**label**	***species***
BIŚNIK CAVE	Department of Palaeozoology, zoological institute, university of Wroclaw	NO NAME	ZPalUWr/JB/M/05/Pp/2	tooth	C upper	rx		t		*P. pardus*
GROTTA DELLE OSSA (BG)	Museo Civico di Storia Naturale 'E. Caffi' BG	NESSUN NOME	MCSNB 5127	cranium	cranium			f	f	*P. leo spelaea*
BRISTIE	Museo civico di storia naturale TS	MCSN TS	Vpa 1391	tarsal	calcaneus	lx	a	f	t	*P. leo spelaea*
BARCHE DI SOLFERINO	Museo Civico di Storia Naturale VR	MCSN VR	V.2001	cranium	maxillar			t	f	*Felis sylvestris*
CASTELLON DEL BROSIMO	Museo di Geologia e Paleontologia PD	MU PD	B370	humerus	humerus	lx	a	t	f	*Felis silvestris*
ARAGO	Museo di Paleontologia e Preistoria "Piero Leonardi" FE		CNR 283689	mandible			a	f	f	*P. pardus*
MONTEMERANO	Museo di storia naturale della Maremma GR	MM GR	169035/2	mandible	mandible	rx	a	t	f	*P. leo spelaea*
CAVERNA POCALA	Museo Geologico Giovanni Cappellini BO	NO NAME	IGPC83	tooth	P4 upper			f	f	*P. leo spelaea*
GROTTA POCALA	Museo Naturalistico Archeologico VI	MU PD	25241	mandible		lx	a	t	f	*P. leo spelaea*
BAD SALZUNGEN	Museum fur Naturkunde - Berlin		MB.Ma.30103	femur	femur	lx		t	t	*P. leo spelaea*
TRIAGALNATA PESHTERA	Museum of Carst	NO NAME	3398	tooth	C	rx	old			*P. pardus*
PRAHA-PODBABA	National Museum Prague	NMP Coll. Museum	R65	tooth	C lower		a	t		*P. leo spelaea*
GROTTA DEL CERVO	Undeclared	NO NAME	P37-38-39	interossei	3 interossei					*P. leo spelaea*

For the entire list of specimens (more than 700 findings) please refer to the attached CD. Gray rows indicate museums with more specimens. For the fossils from Equi see the next tables.

Leopard finds from Equi:

inv. n.			element	right or left	age
IGF	184	V	cranium		a
IGF	185	V/1	cranium		a
IGF	185	V/2	premaxillary		o
IGF	6120	V/1	maxillary	l	y
IGF	6136	V	maxillary	r	y
IGF	6137	V	temporal	l	
IGF	10036	V	cranium		a
IGF	15110	V	cranium		a
IGF	15111	V/1	cranium		a
IGF	6132	V	I		
IGF	6138	V	I3	r	a
IGF	185	V/3	C	l	a
IGF	6107	V	C	l	a
IGF	6108	V	C	r	a
IGF	6106	V	P3	r	a
IGF	6115	V	P3	r	a-o
IGF	6109	V	P4	l	a
IGF	6134	V	i2	r	
IGF	6116	V	c	l	a
IGF	5460	V	c	l	y-a
IGF	6105	V	c	l	a
IGF	6110	V	p3	r	a
IGF	6107	V	p4		y
IGF	6113	V	m1	r	a
IGF	6114	V	m1	l	a
IGF	6117	V	incisive		o
IGF	6118	V	incisive	l	a
IGF	6123	V/2	d	l	y
IGF	6123	V/3	d	l	y
IGF	6124	V	d	r	y
IGF	6131	V	d	l	y
IGF	6112	V	d	r	y
IGF	185	V/4	mandible	l	o
IGF	6102	V	mandible	r	a-o
IGF	6103	V	mandible	l	a-o
IGF	6104	V	mandible	r	y-a
IGF	6119	V	mandible	l	y
IGF	6120	V/2	mandible	l	a
IGF	6122	V	mandible	l	y-a
IGF	6123	V/1	mandible	r	y
IGF	6125	V	mandible	r	y
IGF	6135	V	mandible	r	y
IGF	10037	V/1	mandible	l	a
IGF	10037	V/2	mandible	r	a
IGF	15111	V/2	mandible		a
IGF	5336	V	scapula	r	y
IGF	5356	V	scapula	l	a
IGF	5401	V	scapula	l	y
IGF	6157	V	scapula	l	
IGF	6159	V	scapula	l	a
IGF	15118	V	scapula	r	a
IGF	15119	V	scapula	l	a
IGF	5335	V	humerus	r	a
IGF	5341	V	humerus	r	y
IGF	5342	V	humerus	r	a
IGF	5351	V	humerus	r	y-a
IGF	5352	V	humerus	r	ao
IGF	6141	V	humerus	l	y-a
IGF	6164	V	humerus	l	a
IGF	6165	V	humerus	r	a
IGF	6166	V	humerus	l	a
IGF	15116	V	humerus	r	a
IGF	15117	V	humerus	l	a
IGF	5337	V	radius	l	a
IGF	5338	V	radius	l	a
IGF	5339	V	radius	r	a
IGF	5340	V	radius	r	y
IGF	6129	V	radius	r	
IGF	6169	V	radius	r	a
IGF	15113	V	radius	r	a
IGF	15114	V	radius	l	a
IGF	5353	V	ulna	l	y
IGF	5354	V	ulna	l	a
IGF	5355	V	ulna	l	a
IGF	5357	V	ulna	r	y
IGF	6161	V	ulna	r	y
IGF	15115	V	ulna	l	a
IGF	6168	V	scaphoide	l	
IGF	6172	V	scapholunar		
IGF	nn		carpal	r	
IGF	nn5	/1	mc I	r	a
IGF	nn9		mc I	l	a
IGF	5303	V	mc II	l	a
IGF	5305	V	mc II	l	a
IGF	5299	V	mc II	l	y
IGF	5291	V	mc II	l	a
IGF	5321	V	mc II	r	a
IGF	nn8		mc II	l	a
IGF	nn4		mc II	r	a
IGF	5295	V	mc III	r	a
IGF	5301	V	mc III	l	y
IGF	5302	V	mc III	l	a
IGF	5308	V	mc III		
IGF	5314	V	mc III	l	a
IGF	nn3		mc III	r	a
IGF	nn7		mc III	l	a
IGF	s.n. 001		mc III	r	y
IGF	5293	V	mc IV	r	a
IGF	5296	V	mc IV	l	a
IGF	5297	V	mc IV		a
IGF	5298	V	mc IV	r	a
IGF	5307	V	mc IV	r	y
IGF	nn2		mc IV	r	a
IGF	5294	V	mc V	l	a
IGF	5300	V	mc V	l	y
IGF	5309	V	mc V	l	a
IGF	5310	V	mc V	r	a
IGF	5315	V	mc V	r	a
IGF	nn1		mc V	r	a
IGF	nn5	/2	mc V	l	a
IGF	nn6		mc IV	l	a
IGF	6130	V	atlas		
IGF	15112	V	atlas		a
IGF	15120	V	lumbar vertebra		a
IGF	15121	V	caudal vertebra		
IGF	15122	V	caudal vertebra		
IGF	15123	V/1	caudal vertebra		
IGF	15123	V/2	caudal vertebra		
IGF	15124	V	caudal vertebra		
IGF	16123	V	caudal vertebra		
IGF	6153	V	ileum	r	
IGF	6156	V	ileum	l	
IGF	6142	V	coxal	l	a
IGF	6154	V	coxal	r	
IGF	6155	V	coxal	l	a
IGF	nn23		coxal	r	a
IGF	nn24		coxal	l	y

IGF	5347	V	femur	r	a
IGF	5348	V	femur	l	y
IGF	5349	V	femur	r	y
IGF	5350	V	femur	r	y
IGF	5397	V	femur	r	y
IGF	6167	V	femur	l	a
IGF	6171	V	femur	l	a
IGF	6171	V	femur	l	y
IGF	nn25		femur	r	a
IGF	nn45		femur	l	a
IGF	5343	V	tibia	r	y
IGF	5344	V	tibia	l	y
IGF	5345	V	tibia	r	y
IGF	5346	V	tibia	r	y-a
IGF	5398	V	tibia	l	y
IGF	6160	V	tibia	r	y
IGF	6163	V	tibia	r	a
IGF	15125	V	tibia	r	a
IGF	nn46		tibia	l	a
IGF	5334	V	astragalus	r	a
IGF	6145	V	astragalus	r	a
IGF	6146	V	astragalus	r	
IGF	6162	V	astragalus	r	
IGF	nn27		astragalus	r	a
IGF	6143	V	calcaneus	l	a
IGF	6144	V	calcaneus	l	a
IGF	6147	V	calcaneus	r	a
IGF	6148	V	calcaneus	r	
IGF	6149	V	calcaneus	r	a
IGF	6150	V	calcaneus	r	y-a
IGF	6151	V	calcaneus	l	y
IGF	nn26		calcaneus	r	a
IGF	nn47		calcaneus	l	a
IGF	6697	V	cuboid		
IGF	nn28		cuboid	r	a
IGF	nn48		cuboid	l	a
IGF	nn29		navicular	r	a
IGF	s.n. 003		navicular		a
IGF	5311	V	mt II	r	a
IGF	5319	V/1	mt II	l	a
IGF	5312	V	mt III	r	y-a
IGF	5313	V	mt III	l	a
IGF	5317	V	mt III	r	a
IGF	5320	V	mt III	r	a
IGF	5322	V	mt III	l	a
IGF	5323	V	mt III	r	a
IGF	nn32		mt III	r	a
IGF	5292	V	mt IV	r	a
IGF	nn31		mt IV	r	a
IGF	5324	V	mt V	l	y
IGF	5325	V	mt V	r	y
IGF	nn30		mt V	r	a
IGF	5318	V	mt V	l	a
IGF	s.n. 002		mt V	l	a
IGF	5287	V	phalanx I		a
IGF	5289	V	phalanx I		
IGF	5319	V/2	phalanx I		a
IGF	5327	V	phalanx I		y
IGF	5328	V	phalanx I		a
IGF	5329	V	phalanx I		a
IGF	5330	V	phalanx I		a
IGF	5331	V	phalanx I		a
IGF	5331	V	phalanx I		a
IGF	nn10		phalanx I		a
IGF	nn11		phalanx I		a
IGF	nn12		phalanx I		a
IGF	nn13		phalanx I		a
IGF	nn14		phalanx I		a
IGF	nn15		phalanx I		a
IGF	nn16		phalanx I		a
IGF	nn17		phalanx I		a
IGF	nn34		phalanx I		
IGF	nn35		phalanx I		
IGF	nn36		phalanx I		
IGF	nn37		phalanx I		
IGF	nn38		phalanx I		
IGF	nn39		phalanx I		
IGF	nn18		phalanx II		a
IGF	nn19		phalanx II		a
IGF	nn20		phalanx II		a
IGF	nn21		phalanx II		a
IGF	5290	V	phalanx II		a
IGF	nn40		phalanx II		
IGF	nn41		phalanx II		
IGF	nn42		phalanx II		
IGF	nn43		phalanx II		
IGF	nn22		phalanx III		a
IGF	nn44		phalanx III		
IGF	5331	V	phalanx		a
IGF	5333	V	phalanx	r	
IGF	5304	V	metapodius		a
IGF	5306	V	metapodius		a
IGF	5308	V	metapodius		a
IGF	5316	V	metapodius		
IGF	5326	V	metapodius		y-a
IGF	5326	V	metapodius		y-a
IGF	nn33		metapodius		

id_nan_site_publication:

site_name	publication_name
ABIMES de la FAGE	BALLESIO 1975
ALGOZ	BRUGAL et al. 2004
ALLEKOAITZE CAVE	DIEDRICH 2013
APIDIMA CAVE	DIEDRICH 2013
ARBREDA CAVE	DIEDRICH 2013
AVETRANA	PANDOLFI et al. 2011
BAUMANN'S CAVE	DIEDRICH 2013
BIŚNIK CAVE	MARCISZAK 2013
BLANOT CAVE 2	DIEDRICH 2013
BLEADON CAVE	DIEDRICH 2013
BONDENO	SALA 2012
BOQUETE DE ZAFARRAYA	DIEDRICH 2013
BRÃœHL	DIEDRICH 2013
BRECCIA 2	ARGANT et al. 2007
BRECCIA 4	ARGANT et al. 2007
BRECCIA DI SLIVIA	BON et al. 1992; VENTURINI et al. 2010
BRISTIE I	BON et al. 1991
BUCA DEL TASSO	MASSETI et al. 2012
BUCA DELLA IENA	MASSETI et al. 2012
BUCA DELLA IENA (Lucca)	CALOI et al. 1994
BUCA DELLA JENA (Bari)	MELORO 2004
BUCINE	MUSSI et al. 2001
BURGTONNA	VAN KOLFSCHOTEN 2000
CAMPO VERDE	MUSSI et al. 2001
CAPRI	DIEDRICH 2013
CARNELLO	MUSSI et al. 2001
CARREGADO	BRUGAL et al. 2004
CASAL DE' PAZZI	MUSSI et al. 2001
CASAL DO TORQUATO	BRUGAL et al. 2004
CASAL SELCE	SARDELLA et al 2012b
CASALE MONTECCHIO di CASALINA	ARGENTI 2003 2004
CASTEL DI GUIDO	CAPASSO BARBATO et al. 1987; MUSSI et al. 2001; AIAZVI_SACCA' 2009
CASTELLO	BON et al. 1991
CAUNE DE L'ARAGO	MOIGNE et al. 2004
CAVA CASTIGLIANO e CASALE VIOLINO	ARGENTI 2003 2004
CAVA DELLA CROCE	MASSETI et al. 2012
CAVA FILO	PASINI 1968; PASINI 1969; SALA 1985
CAVA PIRRO	PECORELLA 1995
CAVA SAN FAUSTINO	ARGENTI 2003 2004
CAVERNA DEGLI ORSI	BERTO et al. 2011

For the complete list of references see table PUBLICATIONS of the DB, in the attached CD

m_mandible:

site_name	inv. n.	*species*	condilo_infradentale	incisura_angolare_infradentale	condilo_faccia_distale_canino	lunghezza_sinfisi	incisura_angolare_faccia_distale_canino	processo_angolare_corion	processo_angolare_condilo	b_ramo_orizzontale	h_davanti_p3	h_dietro_m1	h_dietro_d4	lunghezza_diastema	b_condilo	note
ABIMES de la FAGE	40946	*P. leo spelaea*												23		
	40947	*P. leo spelaea*												23		
	40945	*P. leo spelaea*												23		
ARAGO	CNR 283689	*P. pardus*	127	123	111	35.5	104.4	56	23		23	25		15	27	lx
	CNR 283689	*P. pardus*	125	122	109	35.5	105	56.6	22		23.4	25		15	26	rx
BAITS CAVE	V 62/559/2	*Felis silvestris*	66.3	64.3	57.6	15.7	54.7	26	12.2	6.4	11.5	12.3		5.8	14	
	V 62/559	*Felis silvestris*				16				5.7	11.8					
BAJÓT	V.60/55	*Felis sylvestris*	63.7	62.4	56	15.4	54.5	27.3	12.2	6	11.2	11.4		8.3	14.2	rx
	V.60/55	*Felis sylvestris*	62	63.3	55.4	14.4	54.5	27.9	12.2	13.6	11.4	11.4		7.7	14.4	lx
BALVE-SANSSOUCI MITTL. HOHLE	Mb.Ma.30038.2	*Felis silvestris*	53.2	50	47.5	11.6	43.8	21.3	10.2	11	8.9	9.4		6.6	11.1	rx
	MB.Ma.30038.1	*Felis silvestris*	53.4	49.9	46.4	12	44	21.6	9.5	4.7	8.8	9.6		6.4	11	lx
BRISTIE	Vpa 383	*P. leo spelaea*				59.7					46	45		24		
BUBASTIS	MB.Ma.30018	*Felis silvestris*									9	10.5				lx
	MB.Ma.30024	*Felis silvestris*									11.2	11.5				rx
	MB.Ma.30027	*Felis silvestris*									10.2	12.7				rx
	Mb.Ma.30023	*Felis silvestris*									11.6	11.3				lx
	MB.Ma.30019	*Felis silvestris*										9.9				lx
	MB.Ma.30025	*Felis silvestris*									12.6	14.7				rx
	Mb.Ma.30026	*Felis silvestris*									13.4	16.5				rx
	MB.Ma.30020	*Felis silvestris*									9.3	12.2				lx
	MB.Ma.30021	*Felis silvestris*									10.4	12.7				lx
	MB.Ma.30022	*Felis silvestris*									9.8	12				lx
BUCO DELLA STREGA	V.7376	*Felis sp.*				13					8			4.5		
BURGTONNA	MB.Ma.628	*Felis silvestris*								6.8		13.7				rx
	MB.Ma.81	*P. leo spelaea*								23.4	51.7			18.7		rx
CAVERNA POCALA	Vpa 5619	*P. leo*	207.5	201.4	176	66.5	166		42.3		43	48		22		
	Vpa 5700	*P. leo*				73.6					51.8	53.3		17		
DECHENHOHLE	Vpa 5701	*P. leo*				79					55			25.4		
	MB.Ma.106 (MB1910)	*P. leo spelaea*								20.5	41	42.5				rx
EQUI	15111.1	*P. pardus*	130.29	108.42	114		109.83		26.26		24.8	28.9		15.04	29.2	lx
	6122V	*P. pardus*						52.74	22.68			22.4		0	22.5	
	10037/1	*P. pardus*	141.3	135.2	121.2	45	116		26.4		28.64	28		15.2	26	
	10037/2	*P. pardus*			120.6		115.3		25.8		29.52	28.64		16	24.52	
	15111.1	*P. pardus*	131.65	124	113.5		107.5	65.21	27.85		24.3	29.26		14.99	29.83	rx
FERRARA	nn	*P. leo spelaea*	226	216	189	63.9	181	101.6	46.7		48	49.5		24.7	49.7	
	nn	*P. leo spelaea*	221.7	216.5	185	64	177	105	47.8		48.5	50		25	51.6	
	G14.EFNI.1000	*P. pardus*	137	131	120	37	112	64.4	28		27.6	30		15	32.5	lx
	G14.EFNI.1000	*P. pardus*	137	128.8	122	37	114	62	27.5		27.6	29		17.5	33	rx
FIRENZE (Sala delle ossa)	C 8439/2	*P. pardus*	161	151.5	138.17	46.27	130.98	75.49	31.12		27.85	30.34		19.56	33.78	rx
	C 8748/2	*P. pardus*	118.25	116.7	103.08	29.69	97	51.5	24.12		18.82	24.12		14.78	25.2	lx
	C 1221/2	*P. pardus*	148.37	144.71	125.2	45.5	121.02	67.8	28.7		28	31.64		13.68	34.1	lx
	C 8748/2	*P. pardus*	118.17	117.55	104	29.69	100.34	52.11	24.6		18.86	23.78		15.61	24.8	rx
	C 1221/2	*P. pardus*	147.15	142.9	123.4	45.5	116.18	66.2	28.6		29.1	32.07		13.04	30.8	rx
	C 8439/2	*P. pardus*	160	153	139.6	46.27	133.4	75.76	31.72		27.01	30.65		20.24	34.4	lx
GAILENREUTH CAVE	MB.Ma.48115.2	*P. leo spelaea*				87				24.5	54	57.4		30.7		lx
	MB.Ma.48115.2	*P. leo spelaea*				87				22.5	54	59.3		30.6		rx
GARKIN	1968VI716	*Hyaenidae*								25.7	43			7.8		rx
GOMBASZÖG	V.24063/6	*P. onca gombaszoegensis*								20		42.3				
	V.24062/3	*P. onca gombaszoegensis*				55.5				17.7	42.7	40.1		18		
	V.24063/1	*P. onca gombaszoegensis*								20.5	40					
GOSLAR (generic)	MB.Ma.44306	*Felis silvestris*	61.3	58.4	52	13	50.5	24.3	9.4	6	9.4	11.4		7.4		lx
	MB.Ma.44312	*Felis silvestris*								4.6	8.4	9.3		4.3		lx
	MB.Ma.44308	*Felis silvestris*	57	54	51	10.7	47.6	23.5	10.7	5.4	9	9.4		6.7	12.2	rx
	MB.Ma.44310	*Felis silvestris*	54.8	51.7	47	11.4	44.6	24	11.4	5	9	10		5	11.4	rx
	MB.Ma.44307	*Felis silvestris*			43.7		42.7		11.4	5	9	10.4		5.7		lx
	MB.Ma.44311	*Felis silvestris*				12.6				5.7	9.7			6.7		rx
	MB.Ma.44309	*Felis silvestris*	54.4	50.7	44.8	13.4	44	22.7	10.8	4.5	8.9	8.7		5.3	10.7	lx
GROTTA DEL BROION	V.10671/1	*P. leo spelaea*				87.1					57.2			30		
	27850	*Felis catus*			53		49		12		10	11			14	

GROTTA DEL CAPRIOLO	pitticapriolo1	*P. pardus*										27.6				
GROTTA DEL CERE'	V.5250	*P. leo spelaea*									24.9		23.2	5.8		
	V.5248	*P. leo spelaea*												16.1		
	V.5251	*P. leo spelaea*									43.7		25.3			
	V.5256	*P. leo spelaea*									33.3			19.1		
GROTTA DEL VAGO	V.9128/2	*Felis sylvestris*	63.4	59.7	56	14.7	52.3	28.64	12		11.2	12		9	14.7	lx
	V.9128/2	*Felis sylvestris*	62.7	60	56	15	52.5	29	12.7		11.5	12		8.2	12.5	rx
GROTTA DELL'ORSO, SAN PRIMO, GABROVIZZA	Vpa 4692	*P. leo*	227	217	199		190		46		46.8	54.3		22.4	56.4	
GROTTA DI EQUI	senza numero	*P. cf. leo spelaea*				53.32					29.11	32.35				
	6103V	*P. pardus*				38					24.6	26.4		15		
	6104V	*P. pardus*	143	138	123		120		28		29	31		14.72	21	
GROTTA DI SLOUP	V.140/2	*P. leo spelaea*	263	248.6	224.24	82	214.5	131	57.4		56	56		24	58	rx
	V.140/2	*P. leo spelaea*				82										lx
GROTTA PAGLICCI	V.5676/2	*Felis sylvestris*									12.2	13.5		5.7		
	V.5676/3	*Felis sylvestris*									11.6	12.6		5.5		
	V.5676/1	*Felis sylvestris*				16.3					11.6	11.8		6.2		
	V.5678/1	*Felis sylvestris*									0	11				
	V.5676/4	*Felis sylvestris*							18						13	
GROTTA POCALA	25264	*P. leo spelaea*				99.7					62	61				
	25241	*P. leo spelaea*							51		43.6	45			57.4	
	25267	*P. leo spelaea*									34	0				
	25236	*P. leo spelaea*				83					53	0				
	25265	*P. leo spelaea*	213	205	183	65	176	120	52		43	44			52.6	
	25266	*P. leo spelaea*										41				
	25263	*P. leo spelaea*	250	221	191	68.5	185	101.6	40		40.6	46.6		25.5	42.6	lx
	25263	*P. leo spelaea*			188		178		41		41.6	47		22	35	rx
	25261	*P. leo spelaea*	253	241	217.6	75	205.2		51.6		51.4	53		21.8		
GROTTE D'AZE	AZE.K.13	*P. leo spelaea*	285.4					141.6			58	60				
HERMANNS CAVE	MB.Ma.14298	*P. leo spelaea*	255	240	215	75.7	203			23.2	49.7	51.3		25.6		lx
IGRIC CAVE	V.60.1785/2	*P. leo spelaeus*						127		24.5	50.6	49.5		19.5		
	V.60.1785/2	*P. leo spelaeus*								25	49.4	50		19.5		
ISTÁLLÓSKŐI CAVE	V.60/49/1	*Falis catus*								5.6	10.9	11.9		7.2		
KŐLYUK	V.63/1927	*Felis cf. domestica*								5.8	9.9	117		7		
KOSTRITZ	MB.Ma.30063.2	*P. leo spelaea*									43.2			20.2		rx
LAMBRECHT CAVE Holocene	V.58/668/5	*Felis silvestris*								5.8	10.6	11.9		5.9		
	V.58.668/1	*Felis silvestris*				15.7				6.3	11.3	12.6		8		
	V.58/668/4	*Felis silvestris*						25.2	10.6	5.8	10	11		6		
	V.58/668/3	*Felis silvestris*	71.3	67.6	62.3	18	59	32	14.2	7	11.9	12.6		7.4	16.7	
	V.58/668/2	*Felis silvestris*	70.3	66.2		17		29.6	13.4	7	11.6	13.6			15.2	
	V.58/668/6	*Felis silvestris*	61	58.6	53.8	14	51.4	5	25.9	12.5	10.8	11.7		5.5	12	
LAUCHSTÄDT	MB.Ma.30066	*P. leo spelaea*		200		67	163		43	21.8	44	47.9		21.6		lx
LIMMERER LOCH	MB.Ma.44348	*Felis silvestris*								5.3	9.6	9.5		5		lx
MONTEMERANO	169035/2	*P. leo spelaea*				76.22					50.4	49.5		26.48		
NANKENDORF CAVE	MB.Ma.50678	*Felis silvestris*	55.9	53.3	48.5	13.6	45.9	22.5	10.4	5.2	9.3	9.7		5.2	10.3	rx
OBERFRANKEN (generic)	MB.Ma.30034	*Felis silvestris*	49	45.5	43	11.5	38.8		8.9	4.8	8.8	8.2		5.1	10.3	lx
OHNE FUNDORTANGABE (no name)	MB.Ma.43395	*Felis silvestris*				13.5				6.4	11.7	12.2		8.6		rx
	MB.Ma.43396	*Felis silvestris*	67	63.6	59.7	13	56.1	29.9	14	6.4	11.5	13.6		6.8	13.8	rx
	Mb.Ma.44382	*P. pardus*									26.3	26.4				lx
PADOVA (Museo di Zoologia)	AGR.MUS.02/2	*P. leo*				78.5					48	53				
PERUGIA Casalina	116/2	*P. leo*	233	228	210	71	202	118	52.7		43.4	53		31.4	59.5	rx
	116/2	*P. leo*	235	225	215		205	114.6	49			53.4			58.6	lx
	124/2	*P. onca*	193	182	162	59	156	90	37		35.5	38		22	47	rx
	124/2	*P. onca*	191	180	164	59	155	89.6	38		37	38		22.4	47	lx
	118/2	*P. pardus*	173	163	150	63	143	87.4	37		32.6	37.4		17	42.4	lx
	4823/2	*P. pardus*	165	158	146	54	141	85.5	34		27.5	33.6		26.3	38	rx
	4823/2	*P. pardus*	167	160	149	54	140	79.5	31.5		27	33		26.4	39	lx
	118/2	*P. pardus*	170	164	153	63	144	84	36.7		34	37.7		19	40	rx
PESCŐ CAVE	V.60/60	*Felis catus*			54.5	15.3	56.6		13.4	6.5	11.6	13		7.3	15	
PHOEBEN	MB.Ma.30067 (MB1911)	*P. leo spelaea*								21.8	43					
PIKERMI	ASII116.2	*Felidae*								6.3	11.8	12.8		8		
	ASII105	*Hyaenidae*				64.6				20	45.3	50.5		6.3		
	ASII125	*Machairodontinae*								15.2	27.3	33.8		26		lx
RABENSTEIN	1894I501	*P. leo spelaea*			160		148		36.4	17.4	38.2	37.6		16	37	lx
ROTER BERG	MB.Ma.30056	*Felis silvestris*				14				4.5	9.1	9.5		8.4		rx
SCHNEIDERLOCH	MB.Ma.44344	*Felis silvestris*	61	56.7	52.7	14.5	48	25.6	11	5.9	10.2	10.6		6.7		rx
SIENA	221/2	*Puma concolor*	112	107.2	98	29.4	93.3	48	22		17.2	20.5		12	26.3	rx
	221/2	*Puma concolor*	112.4	109.3	98.3	29.4	92.4	49	21.4		17.2	20.8		12.7	26	lx
SUSWA	Mb.Ma.30052.2	*P. pardus*	130	126.8	113.3	37.7	107.3	53.4	23.2	12.4	23.6	27		15.1	24.5	rx
	MB.Ma.30051	*P. pardus*				30.4					23.5			11.5		rx
	MB.Ma.30052.1	*P. pardus*	130.8	126	111.4	39.2	108	52.8	21.5	25	23.5	26.7		15.4	24.5	lx
SZELIM CAVE	G 57/285	*Canis lupus*								15	24					
TECCHIA DI EQUI	6059V	*P. leo spelaea*				66					50	47		18.64		
	6120V	*P. pardus*							28.4							
	6123V/1	*P. pardus*	113.62	111.5	103.03	16.19	101.19		22.53				23.81		14.12	
	6102V	*P. pardus*			118		110.5		26		24.8	25.5		13.6	24.6	
TÚRMIZ	Mb.Ma.30032.a (49886)	*Felis silvestris*		49.6		13	43.5	23.7	10.6	4.4	8.7	9.2		5.6		lx

	MB.Ma30032.b (49886)	*Felis silvestris*	54.5	51	49.3	11.7	45.8	25.4	11.7	5	8.9	10.4		5.7		rx
VEREZZI	V.10926	*Felis sylvestris*	67.8	64	59.6		56	31	14.52		11.5	13.34		5.8	14.7	
VÉRTESSZŐLŐS II	V.69.643	*P. onca gombaszoegensis*									40.7			22		
WILDSCHEUER	MB.Ma30028	*Felis silvestris*	56.4	54	49	14.6	46.5	10.4		5.3	10.3	10		4.5		rx
	MB.Ma30031	*Felis silvestris*				13.3				5.5	10	11.4		6		rx
WINTESHOF-WEST	1937II13336	*Pseudaeluridae*			64.7		60.4		19.4	7.9	13.2	15			18.7	lx
ZOOLITHENHOHLE	MB.Ma30078	*Panthea leo spelaea*								24	54.5	50.6				rx
	MB.Ma30081	*P. leo spelaea*								27.5	58	59.4				rx
	MB.Ma30075	*P. leo spelaea*								30	61.5	66.3		23.5		lx
	MB.Ma30072	*P. leo spelaea*	280	265	234	93	215	133	53.4	27	53.7	61.2		23.8		lx
	MB.Ma2002.2	*P. leo spelaea*				86.2				25.2	51.2	57.3		34		rx
	MB.Ma30079	*P. leo spelaea*								30	61.4	60.2				rx
	MB.Ma30074	*P. leo spelaea*				84				25.8	53	58.3		34		lx
	MB.Ma30080	*P. leo spelaea*								30.4	57.3	61.6				rx
	MB.Ma30073	*P. leo spelaea*								24.5	56.2	55.3				lx
	MB.Ma50949	*P. leo spelaea*				90				21.9	59	65		31		lx
	MB.Ma30076	*P. leo spelaea*						130	57	28.4	58	61				rx
	MB.Ma50948	*P. leo spelaea*	267	250	223		212		57.5	25.6	51.7	60.3			64	rx
	MB.Ma50948	*P. leo spelaea*	270	252	233		215		55	26.4	52	58.5			62	lx
	MB.Ma30077	*P. leo spelaea*	255	240	250	77	213	142	62	28	54.8	61.4		31		rx

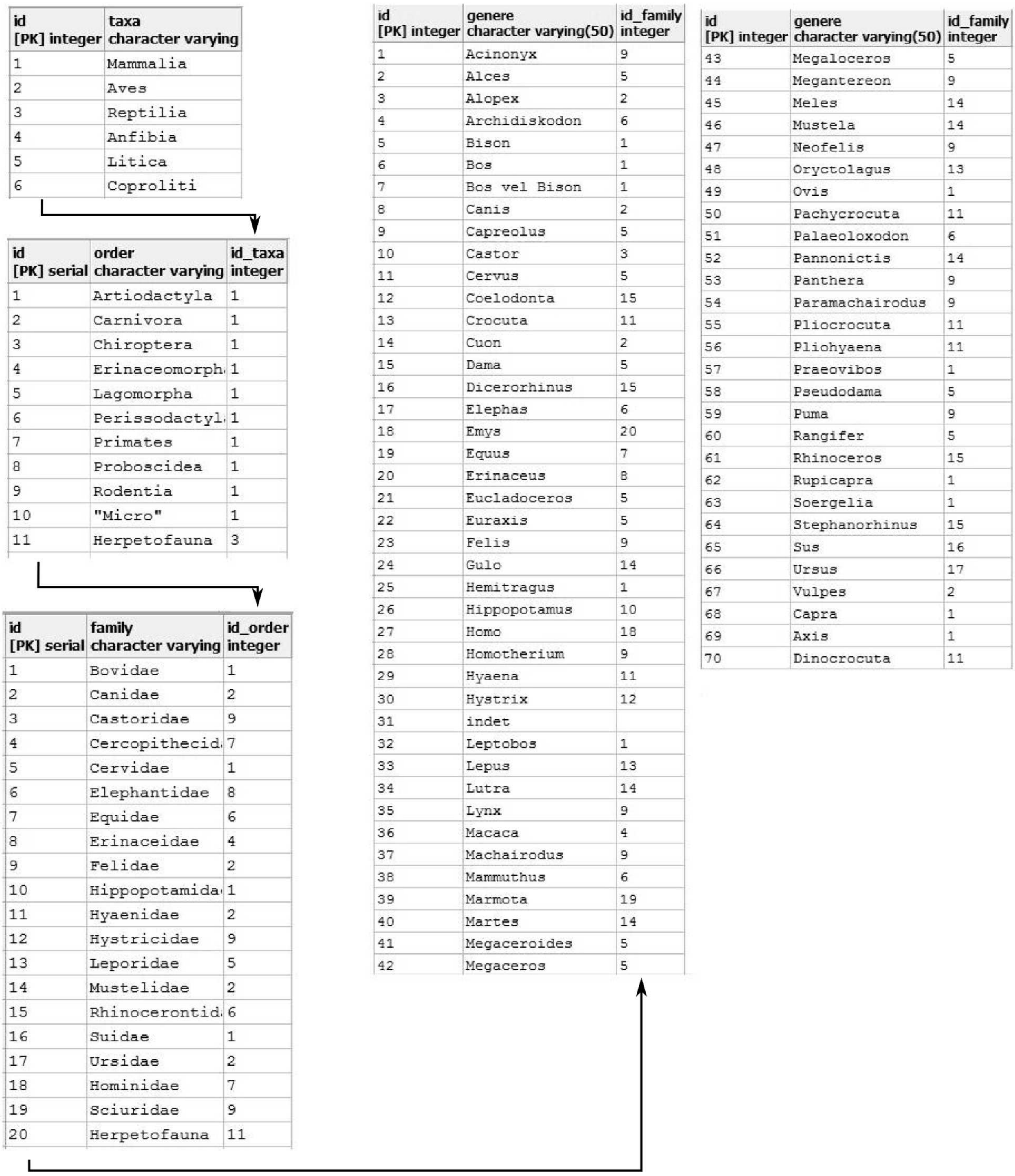
m_lower_teeth:

site_name	inventory_number	species	c_m	p_m	p	m	cl	cb	p3l	p4l	m1l	m1b	note
ABIMES de la FAGE	40950	*P. leo spelaea*							17.9				
	40947	*P. leo spelaea*					26.3	17.9		27.4		14.2	
	40948	*P. leo spelaea*					26.5	17.5					
	40951	*P. leo spelaea*							18.4				
	40952	*P. leo spelaea*							18.4				
	40953	*P. leo spelaea*								28.3			
	40945	*P. leo spelaea*								27.5			
	40946	*P. leo spelaea*		75						28	28.5	13.6	
ARAGO	CNR 283689	*P. pardus*		41.8	26	15.7	11	7.8	11	15	16	7	lx
	CNR 283689	*P. pardus*		42	26.3	16	11.3	8.5	11.2	15	16	7.8	rx
BAITS CAVE	V 62/559/2	*Felis silvestris*	38	24	14.8	10.6			6.6	8.4	10.7	4.2	
	V 62/559	*Felis silvestris*	35.3	23.1	14.3	10.2				8	10.2	4.1	
BAJÓT	V.60/55	*Felis sylvestris*	35	21	12.6	9	5.6	3.4			9	4	rx
	V.60/55	*Felis sylvestris*	34.5	21	12.7	8.6			5.6	7.5	8.7	4.2	lx
BALVE-SANSSOUCI MITTL. HOHLE	MB.Ma 30038.1	*Felis silvestris*	27.4	18.2	11.7	7.6			5.3	6.7	7.7	3.4	lx
	Mb.Ma 30038.2	*Felis silvestris*	28.6	18.3	11.8	7.5	4	3	4.9	7	7.3	3.6	rx
BANRWELL CAVE	MB.Ma 29669	*P. leo spelaea*								27.7			
BIVAK CAVE	1953.IX.24/1	*Lynx lynx*					9.1	6.3					
	1953.IX.24/2	*Lynx lynx*								12			
BRISTIE	Vpa 383	*P. leo spelaea*			41.4				16.6	25.4	26.6	13.3	
	Vpa 377/9	*P. leo spelaea*									28.4	13.4	
	Vpa 377/10	*P. leo spelaea*									29.6	12.2	
	Vpa 377/8	*P. leo spelaea*									27.7	11.6	
BUBASTIS	MB.Ma 30025	*Felis silvestris*		24.7									rx
	Mb.Ma 30026	*Felis silvestris*		22.1	13.3	10				7.2	10	4.5	lx
	MB.Ma 30022	*Felis silvestris*		21.6									lx
	MB.Ma 30024	*Felis silvestris*		22									rx
	Mb.Ma 30023	*Felis silvestris*		25.3									lx
	MB.Ma 30027	*Felis silvestris*		26.7									rx
	MB.Ma 30020	*Felis silvestris*		20.6									lx
	MB.Ma 30021	*Felis silvestris*		21.4									lx
BUCO DELLA STREGA	V.7376	*Felis sp.*		0	19	8				7	8	3.4	
BURGTONNA	MB.Ma 628	*Felis silvestris*		24	15	9			6.6	7.5	9	4	
	MB.Ma 85	*P. leo spelaea*											
	MB.Ma 83	*P. leo spelaea*					26.4	18.9					
	MB.Ma 81	*P. leo spelaea*	117	72.6	46	30.2	24.6	23.5		26.3	30.4	15.2	rx
CASTELLO	V.4468	*P. gombaszoegensis*											
CAVERNA POCALA	Vpa 5701	*P. leo*		78.6	47.4	32			17	28	32.4	16	
	Vpa 5619	*P. leo*									27.4	13.6	
	Vpa 5700	*P. leo*					32	22.4		28.7			
DECHENHOHLE	MB.Ma 106 (MB1910)	*P. leo spelaea*		68	43	28.6					28.5	15.4	rx
EQUI	6077V	*P. leo spelaea*					25	19.5					
	10037/2	*P. pardus*		49.3	31.18	20.5	15.3	10.7	13	19.22	20.4	8.72	
	10037/1	*P. pardus*		50.6	31.8	20.5	15	10.7	13	18.4	20.7	8	
	6113V	*P. pardus*									20	8.64	
	5460V	*P. pardus*					12.6	8					
	15111.1	*P. pardus*		46.69	29.15	17.74	12.53	9.71	12	17.25	18.63	8	lx
	15111.1	*P. pardus*		46	28.7	18	13.63	9.22	12.28	16.97	18.16	8.5	rx
FERRARA	nn	*P. leo spelaea*		71	45.3	27.8	23.5	17	19.32	26	27.8	13.8	
	nn	*P. leo spelaea*		71	45.6	28.3	25	17	19	27	28	14.6	
	G14.EFNI.1000	*P. pardus*		42.6	27	16.7	13	10	9.6	15.5	17	7	lx
	G14.EFNI.1000	*P. pardus*		43	27	17	12.7	10	10.8	15.3	17	7.7	rx
FIRENZE (Sala delle ossa)	C 1221/2	*P. pardus*		50.6	33.8	19.4	15.55	12.05	13.9	19.6	19.4	10.32	rx
	C 1221/2	*P. pardus*		50.81	33.11	18.7	16	11.3	13.75	19.2	19.55	10.1	lx
	C 8439/2	*P. pardus*		48.79	31		13.3	10.7		17.3	20.5		lx
	C 8439/2	*P. pardus*		48.64	31.7		14.09	10.5		17.92	18.57		rx
	C 8748/2	*P. pardus*		42	27	15.5	11.3	7.5	11	15.7	15.5	6.7	lx
	C 8748/2	*P. pardus*		42.27	27.15	15.79	10.5	7	11	15	16	7	rx
GAILENREUTH CAVE	MB.Ma 48115.2	*P. leo spelaea*	134	78.4	47	30.5	23.8	17	19	27	30.6	15	lx
	MB.Ma 48115.2	*P. leo spelaea*	134.2	75.7	45.4	30	23.5	15.5	18.3	26	30.2	14.6	rx
GOMBASZÖG	V.24063/2	*P. onca*					20	15.5					
	V.24063/3	*P. onca*					18.7	15.1					
	V.24063/4	*P. onca*					19.5	15.5					
	V.24062/3	*P. onca*	94.2	60	37.5	23.7	19.5	15.2	16.2	21.6	24.4	11.5	
	V.59.1044	*P. onca gombaszoegensis*					16.3	12.9					
	V.59.1084	*P. onca gombaszoegensis*									22.2	10.6	
	V.59/1041	*P. onca gombaszoegensis*							17.1				
	V.24063/1	*P. onca gombaszoegensis*							16.6	22			
GOSLAR (generic)	MB.Ma 44312	*Felis silvestris*											lx
	MB.Ma 44306	*Felis silvestris*	32.3			7.6	4.8	3.5			7.7	3.4	lx
	MB.Ma 44308	*Felis silvestris*	28.6	17.4	11.6	6.4	3.3	2.7	5	6.6	6.6	3.3	rx
	MB.Ma 44310	*Felis silvestris*	28.2	19.2	13.6	7	4.2	3	5.3	6.6	7	3.2	rx
	MB.Ma 44307	*Felis silvestris*	27.5	18.5	11.7		4.3	3	5.2	6.9	7	3.4	lx
	MB.Ma 44311	*Felis silvestris*	27.5	17.4	11	6.4	3.7	2.8	5	6.3	6.7	2.8	rx
	MB.Ma 44309	*Felis silvestris*	27.2	17.4	11.3	7	3.9	2.3	5	6.3	6.9	3	lx
GROTTA DEL BROION	V.10671/1	*P. leo spelaea*			50				20	29.42			
GROTTA DEL BRUSCO	27850	*Felis catus*		19	12	7			2.3	6.6	7.1	3	
GROTTA DEL CAPRIOLO	pitticapriolo1	*P. pardus*		52							21.1	9.5	
	pitticapriolo3	*P. pardus*									21.2	9.7	

GROTTA DEL CERE'	V.5251	*P. leo spelaea*					23.3	13.9					
	V.5248	*P. leo spelaea*					16.2	11					
	V.5256	*P. leo spelaea*											
GROTTA DEL VAGO	V.9128/2	*Felis sylvestris*		18.4	11.4	7	4.7	3.3	4.7	6.5	7.5	3	lx
	V.9128/2	*Felis sylvestris*		18.5	11.3	7	4.2	3	4.72	6.5	7.5	3.4	rx
GROTTA DELL'ORSO, SAN PRIMO, GABROVIZZA	Vpa 4692	*P. leo*		74.4	45.7	28.8			18.4	29	28.8	14.4	
GROTTA DI EQUI	senza numero	*P. cf. leo spelaea*				21.52	13.81	12.38		18.84	21.49	9.46	
	6075V	*P. leo spelaea*									29.5	0	
	6104V	*P. pardus*		51	32	20					20.4	8.64	
	6103V	*P. pardus*		46	28	19	11.38	8.7	12	16.48	19.32	8.54	
GROTTA DI FUMANE	nn	*P. leo spelaea*									25.8	10.4	
GROTTA DI SLOUP	V.140/2	*P. leo spelaea*		81.8	53	29.4	27.4	19	22	30	30.5	15	rx
GROTTA PAGLICCI	V.5676/3	*Felis sylvestris*		23.3	14.6	9			7	7.86	9	3.9	
	V.5678/1	*Felis sylvestris*									7.7	3.5	
	V.5678/2	*Felis sylvestris*							5.5				
	V.5676/2	*Felis sylvestris*		21	14.32	7.6	6.5	5	6.3	8.24			
	V.5676/1	*Felis sylvestris*		22	14	8.3	5	4	6.68	7.7	8.3	4	
GROTTA POCALA	25266	*P. leo spelaea*								28	30.2	15	
	25258	*P. leo spelaea*											
	25253	*P. leo spelaea*								27.3			
	25252	*P. leo spelaea*									30	15	
	25239	*P. leo spelaea*											
	25238	*P. leo spelaea*		76.7	49	29			19.62	30	29.3	15	
	25265	*P. leo spelaea*		64.5	39.5	26.3				24	26.3	13.4	
	25236	*P. leo spelaea*		77.3	49.7	30				24.5	30.4	16	
	25267	*P. leo spelaea*		76.4	49	29.1				28.4	29.3	14.3	
	25247/14	*P. leo spelaea*							21.38				
	25241	*P. leo spelaea*		67						24.3	26.9	13.3	
	25264	*P. leo spelaea*		78.4	48.24	32	30.7	21.7		29	31	14.1	
	25263	*P. leo spelaea*		72.3	47	27				25.4			
	25263	*P. leo spelaea*		68.9	45	22.4				25			
	25261	*P. leo spelaea*		74.5	47	29			18.5	28			
GROTTE D'AZE	AZE.K.13	*P. leo spelaea*		84.5					20.5		32		
GRUTA DO CALDEIRÄO	215	*Felis silvestris*							36	74	84	36	
	375	*Lynx pardinus*									139	61	
	156	*Lynx pardinus*									136	55	
	855	*Lynx pardinus*							241	248	350	140	
	838	*Lynx pardinus*									209	102	
HÁROMKÚTI CAVE	V.63/1480	*P. leo spelaea*									28	14.3	
HÁRVÖLGYI FÜLKE	V.75.174/2	*Felis cf. silvestris*								7			
	V.75.185/1	*P. leo cf. spelaea*								24.5			
HERMANNS CAVE	MB.Ma14298	*P. leo spelaea*			46		29.3	21	18.9	27.4			lx
IGRIC CAVE	V.60.1785/2	*P. leo spelaea*		74.7	48	27.6			17	26.3	27.4	14	lx
	V.60.1785/2	*P. leo spelaea*		77	52.1	28			18.6	25	28	13.8	rx
ISTÁLLÓSKŐI CAVE	V.60/49/1	*Falis catus*	33.4	21.7	13.5	8.9	4.4	3.4	6	7.6	8.8	4	
	V.59/261	*P. leo spelaea*								25.9			
	V.59/245	*P. leo spelaea*									27.8	14.3	
	V.59/242	*P. leo spleaea*									32	16.2	
KŐLYUK	V.63/1927	*Felis cf. domestica*	31	19.9	12.2	8			5.4	7	8	3.6	
KISLÁNG	V.13327	*P. cf. onca gombaszoegenesis*					16.5	13.7					
LA PARTE	LP-4	*P. leo spelaea*					28	23					
LAMBRECHT CAVE Holocene	V.58/668/4	*Felis silvestris*		20	12.8	7.8			5.8	7.2	8.2	4	
	V.58/668/2	*Felis silvestris*		22.1	14	9			6.1	7.6	8	4	
	V.58/668/5	*Felis silvestris*	32.2	21.1	13.4	8.4	4.8	3.6	6	7.4	7.1	3.7	
	V.58/668/6	*Felis silvestris*		21.7	13.8	8.3			6.4	7.2	8.3	3.9	
	V.58/668/3	*Felis silvestris*	35.8	21.4	14.1	8.4	4.5	3.8	6.9	7.7	8.3	3.8	
	V.58.668/1	*Felis silvestris*		22.8	14.2	9.2			6.2	8	9.2	4	
LAUCHSTÄDT	MB.Ma30066	*P. leo spelaea*	111	66	42.4	27.7			16.9	24.7	27.4	13.7	lx
LIMMERER LOCH	MB.Ma44348	*Felis silvestris*		21.7	12.7	8.8					8.8	3.5	lx
MONTEMERANO	169035/2	*P. leo spelaea*					25.4	14.82		26.7	28.3	0	
NANKENDORF CAVE	MB.Ma50678	*Felis silvestris*	30.4	20.3	13	8.3					8.3	3.6	rx
OBERFRANKEN (generic)	MB.Ma30034	*Felis silvestris*	26	16.9	10.2	7.5	3.9	2.7	4.3	6	7.5	3.4	lx
OHNE FUNDORTANGABE	MB.Ma43396	*Felis silvestris*	35.5	23.7	15.4	9.2	5.3	4	7.2		9.3	4.2	rx
	MB.Ma43395	*Felis silvestris*	33.3	22.4	12.2	9.6				7.2	9.8	3.9	rx
	MB.Ma30007.2	*P. onca*									22.6	11.5	rx
	MB.Ma30007.4	*P. onca*								23			rx
	MB.Ma30007.3	*P. onca*								22.7			lx
	Mb.Ma44382	*P. pardus*		48	30	19			12.6	17.4	19	9	lx
PADOVA (Museo di Zoologia)	AGR.MUS.02/2	*P. leo*		71			24	16	16.5	24	28.5	13.6	
PERUGIA Casalina	116/2	*P. leo*				28.5	23	16.5			28	14	lx
	116/2	*P. leo*		71	45.7	28	24.3	16.7	18	27	28	14.4	rx
	124/2	*P. onca*		57.7	36.2	23.7	20	13.8	14.9	22	24	12.2	lx
	124/2	*P. onca*		56.8	35.5	23.54	20	14	15	21	24	12.5	rx
	118/2	*P. pardus*		53	34	20				20	20	10.5	lx
	118/2	*P. pardus*		53	34.4		18.2	13.3		20			rx
	4823/2	*P. pardus*		48	30	18	15.3	11	13.6	17	18	9	lx
	4823/2	*P. pardus*		48.5	30.5	18	14.7	11.4	13.5	17	18	8.5	rx
PESCŐ CAVE	V.60/60	*Felis catus*		22	14	9			6.5	8.3	9	4.2	
	V.60/62/1	*Lynx lynx*					10	7.3					
PHOEBEN	MB.Ma30067 (MB1911)	*P. leo spelaea*			41.3				15.3	24.4			rx

PIKERMI	ASII116.2	*Felidae*	37	25	15.4	10.7	4.4	4.3	8.4	10.7			
	ASII125	*Machairodontinae*	108.6	70.4	42.3	30	14.5	9.3		27	30	13.3	
	ASII605	*Machairodontinae*							20.8	27.2			rx e lx
QUEDLINBURG	MB.Ma.29597	*P. leo spelaea*								30.3			
RABENSTEIN	1894I501	*P. leo spelaea*		57.4	36.2	21.5			13.8	21.6	21.7	11.4	
ROTER BERG	MB.Ma.30056	*Felis silvestris*	31.2	19.5	12.3	7.5				6.4			rx
	MB.Ma.51507.1 (MB.Ma.29062 12)	*P. cf. leo spelaea*											
	MB.Ma.3221	*P. leo spelaea*					28.8	21.4					
	MB.Ma.30061	*P. leo spelaea*									31.4	16	rx
SÁRKÁNY LYUK	V.60/54	*P. leo spelaea*					21.9	14.5					
SCHNEIDERLOCH	MB.Ma.44344	*Felis silvestris*	29.9	18.4	12	7.3	4.3	3.2	5	6.6	7.4	3.2	rx
SIENA	221/2	*Puma concolor*		40	25	15	10	6.5		12.9	15.1	6.9	lx
	221/2	*Puma concolor*		39	23.8	15.1	9.5	6.8	11		15	7.2	rx
SLIVIA	SL 5	*Homotherium crenatidens*									32.1	12.3	
SUSWA	MB.Ma.30051	*P. pardus*											
	MB.Ma.30052.1	*P. pardus*	75.4	45.5	31	18.5	14.5	9.5	12	19	18.5	8.8	lx
	MB.Ma.30053	*P. pardus*					12.8	9.3					lx
	Mb.Ma.30052.2	*P. pardus*	75.2	47.2	31.6	18.6	14.4	9.6	12	19.4	18.2	8	rx
SZELIM CAVE	G 57/60	*P. leo spelaea*									32.8	16.2	
TÜRMIZ	MB.Ma.30032.b (49886)	*Felis silvestris*	29	18	11.2	7.5	4	3.2	4.8	6.6	7.7	3.6	rx
	Mb.Ma.30032.a (49886)	*Felis silvestris*	25.8	17.7	10.7	6.7			4.6		6.2	3	lx
TECCHIA DI EQUI	6059V	*P. leo spelaea*		73	46.8	28.84	21.5	15.4	18.54	27.44	29	14.4	
	6070V	*P. leo spelaea*								28.3			
	6064V	*P. leo spelaea*											
	6102V	*P. pardus*		46.5	38.54	19			12	17	19	7.68	
	6125V	*P. pardus*											
	6131V	*P. pardus*											
	6114V	*P. pardus*									18.3	17.5	
	6116V	*P. pardus*					13.4	10.8					
	6120V	*P. pardus*									20.6	8.64	
	6123V/2	*P. pardus*											
	6123V/3	*P. pardus*											
	6119V	*P. pardus*											
	6123V/1	*P. pardus*											
	6110V	*P. pardus*							11.48				
UPPONYI I. KŐFÜLKE	V.60/61251	*P. onca gombaszoegensis*								22.8	22.3	10.8	
VÉRTESSZŐLŐS II	V.69.1231	*Homotherium latidens*					9	13.7					
	V.69.648	*P. cf. leo fossilis*								27.7			
	nn	*P. leo fossilis*									27.6	13.9	
	V.69.652/2	*P. leo spelaea*											
	V.69.675	*P. leo spelaea*									32	16.6	
	V.69.674/3	*P. leo spelaea*									30.3	15.8	
	V.69.674/2	*P. leo spelaea*									27.4	14.3	
	V.69.674/1	*P. leo spelaea*									30.7	16.4	
	V.69.643	*P. onca gombaszoegensis*					22.8	16.2	19.3				
VEREZZI	V.10926	*Felis sylvestris*			23.44	9.2			7	8.2	9	4.5	
WILDSCHEUER	MB.Ma.30028	*Felis silvestris*	31.8			8.8							rx
	MB.Ma.30031	*Felis silvestris*	31.6	20.6	12.8	7.9	4.2	3.4	5.7	6.7	7.9	3.5	lx
YENI ESKIHISAR	1968VI792	*Miomachairodontinae*								22.5	26.5	11.2	
ZOOLITHENHOHLE	MB.Ma.30073	*P. leo spelaea*		80.3	50.6	32			21.1	30	32.4	15.6	lx
	MB.Ma.50949	*P. leo spelaea*	140	75.1	56.4	29.7			18.2	27.5	29.6	14.5	lx
	MB.Ma.30076	*P. leo spelaea*		78.2	48.7	30.7					30.6	16.2	rx
	MB.Ma.30077	*P. leo spelaea*	133	76	50.5	29	28			28.4	29.2	14	rx
	MB.Ma.30081	*P. leo spelaea*		82					20.5				rx
	MB.Ma.30075	*P. leo spelaea*		80.3	51.6	30.3			19.8	30.7	30.2	15.9	lx
	MB.Ma.30072	*P. leo spelaea*	140	81		30.3				29.2	30.3	15.7	lx
	MB.Ma.30079	*P. leo spelaea*		74.3	47.3	29			19	27.7	29	13.5	rx
	MB.Ma.30074	*P. leo spelaea*	132.6	72.4	45.3	28.4	25.6	17.4	18.2	26.7	28.3	14.7	lx
	MB.Ma.30080	*P. leo spelaea*		79.7	52	30.7				28	30	15	rx
	MB.Ma.50948	*P. leo spelaea*	135.6	78.3	50.7	30.3	26	18		27.7	30	14.5	lx
	MB.Ma.50948	*P. leo spelaea*	131.5	74.3	44.7	30	26.3	19.6	17	26.5	30.2	14.7	rx
	MB.Ma.2002.2	*P. leo spelaea*	135	73.4	45.2	27.6	25	16.9	18	26.2	27.8	14.1	rx
	MB.Ma.30078	*P. leo spelaea*		80.5						28.5			rx

Specie_



id [PK] integer	taxa character varying
1	Mammalia
2	Aves
3	Reptilia
4	Anfibia
5	Litica
6	Coproliti

id [PK] serial	order character varying	id_taxa integer
1	Artiodactyla	1
2	Carnivora	1
3	Chiroptera	1
4	Erinaceomorph	1
5	Lagomorpha	1
6	Perissodactyl	1
7	Primates	1
8	Proboscidea	1
9	Rodentia	1
10	"Micro"	1
11	Herpetofauna	3

id [PK] serial	family character varying	id_order integer
1	Bovidae	1
2	Canidae	2
3	Castoridae	9
4	Cercopithecid	7
5	Cervidae	1
6	Elephantidae	8
7	Equidae	6
8	Erinaceidae	4
9	Felidae	2
10	Hippopotamida	1
11	Hyaenidae	2
12	Hystricidae	9
13	Leporidae	5
14	Mustelidae	2
15	Rhinocerontid	6
16	Suidae	1
17	Ursidae	2
18	Hominidae	7
19	Sciuridae	9
20	Herpetofauna	11

id [PK] integer	genere character varying(50)	id_family integer
1	Acinonyx	9
2	Alces	5
3	Alopex	2
4	Archidiskodon	6
5	Bison	1
6	Bos	1
7	Bos vel Bison	1
8	Canis	2
9	Capreolus	5
10	Castor	3
11	Cervus	5
12	Coelodonta	15
13	Crocuta	11
14	Cuon	2
15	Dama	5
16	Dicerorhinus	15
17	Elephas	6
18	Emys	20
19	Equus	7
20	Erinaceus	8
21	Eucladoceros	5
22	Euraxis	5
23	Felis	9
24	Gulo	14
25	Hemitragus	1
26	Hippopotamus	10
27	Homo	18
28	Homotherium	9
29	Hyaena	11
30	Hystrix	12
31	indet	
32	Leptobos	1
33	Lepus	13
34	Lutra	14
35	Lynx	9
36	Macaca	4
37	Machairodus	9
38	Mammuthus	6
39	Marmota	19
40	Martes	14
41	Megaceroides	5
42	Megaceros	5
43	Megaloceros	5
44	Megantereon	9
45	Meles	14
46	Mustela	14
47	Neofelis	9
48	Oryctolagus	13
49	Ovis	1
50	Pachycrocuta	11
51	Palaeoloxodon	6
52	Pannonictis	14
53	Panthera	9
54	Paramachairodus	9
55	Pliocrocuta	11
56	Pliohyaena	11
57	Praeovibos	1
58	Pseudodama	5
59	Puma	9
60	Rangifer	5
61	Rhinoceros	15
62	Rupicapra	1
63	Soergelia	1
64	Stephanorhinus	15
65	Sus	16
66	Ursus	17
67	Vulpes	2
68	Capra	1
69	Axis	1
70	Dinocrocuta	11

10. About the Author

Elena was born in 1984 in a tiny island of Venice, between the sea and the Venician lagoon. Like several other children, she was very young when following her passion and hanging around the beaches for uncoltivated gardens she had the opportunity to observe the behavior various animals and to consider relationships among different species. Thanks to sea storms, many different colored shells were washed up on the shore. Moreover, the island is characterized by a proctective barrier built several centuries ago: there on the white and pink rock floor, she could observe circular ammonites spread everywhere.

Here for the first time she wondered why the shells were showing similar features, but sometimes so many different colors? From where did they come from? How long had they been under the sea? And, why such kinds of strange petrified snails were observable on the “murazzi”?

The desire for study doesn't develop for everyone in the same way, and at that time, when the moment to choose her high school came, she just loved maths so she opted for the school for accountants and programmers.

Over the years, however, the idea of traveling in far countries, learning something nobody knows, and the complete lack of interest for a booring office job, persuaded the troubled and nervous Elena to change her path. So, at eighteen, she decided to leave her comforting hometown for a larger city. Padua represents, also today, one of the most active cities for history and heritage in Italy, with a prestigious University where Geology and Natural Sciences faculties are offering students different curricula focusing on research and marketing (often for the offshore oil industry).

During her Msc thesis in Natural History and Museology, Elena finally approached the study of animal skeletal anatomy, and had the opportunity to deals with "ancient bones", primarily experiencing works in fossil conservation and restoration.

For her first paleontological restoration, she first treated fossil palm trees from the Eocene site of Bolca (Verona) hosted in the Padua Museum. Then fossil whales from Salsomaggiore (Parma) and finally the South American *Megatherium* skeleton in Turin. All these, and several other projects, allowed a young and curious woman to extend (sometimes confusing) her knowledge about geological ages, the evolutionary serie of species, and the complexity of skeletal anatomy. Moreover, she realized how many fossils account for the North Italian paleontological heritage.

After three years, the nearest city where to deepen the methodological approach to fossils was the University of Ferrara, and there Elena had change to complete her master degree dealing both with the study of animal fossils and the human-animal relationships.

Finally, she began her doctorate at the Earth Science Department at the University of Florence. Here she had the opportunity (and the privilege) to enlarge her horizons. The field work experiences in Spain, Georgia and Eritrea, and learning about foreign cultures and different paleontological approaches (using only square or GIS instruments) permanently influenced her concept of excavation. Also, getting international grants allowed her to visit foreign museums, in Berlin, Munich and Budapest, guaranteeing the temporal continuity and establishing a productive network for future research.

In the last three years Elena has made an enormous leap ahead towards pure research, developing self-financing and managing skills and experiences for drafting research articles, dealing with different subjects but all perfectly centered within a scientific paleontological network.

Scientific production

Publications:

- Ghezzo E., Bergamo A. (in review). Critical overview about cranial variability of European and African lions (*Panthera leo* ssp.). Annales de paléontologie
- Ghezzo E., Sami M. (in review). Mammiferi del Pleistocene superiore nelle grotte dei Gessi di Brisighella e Rontana. In PIASTRA S., LUCCI P. (eds.) *I Gessi di Brisighella e Rontana-Castenuovo*, Faenza.
- Ghezzo E., Boscaini A., Madurell-Malapeira J., Rook L. (in press). Lynx remains from the Pleistocene of Valdemino cave (Savona, Northwestern Italy), and the oldest occurrence of *Lynx spelaeus* (Carnivora, Felidae). Rendiconti Lincei doi: 10.1007/s12210-014-0363-4
- Ghezzo E., Rook L. (in press, accepted). The remarkable *Panthera Pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology. Quaternary Science Reviews
- Ghezzo E., Rook L. (2014). *Cuon alpinus* (Pallas, 1811) (Mammalia, Carnivora) from Equi (Late Pleistocene, Massa-Carrara, Italy): anatomical analysis and palaeoethological contextualisation. Rendiconti Lincei 25: 491-504
- Ghezzo E., Palchetti A., Rook L. (2014). Recovering data from historical collections: stratigraphic and spatial reconstruction of the outstanding carnivoran record from the Late Pleistocene Equi cave (Apuane Alps, Italy). Quaternary Science Reviews 96: 168-179
- Rossetti S., Ghezzo E. (2014). Segnalazione di una vertebra di orso nell'Abisso Col de la Rizza (Provincia di Pordenone). Quaderni del Museo di Storia Naturale di Ferrara 2: 11-16
- Ghezzo E., Bertè D.F., Sala B. (2014). The revaluation of Galerian Canidae, Felidae and Mustelidae of the Cerè Cave (Verona, Northeastern Italy). Quaternary International 339-340: 76-89

Podium and poster presentations at congressess:

- Ghezzo E. (2014). A review of *Cuon alpinus* from the Equi Cave (Late Pleistocene, Apuane Alps). EAVP (European Association for Vertebrate Paleontology), XII Annual Meeting.Turin June, 24-28, Abstract Book and Field trip guide
- Kotsakis T., Costeur L., Del Favero L., Fornasiero M., Ghezzo E., MaiorinoL., Mietto P., Piras P., Rook L., Sansalone G., Pandolfi L. (2014). Reassessing the (?)Early Oligocene vertebrate

assemblage of Monteviale (Vicenza, Italy). EAVP (European Association for Vertebrate Paleontology).), XII Annual Meeting, Turin June, 24-28, Abstract Book and Field trip guide

- Cenni C., Ghezzo E., Cioppi R., Rook L. (2013). Il leopardo di Equi: analisi morfologica e contestualizzazione cronologica. Giornate di Paleontologia XIII ed. Perugia, 23-25 maggio 2013, Volume dei riassunti
- Ghezzo E., Ponzo M. (2013). Il sito del Villafranchiano medio di Steggio (Possagno, TV): rivalutazione delle specie e nuovi restauri. Giornate di Paleontologia XIII ed, Perugia, 23-25 maggio 2013, Volume dei Riassunti
- Rook L., Ghezzo E., Lordkipanidze D., Tsikaridze N., Delfino M., Longo L. (2012). Archeologia e Paleontologia senza confini: il contributo Italiano al progetto Dmanisi (Georgia). In: Archeologia pubblica in Italia. Università degli Studi di Firenze / Comune di Firenze, Firenze, 29-30 Ottobre 2012
- Ghezzo E. (2012). Revision of *Ursus* and *Marmota* from Grotta del Cerè (Northeastern Italy). Quaternary International, Abstracts: 279-280
- Bartoli C., Cioppi E., Ghezzo E., Rook L. (2012). Canidi e Felidi della Grotta di Equi (Fivizzano, MS). Giornate di Paleontologia XII edizione – Catania, May 24-26 2012; Abstracts Volume: 71.
- Ghezzo E. (2012). Felidi e Ienidi d'Italia e d'Europa del Pleistocene medio e superiore: studio e georeferenziazione dei reperti museali. Giornate di Paleontologia XII edizione – Catania, May 24-26 2012; Abstracts Volume: 86.
- Ghezzo E. (2012). Felidi e Ienidi d'Italia e d'Europa del Pleistocene medio e superiore: studio e georeferenziazione dei reperti museali. (PhD Days)$_3$ – Firenze, May 16 2012; Abstracts Volume: 51- 52.
- Ghezzo E., Cioppi E., Rook L. (2012). Applicazioni GIS per l'informatizzazione e la ricostruzione spaziale dei dati storici del sito pleistocenico di Equi (Fivizzano, MS). Giornate di Paleontologia XII edizione – Catania, May 24-26 2012; Abstracts Volume: 47.

Public conferences:

- June 26, 2012: Conference at the Natural History Museum of Trieste. Title: “Carnivori, una storia lunga un milione di anni”
- May 15, 2010: Conference at the National Archaeological Museum of Adria (Soprintendenza per i Beni Archeologici del Veneto). Title: “Sepolture animali in contesti sepolcrali del Veneto (Con l’esempio della Biga di Adria)”

Field works:

- Palaeoantropological field-work in Mulhuli Amo site (Buia, Eritrea) Nov 17-Dec 01, 2012
- Archaeological excavation in the Upper and Middle Paleolitic site of “Grotta di Fumane” (Verona, Italy) Sept 04 – 22, 2012
- Dmanisi Paleoanthropology Field School 2012 (Georgia) July 30 –Aug 5, 2012
- Palaeontological exavation in the Pliocene site of Incarcal (Spain) July 01-11, 2012
- Palaeontological excavation in Cava Filo, S. Lazzaro di Savena (Bologna) 2007, 2008, 2011

Work experience in the field of Preparation/Restoration:

- Pre-restoration mapping using CAD Software of *Mammuthus meridionalis* (L'Aquila)	2013
- Restoration of two skeletal horses for the archaeological exhibition: “Venetkens” (www.venetiantichi.it)	2013
- Restoration of Miocene Odontocetes in the GeoPaleontological Museum of Padova (www.unipd.it/musei/geologia)	2010
- Restoration of a hourse conservated in the Archaeological Museum of Oderzo (Treviso)	2010
- Restoration of Zangheri Collection (avifaunal embalmed) in the Natural History Museum of Verona	2009
- Disassembly and assembly of an entire skeleton of *Loxodonta africana* at Natural History Museum,Turin	2009
- Restoration of a dinosaur model (*T. rex* family) at Natural History Museum,Turin	2009
- Restoration of a *Megatherium* sp. skull and (other bones) at Natural History Museum of Torino	2009
- Restoration of the Bolca vegetation in the University collections of Padova and Modena Universites	2007-2008
- Modelling of two whales bones specimens in the Salsomaggiore Museum	2007

Grants and scholarships:

- Deutscher Akademischer Austausch Dienst (https://www.daad.de/en/) grant for research stay at the Naturkunde Museum (Berlin) and at the Staatliche Naturwissenschaftliche Sammlungen Bayerns (Munich). November 2013-December 2013 (two months).
- Synthesys Grant (http://www.synthesys.info) for study visit at the Hungarian Natural History Museum (Budapest). November 2014 (two weeks).

10.1. Future research

2015 will begin with several expectations and research projects. Since 2009 (when new excavations and the discovery of valyable “overlooked” old collections in museum confirmed me that an enormous amount of fossils have yet to be investigated), impressive new studies have started expecially thanks to the promotional work of the Pleistocene site of Equi.

Firsly, last summer the Departments of Earth Science and Biology of the University of Florence began a project for the mithocondrial DNA reconstruction of the leopard from Equi, cooperating also with a local private organization for the conservation of large felids. Recently, salivary samples have been donated by the Tiger Experience organization (from two leopards from Africa and one from Asia). They will be compared to fossils with the expectance that they will shed light on the evolutive and distributional trends of this large Pleistocene hunter. Similar research has never been done in Europe, mostly because of the limited number of findings, and because the evolutive history of this elusive predator was based on Asian and African comparisons, the latter putatively recognized as the area of origin of the species.

Another characteristic of Equi is the imbalancee relationship among species, with a large amount of carnivorans in respect to herbivores. In this new year I plan to investigate it within a paleoecological perspective, studying the environments and behaviors of modern species and especially the relationship between these species and bears. As previously explained, the presence of several young leopards implies a changed behavior, and I want to investigate if a similar divergent trend existed for the other carnivorans.

Given that the most frequent species at Equi is the wolf (after the bear), the morphology of this large hunter will be also analyzed, comparing it to the modern Tuscan populations, using the osteological collection of the Italian State Forestry Corps.

The large felids are going to keep me busy also in the new year, with the analysis of the intriguing *Homotherium* from Pirro. These fossils are from three different animals, one adult and two immature and the morphological development and ontogeny of the species will be investigated for the first time.

Other focuses have been established in the last three years. Among these, in the first months of 2015 a revision of Pleistocene fauna from Grotta Pocala will be concluded as a master Thesis at the University of Padua (for wich I am co-tutor), and this research will be edited and finally published.

The paleontological heritage from Veneto also allowed paleontologists to recover Early Oligocene findings from Monteviale (Vicenza). Even though this fauna lies outside the goal of my thesis project, in 2015 the study of these exciting fossil materials will be one of my goals.

Since there are many other things to do in the next years and ideas for future projects are much more that the available time... I really hope to continue contributing to unveil and narrate the exciting story of fossils.

11. Acknowledgments

E' indispensabile alla fine di questo percorso riconoscere la mia gratitudine verso tutte quelle persone ed istituzioni che hanno ispirato, influenzato e promosso il mio lavoro e la mia vita professionale.

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Non ci sono parole, invece, per dichiarare apertamente quello che Alberto ha fatto e continua a fare ogni giorno per noi. Questo testo non avrebbe mai visto la luce se non fosse stato lui a spronarmi e sostenermi per tutto questo tempo, dandomi tutto il suo amore e tenendomi stretta nei momenti (numerosi) di sconforto.

Realizzare che il tuo lavoro ha valore aiuta ad essere più consapevole nello studio e produttiva nei risultati. Per questo motivo, professionalmente, è doveroso ringraziare in questa sede coloro che hanno facilitato il mio lavoro facendomi accedere liberamente alle collezioni e nei magazzini dei musei, luoghi in cui si nascondono tesori inimmaginabili, in particolar modo Mariagabriella Fornasiero del Museo di Geologia e Paleontologia dell'Università di Padova,

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Ringrazio la Società Paleontologica Italiana per il supporto che fornisce annualmente ai giovani paleontologi italiani, per essere il luogo pulsante di incontro e scontro di diversi mondi paleontologici.

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