



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



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ABSTRACT

European leopard sites in Europe demonstrate Early/Middle Pleistocene out of Africa lowland, and Late Pleistocene Asian alpine migrations being driven by climatic changes. Four different European Pleistocene subspecies are known. The final European Late Pleistocene “Ice Age leopard” *Panthera pardus spelaea* (Bächler, 1936) is validated taxonomically. The skull shows heavy signs of sexual dimorphism with closest cranial characters to the Caucasian *Panthera pardus ciscaucasica* (Persian leopard). Late Pleistocene leopards were distributed northernmost, up to S-England with the youngest stratigraphic records by skeletons and cave art in the MIS 2/3 (about 32,000–26,000 BP). The oldest leopard painting left by Late Palaeolithics (Aurignacians/Gravettians) in the Chauvet Cave (S-France) allows the reconstruction of the Ice Age leopard fur spot pattern being close to the snow or Caucasian leopards. The last Ice Age glacial leopard habitat was the mountain/alpine boreal forest (not mammoth steppe lowland), where those hunted even larger prey such as alpine game (Ibex, Chamois). Into some lairs, those imported their prey by short-term cave dwelling (e.g. Baumann’s Cave, Harz Mountains, Germany). Only Eurasian Ice Age leopards specialized, similar as other Late Pleistocene large felids (steppe lions), on cave bear predation/scavenging partly very deep in caves. In Vjetrenica Cave (Dinarid Mountains, Bosnia Herzegovina), four adult leopards (two males/two females) of the MIS 3 were found about two km deep from the entrance in a cave bear den, near to one cave bear skeleton, that remained articulated in its nest. Leopards died there, partly being trapped by raising water levels of an active ponor stream, but seem to have been killed possibly either, similar as for lions known, in battles with cave bears in several cave bear den sites of Europe (e.g. Baumann’s Cave, Wildkirchli Cave, Vjetrenica Cave). At other large cave sites, with overlap of hyena, wolf and dhole dens at the cave entrances, leopard bones with bite damages indicate their remains to have been imported and consumed by predators in alpine regions due to reduced prey availability. The best models for the competition/taphonomy of large predators – felids, hyenids, canids – within large cave bear dens of Europe is represented in combination of the Zoolithen Cave and Vjetrenica Cave taphonomy.

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1. Introduction

1.1. Pleistocene leopard sites in Europe and their dating

Pleistocene leopards are known from different time periods all over Europe with the most known sites in the Late Pleistocene

(Fig. 1, Table 1). First palaeobiographical maps (see Fischer, 2000) can be much extended now including herein 78 sites which separate four preliminary “subspecies” within the Early to Late Pleistocene time frame (Figs. 1 and 2). Modern DNA studies about extant leopards which failed most recent for the Pleistocene record (Rozhnov et al., 2011) are important to understand the taxonomy and phylostratigraphic record of extinct forms. However, even if in future those will be positive for younger aged specimens, there remains a fossil gap in knowledge between the Last Glacial Maximum and Holocene that will link the evolutionary relationships to the ten modern leopards of the world (cf. Fig. 2).

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Fig. 1. Sites with Pleistocene leopard *Panthera pardus* subsp. palaeobiogeography (map showing interstadial within glacial of Late Pleistocene) in Europe (Lartet, 1867; Bourguinat, 1879; Costa, 1886; Issele, 1892; Boule, 1919; Mochi, 1911; Regalia, 1911; Soergel, 1914; Del Campana, 1914; Simonelli, 1916; Battaglia, 1918; Schmidgen, 1922; Fabiani, 1923; Fraipont, 1923; Boule and Vileneuve, 1927; Rüger, 1928; Leonardi, 1935; Bächler, 1936; Kretzoi, 1938; Wettstein, 1938; Boursiac, 1939; Schütt, 1940; Koby, 1946; Schmid, 1949; Vanzo, 1954; Vialli, 1957; Kurtén, 1968; Lumley-Woodyear, 1969; Schütt, 1969a,b; Malez and Pepeonik, 1969; Tozzi, 1970; Thenius, 1971; Hemmer, 1971; Pillard, 1972; Sorbini and Durante Pasa, 1974; Kotsakis and Palombo, 1979; Groiss, 1979; Lumley et al., 1984; Estévez, 1987; Lumley et al., 1988; Bassiakos, 1993; Valensi, 1994; Tournepiche, 1996; Nagel, 1997; García et al., 1997; Spassov and Raychev, 1997; Otte et al., 1998; Caceres et al., 1998; Nagel, 1999; Aourag, 1999; Tsoukala, 1999; Argant, 1991; Fischer, 2000; Koumouzelis et al., 2001; Walker, 2001; Tournepiche, 2001; Quam et al., 2001; Georgiadou-Dikaoulia et al., 2002; Rabeder, 2003; Barroso Ruiz et al., 2003; Currant, 2004; Moulle et al., 2005; Moigne et al., 2006; Koenigswald et al., 2006; Testu, 2006; Crégut-Bonnoure et al., 2010; Marciszak et al., 2011; Miracle and Brajković, 2010; Baryshnikov, 2011; Corral, 2012; Miculinić, 2012; Diedrich, 2013b, cf. Table 1).

1.2. First European leopards at the Pliocene/Pleistocene boundary

Using the fossil bone record, felids already diverge in the Miocene about 7–10 Ma ago (Johnson et al., 2006). Leopard mitochondrial gene sequence data of modern species, which can not include very old material, suggested instead, that the general felid divergence began not before the Pliocene, about 6.0 Ma (Davis et al., 2010). Based on this, a diversification of the first leopard-like felids must be expected within the Miocene–Pliocene boundary. The oldest believed leopard fossil specimens were mentioned from eastern Africa (Laetoli) and are dated around 3.8 Ma to the late Pliocene (Barry, 1987; Werdelin and Levis, 2005; Christiansen, 2008). Further evidence for early leopards comes from the oldest tiger skull from China (Asia) that includes leopard-like features. This fossil dated the leopard/jaguar felid split also before 2.5 Ma at the boundary of the Plio-/Pleistocene (Mazák et al., 2011). This indicates an early presence and already wide-distribution of leopards in Africa and Eurasia.

In Africa, few younger fossils assigned to “*Panthera pardus* subsp.” are dated approximately 2.0–1.8 Ma into the Villafranchian

(Werdelin and Levis, 2005; Fig. 2). The oldest Late Pliocene/Early Pleistocene leopards have been found at several open air sites, mainly over Europe, but with little and diagnostic material (Table 1, Fig. 1: Soergel, 1914; Boursiac, 1939; Thenius, 1965, 1971; Kotsakis and Palombo, 1979; Moulle et al., 2005). The single bones are from an open landscape adapted leopard which was not using caves, similar as for the ethology of modern African leopards (e.g. Myers, 1980). Snow leopards (*Panthera uncia*) seem to be present in Asia (Siwaliks, Pakistan) supposed to exist since the Early Pleistocene (1.4–1.2 Ma) (Brandt, 1870; Tscherski, 1892), which studies are historically and not validated modern. Molecular-phylogenetic evidence suggested that the origin of all the modern *P. pardus* subspecies (Fig. 2) evolved only in Africa, most probably about 825,000–470,000 BP (middle Middle Pleistocene), the Cromerian Complex (Johnson and O'Brien, 1997; Uphyrkina et al., 2001; Johnson et al., 2006; Fig. 2), which is in contrast to the fossil record as mentioned above. All results implicate evolution and migratory waves starting first most probably only from Africa. Such migration waves to Europe can be recorded several times in the early to middle Pleistocene (Fig. 2), but it was also hypothesized

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