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First fossil record of leopard-like felid (*Panthera* cf. *pardus*) from alluvial deposits of the Po River in northern Italy

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ABSTRACT

A slender right felid tibia has been found in river deposits of the Po River in the territory of Cremona (Northern Italy). The fossil, found in allochthonous position within an alluvial bar, shows an overall slenderness and subtlety, different shape of the shaft from lateral view, or less pronounced medial malleolus, corresponding in morphology and dimensions rather with tibiae of modern leopards than with shinbones of larger pantherines or feline cats. The bone is, however, faintly rounded (surface erosion of the edges in particular on the head of the tibia), indicating a limited transport (rafting). Based on that, it is determined as *Panthera* cf. *pardus* only. The whole mammalian fossil record from the site consists predominantly of large herbivores (*Elephas* (*Palaeoloxodon*) *antiquus*, "*Dihoplus*" (*Stephano-rhinus*), *kirchbergensis, Bison priscus, Megaloceros giganteus, Mammuthus primigenius, Alces alces, Cervus elaphus*), whereas carnivores (*Ursus arctos, Crocuta crocuta* ssp., *Canis lupus, Vulpes vulpes*) are very rare and composed only by a few specimens. The species composition indicates probably a mixing of different faunal assemblages from warm (interglacial) and cold (glacial) periods of the Late Pleistocene.

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1. Introduction

The recent geographical distribution of the leopard (Panthera *pardus*) stretches from Africa to East Asia. During the Pleistocene, however, this felid inhabited Europe, but never penetrated to North America (Turner and Antón, 1997). The oldest European fossil record of the leopard is mentioned from French site of Le Vallonnet (Vallonnet Cave) dated to the period 1.0-0.9 Ma ago (Moulle et al., 2005; Madurell-Malapeira et al., 2014), although Hemmer (2001) attributed all Early Pleistocene leopard fossils to Puma pardoides. Middle Pleistocene remains of leopards are known from the Iberian Peninsula (Sanchis et al., 2015) through Western and Central Europe to the south of the Old Continent (Sabol, 2008). Even at the beginning of the Last Glacial, the species was extended here from the south to Poland. With the intense climate changes, however, leopards gradually retreated southward and had occurred only in isolated areas at the end of the Pleistocene Period (Musil, 1986). They probably survived for longer only in the Iberian Peninsula (Late Glacial – Early Holocene; Sauquó and Cuenca-Bescós, 2013; Sanchis et al., 2015) and in Eastern Europe even until historical times (Spassov and Raychev, 1997).

A relatively rich fossil record of leopards comes from the Apennine Peninsula, whence minimally 32 Pleistocene sites are so far referred (Maviglia, 1952; Diedrich, 2013; Sauquó and Cuenca-Bescòs, 2013; Pacher and Rabeder, 2016). The postcranial bones are, however, much more rare in the fossil record than finds of cranial skeleton and teeth. In summer 2014, however, a new well-preserved leopard-like tibia was discovered on the alluvial bar of the Po River right bank in Cremona (Northern Italy), close to the harbour entrance (Fig. 1). The area, which is well-known for its numerous palaeontological Quaternary record, composes of a crescent-shaped meander bar (about 1 km), located downstream the big meander of Isola Serafini, in which converges the Adda River.

Ever since the 1970s large fossils and palaeontological evidence have been discovered in this area which do not show signs of having been transported by the river probably due to the intense erosion process generated by the natural morphology of the river, the hydrodynamic context generated by the confluence with the Adda river, the current generated by the functioning of the Isola

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Fig. 1. Location of the site near Cremona in northern Italy, where leopard-like tibia was found.

Table 1

Panthera cf. pardus, measurements of the right tibia from alluvial deposits of the Po River near Cremona in northern Italy.

Panthera cf. pardus (tibia dext.), Po River (Italy)	
(1) Maximum length	239.4 mm
(2) Length of the tibial crest	71.5 mm
(3) Maximum anteroposterior diameter of the proximal epiphysis	45.5 mm
(4) Maximum transverse diameter of the proximal epiphysis	42.0 mm
(5) Breadth of the poplitea cavity	10.1 mm
(6) Minimum anteroposterior diameter of the diaphysis	23.3 mm
(7) Minimum transverse diameter of the diaphysis	18.7 mm
(8) Maximum anteroposterior diameter of the distal epiphysis	21.9 mm
(9) Maximum transverse diameter of the distal epiphysis	29.0 mm
(10) Anteroposterior diameter of the distal articular surface	14.5 mm
(11) Transverse diameter of the distal articular surface	21.9 mm

Serafini hydroelectric power station and the possible presence of surface Pleistocene fossiliferous strata.

The found leopard-like fossil is the first record of large felid from the Po River. It is a part of the mammalian assemblage, consisting predominantly of large herbivores (*Elephas (Palaeoloxodon) antiquus*, "Dihoplus" (Stephanorhinus) kirchbergensis, Bison priscus, Megaloceros giganteus, Mammuthus primigenius, Alces alces, Cervus elaphus). Carnivores, such as Ursus arctos, Crocuta crocuta ssp., Canis lupus and Vulpes vulpes, are very rare and composed only by one or few specimens. The species composition indicates a typical river mixing of different faunal assemblages from warm (interglacial) and cold (glacial) periods of the Late Pleistocene.

The focus of the present paper is the paleontological description of the first leopard-like fossil record from the alluvial sediment of Po River, considering taphonomy, the morphology, the aging and the relationship with other species recorded at the region in the Late Pleistocene of northern Italy.

2. Material and methods

The found grey-brown and faintly rounded tibia (MSDP 321) is housed in the Museo Paleoantropologico del Po in San Daniele Po (CR), Italy. The bone colouring is typical for the fossil record from alluvial sediments of the Po River, namely partially mineralised remains containing pyrite, limonite, hematite, goethite, manganese, and manganocalcite (Persico et al., 2012). These minerals indicate an anoxic environment of the fossilization, characterized by abundant carbonificated organic plant matter and subsequent reworking in an oxidizing environment. The surface erosion of the edges in particular on the bone head indicates a limited transport (rafting). Traditional morphometric analysis of osteological remains was employed for precise determination of the felid bone. The measured data is in millimetres; with measurements taken to the



Fig. 2. Measurements of found tibia according to the methodology of Wojtusiak (1953), Gonzáles (2003), and Barycka (2008). For numbered dimensions see Table 1.

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Fig. 3. Panthera cf. pardus, tibia dext. from alluvial deposits of the Po River near Cremona in northern Italy. The surface erosion, indicating a limited transport (rafting) is observed mainly on the bone head and tibial crest. a – anterior view, b – posterior view, c – medial view, d – lateral view, e – dorsal view, f – plantar view.

nearest 0.1 mm with engineering vernier calipers, 0.3 mm standard deviation, 0.1 mm dispersion, and 0.42% random error (Table 1). The basic morphological terminology and measuring methods of fossil remain were borrowed from Wojtusiak (1953), Gonzáles (2003), and Barycka (2008) (Fig. 2).

The found fossil record is compared to leopard, cheetah, lion and cave lion osteological remains housed in the Slovak National Museum – Natural History Museum in Bratislava, Slovak Museum of the Nature Protection and Speleology in Liptovský Mikuláš (Slovakia), the Anthropos Museum in Brno (Moravia, Czech Republic) and the Natural History Museum in Lyon (France), together with data published in scientific monographs and magazines.

3. Description and comparison

Family Felidae Fischer de Waldheim, 1817. Subfamily Pantherinae Pocock, 1917. Genus *Panthera* Oken, 1816.

Panthera cf. pardus (Linnaeus, 1758) (Fig. 3).

The right tibia is similar in length with tibia of modern leopard, but its shaft is more slender and elongated (but not as tibia of cheetah); with the smallest anteroposterior and transverse diameter smaller than in *Homotherium*, *Xenosmilus*, *Smilodon* and big species of *Panthera* (lions and tigers). The Po tibia is only about twothirds the length of the adult tibia in *Panthera spelaea* male and even smaller than the tibia of *P. gombaszogensis* from French site of Château (Argant and Argant, 2011: Pl. 4 and Tab. 5), the size of which resembles more tibiae of homotheres. On the other hand, its length is similar to the tibial length of large-sized specimens of lynxes, but it has distinctly wider and more robust diaphysis than tibiae of these feline cats (Fig. 4). And although it resembles the shinbone of *Acinonyx* in size (Fig. 4), there is a marked difference in the morphology of proximal and distal epiphyses.

The proximal head is relatively narrower and more triangular in dorsal view than in *P. pardus* what is caused by the erosion. Its circle-shaped lateral articular surface is smaller than the medial one and shifted more posteriorly. The medial condyle of the tibia head was probably more robust than the lateral condyle. The tibial tuberosity for the attachment to the patellar ligament is rounded, and the anterior crest-shaped tibial tubercle is low and relatively narrow and straight. None line for soleus muscle is preserved on the posterior shaft face. The shaft itself is straight rather than bowed, resembling a condition rather in the lion than in the leopard, and differs from slightly S-curved tibial shaft of homotheres. The medial malleolus is less pronounced like in large pantherine cats but more conspicuous like in machairodontine cats, slightly exceeding the level of the rest of the bone distal end despite

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its erosion and thus corresponds rather to the malleolar process in modern leopard. The lateral articular surface (lateral trochlea) of the distal epiphysis is latero-medially narrower and shallower than the medial one (medial trochlea). The malleolar sulcus is indistinct.

The found tibia shows an overall slenderness and subtlety in comparison with tibiae of larger felids, corresponding in morphology and dimensions rather with the tibia of modern leopard. The bone is, however, affected by surface erosion caused by rafting in the water environment. Based on that, it is determined as *Panthera* cf. *pardus* only.

4. Discussion

Panthera pardus is the largest spotted cat in today's Africa and Asia, divided into several subspecies. It is an opportunistic predator in the wild (Miththapala et al., 1996; Uphyrkina et al., 2001; Sunquist and Sunquist, 2002), showing a great size variability within its range. Generally, larger size is recorded from animals in open country than in the forest (Hayward et al., 2006). The species is highly adaptable to environmental changes, for this reason it can live in a wide range of habitats: cover forest or mountain, from sea level up to over than 5000 m (Sunquist and Sunquist, 2002).

The phyletic origin of leopard defined with molecular analyses indicate that African leopards are the most primitive ones; those from western and central Asia evolved later from African ancestors (Miththapala et al., 1996; Uphyrkina et al., 2001). Based on the mitogenomic analyses, Lei et al. (2011) estimate *P. pardus* origins at about 4.35 Ma ago, a time older than the first unchallenged pale-ontological evidence of the species in Africa at ca 2.0 Ma ago (Werdelin and Peigne, 2010). The incongruity about the leopard earlier appearance and differentiation is still far from being resolved.

The first occurrence of leopards in Europe is dated to the Early Pleistocene, to the period about 1.0 Ma ago (Madurell-Malapeira et al., 2014). The fossil record of leopards in European Pleistocene, however, shows certain differences in morphological and metrical characters and many authors attempted to recognize fossil subspecies from morphological analyses, especially of dentition (Boule, 1906; Schütt, 1969; Bonifay, 1971; Hemmer, 1971; Kotsakis and Palombo, 1979; Spassov and Raychev, 1997; Diedrich, 2013). Ghezzo and Rook (2015) emphasize that if intraspecific variability was taken into account, the four recognized subspecies *Panthera pardus begoueni* (Fraipont, 1923), *Panthera pardus sickenbergi* (Schütt, 1969), *Panthera pardus antiqua* (Cuvier, 1835), and *Panthera pardus spelaeus* (Bachler, 1936) should be better considered as a single chronospecies *P. pardus* Linnaeus, 1758.

Probably it is captured also in the territory of Italy, where the fossil record of leopards is so far known from Early Pleistocene localities Olivola and Villa Spinola (Kotsakis and Palombo, 1979), Middle Pleistocene sites Grotta di Campagna (Costa, 1886), Grotte di Cerè (Ghezzo et al., 2014), Isernia (Sauqué and Cuenca-Bescós, 2013), Serbaro di Romagnano (Kotsakis and Palombo, 1979), Soave Monte Tenda, Soave–Sentiero and Valdemino (Sauqué and Cuenca-Bescós, 2013), and chiefly from Late Pleistocene deposits of many caves, such as Buca del Tasso (Fabiani, 1923), in Capri Island (Bataglia, 1918), Castelcivita (Sauqué and Cuenca-Bescós, 2013),

Grotta degli orsi (Saugué and Cuenca-Bescós, 2013), Grotta delle Arene candile (Saugué and Cuenca-Bescós, 2013), Grotta del Fossellone, Grotta del Pastore (Del Campana, 1914), Grotta delle Fate (Issel, 1892), Grotta di Cucigliana (Mochi, 1911), Grotta di Fumane (Tagliacozzo et al., 2013), Grotta di Sambughetto (Maviglia, 1952), Grotta di S. Agostino (Tozzi, 1970), Grotta di S. Bernardino, Grotta di S. Lucia superiore (Saugué and Cuenca-Bescós, 2013). Grotta di Grimaldi (Boule, 1919), Grotta di Ingarano, Grotta di Madonna dell'Arma (Sauqué and Cuenca-Bescós, 2013), Grotta di Pocala (Leonardi, 1935), Grotte di Equi (Ghezzo and Rook, 2015), Monte Cucco (Simonelli, 1916), Monte Sacro (Kotsakis and Palombo, 1979), Riparo tagliente (Sauqué and Cuenca-Bescós, 2013) and Zandobbio (Vialli, 1957) (Fig. 5). Generally, the leopard fossil record is scarcer in northern part of Italy (Italian Alps) than in southern sub-alpine parts of the Apennine Peninsula (Diedrich, 2013; Pacher and Rabeder, 2016).

Alluvial deposits of Po River represent next Italian leopard site, situated south of the Alps. Based on the whole faunal assemblage found here, consisting of interglacial (e.g. *Elephas* (*Palaeoloxodon*) antiquus and "Dihoplus" (Stephanorhinus) kirchbergensis) and glacial elements (e.g. Mammuthus primigenius), the age of found leopardlike tibia corresponds in all likelihood with the Late Pleistocene Period. The recent occurrence of modern leopard is connected with moderate climatic conditions in lowland forest, mountains, grassland, brush country, and semi-arid desert of Africa and Asia what can be also assumed for fossil representatives from the palaeoenvironmental viewpoint. Although this felid nowadays commonly exists in mountains at the altitude approximately 3500 m, and has also been recorded at 4500 to 5000 m a.s.l. (Mazák, 1980; Sunguist and Sunguist, 2002), it seems that European extinct specimens migrated into montane areas and northern regions only occasionally with the highest noted fossil record in Ranggiloch site, situated at an elevation of 1845 m (Pacher and Rabeder, 2016). Based on abovementioned data, the existence of Po leopard-like felid could be connected rather with a warm period (Last Interglacial or some of Last Glacial interstadials?) than with a cold period of stadial character (Fig. 6), but surely with a period before the LGM which probably represents the occurrence termination of Pleistocene leopards in most of European territory.

Common carnivoran guilds, recorded in Pleistocene deposits of European sites, frequently contain a Felidae – Ursidae – Canidae assemblage. Their remains, however, can be also found in hyena dominated fossil assemblages (in hyena dens), but these as a result of hyena activity do not reflect the natural composition. The Middle Pleistocene carnivoran assemblage consists of *Panthera fossilis/ P. gombaszogensis* – Ursus deningeri – Canis mosbachensis (Argant et al., 2007; Musil, 2014), whereas the Late Pleistocene assemblage is characterized by the association *Panthera spelaea/P. pardus* – Ursus spelaeus – Canis lupus (Diedrich, 2013) or Lynx sp. – Ursus arctos – Canis lupus, for example from Spain site of Los Rincones (Ghezzo and Rook, 2015). From this point of view, the common occurrence of bear (Ursus arctos) and wolf (Canis lupus) in Po fluvial deposits is interesting, although fossils may not be coeval with the studied leopard-like tibia find.

Diedrich (2013) tried to infer the leopard sex dimorphism in fossil record from the size of crania and postcranial elements,

Fig. 4. Scatter diagrams for the tibial maximum length and transverse width of epiphyses and diaphysis of various felid taxa. Tibiae of fossil (f) and recent (r) representatives of *Panthera pardus* form a distinct cluster, differentiated from clusters of machairodontine cats and large-sized pantherines. Leopard tibiae are metrically similar to tibiae of extinct and extant representatives of lynxes. Their diaphyses are, however, wider and more robust than the tibial diaphyses of feline cats, indicated also by different values of regression lines (middle diagram). The white arrow in the uppermost and the lowermost diagrams shows an assumed position of the Po tibia without the surface erosion caused by rafting in the water environment. *Homotherium* sp. includes species *H. ischyrus*, *H. serum*, and *H. crenatidens* (data source: Merriam and Stock, 1932; Wojtusiak, 1953; Meade, 1961; Ballesio, 1963; Mawby, 1965; Dietrich, 1968; Bonifay, 1971; Vereshchagin, 1971; Kurtén, 1978; Geraads, 1997; Martin et al., 2011; Argant and Argant, 2011; Hearst et al., 2011; Diedrich, 2013; Ghezzo and Rook, 2015; and personal observation).

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Fig. 5. Sites with fossil record of Pleistocene *Panthera pardus* in Italy: 1 – Grotta di Fumane; 2 - Grotte di Cerè; 3 – Serbaro di Romagnano; 4 - Soave – Sentiero; 5 - Soave Monte Tenda; 6 - Riparo tagliente; 7 - Grotta di S. Bernardino; 8 - Grotta degli orsi; 9 - Grotta di Pocala; 10 – Zandobbio; 11 - Grotticelle di Sambughetto; 12 – Olivola; 13 – Grotta di Grimaldi; 14 – Grotta di Madonna dell'Arma; 15 - Grotta delle Fate; 16 – Grotta di S. Lucia superiore; 17 – Grotta delle Arene candide; 18 – Grotta di Valdemino; 19 - Villa Spinola; 20 - Cremona, Po River; 21 – Grotta di Equi; 22 – Grotta di Cuncigliana; 23 - Buca del Tasso; 24 - Monte Cucco; 25 - Monte Sacro; 26 – Grotta di Campagna; 27 - Isernia; 28 – Grotta delle Fasellone; 29 – Grotta di S. Agostino; 30 – Grotta del Pastore; 31 - Capri Island; 32 – Grotta di Castelcivita; 33 – Grotta di Ingarano (Diedrich, 2013; Sauqué and Cuenca-Bescós, 2013; Ghezzo and Rook, 2015).

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Fig. 6. The reconstruction of the Po tibia potential owner ([©] by Emiliano Troco, 2015).

including also tibiae. Unfortunately, two compared shinbones from the Baumann's Cave and the Vjetrenica Cave (in addition to incorrectly used dimensions) cannot be regarded as a decisive evidence for the sex determination. And although the general rule that males are larger than females could be considered valid, the size variability does not allow per se inferring the genders. Thus, the morphology should be preferable to size analysis for sex determination (Ghezzo and Rook, 2015). The described tibia from Po River is similar in length to the leopard tibia from the Vjetrenica Cave (attributed by Diedrich (2013) to a male), but it is more slender in diaphyseal portion, corresponding more with the leopard tibia from the Baumann's Cave (attributed by Diedrich (2013) to a female) or extant relatives (Fig. 4). Because the morphological differences between tibiae of leopard males and females are not so far adequately defined, it is impossible to assign the Po fossil remain to one of two genders, although its attribution to a large female is not fully excluded. The record probably indicates only wide intraspecific variability, observed also in leopard humerus and radius from Equi site (Ghezzo and Rook, 2015). On the other hand, the larger dimension of studied fossil can indirectly indicate rather more open environment than the presence of dense forest in the area of Po River in the time of its deposition.

5. Conclusion

The leopard-like right tibia, found in alluvial deposits of the Po River, represents the first fossil record of large pantherine cat in the north Italian territory of Cremona. The Po shinbone shows different morphological and metrical characters in comparison with tibiae of machairodontine and larger pantherine cats as well as with felines such as lynxes, corresponding rather with tibiae of modern leopards. But it is determined as Panthera cf. pardus only because of its surface erosion caused by rafting in the water environment. The studied bone belonged to larger specimen (maybe to a large female (?) on the basis of its measurements and overall slenderness); with the possible indirect impact on the palaeoenvironmental reconstruction of the finding area in the time of fossil deposition. Based on the whole mammalian fossil record from the site, consisting of mixed interglacial and glacial elements (straight-tusked elephant, Merck's rhinoceros, steppe bison, Irish elk, woolly mammoth, elk, red deer, brown bear, spotted (cave) hyena, wolf, and red fox), the leopard-like tibia is dated to the Late Pleistocene. Its occurrence, however, is probably connected rather with a warm period (Eemian or a Last Glacial interstadial) than with stadials of the Last Glacial. The fossil remain was, however, certainly deposited before the LGM Period, which is probably the termination of the occurrence of Pleistocene leopards in Europe except for the Iberian Peninsula and

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the European eastern areas.

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References

- Argant, A., Argant, J., 2011. The Panthera gombaszogensis story: the contribution of the Château breccia (Saône-et-Loire, Burgundy, France). Quaternaire, Hors-série 4, 247–269.
- Argant, A., Argant, J., Jeannet, M., Erbajeva, M., 2007. The big cats of the fossil site Château Breccia Northern Section (Saône-et-Loire, Burgundy, France): stratigraphy, palaeoenvironment, ethology and biochronological dating. Cour. Forschungsinstitut Senckenberg 259, 121–140.
- Bachler, E., 1936. Das Wildkirchli. Eine Monographie. Buchdruckerei H. Tschudy, St. Gallen.
- Ballesio, R., 1963. Monographie d'un Machairodus du Gisement Villafranchien de Senèze: Homotherium crenatidens Fabrini. Trav. Lab. Géologie 9, 8–43.
- Barycka, E., 2008. Middle and Late Pleistocene Felidae and Hyaenidae of Poland. Fauna Poloniae — Fauna Polski 2ns. Museum and Institute of Zoology Polish Academy of Science, Warszawa.
- Bataglia, R., 1918. Le industrie e le faune pleistoceniche d'Italia. Riv. Antropoligia 23, 1–102.
- Bonifay, M.-F., 1971. Carnivores quaternaires du sud-est de la France. Mémoires du Museum national d'Histoire Naturelle, Series C, 1–339.
- Boule, M., 1906. Les grands chats des cavernes. Annales de Paléobiologie, t. I, pp. 69–95.
- Boule, M., 1919. Géologie et Paléontologie. Les Grottes Grimaldi 1 (4), 237-362.
- Costa, O.G., 1886. Descrizione degli avanzi scheletrici renvenuti nella grotta ossifera di Campagna. Atti dell'Accademia delle Sci. Fis. Mat. Napoli 8 (3), 1–16.
- Cuvier, G., 1835. Recherches sur les ossements fossiles où l'on rétablit les caractères de plusieurs animaux dont les révolutions du globe ont détruit les espèces, vol.
 4. G. Dufour et E. d'Ocagne, Paris.
- Del Campana, D., 1914. Sopra alcuni resti di mammiferi quaternary della Grotta del Pastore (Grotta della Livrea) in provincial di Genova. Achaeologica Anthropol. Etnologica 44 (1), 1–6.
- Diedrich, C.G., 2013. Late Pleistocene leopards across Europe northernmost European German population, highest elevated records in the swiss Alps, complete skeletons in the bosnia herzegowina dinarids and comparison to the ice age cave art. Quat. Sci. Rev. 76, 167–193.
- Dietrich, W.O., 1968. Fossile Löwen im europäischen und afrikanischen Pleistozän. Palaeontologische Abhandlungen, Abt. A – Paläozoologie 3 (2), 324–366.
- Fabiani, R., 1923. La fauna mammalogica quaternaria della Bucca del Tasso. Archaeol. Anthropol. Etnologica 52, 10–20.
- Fraipont, C., 1923. Crâne de Panthère ou de Lynx géant provenant de la caverne de Trois Frères (Ariège). Rev. Anthropol. 33, 42.
- Geraads, D., 1997. Carnivores du Pliocène terminal de Ahl Al Oughlam (Casablanca, Maroc). Geobios 30 (1), 127–164.
- Ghezzo, E., Berté, D.F., Sala, B., 2014. The revaluation of Galerian Canidae, Felidae and mustelidae of the Cerè cave (verona, Northeastern Italy). Quat. Int. 339–340, 76–89.
- Ghezzo, E., Rook, L., 2015. The remarkable *Panthera pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology. Quat. Sci. Rev. 110, 131–151.
- Gonzáles, F.L., 2003. Paleontology and Taphonomy of Pleistocene Macromammals of Galicia (NW Iberian Peninsula). Laboratorio Xeolóxico de Laxe, serie Nova Terra, O Castro, 1–323.
- Hayward, M.W., Henschel, P., O'Brien, J., Hofmeyr, M., Balme, G., Herley, G.I.H., 2006. Prey preferences of the leopard (*Panthera pardus*). J. Zool. 270, 298–313. http:// dx.doi.org/10.1111/j.1469-7998.2006.00139.x.
- Hearst, J.M., Martin, L.D., Babiarz, J.P., Naples, V.L., 2011. Osteology and myology of Homotherium ischyrus from Idaho. In: Naples, V.L., Martin, L.D., Babiarz, J.P. (Eds.), The Other Saber-tooths. Scimitar-tooth Cats of the Western Hemisphere. The Johns Hopkins University Press, pp. 123–183.
- Hemmer, H., 1971. Zur kenntnis pleistozäner mitteleuropäischer leoparden (*Pan-thera pardus*). Neues Jahrb. für Geol. Paläontologie, Abh 138 (1), 15–36.

- Hemmer, H., 2001. Die Feliden aus dem Epivillafranchium von Untermaßfeld. In: Kahlke, E.-D., et al. (Eds.), Das Pleistozän von Untermaßfeld bei Meiningen (Thüringen), Teil 3. Monographien des Römisch-Germanischen Zentralmuseums Mainz, pp. 699–782 vol. 40(3).
- Issel, A., 1892. Liguria geologica e prehistorica II. Genova, p. 376.
- Kotsakis, T., Palombo, M.R., 1979. Un cranio di *Panthera pardus* (L.) del Pleistocene medio-superiore di Monte Sacro (Roma). Geol. Romana 18, 137–155.
- Kurtén, B., 1978. The Lynx from Etouaires, Lynx issiodorensis (crozet & Jobert), late pliocene. Ann. Zool. Fenn. 15. 314–322.
- Lei, W., Xiao Bing, W., Li Xin, Z., Zhi Gang, J., 2011. Mitogenomic analysis of the genus *Panthera*. Sci. China 54 (10), 917–930.
- Leonardi, P., 1935. Nuovi resti di mammiferi pleistocenici della caverna Pocala. Atti Mus. Civ. Storia Nat. Trieste 13 (1), 4–5.
- Linnaeus, C., 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I (in Latin). Laurentius Salvius, Holmiæ (Stockholm).
- Madurell-Malapeira, J., Ros-Montoya, S., Espigares, M.P., Alba, D.M., Aurell-Garrido, J., 2014. Villafranchian large mammals from the Iberian Peninsula: paleobiogeography, paleoecology and dispersal events. J. Iber. Geol. 40 (1), 167–178.
- Martin, L.D., Babiarz, J.P., Naples, V.L., 2011. The osteology of a Cookie-cutter cat, Xenosmilus hodsonae. In: Naples, V.L., Martin, L.D., Babiarz, J.P. (Eds.), The Other Saber-tooths. Scimitar-tooth Cats of the Western Hemisphere. The Johns Hopkins University Press, pp. 43–98.
- Maviglia, C., 1952. Le cosidette "fibbie" del Musteriano alpino rinvenute a Sambughetto Valstrona (Novara). Atti del I Congr. Internaz.di Studi Liguri, Monaco-Bordighera, 10–17/4/1950, Bordighera.
- Mawby, J.E., 1965. Machairodonts from the late Cenozoic of the panhandle of Texas. J. Mammal. 46, 573–587.
- Mazák, V., 1980. Zvířata Celého Světa 7. Velké Kočky a Gepardi. Státní zemědělské nakladatelství, Praha.
- Meade, G.E., 1961. The saber-toothed cat, *Dinobactis serus*. Bull. Tex. Meml. Mus. 2, 23–60.
- Merriam, J.C., Stock, Ch, 1932. The Felidae of rancho La brea. Carnegie Institution Wash. Publ. 442, 1–227.
- Miththapala, S., Seifensticker, J., O'Brien, S.J., 1996. Phylogeographic subspecies recognition in leopards (*Panthera pardus*): molecular genetic variation. Conserv. Biol. 10 (4), 1115–1132.
- Mochi, A., 1911. Faune Riss-Würmiana, Würmiana e Post-Würmiana e industriea paleolotica superiore nella Grotta di Cucigliana (Monti Pisani). Riv. Antrhropologica 16 (2–3), 259–272.
- Moulle, P.-E., Echassoux, A., Lacombat, F., Desclaux, E., Bailon, S., 2005. L'environnement animal des premiers habitants de l'Europe méditerrannéenne: les grands mammifères contemporains de l'homme du Vallonnet, données taxonomiques et biostratigraphiques pour la deuxième moitié du Pléistocène inferieur. In: Molines, N., Moncel, M.-H., Monnier, J.L. (Eds.), Les premiers peuplements en Europe. Colloque international: données récentes sur les modalités de peuplement et sur le cadre chronostratigraphique, géologique et paléogéographique des industries du Paléolithique ancien et moyen en Europe (Rennes, 22-25 Sept. 2003), John and Hedge, Oxford, BAR Intern. Series S1364, pp. 105–113.
- Musil, R., 1986. Paleobiography of terrestrial communities in Europe during the last glacial. Sborník Národního muzea v praze – acta musei Nationalis pragae. XLI B 1985 (1–2), 1–89.
- Musil, R., 2014. The unique record of za hájovnou cave. Acta musei Nationalis pragae. Ser. B – Hist. Nat. 70 (1–2), 7–26.
- Pacher, M., Rabeder, G., 2016. The leopard (*Panthera pardus*), the rare hunter of the Alpine area during the Upper Pleistocene. Cranium 33 (1), 43–47.
- Persico, D., Ravara, S., Mantovani, E., 2012. Primo ritrovamento di un livello di provenienza dei vertebrati fossili delle alluvioni dell'Adda e del Po, in provincia di Cremona. Pianura 20, 6–37.
- Sabol, M., 2008. Fosílne Mäsožravce Kenozoika Slovenska. Habilitation Thesis. Comenius University in Bratislava, Slovakia.
- Sanchis, A., Tormo, C., Sauque, V., Sanchis, V., Díaz, R., Ribera, A., Villaverde, V., 2015. Pleistocene leopards in the Iberian Peninsula: new evidence from palaeontological and archaeological contexts in the Mediterranean region. Quat. Sci. Rev. 124, 175–208.
- Sauqué, S., Cuenca-Bescós, G., 2013. The iberian Peninsula, the last European refugium of *Panthera pardus* Linnaeus 1758 during the upper Pleistocene. Quaternaire 24 (1), 35–48.
- Schütt, G., 1969. Panthera pardus sickenbergi n. subsp. aus den Mauerer Sanden. Neues Jahrbuch für Geologie und Paläontologie. Monatshefte 5, 299–310.
- Simonelli, V., 1916. I mammiferi fossili della Caverna di Monte Cucco. Mem. della R. Accad. delle Sci. dell'Istituto Bologna 7 (3), 271–286.
- Spassov, N., Raychev, D., 1997. Late Würm Panthera pardus remains from Bulgaria: the European fossil leopards and the question of the probable species survival until the Holocene on the Balkans. Hist. Nat. Bulg. 7, 71–96.
- Sunquist, M., Sunquist, F., 2002. Wild Cats of the World. The University of Chicago Press, Chicago and London.
- Tagliacozzo, A., Ronaldini, M., Fiore, I., Gala, M., Peresani, M., 2013. Animal Exploitation Strategies during the Uluzzian at Grotta di Fumane (Verona, Italy). In: Côark, J.L., Speth, J.D. (Eds.), Zooarchaeology and Modern Human Origins: Human Hunting Behaviour during the Later Pleistocene, Vertebrate Paleobiology and Paleoanthropology. Springer Science & Business Media, Dordrecht, pp. 129–150.

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Tozzi, C., 1970. La Grotta di S. Agostino (Gaeta). Riv. Sci. Preistoriche 25 (1), 1–87. Turner, A., Antón, M., 1997. The Big Cats and Their Fossil Relatives. Columbia University Press, New York.

Uphyrkina, O., Johnson, W., Quigley, H., Miquelle, D., Marker, L., Bush, M., O'Brien, S.J., 2001. Phylogenetics, genome diversity and origin of modern leopard, *Panthera pardus*. Mol. Ecol. 10, 2617–2633.

Vereshchagin, N.K., 1971. Cave lion and its history in Holarctic area and in USSR. Tr.

Zool. instituta 49, 123–199 (in Russian).

- Vialli, V., 1957. I vertevrati della breccia ossifera dell'interglaciale Riss-Würm di Zandobbio (Bergamo). Atti Soc. Ital. Sci. Nat. 96 (1-2), 51-84.
 Werdelin, L., Peigne, S., 2010. Carnivora. In: Werdelin, L., Sanders, W.J. (Eds.),
- Werdelin, L., Peigne, S., 2010. Carnivora. In: Werdelin, L., Sanders, W.J. (Eds.), Cenozoic Mammals of Africa. University of California Press, pp. 603–657. Meiniegie K. (1922). Screenbill Juna isokingingunger (Felic analoga Calde), a isokingi Meiniegie K. (1923).
- Wojtusiak, K., 1953. Szczątki Iwa jaskiniowego (Felis spelaca Goldf.) z jaskini "Wierzchowskiej Górnej". Acta Geol. Pol. III, 573–592.