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Remains of Canidae and Felidae from Południowa Cave (Sudetes Mts., SW Poland)

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Południowa Cave is a locality that has been known for more than 500 years, where at least three or even four different faunal assemblages have been found. The oldest faunal elements are represented by the rodent *Baranomys loczyi*, and the carnivores *Baranogale helbingi* and *Mustela pliocaenica*, being the only Pliocene finds in the Sudetes Mts. caves. The second faunal assemblage is dated back to the early Middle Pleistocene and consists of the following taxa: *Sorex* sp., *Rhinolophus* aff. *ferrumequinum*, *Glis sackdilligensis*, *Pliomys coronensis*, *Pliomys episcopalis*, *Mimomys* sp., *Lycaon lycaonoides*, *Canis mosbachensis*, *Vulpes vulpes*, *Ursus deningeri*, *Ursus arctos* ssp., *Ursus* cf. *thibetanus*, *Gulo gulo schlosseri*, *Meles meles atavus*, *Martes vetus*, *Mustela strandi*, *Mustela palerminea*, *Mustela praenivalis*, *Panthera spelaea fossilis*, *Homotherium latidens latidens*, *Panthera gombaszoegensis gombaszoegensis*, *Acinonyx pardinensis intermedius*, *Felis* cf. *silvestris*, *Pachycrocuta brevirostris* and *Capreolus* sp. The third assemblage is dated back to the Late Pleistocene (MIS 3), and consists of *Glis glis*, *Arvicola* sp., *Canis lupus spealeus*, *Ursus* ex. gr. *spelaeus*, and *Martes martes*. Finally, the youngest fauna, dated as MIS 1, is represented by *Arvicola* sp., *Apodemus* sp., *Lepus* sp., *Cricetus cricetus*, *Ursus arctos arctos*, *Meles meles*, *Martes martes*, and *Capreolus capreolus*. Possible relationships that may be inferred include the impact of new species in the disappearance of ancient carnivores.

Key words: Middle Pleistocene, Sudetes, competition, extinction, *Homotherium.*

INTRODUCTION

Over the last 30 years, there has been significant progress in the understanding of environmental changes in Europe during the Middle Pleistocene, and of the significance of these changes for the development of extant biota (Strani, 2021). The biochronological context of this interval within Central Europe is relatively abundant. The Middle Pleistocene fossil record of Poland is well documented. Its complex physiography, climatic heterogeneity, and geographical and ecological barriers are factors in analysing changes in taxonomic composition and diversity as well as for more precise comparison of faunal dynamics between different regions. The Early Pleistocene Polish carnivore assemblages originated from a mosaic of species of African and Eurasian origin. Over time, several important taxa dispersed across a large territory while other forms retreated and vanished. During the Middle Pleistocene, the territory of present-day Poland experienced a long and complex history of species turnover, invasions, competitive exclusion and prolonged survival of some taxa in refugia (Wolsan, 1989, 1990, 1993; Marciszak et al., 2020, 2021a–d, 2023a). Located on the northern fringe of the Carpathian-Sudetes arch and acting as a natural corridor through the European continent, the territory of modern Poland is among the key areas for estimating changes in faunal composition over time.

The Middle Pleistocene (MIS 19-6) was a very dynamic period in the history of Europe. Ecological shifts observed at that time and consequent species turnover led to the appearance of modern habitats. Early Pleistocene faunal assemblages were replaced by those more similar in taxonomic composition to extant assemblages (Fejfar and Heinrich, 1979, 1980, 1983, 1988; Fejfar and Horáček, 1983; Fejfar et al., 1998; Sala and

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Masini, 2007; Kahlke et al., 2011; Kahlke, 2014; Palombo, 2016). A thorough study of Middle Pleistocene faunas is crucial for establishing the biochronological background and reconstructing environmental changes that might have caused species turnover (e.g., Berto et al., 2021; Krokhmal' et al., 2021, 2023). Carnivores, together with other mammals, play a significant role in terms of biochronology and climate reconstruction. The history of these changes in western and southern Europe is well documented, while Central Europe remains a relatively poorly known area in this aspect.

There has been an obvious gap in the reconstruction of the Middle Pleistocene world of the long-gone carnivores since material from this interval from the Sudetes area has never been noted. Only Zotz (1939) suggested that some materials and deposits from Południowa Cave may be of Middle Pleistocene age, but these were never an object of more detailed studies. It would take over 70 years for this situation to change. Research into material in some local museums and private collections allows us to rediscover this locality, and show the remains it contains are extraordinary. Unfortunately, its original wealth has been irretrievably lost, and the finds presented here are probably a small part of the former, extraordinary palaeontological wealth. Much of this material remains undiscovered and undescribed, but the search continues, and new material appears every few months. However, already at this stage, the potential of this site, that has been destroyed, is clear. In order to illustrate at least a small part of the extraordinary finds from this site, as well as to introduce Południowa Cave to the scientific world, we have compiled a history of research and made a detailed study of the carnivores, the most numerous amnd significant mammals from this site.

GEOLOGICAL SETTING

GEOLOGY

Połom (Germ. *Kitzelberg*) is a domed mountain 667 m a.s.l. located in the Kaczawa Mts., in the western part of the Sudetes Mts. (SW Poland; Figs. 1 and 2). The mountain has steep, concave-convex slopes and rises above the Kaczawa River valley and the town of Wojcieszów. Similarly to the nearby Młyniec (Miłek) mountain, it is built of carbonate rocks, crystalline limestones and marbles, forming a 20 km-long NW–SE belt of hills. The Cambrian age of the limestones was established based on fossils found there (Gürich, 1882, 1890; Zimmermann and Berg, 1932; Schwarzbach, 1936; Gunia, 1967). This was disputed by Skowronek and Steffahn (2000), who, on the basis of foraminiferal and vertebrate assemblages, determined the age of the rocks to be no older than Ordovician. However, more recent studies of archaeocyathids found there allow dating to the middle part of the Lower Cambrian (Białek et al., 2007). The marbles are accompanied by intercalations of phyllite, calcareous shale, sericite-chlorite shale, carbonate-quartz-sericite shale, and a succession of greenschists around (Baranowski and Lorenc, 1981; Baranowski et al., 1990; Kryza et al., 1992). These rocks belong to a geological unit termed the Kaczawa complex. Veins of younger rhyolite cut this sequence.

The marbles of Połom have a varied chemical composition, allowing seven lithotypes to be distinguished (Lorenc, 1984). The content of CaO in the rocks ranges from 36 to 54%, and the content of insolubles reaches 20% (Pulina, 1977, 1996; Lorenc, 1984). The marbles are up to 500 m thick, they are foliated and folded dip to the N and NNW at various angles, mostly between 45 and 80° (Baranowski and Lorenc, 1981). They are characterised by strong fracturing, mostly along WNW–ESE, NW–SE, and NE–SW directions (Rogala, 2003). This was conducive to the development of karst landforms, including karst sink troughs and caves, mostly filled with sediments. Among these the Gwiaździsta Cave (565 m long), the Nowa Cave (227 m long), Szczelina Wojcieszowska (112.6 m deep – the deepest in the Sudetes Mts.), Jasna Cave (95 mlong), and Kryształowa Cave (130 m long with spectacular speleothems) stand out. The number of caves in the Wojcieszów region are unique in the Sudetes Mts., considering the small area occupied by karst rocks.

Intensive faunal, palaeontological and archaeological research conducted in the Wojcieszów region in the 1920s and 1930s made it possible to draw the first conclusions concerning the age of the cave deposits and the evolution of landforms. The first interpretation of the genesis of the caves was made by Zotz (1939). In the deposits of the Wschodnia Cave, situated 290 m above the Kaczawa valley, he found granite river gravels originating from the nearby Karkonosze Mts., and assigned to them a Pliocene age. Detailed studies of the karst of Połom led to a hypothesis of cyclic development of the karst phenomena (Pulina, 1977). The occurrence of three basic sequences of karst caves found by Zotz (1939) (260–280, 150–210, and 30–70 m above the bottom of the Kaczawa valley) was inferred to correspond to the height of three planation levels in the Western Sudetes (Jahn, 1953). Their ages were stated as Late Cretaceous, Paleogene, and Neogene. According to this hypothesis, with the deepening of the valleys because of successive erosional phases following uplift phases of the Western Sudetes, the higher cave levels were deprived of water flow and became a proxy of the position of the valley floor during periods of limited erosion. The opinions of Pulina (1977) were supported by observations and dating of fossiliferous calcite deposits made on 10 caves known at the time, which had a total passage length of 290 m. Further knowledge of the Połom karst, within which more than 2700 m of cave passages were known at the beginning of the 21st century, allowed us to question the existence of cave horizons *sensu* Pulina (1977): Rogala (2003) noted that most cave passages of Połom are steep or vertical, and lithological or structural controls on their development are clear, such as the contact between limestones and shales in the Za Sztolnią, Ostrych Kantów and Zaciskowa caves, the interstratal fractures in the Północna Duża and Naciekowa caves, and the vertical fissures in Jasna and Aven in the Połom caves. The occurrence of most of the known cave openings coincides with the occurrence of limestone lithotypes C and A, characterised by a high CaO content, whereas no such openings are found in limestone types D1 and D2 (Lorenc, 1984; Rogala, 2003). These phenomena were thus not related to the date of formation of the caves, but they stressed the role of long-term differentiation of the erosional-denudational morphology of the Sudetes in the conditions of ongoing tectonic activity (Rogala, 2003). Full reconstruction of karst landforms and deposits in the Wojcieszów region is difficult. Some of the caves identified in the past have been destroyed by marble quarrying conducted since the middle of the 18th century, and developed on an industrial scale since 1893. Active quarries surround the top of Mt Polom from two sides.

SITE

Południowa Cave was located on the southern slope of Połom Mountain, on the third mining floor of the quarries from the top. The site was known under many German names: Kitzelhöhle, Kitzelloch, Kitzelberghöhle, Kitzelkirche, Kützelloch, Kützellkirche and Teufelskeller.

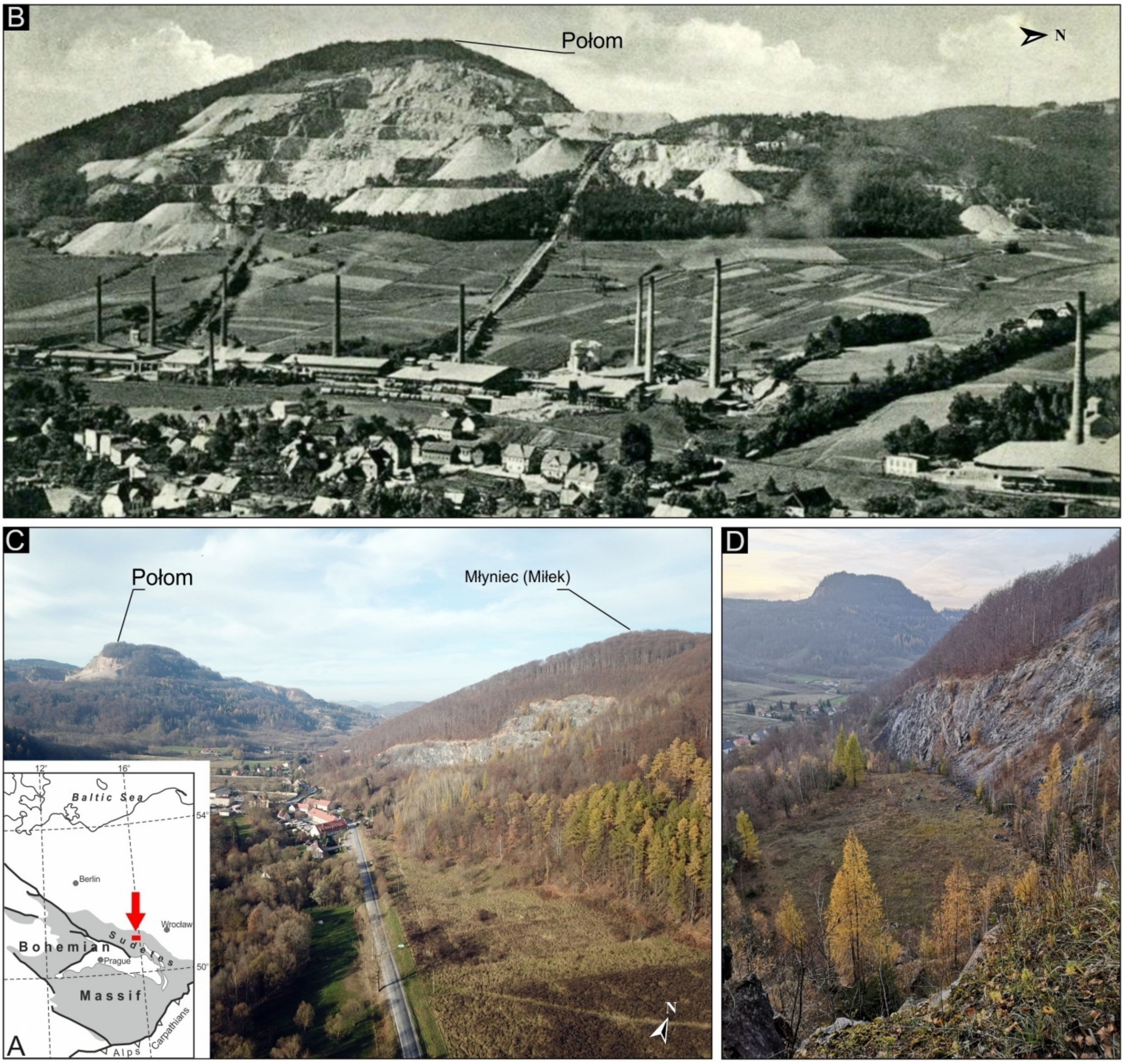

Fig. 1. Different photos of Mount Połom

A – location of Mount Połom within the Sudetes; **B** – above the Kaczawa River valley and the town of Wojcieszów (Germ. *Kauffung*) in the Kaczawa Mts. in 1915–1930 (old postcard, author unknown); **C**, **D** – nowadays (photo M. Kasprzak)

The history of discovering the caves in the Mount Połom in general, and particularly of Południowa Cave (50°57’17” N 15°55’23” E, 620 m a.s.l.) is linked with the Prussian king Frederick II the Great, who ordered the provision of marble to build his Sanssouci Palace in Potsdam in 1742. In 1746, the marble resources in Wojcieszów were explored and mining began for its construction.

However, Południowa Cave was known long before quarrying operations began in the area (Beckmann, 1710). The first mention of the cave dates to 1476, when the name “devil’s basement” (Germ. Teufelskeller) appeared for the first time (Bruzen de la Martiniere and Wolff, 1744; Bruzen de la Martiničre, 1746; Kaluza, 1818; Gehler, 1829; Schmidt, 1830). In the mid-19th century, it was reported that the “stalactite cave” in Połom, or Kitzelloch, once famous for its beautiful dripstone cover and huge stalactites, retained only small fragments of its former beauty (Milde, 1859). Despite progressive degradation, the cave in later years was still mentioned in various publications (Scharenberg, 1862; Beck, 1908). In 1921, the length of its preserved part was ~30 m (Arndt, 1921, 1923, 1925). In the 1930s, Zotz (1939) reported that there was more than 20 m left, while less than 20 years later, the cave was only 10 m long (Sawicki, 1952; Kowalski, 1954).

However, it was not until 1895 that large limestone workings (*Kalkwerk Tschirnhaus*) were built, exploiting these rocks on a mass scale, and that attention was drawn to the cave finds, providing new information about them (Bieroński et al., 2007). Excavations in Południowa Cave were carried out by Zotz (1937, 1939; Fig. 3). At that time, the cave was developed into an elongated L-shaped corridor, ~20 m long, up to 3 m high and

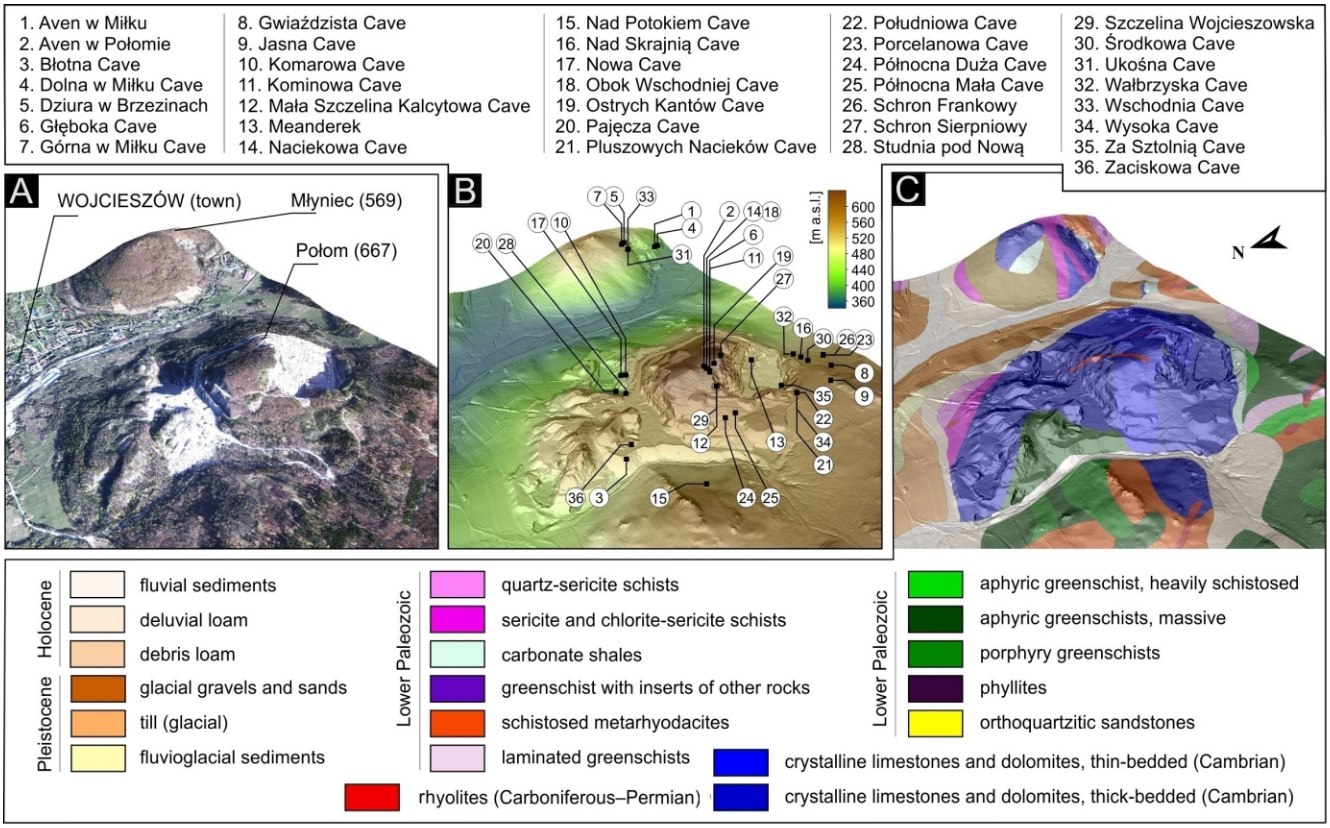

Fig. 2. Terrain situation of the study area in oblique view

A – land use; **B** – landform and location of caves; **C** – geological map, simplified. Sources: DTM and orthophotomap from the PZGiK (State geodetic and cartographic resource in Poland/geoportal.gov.pl), Detailed geological map of the Sudetes Mts. 1:25 000, sheet Wojcieszów (Cwojdziński and Kozdrój, 1995), Central Geological Database (CGD) of the Polish Geological Institute. Note: the location of caves according to the CDG is generalised in some cases

1.5–3 m wide (Fig. 4). The bottom of the cave was filled with yellow clays, preserved only within depressions of the rock floor. Above this was breccia formed by a mixture of weathered granite clasts, quartz, inclusions of quartz gravel, terra rossa clays, and limestones. Above were reddish crystalline calcite plates mixed with terra rossa clay. Above these were brown clays (Fig. 4). A coarsely crystalline calcite plate covered a large portion of the succession (Zotz, 1939).

A report by the Museum of the Earth of the Polish Academy of Sciences, Warsaw, dated 31.08–3.09.1952, stated that the cave was almost destroyed. Finally, one of the excavations was re-examined and part of the silt in its vicinity was dug up. The bottom of the excavation was made of yellow kaolinitic clay; above there was a breccia, made of an admixture of various Kaczawa rocks and aplite gneiss. The ceiling was made of brown clay containing Pleistocene animal bones and Palaeolithic artifacts (Pulina, 1977, 1996; Bieroński et al., 2007).

There are relatively few published studies of the Południowa Cave fauna (Anonymous, 1812; Gerhard, 1816; Oeynhausen, 1822; Glocker, 1832; Henschel, 1834). On a spoil heap of a destroyed part of the cave, a mandible of a brown bear *Ursus arctos* Linnaeus, 1758 was found (Römer, 1874), among hundreds of cave bear bones, clearly contradicting subsequent reports of the lack of large mammal bones in the cave. This finding was later reported by other researchers (Gürich, 1885, 1890; Pax, 1921, 1925; Kowalski, 1959). Several studies concerned the extant invertebrate fauna found in preserved parts of the cave (Gerbardt, 1910; Arndt, 1921, 1923). Additionally, the presence of *Barbastella barbastellus* (Schreber, 1774) hibernating in a cave was noted (Seidel, 1927). Near the entrance were discovered remains of insectivorans, bats and rodents (Langenhan, 1904a–d). Revision of this material, together with some provided by Wenke (1933), revealed the presence of an undetermined shrew *Sorex* sp. (maxilla with two molars), several tens of remains of *Rhinolophus ferrumequinum* (Schreber, 1774) (including, among others, the maxilla from C1 and P4, parts of three left mandibles from c1-m3, m1-m3 and p2-p3 and part of of a right mandible from i3, p2 and p4-m3 as well as numerous isolated teeth), an isolated m1 of *Baranomys loczyi* Kormos, 1933 and a right m1 of *Glis* sp., morphologically closely related to *Glis sackdillingensis* (Heller, 1930, 1937). On a spoil heap near the Południowa Cave, a canid skull, approximately 200 mm long, was found (Langenhan, 1904b). Zotz (1939), at the same level as Langenhan (1904a-d) though a little deeper inside the cave, found a strongly cemented breccia with the remains of *Myotis* sp., and also a heel bone of the cave bear *Ursus spelaeus* Rosenmüller, 1794, in the cave chamber (Zotz, 1939).

Although Wenke (1933) signalled numerous finds from the 1920s of mammalian bones near the site or in a spoil heap surrounding it, these remains have never been properly studied. After extraction, this material was deposited in the quarry collection and sent to numerous museums, including those in Jelenia Góra, Jawor, Bolków, Wrocław, Legnica, Wałbrzych, Chocianów, Görlitz and Berlin. Many of these remains were also concentrated in private collections, mainly in Germany, where they are still present. On the other hand, after nationalisation of the quarries in and within Mount Połom, a significant

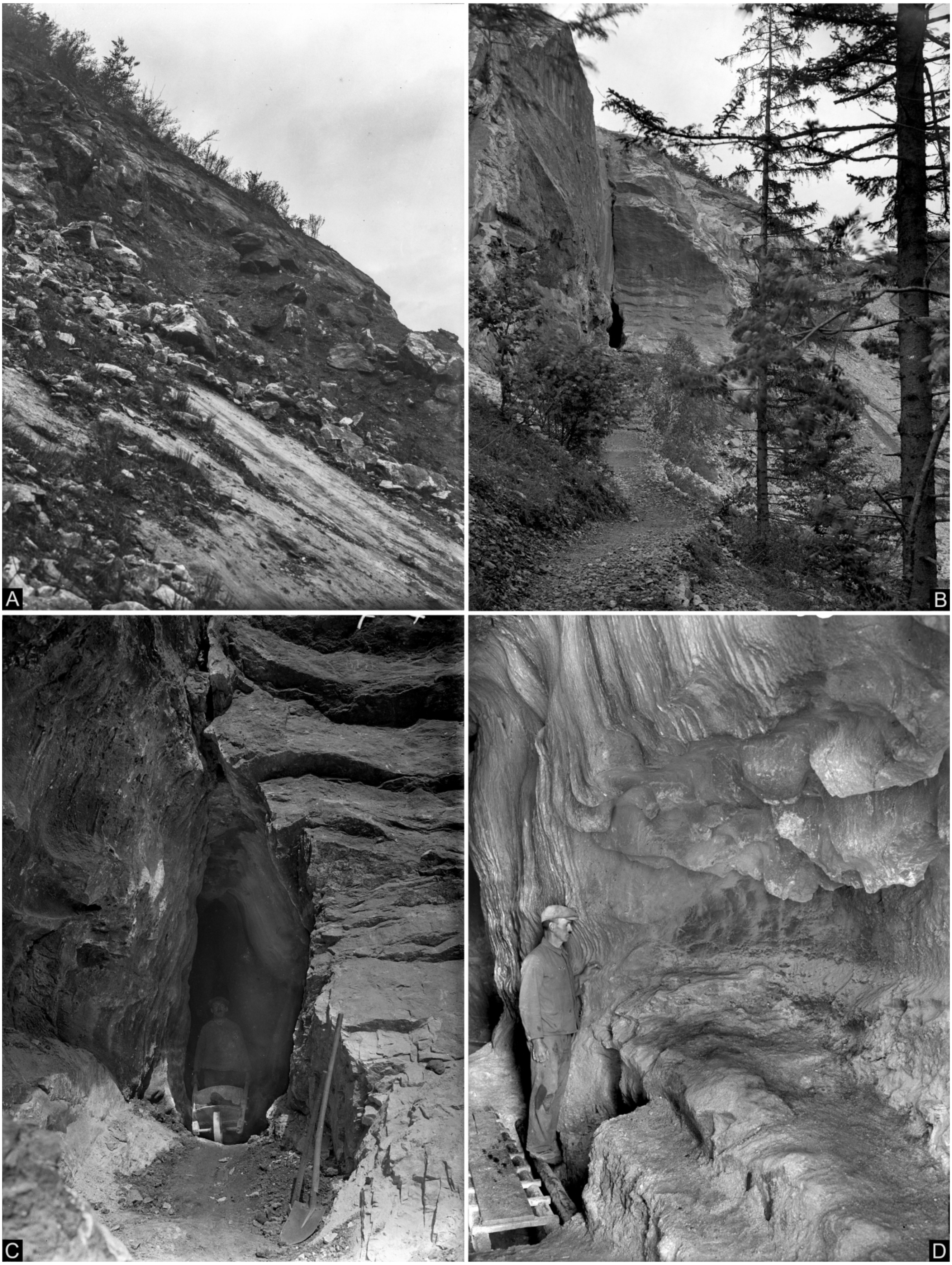

Fig. 3. Historical photos from 1936 showing Południowa Cave

A – a waste heap below the cave; **B** – a path leading to the preserved part of the cave, and representing a part destroyed earlier; **C** – excavations in the preserved part; **D** – a chamber with remnants of dripstone. Source: Archaeological Museum, Branch of the City Museum of Wrocław

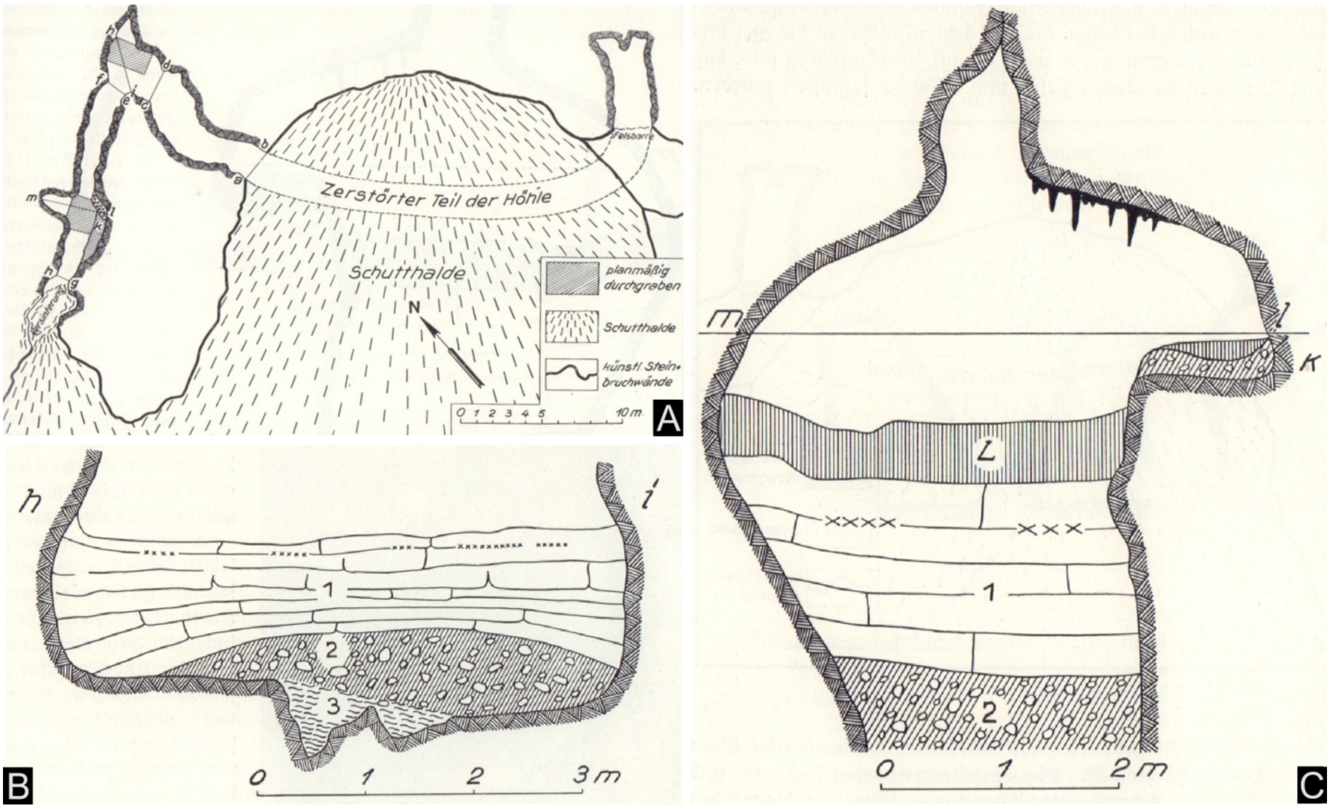

Fig. 4. Południowa Cave

A – ground plan (after Zotz, 1939: 55, fig. 49); **B** – frontal cross-section (1 – yellow clays; 2 – breccia formed of a mixture of weathered granite clasts, quartz, inclusions of quartz gravel, red terra rossa clays and limestones; 3 – reddish, crystalline calcite plates mixed with red terra rossa clay; after Zotz, 1939: 57, fig. 51); **C** – lateral cross-section (after Zotz, 1939: 56, fig. 50)

part of their collections was transferred to the Department of Palaeozoology (University of Wrocław). The last 10 years has been a period of documenting this material, which allowed significant expansion of the Południowa Cave faunal list. In 1952–1976, several rescue expeditions were organised to save bone remains, excavated during quarrying. During such expeditions, bone remains were also found within the heap and mounds of the still-existing cave. Museum inquiries, mainly those in Germany, also produced some material. Together with the remains from Polish and German private collections, they made it possible to compile a list of the remains, analysis of which allowed creation of the faunal list presented herein. Revision of the remains is still incomplete. Each year brings new finds, and probably a significant part of the bone material has not yet been identified. However, even the material found so far shows how much palaeontological potential was present at this site and what a gem was destroyed by the quarrying. It also constitutes a reminder of the need to preserve still-existing caves in further mining activities on Mount Połom.

MATERIAL AND METHODS

The carnivore material from Południowa Cave analysed in this paper is mostly housed in the Department of Palaeozoology of the University of Wrocław, Poland. Some specimens are also in private collections. Measurements were taken point to point, with the landmark system, to the nearest 0.01 mm. A standard published measurement scheme was applied and modified (Boudadi-Maligne, 2010). The definition and subdivisions of mammal zones and their correlation with the chronostratigraphic scale and MN zones follow Kahlke et al. (2011). The nomenclatural codification follows the current (fourth) edition of the International Code of Zoological Nomenclature (ICZN, 2000). Capital and lower case letters, C/c (canines), I/i (incisors), P/p (premolars), and M/m (molars), refer to upper and lower teeth, respectively. Standard body mass estimates using dental or skeletal parameters were used (Hemmer, 2001; Hemmer and Kahlke, 2022). Abbreviations used here are the following: B – breadth, Ba – mesial breadth, Bp – distal breadth, L – length, mm – millimetre, mc – metacarpal, mt – metatarsal, pa – paracone, pad – paraconid, pr – protocone, prd – protoconid.

SYSTEMATIC PALAEONTOLOGY

Class Mammalia Linnaeus, 1758
Order Carnivora Bowdich, 1821
Suborder Caniformia Kretzoi, 1943
Family Canidae Fischer de Waldheim, 1817
Genus *Lycaon* Brookes, 1827
Lycaon lycaonoides (Kretzoi, 1938)
(Fig.5A)

Material. – Worn, left C1 (JP.1.1); left M2 (JP.1.6); right p1 (JP.1.2); right p2 (JP.1.3); right half of m1 (JP.1.4); talonid of right m1 (JP.1.5); right m2 (JP.1.7); proximal half of right metacarpal 3 (JP.1.8); phalanx 1 (JP.1.9).

Measurements. – Table 1.

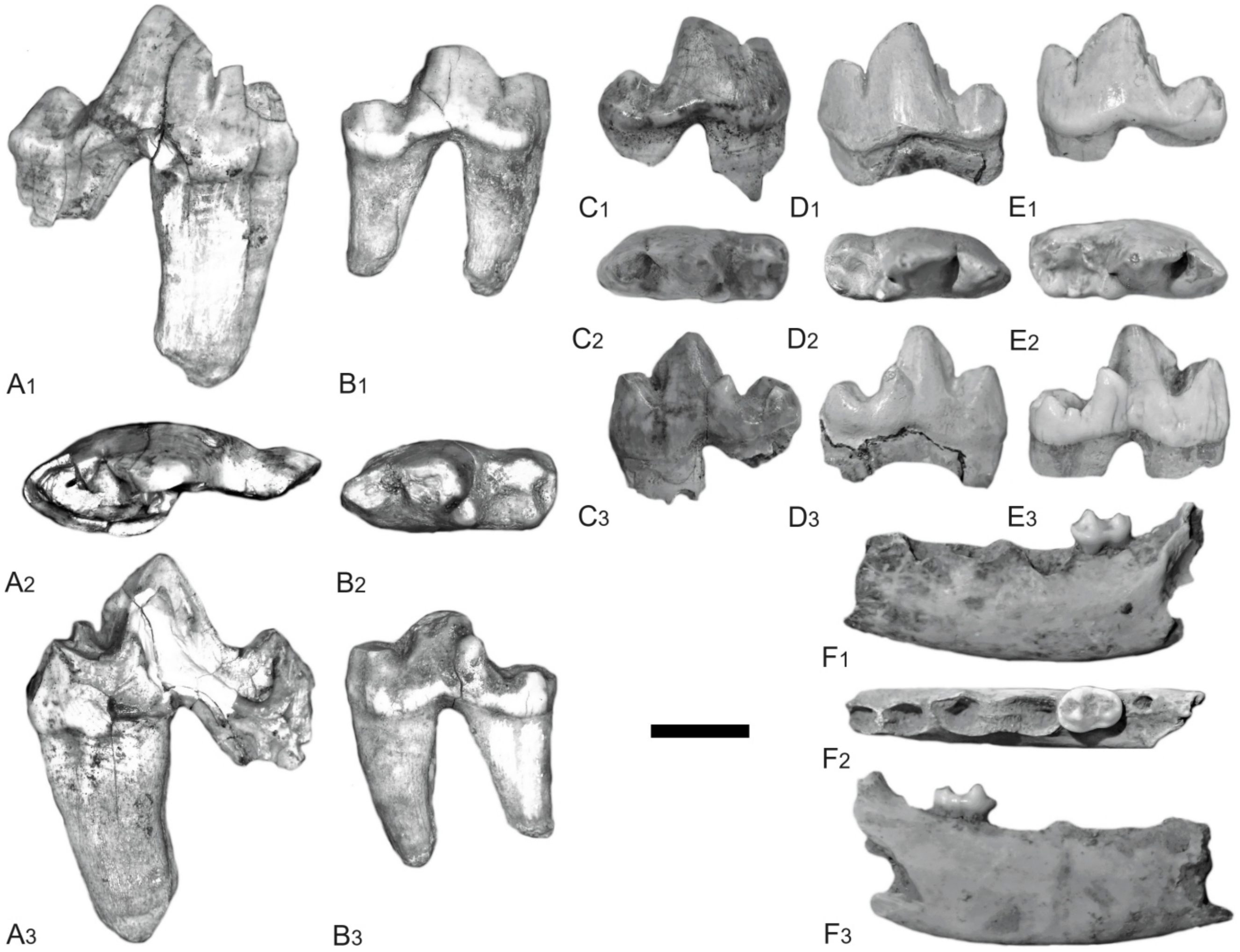

Fig. 5. Remains of canids from Południowa Cave

Lycaon lycaonoides: **A** – right m1 (JP.1.5). *Canis mosbachensis*: **B** – right m1 (JP.2.13); **C** – right m1 (JP.2.14); **D** – left m1 (NN); **E** – left m1 (NN). *Vulpes vulpes*: **F** – left mandible (JP.3.1). All specimens shown at the same scale (12 mm), 1 – buccal view; 2 – occlusal view; 3 – lingual view

Description. – The C1 (JP.1.1) is strong and robust, curved distally and strongly flattened bucco-lingually. The crown is proportionally short, with smooth distal edges accompanied by hollows. The tooth bears a thin but well-defined mesio-lingual and distal crest, running from its apex to the base. The M2 (JP.1.6) is large and sub-triangular in occlusal view, with two low-crowned and similarly sized main cusps, the paracone and metacone. The hypocone and entocone are not present, while the protocone is closely associated with the lingual margin, with the present postprotocrista structure. The

Table 1

Measurements of *Lycaon lycaonoides* remains from Południowa Cave

Bone/tooth	Cat. no.	L	B	L tr	L ta	B tr	B ta	
C1	JP.1.1	19.24	14.45					
M2	JP.1.6	15.38		11.05	8.87			
p1	JP.1.2	10.54	7.46					
p2	JP.1.3	17.72	8.87					
m1	JP.1.4	34.87		26.87	13.56	14.46		
m1	JP.1.5				13.87		11.95	
m2	JP.1.7	17.48			9.44	11.84	9.95	
		L	pL	pB	mL	mB	dL	dB
mc 3	JP.1.8		22.72	14.34	13.52	13.24		
ph 1	JP.1.9	50.94	14.97	17.79	9.36	11.64	10.34	14.96

crown bears a strong lingual cingulum, while the buccal cingulum is rather weakly developed. The p1 (JP.1.2) is a small, monocuspid, single-rooted tooth, with a vestigial distal cingulum. The p2 (JP.1.3) is high, long and relatively robust. The crown lacks a mesial cuspid but bears a large distal cingular projection and a moderately large, centrally positioned distal cuspid. The m1 is large and relatively narrow. A well-developed paraconid and particularly high protoconid are separated by a deep lingual valley. The protoconid holds two grooves, the first one sharp and thin in its mesial surface, running from the apex to the valley between it and the paraconid. The second, strong crest is located on the distal margin of the protoconid and runs from its apex to that of the metaconid. The metaconid is strongly reduced, closely associated and situated behind the protoconid. The trigonid is long and high in relation to the tooth length, while the talonid is short and slightly narrower. The lingual margin of the crown is almost straight, while on the buccal side, only a protoconid margin is moderately curved. The talonid bears a centrally positioned, large and dominant hypoconid. There is also a sharp and thin crest that connects the hypoconid with the lingual margin of the talonid. The entoconid is not present, and in its place, only a vestigial crest-like structure is present, even if the hypoconid often retains a trace of connecting ridge. The cingulum is poorly developed on the distal wall. The m2 is not markedly reduced relative to m1, oval-shaped and tricuspid, with a broad and long trigonid and short and narrow talonid. The m2 bears a large but low protoconid, which occupies 2/3 of its surface. Near it is situated a greatly reduced metaconid, and apexes of both cusps are connected by a thin and sharp ridge. The mesially placed hypoconid is small and equal-sized to the metaconid. The present entoconid is so rudimentary that it is not differentiated from the lingual talonid crest. On the distal-lingual wall of the talonid, a series of vestigial cuspids is present. A stronger cingulum is present only on the mesio-lingual margin.

Remarks. – The bones from Południowa Cave indicate a large and robust dog, comparable in size with the largest extant wolves. These remains differ from *Canis* specimens by a larger size and stouter build, so much so that there is no possibility of confusion. The specimens can be distinguished also morphologically, in particular by the presence of enlarged and robust canines.

Canis mosbachensis Soergel, 1925
(Fig. 5B–E)

Material. – Worn, right C1 (JP.2.1, JP.2.2, JP.2.3); worn leftC1 (JP.2.4); right P2 (JP.2.5); trigon of right P4 (JP.2.6); left part of P4 (JP.2.7); right part of P4 (JP.2.8); crown of left M1 (JP.2.9); left M1 without trigon portion (JP.2.10); trigonid of left m1 (JP.2.11); worn trigonid of left m1 (JP.2.12); worn, right m1 (JP.2.13); right m1 (JP.2.14); shaft of left humerus (JP.2.15); left metatarsal 3 (JP.2.16); left metacarpal 4 (JP.2.17); left metacarpal 5 (JP.2.18); left metatarsal 2 (JP.2.19); proximal half of tleft metatarsal 5 (JP.2.20); right talus (JP.2.21); phalanx 1 without proximal epiphysis (JP.2.22, JP.2.23).

Measurements. – Table 2.

Description. – The C1 is flattened laterally and relatively thin mesio-distally and bears weak mesio-lingual and distal crests running from its apex to its base. Compared to the C1 of *Ly. lycaonoides*, they are smaller, with proportionally longer, more curved, and less massive crowns. The long and narrow P2 bears a moderately large distal cuspid situated in the middle of an elongated distal cingular projection. On the distal margin of the distal cingular projection, something like a small, second cuspid is present, which may be an elevation of the distal cingular projection. The cingulum is well-developed on the lingual side. The P4 is relatively long and narrow, with almost straight buccal and lingual margins. The paracone is high, bears a crest across the mesial border from its apex to the base of the crown. It is clearly separated from the small and low protocone, whose mesial margin is aligned with that of the paracone. The metacone is blade-like and is clearly separated from the paracone by a deep valley; its distal part slightly curves buccally. The cingulum is strongly developed in the lingual margin of the metacone.

The M1 is a triangular-shaped tooth with a broader but proportionally less expanded trigon than in *Ly. lycaonoides*, with a longer and narrower talon. The crown has slightly convex mesial margin and concave distal one. The paracone is the largest and highest among the cusps, and exceeds in size and height the metacone; however, the difference is less well expressed than in *Ly. lycaonoides*. The small and low protocone is connected by a thin and sharp crest with a small but clearly distinguished entocone. On the mesial part of the talon is situated a small protoconule, while the low and elongated hypocone is developed into a strong crest-like structure. The main basin between the trigon and the talon is relatively restricted and shallow, as is the basin between the protocone and hypocone. The cingulum is well developed on its mesial and disto-buccal margins, while the buccal cingulum is weak. The m1 is relatively short and broad, with a proportionally long (~30 % of the tooth's length) and wide talonid, which is only almost as wide as the trigonid. The trigonid is high, with a massive protoconid separated from the high paraconid by a deep valley, less prominent than that in *Ly. lycaonoides*. The metaconid is moderately large and situated disto-lingually to the protoconid. The talonid bears a large and prominent hypoconid and disto-lingually positioned small entoconid, connected distally by a crest. The talon basin for the protocon is broad and deep. Behind the metaconid occur a small but prominent metastylid and hypoconulid.

Remarks. – Due to a particular pattern of features shared by all large canids (e.g., the retention of primitive dental characteristics), the taxonomy of Middle Pleistocene wolves in Europe is debatable. The occurrence of these characteristics complicates a clear taxonomic determination of true diagnostic characters that define interspecific and/or intersubspecific variability (Mecozzi et al., 2017, 2018; Mecozzi and Bartolini-Lucenti, 2018). In this paper, the prevailing consensus that *Ca. mosbachensis* was the ancestor of *Ca. lupus* is accepted (Sotnikova and Rook, 2010; Sardella et al., 2014; Mecozzi et al., 2017, 2018; Mecozzi and Bartolini-Lucenti, 2018). The wolf remains from Południowa Cave correspond well to a small, gracile form known from a number of European late Early and Middle Pleistocene sites, e.g. Belle-Roche (Kleczko, 1999), Westbury-sub-Mendip (Bishop, 1982; Turner, 1999), West Runton (Lewis et al., 2010), Mosbach 2 (Soergel, 1925), Mauer (Freudenberg, 1914; Rüger, 1928) and Stránská Skála (Schirmeisen, 1926; Stehlík, 1934; Musil, 1972, 1995). In size and shape, it is similar to wolves from those sites. The specimens described are strongly distinct from those of the earliest true wolf *Canis lupus lunellensis* Bonifay, 1971, which appeared not earlier than MIS 11 (Bonifay, 1971; Boudadi-Maligne, 2010; Brugal and Boudadi-Maligne, 2011; Brugal et al., 2020; Marciszak et al., 2023a, b). Apart its smaller size and lesser posture, it differs from *Ca. l. lunellensis* in a straighter lower tooth row, parastyle of M1 united with preparacrista, p4 with a second distal cuspid, m1 with a strong buccal cingulum and two

Table 2

Measurements of *Canis mosbachensis* remains from Południowa Cave

Bone/tooth	Cat. no.	L	B	L tr	L ta	B tr	B ta	
C1	JP.2.1	11.15	7.47					
C1	JP.2.2	11.37	8.17					
C1	JP.2.3	12.11	7.38					
C1	JP.2.4	9.57	7.57					
P2	JP.2.5	10.08	4.41					
P4	JP.2.6						10.09	
P4	JP.2.7	22.24	7.56					
P4	JP.2.8	21.97	8.38					
P4	JP.2.27	22.87					9.69	
M1	JP.2.9	17.32		14.04	10.76			
M1	JP.2.10	17.66		13.89	11.04			
m1	JP.2.11	23.87		15.64		8.74	8.56	
m1	JP.2.12	23.37		15.94		9.24	8.49	
m1	JP.2.13	24.45		17.36		9.66	9.27	
m1	JP.2.14	22.64		15.74		8.67	8.22	
m1	JP.2.24	24.37		17.14		9.04	8.57	
m1	JP.2.25	24.15		17.25	7.11	9.64	8.84	
		L	pL	pB	mL	mB	dL	dB
humerus	JP.2.15				15.27	17.82		
mc 4	JP.2.17	71.87	12.76	8.67	5.14	6.54	9.78	8.89
mc 4	JP.2.26		10.74	7.36	7.18	7.25		
mc 5	JP.2.18	63.13	11.42	11.65	6.02	8.58	10.61	11.54
talus	JP.2.21	27.05	21.94					
mt 2	JP.2.19	69.16	12.64	5.18	5.47	5.95	7.96	8.07
mt 3	JP.2.16	63.74	10.82	8.36	5.34	6.45	8.72	9.72
mt 5	JP.2.20		8.34	11.32	7.54	5.76		
ph 1	JP.2.22				6.06	5.59	6.48	7.54
ph 1	JP.2.23		8.16	8.84	5.25	5.84		

well-developed talonid cusps, hypoconid and entoconid connected by a thick transversal crest, and bicuspid m3 (Tedford et al., 2009; Mecozzi and Bartolini-Lucenti, 2018; Mecozzi et al., 2021).

Comparison of the material from Południowa Cave with that from other late Early and Middle Pleistocene European wolf palaeopopulations documented its similarity to those dated between 1.1 and 0.7 Ma. A size comparison of lower carnassials (m1) showed that *Ca. mosbachensis* was comparatively large through the timespan between 1.1 and 0.7 Ma (Bonifay, 1971; Boudadi-Maligne, 2010; Brugal and Boudadi-Maligne, 2011; Brugal et al., 2020; Marciszak et al., 2021b, 2023a). No substantial differences in size were found between the sites. A comparison showed that populations of these canids formed a biometrically homogeneous group. Slightly larger measurements are characteristic for populations younger than 0.6 Ma, like those from Mosbach 2, Hundsheim and Mauer, but the differences are insignificant. Up to MIS 11 (~0.4 Ma), wolves only slightly differed in size, and real increases in size started after MIS 11, with the appearance of *Ca. l. lunellensis* (Bonifay, 1971; Boudadi-Maligne, 2010; Brugal and Boudadi-Maligne, 2011; Brugal et al., 2020; Mecozzi et al., 2021, Marciszak et al., 2021b, 2023a).

Vulpes vulpes (Linnaeus, 1758)
(Fig. 5F)

Material. – Left I1 (JP.3.2); left I3 (JP.3.3, JP.3.4); left C1 (JP.3.5); right C1 (JP.3.6, JP.3.7, JP.3.8); left P4 (JP.3.9); right i2 (JP.3.10); left i3 (JP.3.11); left c1 (JP.3.12); right c1 (JP.3.13); right hemimandible with a damaged ramus and preserved p4-m1 (JP.3.1).

Description. – Upper incisors are similar in size and shape to those in extant *Vu. vulpes*. The I1 and I2 have a triangular lingual outline and have two basal cuspids on each side of the main cusp, which are smaller. Also, the lingual cingulum is less developed. The canine-like I3 has a moderately distal-lingual cingulum, which does not bulge into the lingual side. The crown is slightly shorter and narrower, not so expanded as in modern *Vu. vulpes*. The canine is like that of *Vu. vulpes*, flattened laterally and narrow mesio-distally, proportionally slightly shorter, less curved and with a weak mesio-lingual cingulum. The P4 is long and narrow, with straight buccal and lingual margins. The paracone is high and bears a sharp and thin crest running across the mesial border from its apex to the base of the crown. The paracone is clearly separated by the wide, V-shaped valley from the broad and long protocone, the mesial margin of which is strongly pushed forwards mesio-lingually. The blade-like metacone is long and low, narrowing distally, and its distal part slightly curves buccally. A stronger cingulum is situated on the lingual margin of the metacone. Lower incisors and canines are indistinguishable in size and shape from those of extant *Vu. vulpes*. Both m1 belong to very large and robust individuals, slightly exceeding those even in the largest modern *Vu. vulpes*.

The hemimandible has an elongated and stout mandibular body, with a straight lower margin in its mesial part. The latter is slightly convex distally under the m1. The body is thicker ventrally. The body massiveness increases distally, with the highest point at the level of m2–m3. The triangular, mesial margin of the shallow masseteric fossa reaches the m3. Two mental foramens are situated at a similar level. Premolars are separated by short diastemas, while molars are set closely together. The main axes of the tooth row coincide and are slightly curved. Similarly, the p4 is located lower than the m1 paraconid.

The p4 is an elongated tooth with a strong mesial cingulum. The distal cingular projection, distal cuspid, and lingual cingulum are well developed. The occlusal morphology of the distal portion of the p4 is mesio-distally elongated and oval. The distal margin shows a rounded outline. The m1 is an elongated, relatively slender and bucco-lingually compressed tooth. On the lingual side, the m1 protoconid possesses a gentle inflexion on its lingual side. The notch is strongly developed and marked. The m1 metaconid possesses a strongly developed metaconid, clearly separated from the protoconid. There is a transverse cristid between the ento- and hypoconid. Lingual cuspids are not markedly reduced and located mesially to the m1 entoconid. Among these, there are a reduced entoconulid and enlarged entoconulid. The m1 distal margin is characterised by the presence of a distal cristid arising from the distinct hypoconulid and distal accessory cuspids in place of a cingulid. The hypoflexid is on the m2 buccal side, making the latter oval. A prominent buccal cingulid is situated on the mesio-buccal side of the protoconid. Compared to other cusps on m2, it is enlarged and extends prominently distally on the buccal side of the hypoconid. The m2 also shows the presence of a large entoconid and a mesial accessory cuspid. The m3 is relatively large in relation to the m1 and rounded in occlusal outline. The buccal protoconid and the lingual metaconid, two main cusps, are similar in size, although the protoconid seems slightly higher and larger than the metaconid.

Remarks. – The fox remains from Południowa Cave differ morphometrically from other Early and early Middle Pleistocene European foxes: *Vulpes alopecoides* (Del Campana, 1913), *Vulpes praeglacialis* (Kormos, 1932), and *Vulpes praecorsac* Kormos, 1932. The incisor arch is more curved than in those species. The I1 and the I2 have stronger developed mesial lobes, with a weak lingual cingulum. The I3 is higher, more elongated and broadened, in particular, at the lingual cingulum, as in *Vu. vulpes*. The C1 is longer and more curved. Based on these parameters and the indistinguishability of the fox remains collected in Południowa Cave from *Vu. vulpes*, we attributed them to this species.

Family Ursidae Fischer de Waldheim, 1817
Genus *Ursus* Linnaeus, 1758
Ursus deningeri von Reichenau, 1904
Ursus ex. gr. *spelaeus*
Ursus arctos ssp.
Ursus cf. *thibetanus* Cuvier, 1823

We do not describe the ursid remains here since these have already been studied. The remains of *Ur. deningeri* from Południowa Cave belong to a typical representative of the deningeroid-spelaeoid lineage, with traits characteristic for early Middle Pleistocene individuals. Analysis showed its similarity to other European populations of *Ur. deningeri* from the Gombasek, Koněprusy Caves, and Kozi Grzbiet sites. *Ur. deningeri* from Południowa Cave was shown to be less evolved than those in later populations, dated 650–450 ka (Wagner and Čermák, 2012). Other than the most common *Ur. deningeri*, arctoid and black bear remains have also been found. Those of *Ur. arctos* from Południowa Cave are noteworthy due to the presence of different subspecies and ecomorphs.

Family Mustelidae Fischer de Waldheim, 1817
Gulo gulo schlosseri (Kormos, 1914)
Meles meles atavus Kormos, 1914
Martes vetus Kretzoi, 1942
Martes martes (Linnaeus, 1758)
Baranogale helbingi Kormos, 1934
Mustela strandi Kormos, 1934
Mustela pliocaenica Stach, 1957
Mustela palerminea (Petényi, 1864)
Mustela praenivalis Kormos, 1934

As with the ursids, the mustelids are also the subject of a separate publication, since their remains are still under study. Their relatively numerous and well-preserved material is especially important in biostratigraphic and palaeoecological contexts. Among the most noteworthy records, there is a partially damaged cranium of *Ma. vetus* and the presence of such enigmatic and rare species as *Mu. strandi* and *Mu. pliocaenica*. Since the mustelid remains are so diverse and valuable, they were analysed in detail in a Eurasian context.

Family Felidae Fischer de Waldheim, 1817
Subfamily Pantherina Pocock, 1917
Genus *Panthera* Oken, 1816
Species *Panthera spelaea* (Goldfuss, 1810)
Panthera spelaea fossilis (von Reichenau, 1906)

Material. – Crown of right p4 (JP.13.1), right m1 (KP.13.2), right metacarpal 4 (JP.13.4), left metatarsal 3 (JP.13.3), stored in ZPal UWr. Right femur, tibia and metatarsal 3 and left metacarpal 5 are stored in a private collection in Dresden.

Measurements. – Table 3.

Description. – The p4 is large, longer than the m1 (L p4/L m1 index is 101.3) tooth with a robust crown. The protoconid is short and high. The buccal margin is straight, and the lingual margin is noticeably expanded, creating a broad and smooth area. Both cusps are equal in size, large, rounded and high. The hypoconid is poorly distinguished from the strong distal cingulum, while the paraconid is clearly separated from the protoconid by a wide, V-shaped valley. After the hypoconid, a small but distinctive metaconid is visible (Fig. 6). The m1 is oval and robust. The long and low paraconid has a particularly expanded mesial wall. The protoconid is slightly longer and much higher than the paraconid, and its distal wall is visibly sloped. The notch between the main cusps is deep, narrow and V-shaped. The lingual side from the bottom of the cingulum to

Table 3

Measurements of felid remains from Południowa Cave

Panthera spelaea fossilis								
Bone/tooth	Coll. no.	L	L pa	H pa	L pr	L pr	H in	B
p4	JP.13.1	33.44	15.12	21.74	14.25	17.88		
m1	JP.13.2	32.94	19.93	19.04	18.75	18.94	12.24	18.66
		L	pL	pB	mL	mB	dL	dB
femur	NN	497.65	74.15	127.19	41.29	44.56	112.16	114.66
tibia	NN	445.86	123.64	118.19	49.74	44.76	64.93	81.16
mc 4	JP.13.4	157.88	36.49	27.95	19.44	20.56	31.66	31.49
mc 5	NN	134.56	34.59	35.64	27.48	28.16	23.17	36.86
mt 3	JP.13.3	177.45	42.79	32.56	20.66	24.39	31.59	31.78
mt 3	NN	177.86	45.78	34.66	21.49	25.29	32.86	31.97
Panthera gombaszoegensis gombaszoegensis								
		L	L pa	H pa	L pr	L pr	H in	B
m1	NN	25.78	13.29	14.24	14.41	17.21	7.37	12.44
Acinonyx pardinensis intermedius								
m1	NN	19.45	9.54		12.79	12.31		8.89
Homotherium latidens latidens								
m1	NN	30.97		12.06		16.78		11.97

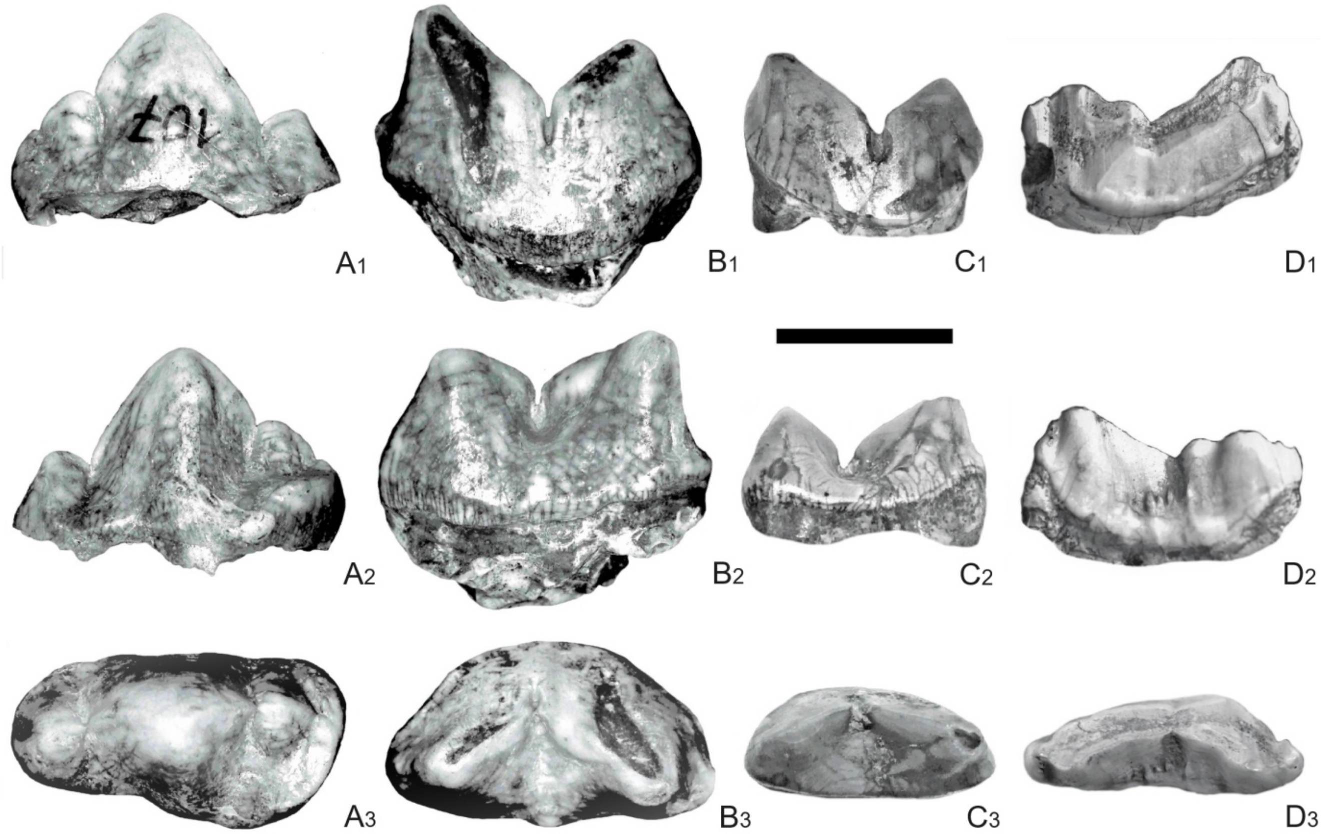

Fig. 6. Isolated teeth of large felids from Południowa Cave

Panthera spelaea fossilis: **A** – right p4 (JP.13.1); **B** – right m1 (JP .13.2). **C** – left m1 of *Panthera gombaszoegensis gombaszoegensis* (NN). **D** – left m1 of *Homotherium latidens latidens* (NN). **E** – right m1 of *Acinonyx pardinensis intermedius* (NN). All specimens shown at the same scale (12 mm); 1 – buccal view; 2 – occlusal view; 3 – lingual view that of the notch between the paraconid and the protoconid is high. The crown is relatively high and elongated in lateral view. A well-developed bulge is situated between the paraconid and the protoconid on the lingual margin in the middle part of the crown. It rises into a small cusp-like formation. The strongly developed lower margin of the cingulum rises considerably upwards, buccally and lingually, in a distal direction under the protoconid. A zigzag enamel structure formed by the lower margin of the cingulum is placed on the border between the protoconid and the talonid on the buccal and lingual sides. The talonid is elongated and well developed.

Remarks. – Distinctions between *Pa. s. fossilis* and *Pa. s. spelaea* are the most clearly visible on p4, and the mean difference is significant even though the range of variability generally overlaps. *Pa. s. fossilis* has a proportionally shorter and higher protoconid and a broader crown. The mean of the index of the protoconid length to the total crown length is ~46 for *Pa. s. fossilis* and ~52 for *Pa. s. spelaea*. In the occlusal view, the mesial part is broad, the middle part is double-sided concave and the distal part is convex on the lingual and buccal sides. Additional cuspids, a mesial paraconid, and distal hypoconid, are poorly reduced as well as high and mostly equal in size (Schütt, 1969; Maciszak et al., 2019). In lingual view, the distinction between the main cusp and additional cuspids are less marked, and the hypoconid especially is closely associated with the strong distal cingulum. The tooth is proportionally longer as regards the L p4/L m1 index. The mean index of p4 length to m1 length is 98.6 (87.3–101.4, n = 15) for *Pa. s. fossilis* and 93.4 (83.3–107.5, n = 118) for *Pa. s. spelaea*. In the lion from Południowa Cave this index is ~100, while in stratigraphically younger lions from Biśnik and Wierzchowska Górna caves the index is between 95–97 (Marciszak et al., 2019). The breadth-to-length index for *Pa. s. fossilis* is greater than 50 (Marciszak et al., 2019). The mean index of crown breadth to the total crown length is ~57 for *Pa. s. fossilis* and ~46 for *Pa. s. spelaea*.The lion from Południowa Cave is represented by individuals of gigantic proportions, among the largest known representatives of this group. An immense size and exceptionally stout posture are characteristic of *Pa. s. fossilis*. Lion remains from Południowa Cave have already been described and compared in previous papers summarising knowledge of Polish lions in a Eurasian context (Marciszak et al., 2019, 2020, 2021c, 2023a). The lions from this locality represent *Pa. s. fossilis*.

Panthera gombaszoegensis gombaszoegensis (Kretzoi, 1938)

Material. – Distal half of left P4 (JP.14.1), worn crown of right p3 (JP.14.3), worn crown of left p4 (JP.14.2), distal half of right metacarpal 4 (JP.14.4), stored in ZPal UWr. Right, isolated m1 in a private collection.

Measurements. – Table 3.

Description. – The distal part of the P4 has a moderately long and low paracone. Similar in length, the metastyle ends with a rounded and not very massive distal wall. The buccal and lingual margin of enamel runs sharply up towards the metastyle. The crown bulges only slightly buccally, while the lingual margin is straight. The lingual and distal cingulum is well developed and forms a thick ridge surrounding the crown. The notch between the paracone and the metastyle is moderately pronounced. The p3 is an elongated, large and proportionally robust tooth with an almost straight buccal margin. The transition between the mesial and distal parts of the crown is poorly pronounced, and the protoconid is long and high. The distal cingulum is well-developed and forms a strong ridge on the distal edge. A minute hypoconid, closely associated with the main cusp, is situated after the protoconid. It is oriented slightly bucco-distally. The disto-lingual part of the crown is very slightly expanded. The distal half of the p4 has a straight buccal and expanded lingual part of the crown. The protoconid is large and low, while the proportionally smaller and more oval hypoconid is located almost in the middle of the crown, just after the protoconid. The distinctions between the protoconid, hypoconid and distal cingulum are moderately pointed and developed in form of V-shaped, not very deep and narrow valleys. The disto-lingual cingulum is weakly developed. The distal half of the metacarpal 4 is large and massive. Its morphology and size match well with the mc 4 from other sites. The bone is much smaller than the mc 4 of *Pa. s. fossilis*, but larger and more massive than that in *Pa. pardus*.

Remarks. – The record from Południowa Cave and those from the Tunel Wielki and Kozi Grzbiet caves is dated to the early-mid Middle Pleistocene. This is well corroborated morphometrically, spatially, and temporally with the Eurasian occurrence of *Pa. g. gombaszoegensis*. This was the time when this species was a widespread and relatively common faunal element, the best time for the Eurasian jaguar, judging from the number of sites and its geographical range (O'Regan, 2002; O'Regan and Turner, 2004). However, since the evolutionary history of *Pa. gombaszoegensis* is well documented, there is no reason to believe that any species other than *Pa. g. gombaszoegensis* should be considered (Marciszak and Lipecki, 2022). The records from Draby 3 and Biśnik Cave documented a very late occurrence of this species (Marciszak, 2014; Marciszak and Lipecki, 2022); the jaguar from Biśnik Cave represents one of the last Eurasian survivors of the species. Both these sites documented the time when this once widespread top carnivore disappeared and finally went extinct 350–300 ka.

Homotherium latidens latidens (Owen, 1846)

Material. – Crowns of right p4 and right m1 with worn paraconid, right calcaneus and left metatarsal 3 stored in a private collection.

Measurements. – Table 3.

Description. – The left m1 is quite badly worn and has damaged roots, but its state of preservation makes it possible to clearly identify the tooth as belonging to the genus *Homotherium*. The morphology of this tooth is so unique that it can be recognised even in the case of considerable incompleteness. The tooth has two massive, strongly laterally flattened roots, the front one of which is much larger and more massive. Both roots are additionally fused mostly in the middle part. The mesial triangular root is blunt, while the distal one strongly tapers towards its end. The crown in occlusal view is strongly elongated and slender, slightly arched. The mesial and distal edges of the crown are rounded. From the mesial edge, the crown widens distally and reaches its maximum width at the height of the paraconid. Then the crown diminishes to its narrowest point, which is the talonid. The cheek edge is moderately arched, with a more pronounced curvature at the paraconid level. The lingual edge is straight, with a moderately deep indentation in the middle part. Both cusps are worn, elongated and low, and there is a valley between them, forming a

U-shaped and narrow valley. Para- and protoconid are of similar length, and there is a clearly marked notch on their lingual edge. The talonid is short and rounded, and the distal edge of the protoconid falls steeply into its center. The cingulum on the talonid is strongly developed in the form of a thick shaft. The cingulum surrounding the trigonid is moderately developed. It is arched on the lingual and buccal sides, sloping evenly mesially and rising distally. There is a clearly marked protrusion on the buccal side, in the back part, at the border of the trigonid and talonid.

Acinonyx pardinensis intermedius (Thenius, 1954)

Material. – Right p4, left m1 and right metacarpal 4, stored in a private collection.

Measurements. – Table 3.

Description. – The right p4 is almost complete. In lateral view, the crown is proportionately short and tall, with a compact structure. It is almost completely vertical. Narrow, deep and V-shaped valleys clearly separate all three cusps and the distal cingulum. All three cusps are located almost in one line after each other; only the paraconid is slightly mesio-lingually oriented. The protoconid is triangular in buccal view and rounded in occlusal view. Its mesial and distal edges fall evenly towards the base. It is shifted somewhat mesially. The paraconid and the hypoconid are similar, in the form of blunt cones, the paraconid being slightly larger. The mesial edge of the paraconid falls almost vertically towards the base. Also, the distal edge of the hypoconid is very steep, almost vertical. The mesial edge of the crown is blunt and the cheek edge is slightly arched. The distal edge is rounded, but the distal-lingual part is blunter. In the mesial part, the lingual edge is straight, but from the section between the para- and protonid it gradually widens distally and reaches its maximum width at the level of the hypoconid. The cingulum is strongly developed only in the distal part, forming a thick shaft surrounding the crown. The cingulum line on the lingual and buccal sides is W-shaped, with a clearly marked indentation in the central part of the crown.

The right m1 lacks a large part of the paraconid. The crown is elongated and narrow in occlusal view. The mesial edge is blunt, the distal edge is rounded, while the buccal edge is moderately convex. The lingual edge is almost straight, with a slight concavity in its middle. Paraconid and protonid are of similar length. The protoconid is a relatively tall and prominent cusp, the mesial edge of which forms an open angle with the distal edge of the paraconid. The distal edge of the protoconid, on the other hand, slopes gently towards the talonid. The talonid is slightly reduced, and strongly narrowing distally. In its centre, strongly fused with the distal wall of the protoconid, there is a conical, well-defined cusp. It is distal-lingually oriented. The transition from trigonid to talonid is clearly marked with a pronounced concavity on the buccal side. The cingulum is weakly developed, slightly convex in the medial part. The lingual cingulum is arcuate to the trigonid and then runs almost straight from the middle of the protoconid. The buccal cingulum is convex at the height of the metaconid on the talonid.

Felis silvestris Schreber, 1777

Material. – Lleft femur (JP.17.1).

Description. – This is a long cylindrical bone, except for the proximal 1/3 of the body, where it is slightly flattened cranio-caudally. The head is spherical, with a prominent neck. The trochanteric fossa is narrow and deep, forming a sort of gutter laterally bordered by a prominent intertrochanteric ridge. It is poorly developed, arriving at the same level as the head in height. The lesser trochanter is a slight conical prominence. The shaft appears slightly bowed in its longitudinal extent and widens gradually from a point near the middle of the femur toward the proximal and distal ends. A nutrient foramen on the inner side of the posterior surface of the shaft is situated in the middle between the lesser trochanter and the distal articulation. The greater trochanter rises distinctly above the head level and is obliquely truncated on its lateral side. The outer surface of the trochanter extends further down the proximal extremity of the femur. In the posterior view, the lesser trochanter is situated at a point distinctly below the head. The posterior surface of the neck develops a rounded and prominent tuberosity between the fossa and the head. At the distal end, the condyles are separated by a broad and deep pit surrounded by a slightly marked intercondylar line. The lateral condyle is slightly more developed than the medial one. Facets overhang these condyles and joints to the bones by a supracondylar sesamoid. There is a supracondylar fossa above the lateral condyle. The epicondyles are small, barely discernible. The trochlea is narrower than high and its margins are equal.

Remarks. – *Fe. silvestris* is rare in the Sudetes fauna, recorded so far from 9 localities (Marciszak et al., 2016, 2017, 2020). Probably almost all the Sudetes occurrences, except those from Południowa and Wschodnia caves, are of postglacial or Holocene age. It was not clear before whether these remains belong to *Fe. silvestris* or *Fe. catus* because the earlier identification was based on bones of a little taxonomic value (Frenzel, 1936). Numerous bones were found at the surface and not fossilised. The remains of *Fe. silvestris* are rarely found in Pleistocene deposits of Central Europe (Barycka, 2008; Marciszak et al., 2011a). Most of the so-called "fossil" specimens, whose age was estimated based on biostratigraphy or other indirect evidence, turned out to be postglacial or subfossil individuals.

DISCUSSION

The carnivore guild from Południowa Cave included several ancient species such as *Ly. lycaonoides*, *Ca. mosbachensis*, *Ho. l. latidens* and *Pa. gombaszoegensis* which formed a stable assemblage ~2.0–0.5 Ma (Fig. 7). This paleoguild of ancient carnivores was represented by *Canis etruscus*, *Ursus etruscus* Cuvier, 1823, *Ho. latidens*, *Pa. gombaszoegensis*, *Ac. pardinensis*, *Puma pardoides*, *Pachycrocuta brevirostris*, *Chasmaporthetes lunensis lunensis* and *Pliocrocuta perrieri* (Hemmer, 2001; Turner, 2009; Hemmer and Kahlke, 2022). Among them, *Ly. lycaonoides* held a very high position, and when grouped, it was regarded as the dominant carnivore species. In this respect, Południowa Cave is similar to other central European sites of early and mid-Middle Pleistocene age, dated between MIS 23 and 13, e.g. Koněprusy C 718, Kozi Grzbiet, Stránská Skála, Gombasek and Południowa Cave (Stehlik, 1934; Kretzoi, 1938, 1941; Fejfar, 1961; Musil, 1965, 1967, 1969, 1972, 1995; Thenius, 1972; Kahlke, 1975; Wiszniowska, 1989; Wagner, 2001; Kahlke et al., 2011; Marciszak, 2014; Wagner and Gasparik, 2014; Marciszak et al., 2019, 2020, 2021a–d, 2023a, b; Marciszak and Lipecki, 2022). Most of those species have an Early Pleistocene or even Pliocene origin and belonged to the ancient fauna which slowly disappeared in Europe during the Middle Pleistocene. The rate of this process differed considerably for each of these species. Some of them vanished very quickly, already during the latest Early Pleistocene. Progressive cooling and a decrease in humidity caused significant changes in large mammal assemblages. The renewal of the carnivore guild began with the extinction of *Megantereon cultridens* (Cuvier, 1824), recorded for the last time at ~1.0 Ma in the Vallparadís Section (Madurell-Malapeira et al., 2010) and Untermassfeld (Hemmer, 2001; Hemmer et al., 2022).

Three canids were present in this palaeoguild: *Ly. lycaonoides*, *Ca. mosbachensis*, and *Vu. vulpes*. The extinction of eucyons in the latest Pliocene is correlated in time with the appearance of the first representatives of the genus *Canis* and *Lycaon* in Eurasia. They appeared first in Central Asia 3.4–3.3 Ma (Rook, 1993; Sotnikova, 2001), while the earliest European record from the French site Vialette is dated at 3.2–3.1 Ma (Lacombat, 2006; Lacombat et al., 2008, Sotnikova and Rook, 2010). This implies that wolf-sized forms appeared almost simultaneously in Asia and Europe. Slightly younger (2.8–2.6 Ma) is the Hungarian locality Osztramos 8 (Jánossy, 1986). It is known that *Eucyon* gave rise to the *Canis* in North America 6.5–6.0 Ma (Wang and Tedford, 2007, 2008; Rook, 2009). The westward invasion of *Canis* ended this domination, especially as it emerged in a larger, social, and more advanced form.

Lycaons appeared in Europe relatively shortly after early wolves; they dominated open landscapes for the next 2 My. Canids of the genus *Lycaon* appeared in Europe ~2.6 Ma already in robust build and large form, which did not change for the next 2 My (Bartolini-Lucenti and Spassov, 2022). Their ancestor, *Sinicuon dubius* (Teilhard de Chardin, 1940), from the Tibetan region of Zanda Basin, dated at 3.8–3.4 Ma, reached the size of the large hole *Cuon alpinus* (L m1 22.5 mm; Wang et al., 2014a, b). Its descendants were already much larger, similar in size or exceeding the largest extant wolves (Marciszak et al., 2021b, 2023b). The individuals from the oldest European record of Perrier-Roccaneyra (France, 2.6–2.5 Ma) already have the morphology and size characteristic of the Early Pleistocene lycaones (Bartolini-Lucenti and Spassov, 2022). As shown by size variation analysis, the lycaons underwent only slight changes.

Ca. mosbachensis appeared ~1.5–1.4 Ma and survived almost unchanged until ~0.4 Ma. Only once *Ly. lycaonoides* had disappeared in Eurasia, the first true wolf, *Ca. l. lunellensis*, evolved from *Ca. mosbachensis* during a relatively short time, between 0.4 and 0.35 Ma (Bonifay, 1971; Bishop, 1982; Sotnikova, 2001; Boudadi-Maligne, 2010; Brugal and Boudadi-Maligne, 2011; Sotnikova and Rook, 2010; Sardella et al., 2014; Mecozzi et al., 2017, 2018; Mecozzi and Bartolini-Lucenti, 2018). The wolf increased in size, took a niche occupied so far by the lycaon and became the dominant dog in Eurasian terrestrial ecosystems (García and Virgós, 2007; Marciszak et al., 2021b, 2023b).

The evolutionary history of *Vu. vulpes* started in the early Middle Pleistocene. The first appearances of this species are not older than 0.8 Ma (Madurell-Malapeira et al., 2021). The findings of its remains are known from Stránská Skála (0.8–0.7 Ma; Musil, 1972), L'Escale (0.7–0.6 Ma; Bonifay, 1971), Bed 5 of Westbury-Sub-Mendip (0.6–0.5 Ma; Bishop, 1982), Arago Cave (0.6–0.5 Ma; Crégut, 1979; Moigne et al., 2006), Vallparadís Estació (0.6–0.5 Ma; Madurell-Malapeira et al., 2021) and Hundsheim (0.6–0.5 Ma; Thenius, 1954). Two chronosubspecies have been recognised, *Vulpes vulpes jansoni* Bonifay, 1971 from L'Escale (Bonifay, 1971), and *Vulpes vulpes angustidens* (Thenius, 1954) from Hundsheim (Thenius, 1954; Rabeder, 1976), originally described as an independent species. As compared to extant *Vu. vulpes*, *Vu. v. jansoni* is characterised by a more prominent protocone of P4, M1 with sharp paracone and metacone, strong lingual cingulum, and distinct metaconule and hypocone as well as M2 with a larger hypocone (Bonifay, 1971; Madurell-Malapeira et al., 2021). The main feature distinguishing *Vu. v. jansoni* from the extant *V. vulpes* is the development of the P4 protocone. Nevertheless, as shown by the revision of early *Vulpes* species (Bartolini-Lucenti and Madurell-Malapeira, 2020), the shape and size of this cusp is highly variable in extant *V. vulpes*. Morphologically, it is indistinguishable from specimens of *Vu. vulpes* and falls within the range of its variability (Madurell-Malapeira et al., 2021).

Vu. v. angustidens was described as slightly smaller than the extant *Vu. vulpes*, having m1 with a weaker protoconid, strong mesoconid and ridge connecting hypo- and entoconid, and narrow m2 with a strong mesial cingulum, strong entoconid and metaconid higher than the protoconid (Thenius, 1954). In the revision of the European Middle Pleistocene *Vu. vulpes*, it was noted that similarly dated (0.6–0.5 Ma) individuals from the Vallparadís Section to that from Hundsheim resemble them in the small size of the entoconid and the well-developed entoconulid on the m1 talonid (Madurell-Malapeira et al., 2021). The material from Hundsheim shows also strong similarities with other Middle Pleistocene specimens (Marciszak et al., 2023b). The earliest occurrences of *Vu. vulpes* from Poland are known from Południowa Cave and Rębielice Królewskie 2. These records are dated to 0.7–0.6 Ma. Younger records are those from Tunel Wielki Cave (MIS 14-12) and Draby 3 (MIS 11) (Marciszak et al., 2023b). There are some minor morphometric differences between them and the extant *Vu. vulpes* (Marciszak et al., 2023b). However, as noted by Szuma (2011), the wide geographic range of the extant *Vu. vulpes* and a number of geographic, climatic and biological factors, such as latitude, habitat productivity, different food availability, competition on various levels, genetic diversity and population density resulted in a high variability of this species (Bartolini-Lucenti and Madurell-Malapeira, 2020).

The biostratigraphic value of felids represented in Południowa Cave is very high, and their remains are very informative. The oldest known remains of the lion assigned to *Pa. s. fossilis* were described from the late Early Pleistocene (1.2–0.8 Ma) of Western Siberia and Moldova (Hemmer, 2011; Sotnikova and Foronova, 2014). The presence of this large lion is documented from 62 Eurasian sites dated between 1.2 and 0.3 Ma (Marciszak et al., 2019, 2020, 2021c, 2023a). The feature especially highlighted by many authors (e.g., Kurtén, 1960, 1968; Schütt, 1969; Schütt and Hemmer, 1978; Argant, 1980, 1991, 2000; Argant et al., 2007; Argant and Brugal, 2017; Argant and Argant, 2018) is the large size of *Pa. s. fossilis*. However, recent studies showed that the ranges of *Pa. s. fossilis* and *Pa. s. spelaea* measurements overlap and did not change significantly during the entire Middle Pleistocene (Barycka, 2008; Marciszak et al., 2014, 2019, 2020, 2021c, 2023a). *Pa. spelaea* was a dynamically evolving species; the size of its representatives does not seem to be a very reliable biochronological tool in determining the age of Pleistocene lion finds. This general picture is complicated by the high level of sexual dimorphism, intraspecific variability, local evolution and extinction, climatic conditions, and migrations (Marciszak et al., 2019, 2020).

The occurrence of *Pa. g. toscana* is restricted to the middle Early Pleistocene (2.0–1.7 Ma) of southern and western Europe (Greece, Italy, and the Netherlands; O'Regan, 2002; O'Regan and Turner, 2004; Mol et al., 2011; Marciszak and Lipecki, 2022). The stratigraphically younger (1.6–0.3 Ma) and much more widespread chronosubspecies *Pa. g. gombaszoegensis* has been recognised from almost 80 Eurasian sites, with half of them dated to the Middle Pleistocene, between MIS 19 and 10 (Hemmer, 2001; O'Regan, 2002; Marciszak, 2014; Jiangzuo and Liu, 2020; Marciszak and Lipecki, 2022). *Pa. gomba-*

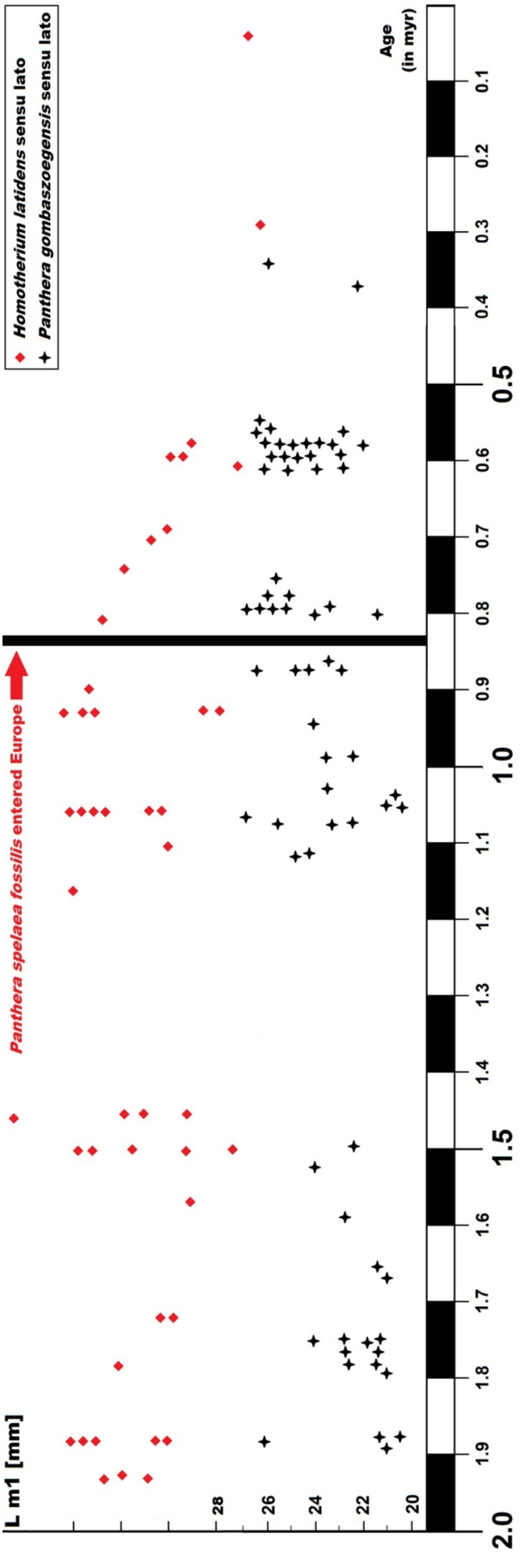

Fig. 7. Comparison of the m1 length of *Homotherium latidens* ssp. (red rhombs) and *Panthera gombaszoegensis* ssp. (black stars)

Note decrease in *Homotherium latidens* size after the arrival of *Panthera spelaea fossilis* in Europe

szoegensis appeared in Eurasia not earlier than 2.0 Ma (O'Regan and Turner, 2004; Mol et al., 2011; Marciszak, 2014). It also fits well with the molecular data since the split of the jaguar lineage is dated to 2.58–2.03 Ma (Davis et al., 2010).

Pa. gombaszoegensis was a permanent member of the carnivore faunal assemblage for more than 1.7 My (2.1–0.3 Ma) and it was the only pantherine cat in the Early Pleistocene of Europe (Hemmer, 2003, 2004; O'Regan and Turner, 2004; Marciszak, 2014; Marciszak and Lipecki, 2022). The evolutionary success of *Pa. gombaszoegensis* is reflected by its enormous geographical range and occurrence of its fossils in a wide variety of habitats (Hemmer, 2001, 2003; Argant et al., 2007; Marciszak, 2014). The species was widespread in the early and mid-Middle Pleistocene of Europe, but since MIS 12 started to decline, and occurrences of this species dated on MIS 11 or later are extremely rare. All these late records are temporally and geographically disparate, and only few Eurasian sites are known from this period: Swanscombe in England (Turner, 1999, 2009), Vertesszöllös 2 in Hungary (Jánossy, 1990), and the Kudaro 1 and 3 caves in the Caucasus (Baryshnikov, 2011). The Polish materials from Daby 3 and especially those from younger (MIS 10-9) layers 19a-d of Biśnik Cave are placed among the youngest Eurasian records of this species (Marciszak, 2014; Marciszak and Lipecki, 2022). Between 0.9–0.8 Ma *Pa. s. fossilis* and *Pa. pardus* also arrived to Europe. All three pantherinae cats coexisted for more than 0.5 My, with some competition between these cats. However, the level of mutual interaction and influence between species is still poorly understood and requires further research. The dominant lion preferred open areas, while jaguar preferred forest and water areas. However, like the modern jaguar, it had considerable ecological tolerance and felt equally comfortable in open areas. The leopard was the most adaptable of the three cats and capable of inhabiting virtually any habitat. Ultimately, *Pa. g. gombaszoegensis* disappears from the fossil record at ~0.3 Ma (Hemmer, 2001, 2003, 2004; O'Regan, 2002; Marciszak, 2014; Jiangzuo and Liu, 2020; Marciszak and Lipecki, 2022). Species of the genus *Homotherium* were present in Africa, Eurasia and both Americas at more than 4 Ma (Hemmer, 2001; Barnett, 2014; Hemmer and Kahlke, 2022). Południowa Cave documented the time when this species was still a dominant, large and widespread felid. It survived in America till MIS 2, although only as a relict with a dwarf stature somewhere on the outskirts of its former range, especially in Eurasia (Reumer et al., 2003). This was possible mainly because of its decreasing size, which reduced competition with the lion and due to its ecological plasticity (Hemmer, 2001; Barnett, 2014; Hemmer and Kahlke, 2022). Remains from Południowa Cave fit well into the general trend of size and mass decrease. *Homotherium* from this locality was a moderately large and gracile animal, and its morphology and stature correspond well to those of other Middle Pleistocene individuals (Hemmer, 2001; Barnett, 2014; Hemmer and Kahlke, 2022). The previous revision showed that *Homotherium* evolved largely csynchronously in different regions of Eurasia, which suggests continuous gene flow within this area (Jiangzuo et al., 2022). It also showed that the subspecies delimitation should be more chronological than geographical (Jiangzuo et al., 2022).

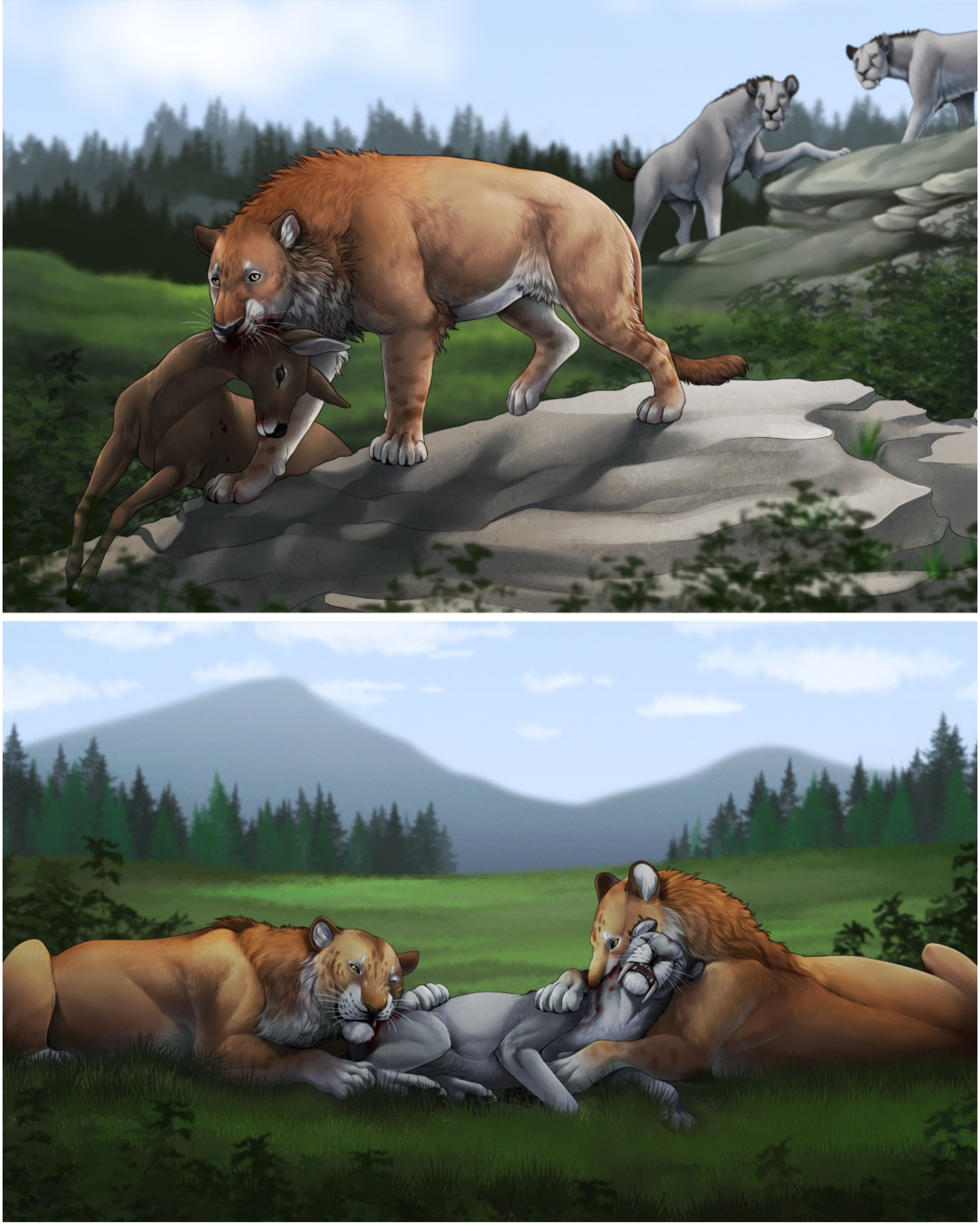

Fig. 8. Until the lion entered Europe, *Homotherium latidens* was the dominant cat and one of the main aggressive scavengers and kleptoparasites of other carnivore carcasses. After *Panthera spelaea fossilis* appeared, everything totally changed. Its size, brutal strength, intelligence and social lifestyle gave it a dominant position in the hierarchy of carnivores. Drawing by W. Gornig

The lion's influence on *Homotherium* was undeniable, but the scale and strength of this influence is difficult to reconstruct. Before the lion's appearance, *Homotherium* was the dominant felid in Eurasian palaeocommunities (Petrucci et al., 2013; Barnett, 2014; Barnett et al., 2020). Members of the genus *Homotherium* were among the most successful carnivore species and have been present in fossil material from the Middle Pliocene (Antón et al., 2005; Barnett et al., 2020). However, during the latest part of the Early Pleistocene, *Homotherium* had noticeably decreased in size and especially in mass (Hemmer, 2001, 2003, 2004). The weight of the Pliocene and Early Pleistocene individuals was estimated at 250–400 kg for ♂♂ and 150–220 kg for ♀♀. The Middle and Late Pleistocene individuals are smaller and more gracile, with weights of 150–220 kg for ♂♂ and 100–130 kg for ♀♀, and could be even less (Hemmer, 2001, 2003, 2004).It is not clear what was the main factor since these gracile homotheres appeared at the same time in different areas within Eurasia (Fig. 7). Lion pressure might have played a significant role in the combination of climate-induced changes in vegetation, exacerbated competition among large carnivores, and the increased pressure from *Homo heidelbergensis* Schoetensack, 1908 (Serangeli et al., 2015). It is virtually unknown how severe was this competition, but it might be cautiously inferred that these similar-sized species, lion and homotherium, competed, and *Homotherium* probably found a way to reduce competitive pressure (Fig. 8). After long co-existence, it occurred in favourable habitats where lion was absent or existed in low densities (Antón et al., 2005, 2014; Bona and Sardella, 2014). Based on palaeontological data, this scenario is difficult to reconstruct since late Middle Pleistocene records of *H. latidens*, younger than 300 ka, are extremely rare. They are concentrated mostly in Central Europe as at Schöningen (330–300 ka; Serangeli et al., 2015; Diedrich and McFarlane, 2017), Steinheim an der Murr (270–250 ka; Adam, 1961), Zoolithen and Balve Caves, both dated to 220–200 ka (Diedrich and McFarlane, 2017). A Portuguese record from Mealhada (250–200 ka; Serangeli et al., 2015) and layer 5a of the French site Artenac Cave (250–200 ka; Serangeli et al., 2015) should be also added to this list. Finally, the so far undescribed Polish material from layer 19b–d of the Biśnik Cave, dated ~350–300 ka, should be also noted.

However, besides the North Sea find, there are no reliable *Homotherium* records in Europe (Reumer et al., 2003). English records from Kent's Cavern and Robin Hood's Cave, dated previously to the Late Pleistocene, were recently re-interpreted as of Middle Pleistocene age (Barnett, 2014; Serangeli et al., 2015). The dating of the last occurrence of the genus *Homotherium* in Eurasia is a matter of debate, even though all the available radiocarbon dates provide an age of ~31–27 ka (Reumer et al., 2003). The lack of evidence of *Ho. latidens* in the Late Pleistocene of Europe makes this record unique, and some authors consider it questionable (Antón et al. 2014, 2022). Based on the presence or lack of some morphological features, it was also suggested that *Ho. latidens* went extinct in Europe during the late Middle Pleistocene (Antón et al., 2014).

Several different demographic scenarios have been proposed to explain the presence of *Homotherium* in Europe during the Late Pleistocene. In Eurasia, the Late Pleistocene *Homotherium* populations may have existed at low population densities. Due to that, they effectively dropped under the "fossil detection threshold," with very few remains in the fossil record. This has been proposed to explain the low abundance of *Homotherium* relics in the Americas (Jefferson and Tejada-Flores, 1993; Rincón et al., 2011; Paijmans et al., 2017). These areas were restricted to small habitats and maybe even called "refugia". *Ho. latidens* survived as long as the second part of MIS 2, and finally disappeared during the latest part of the Last Glacial (Reumer et al., 2003; Antón et al., 2005, 2014, 2022). *Homotherium* from the North Sea might have descended from a Late Pleistocene dispersal from a core paleopopulation in Central Eurasia or Beringia (Paijmans et al., 2017). Like extant large felids, *Homotherium* was a highly mobile carnivore. It may have recolonised Europe during the Late Pleistocene after the resident population went extinct in the Middle Pleistocene. This scenario is consistent with the estimated coalescence timing of the European and American *Homotherium* mitochondrial lineages (216–77 ka) (Paijmans et al., 2017; Barnett et al., 2020). In addition, recent molecular data indicate the occurrence of one macrospecies in Eurasia and North America (Barnett et al., 2020).

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