FOSSIL THERIOFAUNA FROM THE SUDETY MTS (SW POLAND)

THE STATE OF RESEARCH

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This article is dedicated to the memory of Professor Teresa Wiszniowska and Dr Jerzy Bieroński, the Polish pioneers of Sudetic palaeontology

Abstract

The updated faunal list, based on the revision of pre-war German paleontological collections and post-war Polish excavation results and on the literature review, includes 7 taxa of insectivores, 12 bats, 4 lagomorphs, 17 rodents, 20 carnivores and 11 ungulates. For all but one cave (which held the remains of species which could be characteristic of the Middle Pleistocene (e.g. *Ursus deningeri* or *Panthera spelaea fossilis*) or even Pliocene (*Baranomys*)) the material from all the palaeontological and archaeological sites was of Late Pleistocene and Holocene age. The following species are noteworthy: *Baranomys loczyi*, the only reliable Pliocene element in the Sudetic fauna; *Ursus deningeri* for which it is the first record from Sudetic caves; the giant bear *Ursus arctos priscus* which was replaced by a smaller form with development of forests after retreat of the glacier; *Gulo gulo* with its only reliable, postglacial record from Poland; *Panthera pardus* and *Rupicapra rupicapra*, recorded as fossil in the Sudetes for the first time. All the remains of *Ursus spelaeus* from the Sudetes turned out to represent *Ursus ingressus*.

Samenvatting

Een gedeelte van de Duitse paleontologische collectie betreffende de karstgrotten van de Poolse Sudeten zijn opnieuw onderzocht. De vernieuwde faunalijst bevat 7 insectivoren, 12 vleermuizen, 4 haasachtigen, 17 knaagdieren, 20 carnivoren en 11 hoefdieren. Bijna al het materiaal (behalve bij één grot met een midden-pleistocene (e.g. *Ursus deningeri* en *Panthera spelaea fossilis*) of zelfs pliocene (*Baranomys*) ouderdom) is afkomstig uit grotten met een laat-pleistocene en miocene ouderdom. De volgende soorten zijn noemenswaardig: *Baranomys loczyi*, het enige betrouwbare pliocene element in de Sudetische fauna; *Ursus deningeri* welke de eerste vondst is uit een grot in de Sudeten; *Ursus arctos priscus* welke werd vervangen door een kleinere vorm die beter aangepast was aan het bosleven; het enige betrouwbare Poolse postglaciale fossiel van *Gulo gulo*; de fossiele resten van *Panthera pardus* en *Rupicapra rupicapra,* voor het eerst geregistreerd in de Sudeten. Alle resten van *Ursus spelaeus* van de Sudeten zijn hergedetermineerd als *Ursus ingressus*.

1. HISTORY OF RESEARCH IN SUDETIC CAVES

Palaeontological studies in the Sudety Mts focus on karstic caves. These are associated with carbonate rock outcrops which form intercalations of various sizes among non-karstifying rocks. Groups or greater bodies of carbonate rocks are found mainly in two parts of the Sudetes (Fig. 1). In the Western Sudetes the Kaczawskie Mts. (A) and Pogórze Bolkowskie (B) hold the largest areas with karstic formations. In the Eastern Sudetes major carbonate intercalations occur in the massif of Mt. Śnieżnik on the margin of Kłodzko Basin (C), in the Krowiarki range (D), Złote Mts. (E) and Bystrzyckie Mts. (F). Besides, smaller calcareous outcrops exist in other massifs (Bieroński *et al.*, 2007).

Most of the palaeontological sites in the Sudetes were found during quarrying in the 18th and 19th century, but the excavations first started in the first half of the 20th century. Pre-war, German studies in Sudetic caves focussed on two main areas: the region of Wojcieszów in the Kaczawskie Mts and the area between the Krowiarki range and the Złote Mts. The first area Mt. Połom (Kitzelberg), now largely destroyed, is especially noteworthy. Many large caves (for example Południowa Cave (Southern Cave, Kitzelhöhle, Kitzelloch, Kitzelberghöhle), Północna Duża Cave (Big Northern Cave, Witschelhöhle), Wschodnia Cave (Eastern Cave, Hellmichhöhle) and Obok Wschodniej Cave (Near Eastern Cave, Kammerberghöhle) with interesting fauna were found during quarrying. The Mt. Połom quarry has been in operation for more than two hundred years. New caves are constantly discovered and destroyed without any geological or palaeontological documentation, even though a nature reserve existed there for a long time, established already before World War II by the Germans (Pulina, 1977, 1996).

The palaeontological finds of the 1930s were summarised by Zotz (1939) and later critically reviewed by Kowalski (1954, 1959). An abundant material of large mammals

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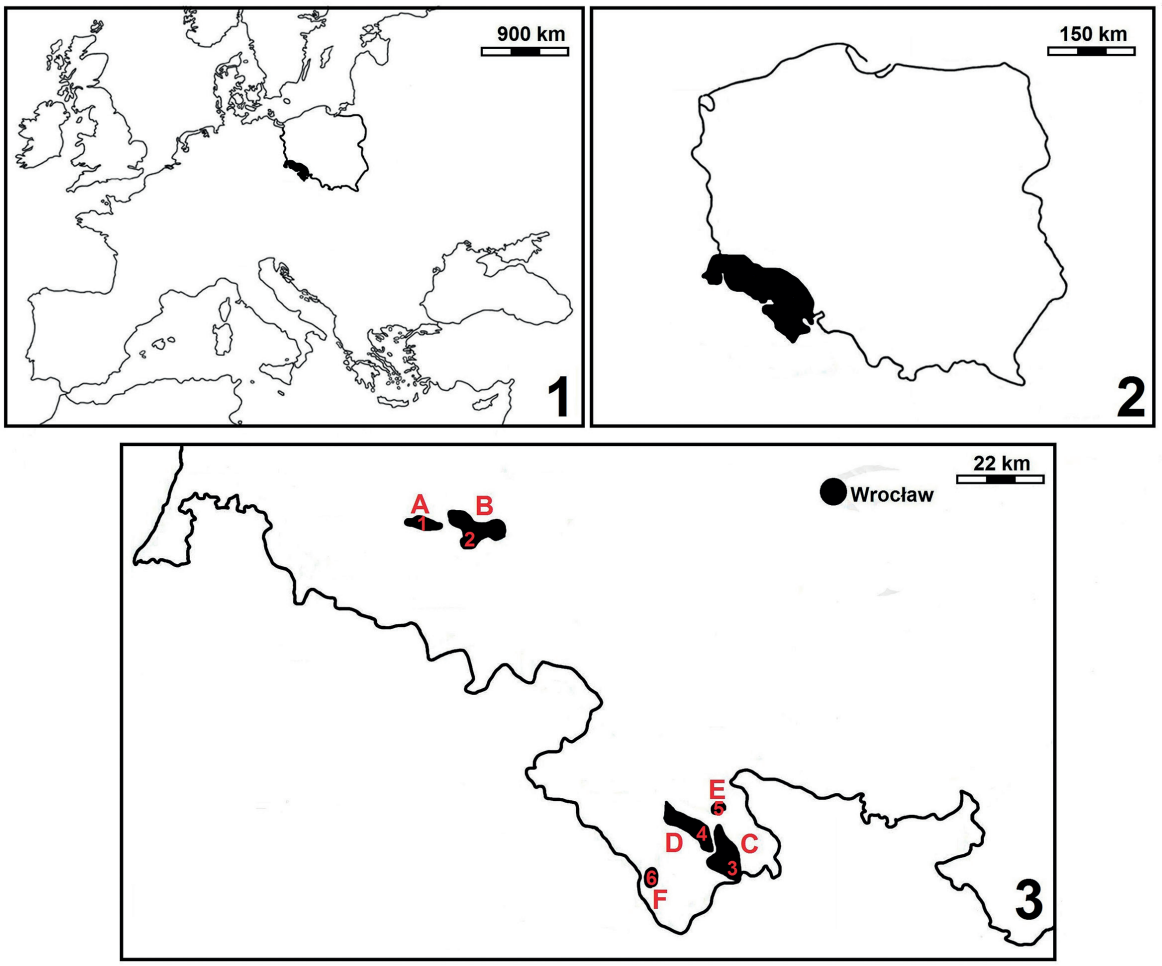

Figure 1: Location of Sudeten Mts in Europe (1), in Poland (2) and karstic areas in Polish Sudeten (3) adjusted after Bieroński et al., 2007

Figuur 1: Locatie van het Sudetengebergte in Europa (1), in Polen (2) en karst regio's in de Poolse Sudeten (3). Aangepast naar Bieroński et al., 2007

A: Kaczawskie Mts (1: Mt Połom with sites Północna Duża, Południowa, Wschodnia and Obok Wschodniej Caves); B: Pogórze Bolkowskie (2: Mt Miłek with sites Małgorzata, Lucia, Trwoga Paleontologa, Panna, Cisowe 1 and 2 Rock Shelters and Tomkowa Niche); C: Śnieżnik Mt (3: Niedźwiedzia Cave); D: Krowiarki range (4: Rogóżka and Na Ścianie Caves); E: Złote Mts (5: Radochowska Cave); F: Bystrzyckie Mts (6: Solna Jama Cave).

(mainly cave bear) together with some artefacts, flint tools and campfire remains, was found in the caves Północna Duża, Wschodnia and Obok Wschodniej. Some bones bearing traces of human interaction, such as a fragment of bear's rib with traces of tool marks on the surface and a drilled hole from Obok Wschodniej Cave, were correlated with the Late Glacial (C14 date 12.2 KA, Poz-27293) (Wiśniewski *et al.*, 2009). A similar age (12.4 Ka, Poz-25407) was obtained for the facial part of the brown bear skull from the Obok Wschodniej Cave. The calvarium, preserved complete with mandible, had extremely worn teeth, and Zotz (1937a; 1937b; 1939; 1951) interpreted it as an object of bear worship, associated with the so called "bear cult" scenario which was known also from other European caves (Pacher, 1997). However, a detailed analysis showed that the teeth were worn in a natural way (Wiśniewski *et al.*, 2009).

In Południowa Cave the situation was more difficult. This site had been known since the early 18th century (Pulina, 1977) and before its final destruction ranked as one of the largest (length 580m) and most beautiful Sudetic caves. Volkmann (1720) described the extremely rich dripstones which covered the cave's walls. In his opinion (Volkmann, 1720: 257): "they were extremely impressive and unbelievably beautiful". Archaeological and palaeontological studies were carried out by F. Heller (1937) and L. Zotz (1939). Zotz dug two trenches, one inside the cave, another just at the entrance. The floor of the deposits in the trench inside the cave was a mixture of yellow loams, intercalations of quartz gravels and limestone. The top was covered with brown loams. From this profile Zotz (1939) described coals of yew, two flint tools and numerous cave bear bones. From the trench at the entrance came breccia composed of dripstone and limestone fragments, mixed with small faunal remains (mainly rodents) and red loams of terra-rossa type (Heller, 1937; Zotz, 1937a; Pulina, 1977; Bieroński *et al.*, 2007). The most important discovery was a new species of hamster *Baranomys langenhani*, more recently re-described as *Baranomys loczyi* Kormos, 1933 (Kowalski, 2001). This Pliocene species disappeared from Europe as early as in the Villanyian (Kowalski, 2001). Heller (1937) described two faunal assemblages from those two trenches. According to him, the trench at the entrance was older and might be dated as Middle Pleistocene with some Pliocene elements, e.g. *Baranomys*. The trench inside the cave was much younger and its deposits were formed in the Late Pleistocene (maybe since the last interglacial). As a proof he mentioned the abundant cave bear material in this profile (Heller, 1937; Bieroński *et al.*, 2007). Zotz (1937a, 1937b, 1939) doubted this and maintained that both assemblages were approximately the same age. He thought that the profile inside the cave was formed of bat guano and remains, while the one at the entrance might be a result of accumulation of pellets of birds of prey and owls (Zotz, 1939). After World War II Kowalski (1954) presented a thorough re-interpretation of the results of the German researches; he found no faunal remains that could indicate an age older than the Late Pleistocene (Bieroński *et al.*, 2007). Finally, shortly before the final destruction of the cave in the late 1950s or early 1960s, survey excavations done by Pulina (1977) yielded new fossil material (mostly large carnivores) which might indicate the presence of Middle Pleistocene deposits inside Południowa Cave.

During a visit to the quarry M. Pulina found another cave, called Naciekowa Cave (Dripstone Cave). The cave was a long, horizontal corridor, which in its middle part expanded into a relatively narrow chamber. The survey excavations yielded abundant fossil material: nine carnivore taxa and also some ungulate remains. The age of the bones was estimated between 45 and 25 ka, and the sediments were mainly composed of red and brown residual loams, partially mixed with limestone rubble. The destruction of the locality as a result of extensive quarrying took place shortly after its discovery (Pulina, 1977, 1996). Pulina's work yielded also sparse material of postglacial or Holocene age from a small rock shelter called Aven on Mt. Połom.

Excavations on Mt. Miłek, initiated by Zotz (1939), focussed on two small rock shelters: Cisowe 1 (length 5 m) and 2 (length 3 m) (Yew Tree Rock Shelter 1 and 2, Eibenloch I, Eibenloch II). In both rock shelters remains of snails, vertebrates, charcoal and a campfire were found. The age of the deposits for Cisowe 1 was estimated as Last Glacial and for Cisowe 2 (Zotz, 1939) as Holocene. In the 1980s more rock shelters were discovered near the top of Mt. Miłek and below the outcrop Cisowe: Małgorzata Rock Shelter (Małgorzata's Rock Shelter), Lucia Rock Shelter (Lucia's Rock Shelter), Trwoga Paleontologa Rock Shelter (Palaeontologist's Fright Rock Shelter), Tomkowa Niche (Tomek's Niche) and Panna Rock Shelter (Maiden Rock Shelter) (Bieroński *et al.*, 2007). Their exploration yielded fossils of snails (49 species in Małgorzata Rock Shelter, 35 species in Lucia Rock Shelter) and small mammals (Pakiet, 1999; Bieroński *et al.*, 2007). Among larger animals, only some remains of medium-sized carnivores such as red fox, badger or wildcat and few roe deer bones were found.

The German palaeontological studies included also the Eastern Sudetes: Rogóżka Cave (Wolmsdorferhöhle) in marble quarry Rogóżka in the Krowiarki range was explored in the 1930s (Bieroński *et al.*, 2007). The excavations carried out by Pax and Zotz showed that the deposits, composed of yellow-brown cave loams, were practically devoid of faunal remains and human artefacts, except for two bird bones and a fragment of spruce timber (Pax & Maschke, 1935; Pax, 1937, Zotz, 1939; Bieroński *et al.*, 2007). Another cave in the same quarry - Na Ścianie Cave (On The Wall Cave) - was discovered in 1985 by a team of explorers from Stronie Śląskie (Pulina, 1996). The studies immediately following its discovery (Bieroński & Wiszniowska, 1994) documented sands and clays which filled the cave, and some subfossil bat remains were found (Bieroński *et al.*, 2007).

The northernmost site, Radochowska Cave (Reyersdorfer Tropsteinhöhle) in the Złote Mts is one of the longest, best known and best studied Sudetic caves. It was known since half of the 18th century, but the palaeontological studies were carried out in the 1930s. The results of Zotz's (1939) excavations in Radochowska Cave and the caves of Mt. Połom provided him with the basis to formulate the hypothesis of the "cave bear cult" among Palaeolithic humans (Bieroński *et al.*, 2007). Finding a complete cave bear skull covered by a rock plate in a niche induced him to interpret it as a ritual burial. The faunal remains found during Frenzel's (1936) and Zotz's (1939) excavations represented Late Pleistocene and Holocene forms. However, more recent, Polish studies (Bieroński *et al.*, 1985) cast doubt on the occurrence of Palaeolithic humans in the site. The tools made (according to Zotz, 1939) by humans could in fact have been shaped by natural processes. The different state of preservation of bones described by Frenzel (1936) and Zotz (1939) might result from re-deposition from another location. Finally, Zotz's "burial plateau" can be explained by sliding of material along the sloping surface of the deposits (Bieroński *et al.*, 1985, 2007).

Niedźwiedzia Cave (Bear Cave), the largest palaeontological site with the most abundant fossil material, was discovered in 1966 in a quarry in the Śnieżnik Massif. The excavations started just after its discovery and progressed in 1967-1970, 1974-1978, 1985-1988 and 1991-1997. Six trenches (each 250 cm deep) were dug, and the excavations yielded remains of more than 38 mammal species (Bieroński *et al.*, 2007, 2009c). The animal remains contained in the deposits are most probably not in situ; the re-deposition due to water and solifluction transport played the major role in deposition in Niedźwiedzia Cave. No unambiguous traces of human occupancy or activity were found in the site, even though earlier authors suspected a possible presence of Palaeolithic man (Paluch, 1970; Świdnicki, 1980). The fauna was dated as Late Pleistocene; AMS and UTh dating indicated an age between 80 and 20 ka (Bieroński *et al.*, 2009c).

Cave bear remains dominated and constituted up to 98% of the whole material (till now more than 150.000 adult bones and a ca. 500.000 juvenile remains were described from the site). Such a vast number of cave bear bones confirmed that Niedźwiedzia Cave should be regarded as a typical cave bear den, a place providing a good shelter for hibernation and breeding. The few herbivore remains (e.g. steppe bison, chamois) may represent leftovers of carnivore prey (Bieroński *et al.*, 2009c).

The Bystrzyckie Mts, with numerous small outcrops of crystalline limestone, are situated on the opposite, western margin of the Kłodzko Basin. The origin of Solna Jama Cave, located in one of the outcrops, is probably associated with water flow from one of the neighbouring streams through the fissured crystalline limestones (Bieroński *et al.*, 2007). Though the cave was known since the 18th century and was already mentioned by Zimmermann (1789) and Scholz (1843), palaeontological studies were done as late as in 1984 and 1985. A small niche, ending with a narrow crevice, was found at the end of the cave. It was filled with sediments (mostly cave loams, with Holocene humus on top) together with loose bone breccia. Survey studies revealed the presence of two different faunal assemblages. One was dated as ca. 40 Ka with ursid remains, while the second, represented by material of 20 mammal species, corresponded to the postglacial period with mosaic habitats in the environs of the cave (Bieroński *et al.*, 2007; Marciszak & Stefaniak, 2016). The presence of parts of a particularly large and robust wolverine skeleton, the only reliable Polish record of the species from the postglacial period, is noteworthy.

2. TAXONOMY

Revision of the material showed presence of 4 species of insectivores, 11 bats, 4 lagomorphs, 15 rodents, 18 carnivores and 10 ungulates. Even more taxa were found, however their taxonomical assignation uncertain (due scanty or badly preserved material) and were classified only for the genus or as the closely undetermined forms. Sometimes the pre-war German determination were also strongly doubtful and in many times were already reject by later authors.

2.1 Insectivores

Erinaceus. The hedgehog is known only from the Holocene layers of four rock shelters on Mt. Miłek (Małgorzata, Trwoga Paleontologa, Cisowe 1 and 2) (Zotz, 1939; Bieroński *et al.*, 2007).

Sorex*/*Crocidura. The only Middle Pleistocene record is an unidentified shrew *Sorex* sp. from the deposits of Południowa Cave (Zotz, 1939; Kowalski, 1959; Rzebik-Kowalska, 2009). Scanty Late Pleistocene material of *Sorex araneus* and *Crocidura suavoeolens* was found in trenches IV and V (Bieroński *et al.*, 2009c). *Sorex araneus* was also a component of the Holocene fauna from rock shelters Małgorzata, Lucia, Tomkowa Niche, Trwoga Paleontologa and Panna (Bieroński *et al.*, 2007). *Sorex minutus* and an unidentified *Crocidura* sp. were found in the postglacial deposits of Solna Jama Cave (Bieroński *et al.*, 2007; Stefaniak *et al.*, 2009).

Talpa europaea. A few mole remains were found in the Late Pleistocene sediments of Wschodnia Cave (Zotz, 1939; Rzebik-Kowalska, 2009) and in the mixed layers (most probably Holocene) of the deposits in Radochowska Cave (Bieroński *et al.*, 1985, 2007).

2.2. Bats

Bats are commonly found in Sudetic caves (Bieroński *et al.*, 2007, 2009c). However, most of the remains are subfossil, which indicates a relatively young age, most probably Holocene. Many remains are postcranial bones which are difficult to identify; such unidentified material was found, for example in a few Holocene sites of Mt. Miłek (rock shelters Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche and Panna) (Bieroński *et al.*, 2007).

Eptesicus nilssoni.A single find of this species, which today is among the most common bats in northern Eurasia, comes from trench IV of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Eptesicus* cf. *serotinus. This fairly large Eurasian bat was reported from Cisowe 1 Rock Shelter (Zotz, 1939).

Myotis. Unidentified remains of a mouse-eared bat were found in caves Radochowska, Południowa and Obok Wschodniej (Zotz, 1939).

Myotis bechsteini. The Late Pleistocene (age uncertain) records of this bat come from Wschodnia Cave and all the trenches of Niedźwiedzia Cave, where also subfossil remains of the species were found (Bieroński *et al.*, 2007).

Myotis brandti. Remnants of this close relative of *Myotis daubentoni* were found in the Holocene sediments of trench VI in Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Myotis daubentoni. Remains of this small bat were found in trenches I, II and III of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Myotis myotis. Few mandibles of this bat were found on the surface of the deposits of Solna Jama Cave, on top of the sediments from trenches I and II in Niedźwiedzia Cave (Bieroński *et al.*, 2007) and in Radochowska Cave (Bieroński *et al.*, 1985). All the records were dated as Holocene.

Myotis mystacinus. This small Western Palaearctic bat appeared in the fossil and subfossil material from all six trenches of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Myotis nattereri. Remains of this medium-sized, vespertilionid bat with Western Palaearctic distribution were found in four trenches of Niedźwiedzia Cave (III to VI) (Bieroński *et al.*, 2007). Most were of postglacial or Holocene age, however a few Late Pleistocene bones were also present (Bieroński *et al.*, 2007).

Plecotus auritus. Holocene records of this species come from Solna Jama Cave (Bieroński *et al.*, 2007) and Radochowska Cave (Bieroński *et al.*, 1985). This species was also found in the fossil and subfossil material in all six trenches of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Rhinolophus* aff. *ferrum equinum. The only record comes from Południowa Cave, but its age is extremely uncertain (Middle or Late Pleistocene) (Bieroński *et al.*, 2007).

Rhinolophus hipposideros. This southern species was found only in Radochowska Cave (Bieroński *et al.*, 1985).

2.3. Lagomorphs

Lepus. Remains of an unidentified hare were found in the Late Pleistocene sediments of Obok Wschodniej Cave and Cisowe 1 Rock Shelter (Bieroński *et al.*, 2007). Hare remains came also from the postglacial/Holocene periods of Cisowe 2 Rock Shelter and Radochowska Cave (Zotz, 1939; Bieroński *et al.*, 2007).

Lepus europaeus. Remains of this most abundant leporid were found in the postglacial/Holocene deposits of Radochowska Cave (Frenzel, 1936), as well as rock shelters Małgorzata, Trwoga Paleontologa, Tomkowa Niche and Cisowe 2 (Bieroński *et al.*, 2007).

Lepus timidus. This species, largely adapted to arctic and mountain habitats, was found only in the postglacial or early Holocene sediments of Małgorzata Rock Shelter (Bieroński *et al.*, 2007).

Ochotona pusilla*/*Ochotona. Few remains of this steppe species, at present limited to Central Asia, were found in Małgorzata Rock Shelter (Bieroński *et al.*, 2007). An unidentified pika was mentioned by Zotz (1939) from Cisowe 1 Rock Shelter.

Oryctolagus cuniculus. This species was mentioned from the uppermost humus layer of Radochowska Cave as well as from rock shelters Małgorzata and Trwoga Paleontologa (Frenzel, 1936; Bieroński *et al.*, 2007). It is also known from archaeological sites in Poland since the early Middle Ages (Nowak, 1968).

2.4. Rodents

***Apodemus* sp.**. Unidentified mouse from genus *Apodemus* was found in Radochowska Cave (Bieroński *et al.*, 1985).

Apodemus sylvaticus. Zotz (1939) mentioned the wood mouse from Cisowe 1 and 2 Rock Shelters. Morphometrically and morphologically the species is very close to the yellow-necked mouse (*Apodemus flavicollis*), so identification of fossil material, especially based on sparse remains, should be regarded with caution.

Arvicola terrestris. Regarded as a semi-aquatic species, the European water vole was found, among other sites, in the Late Pleistocene sediments of Wschodnia Cave and trenches I, II and V of Niedźwiedzia Cave (Bieroński *et al.*, 2007; Stefaniak *et al.*, 2009). It was much more common in the postglacial and Holocene sediments of rock shelters on Mt. Miłek (Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche, Panna and Cisowe 2; Bieroński *et al.*, 2007). It was also present in the deposits of the same age in Solna Jama Cave (Stefaniak *et al.*, 2009) and Radochowska Cave (Zotz, 1939). Probable remains of the species from Cisowe 1 Rock Shelter, (Zotz 1939), also correspond to *A. terrestris*.

Baranomys loczyi. This form (*langenhani* sensu Heller, 1937) is until today the only reliable Pliocene element in the Sudetic fauna (Bieroński *et al.*, 2007).

Castor fiber. Closely associated with water, the Eurasian beaver is quite rare in the Sudetic fauna, represented by scanty material found in Radochowska Cave (Bieroński *et al.*, 1985) and trenches I and II of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Cricetus cricetus. This large steppe rodent was mentioned by Zotz (1939) from Cisowe 1 and 2 Rock Shelters and from Solna Jama Cave (Bieroński *et al.*, 2007, Stefaniak *et al.*, 2009).

Cricetidae indet. Unidentified hamster remains were reported from rock shelters Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche and Panna (Bieroński *et al.*, 2007).

Dicrostonyx gulielmi. This cold-adapted rodent was found in the deposits of the latest part of glaciation or postglacial of rock shelters Małgorzata, Trwoga Paleontologa and Cisowe 1 (Bieroński *et al.*, 2007).

Glis glis. One of the most abundant Sudetic rodents. This species was discovered in the fossil material from the Late Pleistocene Wschodnia Cave, and deposits of uncertain age (Middle or Late Pleistocene) from Południowa Cave (Bieroński *et al.*, 2007). The edible dormouse is also a component of the postglacial/Holocene faunas of rock shelters Małgorzata and Trwoga Paleontologa (Bieroński *et al.*, 2007).

Lemmus lemmus. The Norway lemming, endemic to the northern Fennoscandia, was mentioned only from Cisowe 1 Rock Shelter (Bieroński *et al.*, 2007).

***Microtus* sp. (*Pitymys* sp.)**. The only record of this species was found atCisowe 1 Rock Shelter(Zotz, 1939).

***Microtus* sp**. An unidentified vole was mentioned from Cisowe 1 Rock Shelter (Zotz, 1939), from Solna Jama Cave (Bieroński *et al.*, 2007) and from Radochowska Cave (Zotz, 1939).

Microtus agrestis. Today the field vole mainly occurs in moist grassy habitats; it was a common component of the postglacial and Holocene faunas of rock shelters Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche and Panna (Bieroński *et al.*, 2007).

Microtus arvalis. Like *Microtus agrestis*, the common vole was found in a few rock shelters on Mt. Miłek (Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche and Panna) (Bieroński *et al.*, 2007). It was also mentioned from Radochowska Cave (Bieroński *et al.*, 1985) and from four trenches (I, II, III and V) of Niedźwiedzia Cave (Bieroński *et al.*, 2007).

Myodes glareolus. This most common Sudetic rodent, regarded as a forest-dweller, was represented by numerous remains from most postglacial and Holocene sediments, such as rock shelters Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche, Panna and Cisowe 1, as well as Solna Jama and two trenches (I and II) of Niedźwiedzia Cave (Bieroński *et al.*, 2007). In the last locality, Late Pleistocene age of some individuals cannot be excluded (Bieroński *et al.*, 2009c).

Microtus gregalis. The narrow-headed vole was recorded only from Cisowe 1 Rock Shelter (Zotz, 1939).

Microtus subterraneus*/*Microtus gregalis. The European pine vole occupies a wide range of habitats; it occurred in the fossil material from the five above-mentioned rock shelters on Mt. Miłek (Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche and Panna) (Bieroński *et al.*, 2007). The same is true of the tundra vole, which now occurs in moderately damp tundra or moist meadows and usually near water.

Sciurus vulgaris. The red squirrel was mentioned from Wschodnia Cave, Obok Wschodniej Cave and Cisowe 1 Rock Shelter (Zotz, 1939) as well as from Solna Jama Cave (Bieroński *et al.*, 2007) and Radochowska Cave (Frenzel, 1936). All the records are probably of Late Pleistocene, postglacial, or Holocene age.

2.5. Carnivores

***Canis lupus spelaeus*/*Canis lupus* ssp**. This specialised Late Pleistocene wolf ecomorph, large-sized, robustly built, with slightly shorter limb bones and powerful carnassials, was abundant (more than 350 bones) in all the trenches of Niedźwiedzia Cave. After its first description (Goldfuss, 1823), the form was sometimes mentioned from different European sites, but usually only briefly, and almost never described in detail. The form/subspecies category tends to be employed rather freely in large canid palaeontology. However our preliminary analysis suggested distinct differences compared to the modern European wolf. These differences require a more detailed analysis and are now under study. Remains of a wolf which morphometrically closely resembled those from Niedźwiedzia Cave were also found in Naciekowa Cave. Wolf individuals from Solna Jama Cave, Małgorzata Rock Shelter and Aven on Mt. Połom were smaller and more slender, like the modern wolf. The wolf was also mentioned by Frenzel (1936) from Radochowska Cave.

Crocuta crocuta spelaea. The cave hyena was mentioned from three Late Pleistocene Sudetic sites: Wschodnia Cave, Radochowska Cave and Niedźwiedzia Cave. However, a detailed revision renders the Sudetic records doubtful. Zotz (1939) described lumbar vertebrate, a humerus fragment and two first phalanges as possibly belonging to a hyena (Zotz, 1939: 39). At the same time he remarked that those bones had no taxonomic value and in fact were too small to represent the cave hyena. Zotz (1939: 67) described two tooth fragments from Radochowska Cave, with an indication of their uncertain taxonomic position. In Niedźwiedzia Cave the hyena was reported from all the trenches, but a detailed analysis of all available carnivore fossil material did not confirm the presence of this species. For example, the skull fragment from trench VI, initially identified as cave hyena (Wiszniowska, 1989), turned out to be a large wolf. Likewise, the analysis of Zotz's old collection from Mt. Połom failed to confirm the occurrence of the cave hyena in the site.

Felis silvestris. Zotz (1939) mentioned an unidentified cat from the deposits of Obok Wschodniej Cave. The wildcat was identified based on a few isolated teeth and postcranial bones from the Holocene layers of rock shelters Małgorzata and Trwoga Paleontologa (Bieroński *et al.*, 2007), as well as the postglacial/Holocene layers of Solna Jama Cave and Niedźwiedzia Cave. As to the record from Radochowska Cave, it is not even clear if it was the wildcat or domestic cat, because the identification was based on a femur (Frenzel, 1936). The bone was found in the surface strata of the sediments and was not fossilised. *F. silvestris* is very rarely found in Pleistocene deposits of Central Europe (Barycka, 2008). Most of the so called "fossil" specimens, whose age was estimated based on biostratigraphical or other indirect evidence, turned out to be postglacial or subfossil. The conjecture was confirmed by a few C14 AMS dates, which showed a young age of those remains (Marciszak & Stefaniak, 2016). Except very few bones, most specimens were younger than 12-11 ka.

Gulo gulo. Among the Sudetic caves the wolverine was mentioned from Solna Jama Cave (Bieroński *et al.*, 2007; Stefaniak *et al.*, 2009) and Naciekowa Cave (Marciszak, 2011). The species is a permanent, but not very common, component of the Late Pleistocene faunal assemblage from Poland (Marciszak, 2012; Marciszak & Stefaniak, 2016). The wolverine is not inherently a purely "boreal" or "tundra" species (Döppes, 2001). It can travel long distances and its daily movements may exceed 30 km (Pulliainen, 1993; Pasitschniak-Arts & Larivière, 1995). Straight line distances longer than 300-350 km per month (Gardner *et al.*, 1986) are also known for the wolverine. All the records of *G. gulo* from Poland are of late Middle or Late Pleistocene age (Wojtal, 2007; Marciszak, 2012). It seems that the find from Solna Jama is the only reliable, postglacial record of the species from Poland. Till now the wolverine was not found in any archaeological Holocene sites in Poland (Wyrost, 1994; Sommer & Benecke, 2004; Marciszak & Stefaniak, 2016).

Lynx lynx. The only record of the lynx comes from trench V of Niedźwiedzia Cave, where a maxilla fragment was found in the postglacial/Holocene deposits.

***Martes martes* (also as *Martes* sp. and *Martes* cf. *foina*)**. Kowalski (1959) listed two Pleistocene sites with supposed remains of *Martes foina* in Poland. Both were cited after Ossowski (1885) and Zotz (1939), and most probably the author did not see the material. Already Anderson (1970) suspected misidentification and doubted the geological age of the specimens. Upon revision, the few postcranial bones from Maszycka Cave (Ossowski, 1885) and Wschodnia Cave (Zotz, 1939), labelled as *Martes foina* or *Martes* sp., turned out to be European pine marten *Martes martes*. The stone marten (*Martes foina*) appeared not earlier than the Neolithic period, which was most probably associated with human colonisation (Anderson, 1970). Revisions of the Pleistocene and Holocene mustelid material from the Polish archaeological and palaeontological sites showed that the stone marten was absent in the fossil record (Marciszak, 2012; Marciszak & Stefaniak, 2016).

Zotz (1939) mentioned an unidentified marten from Cisowe 1 and 2 Rock Shelters; most probably those remains represented the European pine marten. This species was also found in the Holocene layers of rock shelters Małgorzata (single canine) and Trwoga Paleontologa (mandible fragment), as well as caves Solna Jama (radius), Biały Kamień (humerus), Kontaktowa (humerus) and Miniaturka (few isolated teeth). The single canine from Radochowska Cave, excavated in the 1980s (Bieroński *et al.*, 1985), was of the same age, as was already emphasised by Frenzel (1936) for the pine marten skull fragment, found near the cave entrance. More than one hundred bones, among them complete skulls, were found in all the trenches of Niedźwiedzia Cave (also in the parts like Sala Mastodonta, discovered in 2012) (Wiszniowska, 1967, 1989; Bieroński *et al.*, 2007, 2009c; Marciszak, 2012, 2014). The markedly larger Late Pleistocene specimens were also characterised by broader and more massive teeth (Marciszak, 2012).

Meles meles. The badger was the most abundant carnivore in the postglacial and Holocene sediments of rock shelters on Mt. Miłek (Małgorzata, Lucia, Trwoga Paleontologa, Tomkowa Niche, Panna and Cisowe 1 and 2; Bieroński *et al.*, 2007). The same age (Holocene) was obtained for the single canines from Solna Jama Cave and Kopułka Cave, and the mandible and a few postcranial bones from trenches V and VI in Niedźwiedzia Cave. Likewise, nearly all the numerous remains from Radochowska Cave, including three complete skulls and fragments of a few skulls date from the Holocene (Frenzel, 1936; Zotz, 1939; Bieroński *et al.*, 1985, 2007, 2009b; Stefaniak & Bieroński, 2009). However, the intact calvarium (complete with mandible) of a very large badger found deep in the profile of trench II in Niedźwiedzia Cave was of Late Pleistocene age. Also the record from Rogóżka Cave (Arndt, 1925) was regarded as subfossil already by the German authors (Pax & Maschke, 1935; Bieroński *et al*., 2009a).

The badger was the most common mustelid in the Late Pleistocene assemblages (Sommer & Benecke, 2004; Mallye, 2007; Marciszak, 2012). It commonly used caves and rock shelters to rest and raise its young. Sheltering in rock crevices or digging burrows in cave deposits, it disturbed the deposit structure. Consequently, finding its remains in a layer does not imply that the age of the remains is the same as or similar to the age of the sediments or other objects found in the same horizon. In the above-mentioned Sudetic caves AMS C14 dating clearly indicated Holocene age of the finds that were previously estimated as Late Pleistocene (except Niedźwiedzia Cave). The wolverine's life style favours accumulation of debris: various organic materials accumulate in its burrows, sometimes in considerable quantities, like in German sites Pisede 1 and 2 (Peters *et al.*, 1973).

Mustela erminea. Fossil remains of the stoat were found in the postglacial/Holocene deposits of rock shelters Małgorzata (two mandibles and isolated P4) and Trwoga Paleontologa (Bieroński *et al*., 2007). The record from Cisowe 2 Rock Shelter, based on a femur classified as *Mustela* cf. *erminea*, seems to be very uncertain because of the lack of morphological features which would clearly separate the stoat and the weasel (Marciszak, 2012). The species was also found during the 1980s excavations in Radochowska Cave (mandible fragment with p3-m1) (Bieroński *et al.*, 2007, 2009b), on the deposit surface in Miniaturka Cave (single canine) and Niedźwiedzia Cave (mandible) (surface of trench VI) (Marciszak, 2012) dated as post-Pleistocene.

Mustela eversmanii. The right mandible from Solna Jama Cave is the first record of the steppe polecat from the Sudetic caves, and one of the few from the Polish Pleistocene. The remaining localities with remains of this species are located in the Częstochowa Upland and dated as the late Middle and Late Pleistocene (Marciszak, 2012; Krajcarz *et al.*, 2014; Marciszak & Stefaniak, 2016).

Mustela nivalis. The most noteworthy find of this smallest mustelid is the calvarium of a minute weasel from Solna Jama Cave; the species is regarded as a possible survivor of the last cool phase in this area (Marciszak & Stefaniak, 2016). Also a much larger male comes from the postglacial sediments of the same site. Other Postglacial/Holocene records of the least weasel come from rock shelters Małgorzata, Trwoga Paleontologa and Cisowe 1 (Zotz, 1939; Bieroński *et al.*, 2007). Single mandibles were found in caves Biały Kamień (postglacial?), Radochowska (Holocene) and in trench IV of Niedźwiedzia Cave (Marciszak, 2012).

The relatively large number of weasel remains in the Sudetic sites is associated with the activity of predators, mainly larger birds of prey and owls (King & Powell, 2007). Studies in the Białowieża Forest show that *Mustela nivalis* remains are found with an average frequency of 0.5% in pellets and faeces of birds and mammals. The registered mortality was 87% within 6 months (Jedrzejewska & Jędrzejewski, 2001).

Mustela putorius. Zotz (1939) mentioned the common polecat from Wschodnia Cave without any detailed stratigraphic context. It was also recorded from the postglacial/Holocene uppermost layers of Cisowe 2 Rock Shelter (Zotz, 1939), Małgorzata Rock Shelter and trench V (surface) of Niedźwiedzia Cave.

Panthera pardus. The second largest cat of the genus *Panthera* was recorded from Mt. Połom: two phalanges and a single canine were found in the material from Naciekowa Cave. In Diedrich's (2013) opinion some mountain populations of leopard, hunting or scavenging hibernating cave bears, might explain the presence of this species in Naciekowa Cave. At the same time, the rarity of its remains in cave sediments can be only partially explained by its elusive, solitary behaviour. Together with wolf, coyote, black bear and a few other large carnivores, the leopard is among the best adapted to different environmental conditions. Its ecological success is due to its opportunistic hunting behaviour, wide range of prey, and ability to adapt to various habitats. In areas like the Sudetes, where montane boreal forests dominated and typical leopard's prey was absent or very rare, such behaviour could ensure the species' survival (Diedrich, 2013).

Panthera spelaea fossilis. The only reliable record of this form comes from the Middle Pleistocene deposits of Południowa Cave, where p4, m1 and two metacarpals were found. All four fossils belonged to one, particularly large lion with ancestral morphology which was typical of the early and mid Middle Pleistocene forms. The dimensions and the shape of the main cusps clearly resembled the early, great lions commonly known as "Cromerian lions", from Mosbach 2, Mauer, La Belle-Roche, Château Breccia, Sima de los Huesos or Westbury-sub-Mendip (Argant *et al.*, 2007). Geologically younger lions from the late Middle Pleistocene (MIS 11-9) were characterised by somewhat more advanced

morphology, quite different from those of the examined individual. The lions from the late Middle Pleistocene (MIS 8-7) of Biśnik Cave and Wierzchowska Górna Cave differed from this individual even more (Marciszak & Stefaniak, 2010; Marciszak *et al.*, 2014).

Panthera spelaea spelaea. Zotz (1939) mentioned cave lion remains from caves Północna Duża and Obok Wschodniej. Our revision of this material confirmed the previous identification. However, the most spectacular material was found in Niedźwiedzia Cave, where more than five hundred bones (among them almost complete skulls) of at least ten individuals were discovered (Wiszniowska, 1978; Barycka, 2008; Marciszak *et al.*, 2014). The cave lion from this site was a massive cat, 400 kg in weight, with relatively short and enormous paws. Males heavily outnumbered females in the material, and only adult individuals were found. The locality is a classical sample of the so called "cave bear den", where large predators, attracted by hibernating bears, visited the cave in search of food. During the Late Pleistocene, speleoid bears hibernated deep inside their caves and cave lions sporadically entered the caves to hunt the herbivorous cave bears. The lion skeletons discovered among the bear skeletons, deep inside Niedźwiedzia Cave, provide evidence of active lion predation on the cave bears (Diedrich, 2012). Also many bones, for example the skull of a young female with two deep holes in the neurocranium (Nowakowski & Stefaniak, 2015), indicate such interactions. However, it was not mainly lions that fed on the cave bears. The large quantities of damaged bones of *Ursus ingressus* with similar kinds of damage show that the cave wolf (cave hyena was almost absent) was the primary scavenger of cave bear carcasses and was largely responsible for the destruction of their remains. Predation and scavenging on cave bears, particularly in montane boreal forests of the Sudetes which were devoid of the mammoth steppe fauna, explains the large numbers of fragmented bones of *Ursus ingressus* found in Niedźwiedzia Cave and suggests similar scenarios in other Sudetic caves.

Vulpes lagopus. Only a few cranial bones (among them an almost complete mandible) of this arctic, cold-adapted species were found in trenches II, IV and VI of Niedźwiedzia Cave.

Vulpes vulpes. The most common canid in Sudetic caves, the red fox was found in the Late Pleistocene and Holocene sediments. Individuals from cooler periods were larger and more massive, while those from warmer periods were smaller and more delicately built. Late Pleistocene records include caves Niedźwiedzia (all trenches), Wschodnia, Naciekowa and Radochowska (Frenzel, 1936; Bieroński *et al.*, 1985). Solna Jama Cave and four rock shelters on Mt. Miłek (Małgorzata, Trwoga Paleontologa, Cisowe 1 and 2) yielded postglacial and Holocene records of the species (Zotz, 1939; Bieroński *et al.*, 2007). In Małgorzata Rock Shelter the red fox material was especially abundant and included also juveniles, indicating that the site was a breeding place.

Ursus deningeri. Mentioned for the first time from Sudetic caves, this characteristic Middle Pleistocene species was identified based on the scanty material from Południowa Cave. Although limited in number, the teeth from this site show a rather ancestral morphology and resemble those from Kozi Grzbiet.

Ursus ingressus. The most common carnivore and the most common of all mammals, it was represented in some localities, for example in Niedźwiedzia Cave, by enormous numbers of individuals (so far ca. 850.000 examined bones). The species, previously determined as *Ursus spelaeus*, was reported from Late Pleistocene sites - caves Wschodnia, Północna Duża, Obok Wschodniej, Radochowska and Solna Jama (Frenzel, 1936; Zotz, 1939; Bieroński *et al.*, 1985, 2007; Stefaniak *et al*., 2009). However, the analysis of mitochondrial DNA (mtDNA) showed that *U. ingressus* was the only speleoid bear from the Sudetic caves (Baca *et al.*, 2012, 2014). The mtDNA haplotypes from Niedźwiedzia Cave formed a single cluster and differed from the haplotypes obtained for cave bears from other European areas. Direct dating (C14, UTh) showed that the species appeared in the Sudetes at least 80 ka, and thus its migration may have preceded the colonisation of the Alps and the Swabian Jura. It is also possible that the migration route ran along the Carpathian-Sudetic arch (Baca *et al.*, 2012, 2014). Preliminary morphometric and morphological analysis also confirmed the distinctness of the Sudetic populations from those from German or Austrian caves. The possibility was already mentioned by Wiszniowska (1976), who found differences between populations from higher and lower situated localities.

Ursus* ex. gr. *spelaeus. This species is represented by cave bear remains from Mt. Połom (among others Wschodnia Cave and especially abundant material from Naciekowa Cave), so far without precise identification. The whole of the material from Naciekowa Cave (more than 5500 bones) is characterised by a very small size and slender build. Also the primitive morphology, with narrow and simply built premolars and molars (P4 without additional cusps, m2 and m3 with poorly developed, straight talonid) and the slim metacarpals/metatarsals, clearly distinguish the population from Naciekowa Cave from the large, advanced, robust *Ursus ingressus* from Niedźwiedzia Cave. Morphometrically the small cave bear resembles the dwarf, Alpine bears (*Ursus ladinicus* and *Ursus eremus*). Though more than a dozen specimens were used, all attempts at DNA analysis failed. We can only suppose, that it cannot be entirely rule out, that the population can be older than Late Pleistocene. Also direct dating methods (C14 and UTh) except one, were unsuccessful. The material requires further analysis and comparison with other untypical cave bear populations from the European late Middle Pleistocene. It is not clear, why all analyses and dating methods failed.

Ursus arctos arctos. A different form of brown bear was discovered in the postglacial and Holocene sediments of some Sudetic caves (Niedźwiedzia, Radochowska): smaller, with more slender build and dentition more advanced than that of *Ursus arctos priscus*. In its size and morphology it is indistinguishable from the recent Carpathian bear. Its appearance in the postglacial period was correlated with the total restructuring of the faunal assemblages and the extinction of the Ice Age giants, which were replaced by smaller and more versatile forms. A mandible of *Ursus arctos arctos* was found on a dump in Południowa Cave (Römer, 1875). A single canine from Cisowe 1 Rock Shelter and a few dozen cranial and postcranial elements from Cisowe 2 and Małgorzaty Rock Shelters as well as Aven on Mt. Połom complete the list of sites with remains of the nominate subspecies of brown bear.

Ursus arctos priscus. Though heavily outnumbered by cave bear remains, also other members of the ursid family occurred in the caves. One of them was the "real king of the Ice Age", an enormous arctoid bear which in size exceeded even the largest recent Kodiak bears. Remains of this huge brown bear were found in caves Niedźwiedzia (Wiszniowska, 1967, 1970, 1989), Radochowska (Frenzel, 1936), Północna Duża and Solna Jama (Marciszak & Stefaniak, 2016), and were especially abundant in Radochowska Cave (about 300 bones) and Niedźwiedzia Cave (70 bones). According to Frenzel (1936), the most noteworthy was the almost complete calvarium found in the deepest part of Radochowska Cave. The dimensions of teeth of this specimen exceeded all known so far specimens (Rode, 1935). The single lower molar from Solna Jama Cave was found in close association with a fibula of *Ursus ingressus*, which was dated as ca. 40 ka (Poz-27294) (Wiśniewski *et al.*, 2009; Marciszak & Stefaniak, 2016).

The important characteristic of *Ursus arctos priscus* was its huge size. This may have been associated only with the

Figure 2: Two main Late Pleistocene Sudeten carnivores: Ursus arctos priscus and Panthera spelaea spelaea in battle in the neighbourhood of Niedźwiedzia Cave

Figuur 2: Twee voorname Laat-Pleistocene Sudetische carnivoren: Ursus arctos priscus en Panthera spelaea spelaea in gevecht in de buurt van de Niedźwiedzia Cave

influence of temperature: according to Bergmann's rule larger individuals are found in harsher climate. However, the issue is more complicated, since large forms are also known from the interglacial/interstadial periods (Musil, 1996; Sabol, 2001a, 2001b). It seems likely that the large size was also associated with a high-protein diet, which the huge bears derived from two sources: hunting and kleptoparasitism. They could roam vast open areas in search of prey and other food, also taking advantage of seasonal abundance of fish, berries and other available food sources (Baryshnikov, 2007). Their size was of considerable advantage during confrontation with other predators, and the abundance of large herds of hoofed mammals could provide the necessary amount of food for such a large predator. The retreat of the glacier was followed by re-construction of the fauna; the open grasslands were replaced by thick forests, with numerous but scattered small and medium-sized species. The world around the huge, hypercarnivorous brown bear changed, and now it offered much more favourable conditions to smaller and more versatile animals. The huge, ancestral, carnivorous brown bear was replaced by a smaller, more omnivorous form, close to the nominate subspecies, which then survived to this day. In conclusion, we agree with many earlier authors (e.g. Thenius, 1956; Mostecký, 1963; Musil, 1964, 1996; Sabol, 2001a, 2001b; Pacher, 2007) on that the true *Ursus arctos priscus* may have represented a different brown bear form which was adapted to open, steppe-like habitats.

2.6. Ungulates

The information on the fossil ungulate fauna from the Sudetes is very scanty and the material from the cave sites excavated before World War II, even when they can be located, is usually very incomplete (Zotz, 1939; Wiśniewski *et al*., 2009). The most abundant assemblage was found in Radochowska Cave, however a critical revision showed that the material was contaminated with remains re-deposited by water (Bieroński *et al*., 2009b).

The identification of the woolly mammoth *Mammuthus primigenius* from Rogóżka Cave (Arndt, 1925) and the woolly rhinoceros *Coelodonta antiquitatis* from Radochowska Cave (Zotz, 1939) was questioned already by some German researches (Bieroński *et al.*, 2009b). Because there are no reliable records of any of the two largest ungulates in the Sudetic caves, they are not included in the faunal lists.

Alces alces. Based on an antler fragment, Frenzel (1936) mentioned the elk from Radochowska Cave and concluded that remains of this species were quite frequent in Silesian lowlands. Also Wenke (1933) reported the elk from one of the caves on Mt. Połom.

***Bison priscus*/*Bison bonasus*?/*Bos* sp**. Steppe bison remains were found in the Late Pleistocene deposits from Sala Mastodonta (rib shaft and tooth fragments) as well as from trenches I and II (talus and carpus bones) (Stefaniak & Ratajczak, 2014). The humerus fragment from Radochowska Cave (Zotz, 1939) and two central bones from the Late Pleistocene deposits of Naciekowa Cave confirmed the presence of an unidentified large bovid. Other finds from Radochowska Cave, such as vertebrae, calcaneus and a sacrum fragment, were assigned to steppe bison, but found in a layer with a great admixture of domestic animals. Other large bovid remains from the uppermost layers of that site were light-coloured and showed no traces of fossilisation, which indicates domestic cattle rather than any wild form (Bieroński *et al.*, 2009b). Besides, Arndt (1925) reported some bison bones from Rogóżka Cave, but already the German researchers (Pax & Maschke, 1935) doubted his identification and regarded the remains as subfossil (Bieroński *et al*., 2009a).

Capreolus capreolus. The European roe deer was mentioned from Radochowska Cave (tibia fragment of very robust animal) (Frenzel 1936) and from Cisowe 1 and 2 Rock Shelters (Zotz 1937a, 1937b, 1939; Bieroński *et al.*, 2007, 2009b). Bieroński *et al*. (2007) and Wiśniewski *et al*. (2009) confirmed the occurrence of this small deer in two rock shelters on Mt. Miłek: Trwoga Paleontologa and Małgorzata, dated as the Atlantic period. Few remains (metacarpal distal epiphysis, a fragment of phalanx I, calcaneus and right tibia)

were mentioned from trenches I, II and V in Niedźwiedzia Cave (Wiszniowska, 1989; Bieroński *et al.*, 2007, 2009c; Stefaniak, 2015). Two phalanges (first and second) were found in the postglacial sediments of Solna Jama Cave (Marciszak & Stefaniak, 2016). Lastly, Rogala *et al*. (1998) provided a brief description of a right mandible, found in Pod Torami Cave. All these records were dated as the postglacial or Holocene, while no Sudetic finds of Pleistocene age are known (Marciszak & Stefaniak, 2016).

Cervus elaphus. Late Pleistocene records of the red deer come from the newly discovered parts of Niedźwiedzia Cave; the material found in a large chamber called Sala Mastodonta included left maxilla with DP3-DP4, isolated teeth (m2, right P4) and radius proximal end (Stefaniak, 2015). AMS C14 dating gave an age of 27870 ± 230 BP (Poz-49732), indicating transition between MIS 3 and MIS 2 (Stefaniak & Ratajczak, 2014). Besides, an upper premolar was found in the profile of Holocene age below Miniaturka Cave (Wiszniowska *et al.*, 1996; Bieroński *et al.*, 2009c). The antler fragment, centrotarsal bone and humerus of young individuals from Cisowe 1 and 2 Rock Shelters were also identified as red deer (Zotz, 1939; Bieroński *et al.*, 2007). Red deer remains were also found in deposits of rock shelters Trwoga Paleontologa and Małgorzata. Frenzel (1936) described fragments of antlers, a mandible with two molars and limb bones of a young individual from Radochowska Cave. According to Frenzel (1936) most were found near the surface and were only poorly fossilised (Bieroński *et al.*, 2009b). Red deer was also mentioned from the Holocene layers of Północna Duża Cave, where a sacrum, three pelvic fragments, a damaged tibia and a metatarsal bone were found (Stefaniak, 2015). During his excavations in Radochowska Cave, Zotz (1939) found a metapodial fragment, identified it as *Cervus* sp. and noted also the presence of ungulates larger than deer; perhaps bovids.

***Equus ferus*/*Equus* sp**. Zotz (1939) described a fragment of a third metatarsal of a very large and robust horse from Radochowska Cave. In his opinion (Zotz 1939) the third metacarpal bone from Obok Wschodniej Cave resembled Przewalski's horse because it was very large. The second phalanx from Radochowska Cave was also quite large (Zotz, 1939). The Postglacial/Holocene horse records from the Sudetic caves indicate the occurrence of another form of horse: smaller, more slender, of tarpan type. Remains of that form (scapula) were found in Cisowe 1 Rock Shelter (Zotz, 1939; Bieroński *et al.*, 2007).

Megaloceros giganteus. The species was listed as *Megaceros* sp. from Radochowska Cave (Zotz 1939), based on two antler fragments and three pieces of metapodials (identification uncertain). It was also found (isolated tooth, carpal bone) in the Late Pleistocene deposits of Naciekowa Cave (Stefaniak, 2015).

Rangifers tarandus. Reindeer remains were only rarely found in the Sudetic caves. Zotz (1939) mentioned the species from Północna Duża Cave (fragment of left mandible and lower molar fragment) (Stefaniak, 2015). A right p4, an intermedium, an accessory bone and the first and second phalanx of this species were found in the material from trenches II and V in Niedźwiedzia Cave. Recently also a fragment of left talus was discovered in the material from Naciekowa Cave (Stefaniak, 2015).

Rupicapra rupicapra. The Chamois (a type of goat antelope and part of the mountain fauna) was for the first time recorded as fossil in the Sudetes, from trench V in Niedźwiedzia Cave, where two phalanges (I and II), milk left i1, left m3 and distal epiphysis of metacarpal bone were found (Wiszniowska & Stefaniak, 1996; Bieroński *et al.*, 2009c; Stefaniak & Ratajczak, 2014).

Sus scrofa. Few remains of a large wild boar of Late Pleistocene age were discovered in trench II in Niedźwiedzia Cave (Wiszniowska, 1989). Later its presence was also confirmed in trench I of that cave (Bieroński *et al.*, 2009c). Wild boar remains were mentioned from some postglacial/Holocene localities in the Sudetes, but it is very uncertain that they represented wild boar and not domestic pig, like the canine fragment from Cisowe 2 Rock Shelter or the remains from rock shelters Małgorzata and Trwoga Paleontologa (Zotz, 1939; Bieroński *et al.*, 2007). It is also unclear if the mandible fragment from Radochowska Cave (Frenzel, 1936) is in fact wild boar or domestic pig (Bieroński *et al.*, 2009c).

Tapirus* cf. *telleri. The single tapir tooth from Mt. Połom (precise locality unknown) most probably represents the Miocene *Tapirus telleri*. It was found among the material from the 1950s survey excavations.

CONCLUSIONS

A detailed revision and re-interpretation of old (usually pre-war) German studies resulted in an up-dated list of the fossil fauna from the Sudetic caves. The list includes ca. 7 insectivores, 12 bat forms, 4 lagomorphs, 17 rodent species, 20 carnivores and 11 ungulates. Apart from Południowa Cave, where the material included species which could be characteristic of older periods of the Pleistocene (Middle Pleistocene, e.g. *Ursus deningeri* or *Panthera spelaea fossilis*) or even Pliocene (*Baranomys*), the fossil material from all the other palaeontological or archaeological sites is of Late Pleistocene and Holocene age (Bieroński *et al.*, 2007).

The German studies from before World War II are at present difficult to verify precisely, because of the damage of the caves or loss of the material. The lack of access to some of the collections renders verification impossible, and during or shortly after World War II many materials were lost; for example Frenzel's huge collection from Radochowska Cave. Even when the material was preserved, the documentation (stratigraphy, excavation plans) was often lost or destroyed. Besides, the German researchers themselves emphasised that in many cases their identifications were uncertain and very doubtful, especially concerning small mammals and distinction between wild and domesticated forms. The part of Zotz's old collection from Mt. Połom (different sites) kept at the Archaeological Museum in Wrocław provides a good example for such uncertain species determination. Re-examination of the old material, which will continue, may make it possible to document its origin in the future.

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