


THE FIRST RADIOCARBON-DATED REMAINS OF THE LEOPARD *PANTHERA PARDUS* (LINNAEUS, 1758) FROM THE PLEISTOCENE OF POLAND

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ABSTRACT. The Pleistocene history of the leopard (*Panthera pardus*) in Europe has been documented by the material obtained from 312 localities, with the last dated ~1.1 Myr. The relatively small and gracile form of the leopard was very rare during the late Early and Middle Pleistocene. Only after the disappearance of the jaguar (*Panthera gombaszoegensis*) did *P. pardus* spread widely in Europe, increasing in size and ecologically substituting *P. gombaszoegensis*. The number of late Middle Pleistocene localities with leopard remains, younger than 300 kyr, increased considerably. The leopard reached the maximum extension of its geographical range in the Late Pleistocene. The Iberian Peninsula was the last European refuge for this cat. Six sites, the Naciekowa, Obok Wschodniej, Radochowska, and Wschodnia Caves from the Sudety Mountains and the Biśnik and Dziadowa Skała Caves from the Kraków-Częstochowa Upland, have documented the presence of the leopard in Poland between MIS 10/9 and MIS 3. These records are from rocky regions with rugged terrain and are located in the territory of Silesia (southern Poland). A newly obtained radiocarbon date (43–42 kyr) from the Radochowska Cave directly confirms the occurrence of *P. pardus* in the Sudety Mountains in the middle part of MIS 3.

KEYWORDS: competition, leopard, occurrence, Pleistocene, relict, survival.

INTRODUCTION

The leopard (*Panthera pardus*) appeared in Europe as a newcomer of African origin 1.2–1.1 Myr ago, with the oldest record known from the Vallonnet Cave (Moullé 1992; Turner 2009; Michel et al. 2017). O'Regan (2002) highlighted that the arrival of *P. pardus* in Europe might have placed pressure on the jaguar (*Panthera gombaszoegensis*). The leopard would have focused on smaller animals, which were at the lower end of the jaguar prey size range (Hemmer 2003, 2004). An unanswered question is why, despite its enormous environmental and hunting adaptability, the occurrence of *P. pardus* in the Middle Pleistocene is limited to a few sites (von Koenigswald et al. 2006). At the same time, the leopard was widespread in Africa and Asia (Geraads 2008; Geraads et al. 2010). It was present in Europe until the end of the Late Pleistocene, even during the very cold and continental climatic phase after the glaciation (Spassov and Raychev 1997). O'Regan and Turner (2004) described *P. pardus* of the Middle Pleistocene as a relatively small cat of a gracile posture and with narrow teeth. The small size of the early leopard may have been a response to reduce competition with other large carnivores (mostly the jaguar) in the areas where these two species coexisted (Nowell and Jackson 1996; Hemmer 2001, 2004; García and Virgós 2007; Marciszak and Lipecki 2021). Only after the disappearance of the jaguar did *P. pardus* spread widely in Europe, increasing in size and ecologically substituting *P. gombaszoegensis* (García and Virgós 2007; Marciszak and Lipecki 2021). The number of late Middle Pleistocene localities with leopard remains, younger than 300 kyr, increased considerably (Diedrich 2013; Sauqué and Cuenca-Bescós 2013). The leopard reached the

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maximum extension of its geographical range during the Late Pleistocene. The spread of *P. pardus* was accompanied by a trend for a size increase, when the initially relatively small and gracile leopard had become larger in size and weight. The size of the largest Late Pleistocene specimens is comparable to that of the small Middle Pleistocene jaguar, and they held the ecological niche that had been occupied by *P. gombaszoegensis* (Hemmer 2004; García and Virgós 2007).

There is a small number of direct dates of *P. pardus*, like that of the Radochowska Cave (Diedrich 2013; Sauqué and Cuenca-Bescós 2013; Sauqué et al. 2017). Every new date is critical to obtain a thorough understanding of the history of the evolution of a species such as the leopard, which is known from numerous sites, but usually only represented by sparse material at each site. In this study, we have dated a leopard sample from the Radochowska Cave. Apart from the new date we have obtained, in addition to the first record of the leopard from Poland (Marciszak et al. 2011a, 2011b), the list of Polish localities with remains of this species has recently increased to six cave sites. We briefly discuss some palaeoecological aspects of this species and possible reasons for its final disappearance from the territory of Europe.

SITE

Radochowska Cave (50°21'31"N, 16°49'9"E; 460–468 m above sea level), is a karst, 265-m-long cave developed in the lenticular marble at the foot of Mount Bzowiec in the Żłote Mountains (eastern Sudety Mountains, southwest Poland). Radochowska Cave was formed during the Pliocene by the leaching of water-soluble marbles in a lens of white marble, partly in contact with schist (grey-yellow, friable rock). It was formed under the erosion made by water filling the entire cross-section of its passages flowing under high pressure. The intensification of erosion of the surrounding slopes at the end of the Pliocene led to deepening of the valley. This caused the channel of a nearby flowing stream to lower (Pulina 1996). A decrease in the karst water level led to dehydration of the area near the cave opening and the formation of hollows. Corridors have been developed along tectonic fissures, and larger halls have been formed at their intersections. In the corridors drained in this way, the alluvial deposition process has begun. The alluvium in the site consists of weathered schist that falls from the cave ceiling and walls, rubble, precipitated calcium carbonate and organic material like animal bones deposited by water from the surface. The alluvium has almost completely filled the cave chambers and passages.

The locality has been known for more than 300 years (Kahlo 1757; Ostrowicz 1881). Shortly afterwards, it became a popular destination for spa patients from Łądek-Zdrój and tourists. From 1933 to 1947, the cave had a permanent custodian and guide, the retired miner Heinrich Peregrin. He also removed a significant part of the sediment while preparing the cave for visits and opening its corridors. Systematic excavations were carried out by J. Frenzel in 1935 and by L. Zotz in 1936. Brown and grey loams represented deposits of this cave with limestone rubble (Utescher 1939). L. Zotz also found quartzite products and pine wood charcoal. In one of the niches, he also found a cave bear's skull with the mandible and three cervical vertebrae. This gave rise to assumptions about the presence of the Paleolithic people in the cave and created a theory of a "bear cult among Paleolithic people" (Zotz 1937a, 1937b, 1939, 1951). The excavations in 1983 were taken to check the results of German studies from the 1930s, and this theory is no longer supported (Bieroński et al. 1985; Wiśniewski et al. 2009; Marciszak et al. 2020). Unfortunately, most of the bone

remains from the pre-Second World War studies have been lost, and thus only a small part could be re-examined. These excavations have revealed two main faunal assemblages. The older, Late Pleistocene fauna is roughly dated at MIS 3, and it contains 23 species (Table 1, Table S2). The second, younger assemblage is dated at MIS 1 and includes 30 species (Table S2; Frenzel 1936, 1937a, 1937b; Pax 1937; Zotz 1937a, 1937b, 1939, 1951; Kowalski 1954; Bieroński et al. 1985, 2007, 2009; Pulina 1996; Stefaniak and Bieroński 2009; Wiśniewski et al. 2009; Marciszak et al. 2016, 2020; 2021a, 2021b, 2021c).

SAMPLES AND METHODOLOGY

The leopard sample from the Radochowska Cave used for dating was taken from a fragment of a left mandible (JR/Pp/1), with preserved p4 alveolus and worn m1, stored in the Department of Palaeozoology, University of Wrocław (Figure 1, Table 2). The sample was pretreated at the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology (MPI-EVA), Leipzig, Germany, using the method described by Talamo and Richards (2011) and Talamo et al. (2021). The outer surface of bone samples is first cleaned by a shot blaster and then 500 mg of whole bone is taken. The samples are then decalcified in 0.5 M HCl at room temperature until no CO₂ effervescence is observed. Then, 0.1 M NaOH is added for 30 min to remove humics. The NaOH step is followed by a final 0.5 M HCl step for 15 min. The resulting solid is gelatinized as described by Longin (1971) at pH 3 in a heater block at 75°C for 20 hr. The gelatine is then filtered in an Eeze-Filter™ (Elkay Laboratory Products [UK] Ltd.) to remove small (> 80 µm) particles. The gelatine is then ultrafiltered with Sartorius “VivaspinTurbo” 30 kDa ultrafilters. Prior to use, the filter is cleaned to remove carbon-containing humectants (Talamo et al. 2021). The samples are lyophilized for 48 hr. The date was corrected for a residual preparation background estimated from a pretreated ¹⁴C-free bone sample, kindly provided by the Mannheim laboratory and pretreated in the same way as archaeological samples (Korlević et al. 2018). To identify the quality of the collagen, the C:N ratio was also estimated. It should be between 2.9 and 3.6, and the collagen yield should not be < 1% of the weight (van Klinken 1999; Talamo et al. 2021). Stable isotopic analysis was performed at MPI-EVA, Leipzig (Lab Code R-EVA), using a ThermoFinnigan Flash EA with a Delta V isotope ratio mass spectrometer. The sample was sent to the Curt Engelhorn Centre for Archaeometry (CEZA) in Mannheim, Germany (lab code MAMS), where it was graphitized and dated (Kromer et al. 2013). All new dates were calibrated by using the program IntCal20, according to Reimer et al. (2020).

RESULTS

Although the dated bone fragment was relatively small, a precise date was acquired (MAMS-42394 in Table 1). The date indicates the middle part of MIS 3 (~43–42 kyr BP). Three more dates were obtained that also fall within the range of MIS 3. The subfossil, a brightly colored and light rib of *Ursus arctos arctos*, was dated to the Romanian period (~1.8–1.7 kyr BP). These dates confirmed the presence of two different faunal assemblages, dated at MIS 3 (older) and MIS 1 (younger). Both assemblages were partially mixed, although bones dated at MIS 3 are grey, brown or black; deeply mineralized; and heavy. Subfossil bones dated at MIS 1 are white or bright grey, lightly mineralized and delicate. These findings confirm the conclusions of Bieroński et al. (1985, 2009) about the mixed character of a part of the sediments in the Radochowska Cave, partial redeposition and a significant role of outside transport in the formation of cave sediments.

Table 1 AMS radiocarbon results dating of carnivores from Radochowska Cave. The newly obtained date of *Panthera pardus* is in bold. All dates were calibrated using the program IntCal20, according to Reimer et al. (2020).

| Species | Bone | Lab code | % coll. | $\delta^{15}\text{N}$ | %C | %N | C: N | ^{14}C age $\pm 1\sigma$ | cal BP 95.4% | cal BP 68.3% | Source |
|-------------------------------|-----------------|-------------------|------------|-----------------------|-------------|-------------|------------|-----------------------------------|--------------------|--------------------|------------------------|
| <i>Ursus arctos arctos</i> | Rib | Poz-97198 | | | 14.2 | 4.1 | | 1840 \pm 30 | 1830–1630 | 1820–1700 | Marciszak et al. 2020 |
| <i>Ursus arctos priscus</i> | Maxilla | Poz-82393 | | | 4.4 | 0.9 | | 34600 \pm 600 | 41130–38140 | 40510–39220 | Marciszak et al. 2020 |
| <i>Panthera pardus</i> | Mandible | MAMS-42394 | 6.9 | 6.6 | 45.2 | 16.5 | 3.2 | 39000 \pm 320 | 42940–42360 | 42780–42480 | This paper |
| <i>Cuon alpinus europaeus</i> | Maxilla | MAMS-48222 | | | 45.7 | | 3.2 | 40480 \pm 380 | 44310–42960 | 43980–43170 | Marciszak et al. 2021b |
| <i>Ursus ingressus</i> | M1 | Poz-28945 | | | 4.7 | 1.2 | | >47000 | | | Bieroński et al. 2009 |

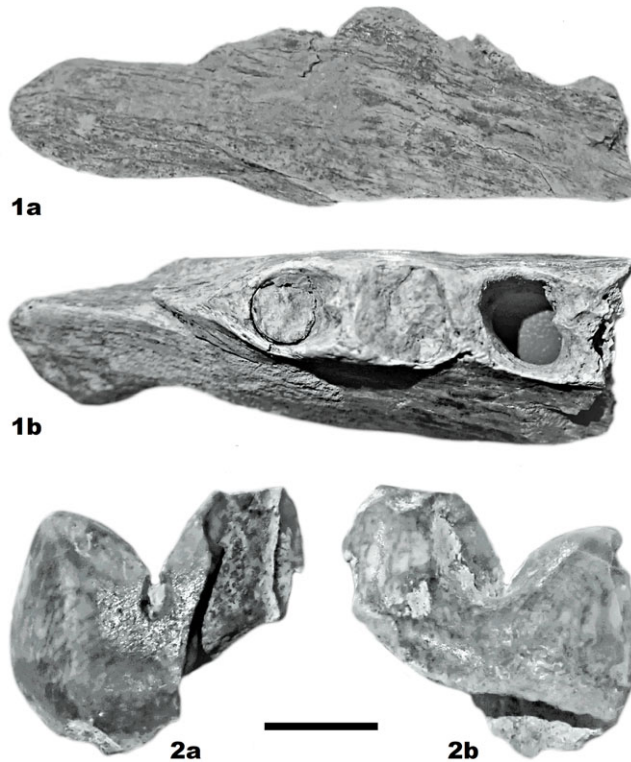


Figure 1 Radiocarbon dated specimen of *Panthera pardus* from Radochowska Cave: 1. fragment of a left mandible (JR/Pp/1, a—buccal view, b—occlusal view); 2. left m1 belonging to the same specimen (a—buccal view, b—lingual view). Scale bar 10 mm.

DISCUSSION

Polish Records of *Panthera pardus* Based on the European Background

A broad query revealed the presence of the leopard at 312 European sites, which cover the timespan of the last ca. 1.1 Myr (Figure 2, Table S1). The list of Polish localities with leopard remains has recently increased to six cave sites. Among them, four are located in the Sudety Mountains (the Naciekowa, Obok Wschodniej, Radochowska, and Wschodnia Caves) and two others are located in the Kraków-Częstochowa Upland (the Biśnik and Dziadowa Skąła Caves). All records are from rocky regions with rugged terrain convenient for ambushes and hiding, and all of them are located on the territory of Silesia (southern Poland). There is a small number of direct dates of *P. pardus*, like the date we have obtained for the Radochowska Cave sample (e.g., Diedrich 2013; Sauqué and Cuenca-Bescós 2013).

The presence of the leopard during MIS 3 at the Sudety Mountains had already been suggested (Marciszak et al. 2016, 2020), but our direct dating has confirmed it. Other Polish records indicate the presence of this species since the late Middle Pleistocene, as confirmed by the study of remains from the lowermost layers 19a–d of the Biśnik Cave, dated at MIS 10/9 (Marciszak et al. 2011a, 2011b). Between MIS 7 and MIS 3, *P. pardus* was probably

Table 2 Radiocarbon results dating of *Panthera pardus* from Europe. All dates were calibrated using the program IntCal20, according to Reimer et al. (2020).

| Site | Bone | Lab code | % coll. | $\delta^{15}\text{N}$ | %C | %N | C: N | ^{14}C age $\pm 1\sigma$ | cal BP 95.4% | cal BP 68.2% | Source |
|-------------------------|-----------------|-------------------|------------|-----------------------|-------------|-------------|------------|-----------------------------------|--------------------|--------------------|---|
| Vraona Cave | | | | | | | | 17805 \pm 1000 | 24200–19300 | 22860–20450 | Nagel 1999 |
| Aintzulo Cave | Skull | Ua-21156 | | | | | | 21705 \pm 355 | 26910–25270 | 26390–25680 | Altuna-Etxabe and Mariezkurrena-Gastearena 2013 |
| Racó del Duc 1 Cave | | Beta-434.367 | | | | | | 25870 \pm 100 | 30310–29970 | 3090–30020 | Sauqué and Sanchis 2017; Sanchis et al. 2019 |
| Vraona Cave | | | | | | | | 24490 \pm 1350 | 32050–26090 | 30130–27410 | Nagel 1999 |
| Equi Cave | Illium | Beta-360175 | | | 19.6 | | | 32910 \pm 260 | 38580–36570 | 37720–36880 | Ghezzi 2014 |
| Allekoaitze Cave | Skull | Ua-21157 | | | | | | 34825 \pm 1375 | 42250–36950 | 41380–38440 | Altuna-Etxabe and Mariezkurrena-Gastearena 2013 |
| Baumann's Cave | | MAM-31740 | 1.9 | | 22.0 | | 2.9 | 37880 \pm 300 | 42470–41970 | 42350–42110 | Pajmians et al. 2018 |
| Radochowska Cave | Mandible | MAMS-42394 | 6.9 | 6.6 | 45.2 | 16.5 | 3.2 | 39000 \pm 320 | 42940–42360 | 42780–42480 | This paper |
| Baumann's Cave | | MAM-31741 | 3.1 | | | | | 40470 \pm 410 | 44330–42940 | 43990–43150 | Pajmians et al. 2018 |
| Baumann's Cave | | MAM-31739 | 1.1 | | 22.4 | | 3.3 | 44710 \pm 630 | 48460–45850 | 47680–46260 | Pajmians et al. 2018 |

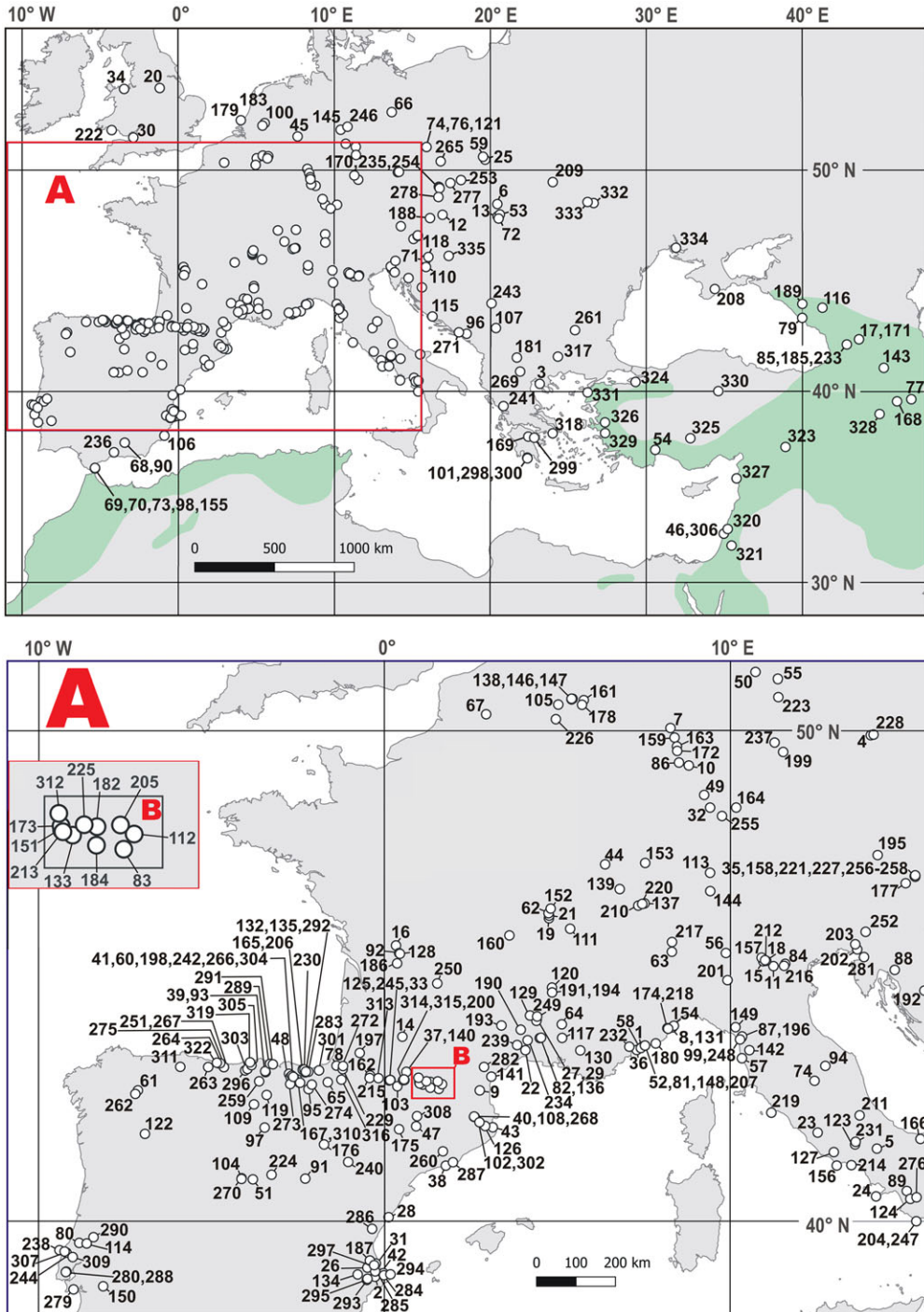


Figure 2 Distribution of the Pleistocene and the Holocene sites with *Panthera pardus* within Europe and southwest Asia. See Table S1 for site numbers. The greenish color indicates the areas where the leopard occurred in historical times and where the extant isolated populations currently living. (After Jacobson et al. 2016. Please see electronic version for color figures.)

present as a rare hunter in Poland. No younger individuals have been found, so nothing is known about the species survival or re-colonization in the Polish territory during the Late Glacial or Holocene. However, this problem with the reconstruction of the European history of *P. pardus*, due to the nearly complete absence of direct dates of its remains, hampers a detailed time resolution of the leopard distribution in Europe (Pacher and Rabeder 2016). The two oldest dates, 88.5 kyr (LEB-14069) and 98.4 kyr (LEB-14070), obtained directly from the remains of a leopard from the Spanish site Artazu VII and based on the amino acid racemization (AAR) method, documented the presence of the species during MIS 5b (Suárez-Bilbao et al. 2016). Three other dates from Baumann's Cave (Germany) and one from the Equi Cave (Italy) also fall into MIS 3 (Table 2). Two conventional dates from the Vraona Cave (Greece) have documented the presence of this species during the MIS 3/MIS 2 transition and MIS 2 (Nagel 1999). These data corroborate well with the occurrence of the Balkan refugee of the species during cool phases—for example, the Last Glacial Maximum (LGM). It also corresponds well with the idea that the leopard seems to have survived up to the LGM in southern and eastern parts of Europe. The history of the last European leopards is still incomplete. The supposed Holocene survival of *P. pardus* in Europe is still highly unresolved and based on quite unclear records—for example, Spassov and Raychev (1997), Bartosiewicz (2001, 2015), and Galik et al. (2012). It is difficult to reconstruct the last occurrence and extinction of *P. pardus* in Europe. The two imprecisely dated records, one Mesolithic from northern Spain (Altuna 1972) and the second from Greece (Nagel 1999), are two indicators that the species could have survived there until the Holocene (Sommer and Benecke 2006; Sauqué and Cuenca-Bescós 2013). The leopard retreated from Europe eastward and south-eastward, but this process has been poorly documented. In western Europe, the Iberian population remained detached from the rest. Multiple post-LGM records indicate their presence and eventual survival until the Middle Holocene in the Iberian Peninsula (Vega del Sella 1930; Altuna 1972; Sauqué and Cuenca-Bescós 2013). This area seems to have been the last refuge for the European leopard, similarly to the last European dhole *Cuon alpinus europaeus* Bourguignat, 1868 (Pérez Ripoll et al. 2010; Sanchis et al. 2019, 2020; Marciszak et al. 2021b).

Disappearance of *P. pardus* in Europe: a Working Hypothesis

The Polish fossil record is highly incomplete and, for this reason, the species succession history in Poland should be treated with caution. The presence of *P. pardus* in Poland was restricted to highland and mountain areas of Silesia. This animal probably avoided open, extensive Bohemian, Moravian, and Silesian grasslands because of the presence of other large, fast-moving and social carnivores, like the steppe wolf or the cave hyena. Both species constituted a serious threat for a solitary cat, especially when trees or other potential shelters were absent or very rare (Eaton 1979).

Regarding the disappearance of the leopard in Europe, the key questions are not only when but also why. First, we must clearly state that our discussion is based on hypotheses and not proven facts. Only positive evidence is reliable in palaeontology due to the incompleteness of the fossil record. The absence of leopard remains in some regions or chronological intervals does not necessarily mean that they were absent from the surroundings. It is possible that the remains were not preserved or have not yet been identified or excavated. Sudeten cave regions favor fossil bone preservation, but open, extensive Bohemian, Moravian, and Silesian grasslands do not. Hence, only knowing the geographic or chronological

distribution of the localities is not enough to draw conclusions about the distribution of past populations. Second, the deductions on population replacements over time and on interspecies relationships are difficult to support by using only the fossil record. Genetics and/or isotopic dating are crucial to conclude about ecological relationships.

The leopard is an extremely adaptive carnivore: it is now able to inhabit highly urbanized areas. Unlike, for example, the lion, the progressive warming and the associated increase in afforestation should have no negative impact on the leopard population (Nagel et al. 2018). On the contrary, forested areas gave it shelter and the density of potential prey—for example, deer, which was quite sufficient. *P. pardus* probably found a favorable ecological niche in the Sudety Mountains during the Late Pleistocene, when there were coniferous forests with some number of deciduous trees growing mostly in valleys during warmer periods. The presence of trees is an important factor for their environment, while deep snow cover is a limiting one (Heptner and Naumov 1967; Jacobson et al. 2016). However, even if the presence of trees is one of the crucial factors for this species, the ecologically extremely flexible leopard could have been adapted even for the coolest phases of the Late Pleistocene (i.e., the LGM), which was characterized by nearly treeless and rocky habitats (Nagel 1999). Despite the fact that *P. pardus* is not a typical cave dweller, recent leopards use caves to catch their prey to avoid competitors like lions and spotted hyenas in treeless regions (Brain 1981; de Ruiter and Berger 2000, 2001; Hayward et al. 2006; Diedrich 2013; Yang et al. 2018). In African cave regions, up to 33% of the carcasses are dragged by leopards into deeper cave parts to avoid conflicts with lions and hyenas. Simultaneously, only 7% of prey remains were pulled up into trees, which were located more than 500 m from those caves. In cases where trees grow near the entrances, 83% of carcasses were stored in caves and only 17% in trees (de Ruiter and Berger 2001; Diedrich 2013). Leopards drag even larger carcasses very deeply into caves, especially to avoid stealing by hyenas, which cannot climb slopes within those caves (de Ruiter and Berger 2001; Diedrich 2013). If possible, they usually preferred small rock shelters with narrow entrances that made them less accessible to lions. In that context, the area of the Sudety Mountains, full of such small rock shelters, can be regarded as a potential preferable habitat for the leopard.

According to Diedrich (2013: 189), this ibex/chamois/deer prey-adapted felid is extremely rare in lowlands. The remains of *P. pardus* have not been found in any of the open-air faunal assemblages in Poland (Wolsan 1989; Marciszak et al. 2019). This scenario has already been discussed for Balkan sites, where the situation is similar to those in Silesia and the Sudety Mountains (Spassov and Raychev 1997). This cat also preferred rocky regions with a rugged terrain that are convenient for ambushes and hiding (Heptner and Sludskij 1972; Spassov and Raychev 1997; Jacobson et al. 2016). The leopard lived in relatively low densities while the density of the wolf population is high (Heptner and Sludskij 1972; Sludskij 1976; Spassov and Raychev 1997). The lowlands surrounding the Sudety Mountains (Bohemian, Moravian, and Silesian) were overwhelmed by packs of robust steppe wolves, whose remains have been recorded regularly from open-air sites (Herr 1924; Kowalski 1959; Wiśniewski et al. 2009; Marciszak et al. 2019, 2020). In addition, the presence of wolves might be a limiting factor, because as a solitary hunter, the leopard usually avoided aggressive competitions with large dogs (Heptner and Sludskij 1972; Eaton 1979; Spassov and Raychev 1997; Miquelle et al. 2005). Given the similar size of wolves and leopards, in a one-on-one confrontation, the leopard has an advantage, but the confrontation of a solitary cat with a pack of wolves is a different story (Figure 3). In this regard, we agree with the hypothesis proposed by Spassov and Raychev (1997) that a set of



Figure 3 Scenes showing conflict between the leopard *Panthera pardus* with one of his main competitors during the Late Pleistocene, cave wolves *Canis lupus spelaeus* near the Radochowska Cave. (Drawing by W. Gornig.)

different factors caused the species not to form vital populations after the LGM (GS-2.1a interval, 17.5–14.7 kyr), when intensive deglaciation processes started. Among them, there are a lack of sufficient food sources combined with a relatively small number of adequate rocky shelters, the high density of the wolf population, and intense human pressure. Isolated, relict populations such as those in the Iberian Peninsula, which survived without probable contact with the North African populations, were probably exterminated by humans at a fairly early date. Eastern re-colonization, in turn, was probably hindered or even prevented by a strip of wide, almost treeless plains that effectively cut off central and western Europe from the eastern populations of *P. pardus*, where the leopard has survived (Bartosiewicz 2001).

CONCLUSIONS

A critical revision of all available literature sources shows the presence of *P. pardus* at 312 European sites, with the last documented ~1.1 Myr. Among them, there are six Polish records (five of which are new), including four sites located in the Sudety Mountains (the Naciekowa, Obok Wschodniej, Radochowska and Wschodnia Caves), as well as two localities in the Polish Jura (the Biśnik and Dziadowa Skała Caves). All records are from rocky regions with rugged terrain convenient for ambushes and hiding, located in the territory of Silesia (southern Poland). These records document the probable presence of the species in Poland between MIS 10/9 and MIS 3. In addition, a newly obtained radiocarbon date of 43–42 kyr from the Radochowska Cave directly confirms the occurrence of *P. pardus* in the Sudety Mountains in the middle part of MIS 3. Together with other AMS dates from this site, we can confirm the presence of two faunal assemblages, one of which is older (MIS 3), and another that is younger (MIS 1). The post-LGM history of *P. pardus* in Europe has been poorly defined. Only the Iberian Peninsula, with numerous records of *P. pardus* dated in the range of 17–11 kyr or even later, can be regarded as a reliable documentation of the last European refugium for this cat. Eastern or southern European records are usually based on imprecisely dated records, and it is still full of ambiguities. A set of different factors probably underscored the inability of the species to establish vital populations after the LGM, including a lack of sufficient food sources combined with a relatively small number of adequate rocky shelters, a high density of the wolf population

and human pressure. Isolated relict populations were probably exterminated by humans at a fairly early date. Eastern re-colonization, in turn, was probably hindered or even prevented by a strip of wide, almost treeless plains that effectively cut off central and western Europe from eastern populations of *P. pardus*, where the leopard has survived.

REFERENCES

- Altuna J. 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa, con catalogo de los mamíferos cuaternarios del Cantábrico y del Pirineo occidental [Mammalian fauna of the prehistoric sites of Guipúzcoa, with a catalog of the quaternary mammals of the Cantabrian Sea and the western Pyrenees]. *Munibe* 24:1–464. In Spanish.
- Altuna-Etxabe J, Mariezkurrena-Gastearena K. 2013. Cráneos de pantera en Allekoaitze (Ataun) y Aintzulo (Errezil) (Gipuzkoa) [Panther skull in Allekoaitze (Ataun) and Aintzulo (Errezil) (Gipuzkoa)]. *Kobie, Paleoantropologia* 32:29–37. In Spanish.
- Bartosiewicz L. 2001. A leopard (*Panthera pardus* L. 1758) find from the late Middle Ages in Hungary. In: Buitenhuis H, Prummel W, editors. *Animals and man in the past* ARC-Publicatie, Groningen 41:151–160.
- Bartosiewicz L. 2015. Every skin teeth ain't a laugh: medieval leopard find from Hungary. *E-Journal* 2015:1–8.
- Bieroński J, Burdukiewicz JM, Socha P, Stefaniak K, Hercman H, Nadachowski A. 2009. Palaeogeographical, archeological and palaeozoological studies in the Radochowska Cave. *Studies of the Faculty of Earth Sciences, University of Silesia* 56:455–475.
- Bieroński J, Burdukiewicz JM, Wiszniowska T. 1985. Wyniki nowych badań Jaskini Radochowskiej [Results of new research of the Radochowska Cave]. *Śląskie Sprawozdania Archeologiczne* 26:5–18. In Polish.
- Bieroński J, Socha P, Stefaniak K. 2007. Deposits and fauna of the Sudetic caves—the state of research. *Studies of the Faculty of Earth Sciences, University of Silesia* 45:183–201.
- Brain CK. 1981. *The hunters or the hunted? An introduction to African cave taphonomy*. Chicago: The University of Chicago Press. 365 p.
- de Ruiter DJ, Berger LR. 2000. Leopards as taphonomic agents in dolomitic caves—implications for bone accumulations in the hominid-bearing deposits of South Africa. *Journal of Archaeological Science* London 27:665–684.
- de Ruiter DJ, Berger LR. 2001. Leopard (*Panthera pardus* Linnaeus) cave caching related to anti-theft behaviour in the John Nash Nature Reserve, South Africa. *African Journal of Ecology* 39:396–398.
- Diedrich CG. 2013. Late Pleistocene leopards across Europe—northernmost European German population, highest elevated records in the Swiss Alps, complete skeletons in the Bosnia Herzegovina Dinarids and comparison to the Ice Age cave art. *Quaternary Science Reviews* 76:167–193.
- Eaton RL. 1979. Interference competition among carnivores a model for the evolution of social behavior. *Carnivore* 2(1–2):9–16.
- Frenzel J. 1936. Knochenfunde in der Reyersdorfer Tropfsteinhöhle [Bone finds in the Reyersdorf Stalactite Cave]. *Beiträge zur Biologie des Glatzer Schneeberges* 2:121–134. In German.
- Frenzel J. 1937a. Die Reyersdorfer Tropfsteinhöhle, ein schlesisches Naturdenkmal [The Reyersdorf Stalactite Cave, a Silesian natural monument]. *Schlesische Heimat* 1:6–11. In German.
- Frenzel J. 1937b. Die Apterygotenfauna des Glatzer Schneeberges [The apterygote fauna of the Glatzer Schneeberg]. *Beiträge zur Biologie des Glatzer Schneeberges* 3:249–321. In German.
- Galik A, Horejs B, Nessel B. 2012. Der nächtliche Jäger als Beute. Studien zur prähistorischen Leopardenjagd [The nocturnal hunter as prey. Studies in prehistoric leopard hunting]. *Prähistorische Zeitschrift* 87(2):261–307. In German.
- García N, Virgós E. 2007. Evolution of community composition in several carnivore palaeoguilds from the European Pleistocene: the role of interspecific competition. *Lethaia* 40:33–44.
- Geraads D. 2008. Plio-Pleistocene Carnivora of northwestern Africa: a short review. *Comptes Rendus Paleovol* 7:591–599.
- Geraads D, Raynal J-P, Sbihi-Alaoui F-Z. 2010. Mammalian faunas from the Pliocene and Pleistocene of Casablanca (Morocco). *Historical Biology* 22:275–285.
- Ghezzi E. 2014. *The Late Pleistocene site of Equi (Massa, Apuane Alps): reevaluation of historical data and new discoveries* [PhD thesis]. Firenze: Università Firenze.
- Hayward MW, Henschel O, O'Brian J, Hofmeyr M, Balme G, Kerley GHI. 2006. Prey preferences of the leopard (*Panthera pardus*). *Journal of Zoology* 270:298–313.
- Hemmer H. 2001. Die Feliden aus dem Epivillafranchium von Untermaßfeld bei Meiningen (Thüringen) [The felids from the Epivillafranchian of Untermaßfeld near Meiningen (Thuringia)]. *Monographien des Römisch-Germanischen Zentralmuseums Mainz* 40:699–782. In German.
- Hemmer H. 2003. Pleistozäne Katzen Europas—eine Übersicht. *Cranium* 20:6–22.

- Hemmer H. 2004. Notes on the ecological role of European cats (Mammalia: Felidae) of the last two million years. In: Baquedano E, Rubio Jara S, editors. *Zona Arqueológica 4. Miscelánea en homenaje a Emiliano Aguirre*. Paleontología 2:214–232.
- Heptner VG, Naumov NP (1967) Mlekopitayushchiye Sovetskogo Soyuz. Tom II, Chast 2. Plotoyadnyye (ginyeny i koshki) [Mammals of the Soviet Union. Volume II, Part 2. Carnivora (hyenas and cats)]. Vysshaya Shkola, Moscow. In Russian.
- Heptner VH, Sludskij AA. 1972. Mlekopitayushchie Sovetskogo Soyuz. Vol. 3. Carnivores (Feloidea) [Mammals of the Soviet Union. Vol. 3. Carnivores (Feloidea)]. Vysshaya Shkola, Moscow. 784 p. In Russian.
- Herr O. 1924. Diluviale und altalluviale Säugetierreste aus der Oberlausitz [Diluvial and old alluvial mammalian remains from Upper Lusatia]. *Abhandlungen der Naturforschenden Gesellschaft zu Görlitz* 29:92–101.
- Jacobson AP, Gerngross P, Lemeris JR Jr, Schoonover RF, Anco C, Breitenmoser-Würsten C, Durant SM, Farhadinia MS, Henschel P, Kamler JF, Laguardia A, Rostro-García SR, Stein AB, Dollar L. 2016. Leopard (*Panthera pardus*) status, distribution, and the research efforts across its range. *PeerJ* 4:1974.
- Kahlo JG. 1757. *Denkwürdigkeiten der Königlichen preussischen souverainen Grafschaft Glatz*. Berlin und Leipzig. 228 p.
- Korlević P, Talamo S, Meyer M. 2018. A combined method for DNA analysis and radiocarbon dating from a single sample. *Scientific Reports* 8(1):4127.
- Kowalski K. 1954. *Jaskinie Polski, tom 3 [Caves of Poland, volume 3]*. Wiedza Powszechna: Warszawa. In Polish.
- Kowalski K. 1959. *Katalog ssaków plejstocenu Polski [Catalog of mammals of the Pleistocene of Poland]*. Państwowe Wydawnictwo Naukowe, Warszawa. In Polish.
- Kromer B, Lindauer S, Synal H-A, Wacker L. 2013. MAMS—a new AMS facility at the Kurt-Engelhorn-Zentre for archaeometry, Mannheim, Germany. *Nuclear Instruments and Methods in Physics Research Section B: Beam Interactions with Materials and Atoms* 294:11–13.
- Longin R. 1971. New method of collagen extraction for radiocarbon dating. *Nature* 230:241–242.
- Marciszak A, Gornig W, Kropczyk A. 2021a. Radochowska Cave (Sudety Mts, SW Poland) — one of the European caves with bear cult? In: Döppes D, Friedland SN, Roendahl W, editors. *Abstract Book of the 26th International Cave Bear Symposium 2021*, Reiss-Engelhorn-Museen, Mannheim, Germany, 30th September–3rd October 2021. p. 25–26.
- Marciszak A, Kotowski A, Przybylski B, Badura J, Wiśniewski A, Stefaniak K. 2019. Large mammals from historical collections of open-air sites of Silesia (southern Poland) with special reference to carnivores and rhinoceros. *Historical Biology* 31(6):696–730.
- Marciszak A, Krajcarz MT, Krajcarz M, Stefaniak K. 2011a. The first record of leopard *Panthera pardus* Linnaeus, 1758 from the Pleistocene of Poland. *Acta Zoologica Cracoviensia* 54A(1–2):39–46.
- Marciszak A, Kropczyk A, Lipecki G. 2021b. The first record of *Cuon alpinus* (Pallas, 1811) from Poland and the possible impact of other large canids on the evolution of the species. *Journal of Quaternary Science* 36(6):1101–1121.
- Marciszak A, Lipecki G. 2021. *Panthera gombaszoegensis* (Kretzoi, 1938) from Poland in the scope of the species evolution. *Quaternary International*. doi: 10.1016/j.quaint.2021.07.002.
- Marciszak A, Lipecki G, Pawłowska K, Jakubowski G, Ratajczak-Skrzatek U, Nadachowski A. 2021c. The Pleistocene lion *Panthera spelaea* (Goldfuss, 1810) from Poland—a review. *Quaternary International* 605–606:213–240.
- Marciszak A, Sobczyk A, Kasprzak M, Gornig W, Ratajczak U, Wiśniewski A, Stefaniak K. 2020. Taphonomic and paleoecological aspects of large mammals from Sudety Mts (Silesia, SW Poland), with particular interest to the carnivores. *Quaternary International* 546:42–63.
- Marciszak A, Socha P, Nadachowski A, Stefaniak K. 2011b. Carnivores from Biśnik Cave. *Quaternaire. Hors-serie* 4:101–106.
- Marciszak A, Stefaniak K, Gornig W. 2016. Fossil theriofauna from the Sudety Mts (SW Poland). The state of research. *Cranium* 33(1):31–41.
- Michel V, Shen CC, Woodhead J, Hu H-M, Wu CC, Moullé PE, Khatib S, Cauche D, Moncel MH, Valensi P, Chou YM, Gallet S, Echassoux A, Orange F, Lumley Hd. 2017. New dating evidence of the early presence of hominins in Southern Europe. *Scientific Reports* 7:10074.
- Miquelle DG, Stephens PA, Smirnov EN, Goodrich JM, Zaumyslova OY, Myslenkov AE. 2005. Tigers and wolves in the Russian Far East: competitive exclusion, functional redundancy and conservation implications. In: Ray JC, Berger J, Redford KH, Steneck R, editors. *Large carnivores and the conservation of biodiversity*. Washington, DC: Island Press. p. 179–207.
- Moullé PE. 1992. *Les grands mammifères du Pléistocène inférieur de la grotte du Vallonet (Roquebrunne-Cap Martin-Alpes Maritimes). Etude paléontologique des Carnivores, Equidés, Suidés et Bovidés [The large mammals of the Lower Pleistocene from Vallonet cave (Roquebrunne-Cap Martin-Alpes Maritimes). Paleontological study of Carnivores, Equidae, Suidae and Bovidae]* (PhD thesis). Paris: Muséum National d'Historie Naturelle. In French.
- Nagel D. 1999. *Panthera pardus vraonensis* n. ssp., a new leopard from the Pleistocene of Vraona/

- Greece. Neues Jahrbuch für Geologie und Palaontologie Monatshefte 1999:129–150.
- Nagel D, Lindenbauer J, Kavcic-Graumann N, Rabeder G. 2018. Subtropical steppe inhabitants in the Late Pleistocene cave faunas of eastern Middle Europe. *Slovenský kras* 56(1):99–110.
- Nowell K, Jackson P. 1996. Wild cats-status survey and conservation action plan. IUCN: Gland.
- O'Regan HJ. 2002. A phylogenetic and palaeoecological review of the Pleistocene felid *Panthera gombaszoegensis* [PhD thesis]. Liverpool (UK): Liverpool John Moores University.
- O'Regan HJ, Turner A. 2004. Biostratigraphic and palaeoecological implications of new fossil material from the Plio-Pleistocene site of Tegelen, The Netherlands. *Palaeontology* 47:1181–1193.
- Ostrowicz A. 1881. Landek w hrabstwie Kłodzkim na Śląsku [Landek in the Kłodzko County in Silesia]. Nakładem autora, Poznań. In Polish.
- Pacher M, Rabeder G. 2016. The leopard (*Panthera pardus*), the rare hunter of the Alpine area during the Upper Pleistocene. *Cranium* 33(1):42–50.
- Paijmans JLA, Axel Barlow A, Förster DW, Henneberger K, Meyer M, Nickel B, Nagel D, Havmøller RV, Baryshnikov GF, Joger U, Rosendahl W, Hofreiter M. 2018. Historical biogeography of the leopard (*Panthera pardus*) and its extinct Eurasian populations. *BMC Evolutionary Biology* 18:156.
- Pax F. 1937. Die Höhlenfauna des Glatzer Schneeberges. 10. Wandlungen des Tierlebens in der Wolmsdorfer Tropfsteinhöhle [The cave fauna of the Glatzer Schneeberg. 10. Changes in animal life in the Wolmsdorf Stalactite cave]. Beiträge zur Biologie des Glatzer Schneeberges 3:289–293. In German.
- Pérez Ripoll M, Morales Pérez JV, Serra AS, Aura Tortosa JE, Sarrion Montañana I. 2010. Presence of the genus *Cuon* in Upper Pleistocene and initial Holocene sites of the Iberian Peninsula: new remains identified in archaeological contexts of the Mediterranean region. *Journal of Archaeological Science* 37:437–450.
- Pulina M. 1996. Jaskinie Sudetów [Caves of the Sudetes]. *Polskie Towarzystwo Przyjaciół Nauk o Ziemi, Warszawa*. In Polish.
- Reimer PJ, Austin WEN, Bard E, Bayliss A, Blackwell PG, Bronk Ramsey C, Butzin M, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Hajdas I, Heaton TJ, Hogg AG, Hughen KA, Kromer B, Manning SW, Muscheler R, Palmer JG, Pearson C, van der Plicht J, Reimer RW, Scott EM, Southon JR, Turney CSM, Wacker L, Adolphi F, Büntgen U, Capano M, Fahrni S, Fogtman-Schulz A, Friedrich R, Köhler P, Kudsk S, Miyake F, Olsen J, Reining F, Sakamoto M, Sookdeo A, Talamo S. 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* 62(4):725–757.
- Sanchis A, Gómez-Olivencia A, Real C et al. 2020. Pleistocene dhole (genus *Cuon*) populations from the Iberian Peninsula: morphometry, taxonomy and evolution. *Colloque Hommes-Canidés, Monographies Ausonius*. In: Boudadi-Maligne M, Mallye J-B, editors. Relations hommes—canidés de la Préhistoire aux périodes modernes, Ausonius Éditions, Bordeaux. p. 135–152.
- Sanchis A, Real C, Sauqué V, Núñez-Lahuerta C, Égüez N, Tormo C, Pérez Ripoll M, Carrión Marco Y, Duarte E, la Rasilla M. 2019. Neanderthal and carnivore activities at Llonin Cave, Asturias, northern Iberian Peninsula: faunal study of Mousterian levels (MIS 3)—general palaeontology, systematics, and evolution (taphonomy and fossilization). *Comptes Rendus Palevol* 18:113–141.
- Sauqué V, Cuenca-Bescós G. 2013. The Iberian Peninsula, the last European refugium of *Panthera pardus* Linnaeus 1758 during the Upper Pleistocene. *Quaternaire* 24:35–48.
- Sauqué V, Sanchis A. 2017. Leopards as taphonomic agents in the Iberian Pleistocene, the case of Racó del Duc (Valencia, Spain). *Palaeogeography Palaeoclimatology Palaeoecology* 472:67–82.
- Sauqué V, Sanchis A, Madurell Malapeira J. 2017. Late Pleistocene leopards as a bone accumulator: taphonomic results from S'Espasa cave and other Iberian key sites. *Historical Biology* 30(2):821–834.
- Sludskij A. 1976. Leopard. In: *Large carnivore*. Forest Newspaper 14:58–81.
- Sommer RS, Benecke N. 2006. Late Pleistocene and Holocene development of the felid fauna (Felidae) of Europe: a review. *Journal of Zoology* 269(1):7–19.
- Spassov N, Raychev D. 1997. Late Wurm *Panthera pardus* remains from Bulgaria: the European fossil leopards and the question of the probable species survival until the Holocene on the Balkans. *Historia naturalis Bulgarica* 7:71–96.
- Stefaniak K, Bieroński J. 2009. Caves and rock shelters of the Eastern Sudetes-catalogue of important speleological features. *Studies of the Faculty of Earth Sciences University of Silesia* 56:515–534.
- Suárez-Bilbao A, Garcia-Ibaibarriaga N, Castaños J, Castaños P, Iriarte-Chiapusso M-J, Arizabalaga A, Torrese T, Ortiz JE, Murelaga X. 2016. A new Late Pleistocene non-anthropogenic vertebrate assemblage from the northern Iberian Peninsula: Artazu VII (Arrasate, Basque Country). *Comptes Rendus Palevol* 15:950–957.
- Talamo S, Fewlass H, Maria R, Jaouen K. 2021. “Here we go again”: the inspection of collagen

- extraction protocols for ^{14}C dating and palaeodietary analysis. *STAR* 7(1):62–77.
- Talamo S, Richards M. 2011. A comparison of bone pretreatment methods for AMS dating of samples >30,000 BP. *Radiocarbon* 53:443–449.
- Turner A. 2009. The evolution of the guild of large Carnivora of the British Isles during the Middle and Late Pleistocene. *Journal of Quaternary Science* 24:991–1005.
- van Klinken GJ. 1999. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *Journal of Archaeological Science* 26:687–695.
- Utescher K. 1939. Die Entstehung schlesischer Höhlenlehme nach ihrer chemischen Untersuchung [The formation of Silesian cave clay according to its chemical analysis]. In: Zotz L, editor. *Die Altsteinzeit in Niederschlesien*. Kabitsch Verlag, Leipzig. p. 122–142. In German.
- Yang H, Zhao X, Han B, Wang T, Mou P, Ge J, Feng L. 2018. Spatiotemporal patterns of Amur leopards in northeast China: influence of tigers, prey, and humans. *Mammalian Biology* 92:120–128.
- Vega del Sella R. 1930. Las cuevas de la Riera y Balmori (Asturias) [The caves of La Riera and Balmori (Asturias)]. *Memoria Comisión de Investigaciones Paleontológicas y Prehistóricas* 13:1–116. In Spanish.
- von Koenigswald W, Nagel D, Menger F. 2006. Ein jungpleistozäner Leopardenkiefer von Geinsheim (nördliche Oberheinebene, Deutschland) und die stratigraphische und ökologische Verbreitung von *Panthera pardus* [A Late Pleistocene leopard pine from Geinsheim (Northern Upper Hein Plain, Germany) and the stratigraphic and ecological distribution of *Panthera pardus*]. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2006:277–297. In German.
- Wiśniewski A, Stefaniak K, Wojtal P, Zych J, Nadachowski A, Musil R, Badura J, Przybylski B. 2009. Archaeofauna or palaeontological record? Remarks on Pleistocene fauna from Silesia. *Sprawozdania Archeologiczne* 61:1–62.
- Wolsan M. 1989. Drapieżne [Carnivora]. *Folia Quaternaria* 59–60:177–197. In Polish.
- Zotz LF. 1937a. Die schlesischen Höhlen und ihre eiszeitlichen Bewohner [The Silesian Caves and their Ice Age inhabitants]. Wilhelm Gottlieb Korn Verlag, Breslau, 38 pp. In German.
- Zotz LF. 1937b. Altsteinzeitlicher Bärenkult in den Sudeten [Palaeolithic bear cult in the Sudetes]. *Altschlesische Blätter* 1–2:4–7. In German.
- Zotz LF. 1939. Die Altsteinzeit in Niederschlesien [The Paleolithic in Lower Silesia]. Kabitsch Verlag, Leipzig. In German.
- Zotz LF. 1951. Altsteinzeitkunde Mitteleuropas [The Paleolithic in Lower Silesia]. F. Enke Verlag, Stuttgart. In German.