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Mustelids (Carnivora, Mammalia) from the Ciemna Cave (southern Poland) as an example of Late Pleistocene small carnivore assemblage

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Abstract. Five mustelid species were found in the Ciemna Cave, in layers 13-1 dated at MIS 5-1: *Gulo gulo, Meles meles, Martes martes, Mustela erminea* and *Mustela nivalis*, with the remains of *M. martes* being the most abundant. They were represented almost exclusively by cranial material, mandibles and isolated teeth. Metrically and morphologically most of the remains corresponded to the modern European forms. Only few isolated teeth of *M. martes* belonged to a great, robust form which was characteristic of cooler phases of the Late Pleistocene and beginning of the Holocene. Another cold-adapted mustelid, represented by a single, damaged calcaneus, was *G. gulo*. Few bones showed traces of carnivore activity, which can be regarded as one of the accumulation factors, other possible factors being water and accidents.

Key words: Size comparison, ratio, species identification, carnivore activity.

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I. INTRODUCTION

The Ciemna Cave (Jaskinia Ciemna, 50°11’48”N, 19°49’54”E, 410 m a. s. l.) sensu VALDE-NOWAK et al. (2014) covers the Main Chamber of the partially preserved cave system of the same name. It is located on the left slope of the Prądnik Stream Valley, 62 m above the valley bottom and 372 m a. s. l. (Fig. 1). Developed in the Upper Jurassic lime-

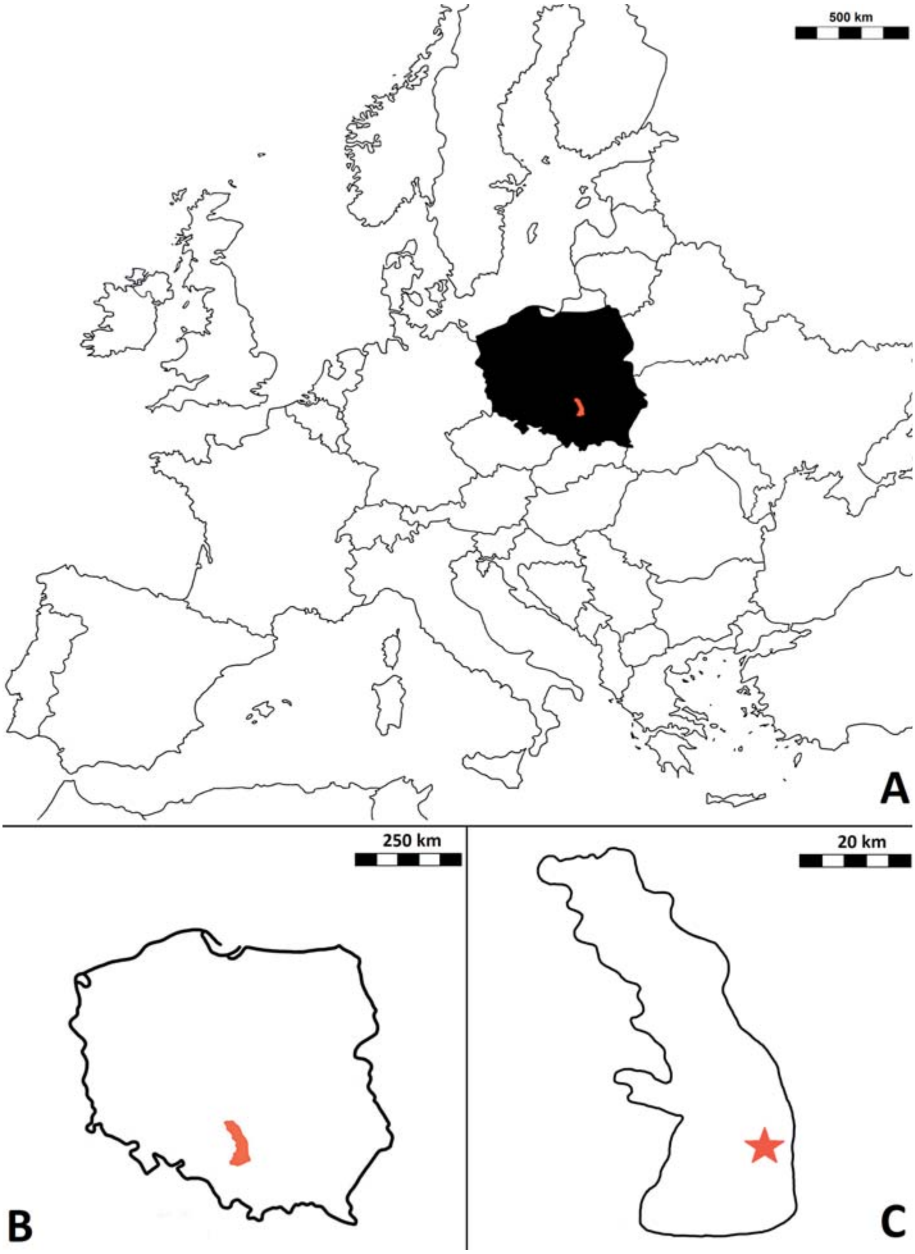

Fig. 1. Location of the Kraków-Częstochowa Upland in Europe (A) and in Poland (B), and location of the Ciemna Cave in the Upland (C).

stone, Ciemna is one of geologically oldest and largest caves in the Ojców Upland, with particularly large main chamber (MADEYSKA 1977; GRADZIŃSKI et al. 2007). The Main Chamber is developed into an elongated, NE-oriented hall (length x width x height = 88 m x 23-10 m x 8 m) which passes into a much smaller, elongated hall of SE orientation. At the end this chamber turns into an NE-oriented, narrowing corridor 60 m long. The entrance is covered and only few, rather damaged speleothems are present (GRADZIŃSKI et al. 2003; VALDE-NOWAK et al. 2014). Recent investigations confirmed that in the past the entrance was probably much wider (VALDE-NOWAK et al. 2014).

The Ciemna Cave has been explored since the second half of the 19th c., mainly by archeologists (OLSZYŃSKI 1871). The site is regularly mentioned in literature as one of the typical Middle Paleolithic sites in Central Europe, even though the results of excavations remain largely unpublished. The locality is especially well known for its Micoquian artefacts, which were the base for defining a separate cultural unit called Prądnik industry (VALDE-NOWAK et al. 2014). The first excavations were conducted at the beginning of the 20th c. (CZARNOWSKI 1924), and focused mainly on Holocene layers. Excavations in the cave part called Oborzysko Wielkie started in 1912 and were followed by exploration carried out by in 1918 and 1919 (KRUKOWSKI 1924, 1939-1948), and then after World War II, between 1963 and 1968 (KOWALSKI 2006). New interdisciplinary studies in the previously unexplored main chamber started in 2007 and are still underway (VALDE-NOWAK et al. 2014).

All these excavations yielded numerous mammal remains: *Talpa europaea*, *Crocidura leucodon*, *Neomys fodiens*, *Sorex minutus*, *Sorex araneus*, *Sorex* cf. *runtonensis*, *Lepus timidus*, *Sciurus vulgaris*, *Muscardinus avellanarius*, *Sicista betulina*, *Cricetus cricetus*, *Cricetulus migratorius*, *Dicrostonyx gulielmi*, *Lemmus lemmus*, *Clethrionomys glareolus*, *Arvicola terrestris*, *Microtus* cf. *arvalis*, *Microtus* cf. *agrestis*, *Microtus subterraneus*, *Microtus oeconomus*, *Microtus gregalis*, *Apodemus* cf. *flavicollis*, *Apodemus* cf. *sylvaticus*, *Canis lupus*, *Vulpes vulpes*, *Vulpes lagopus*, *Vulpes* sp., *Ursus ingressus*, *Ursus* sp., *Ursus arctos priscus*, *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela erminea*, *Mustela nivalis*, *Panthera spelaea spelaea*, *Lynx lynx*, *Crocuta crocuta spelaea*, *Equus* sp., *Coelodonta antiquitatis*, *Mammuthus primigenius*, *Capreolus capreolus*, *Cervus elaphus*, *Rangifer tarandus*, Cervidae indet, *Bos*/*Bison* sp., *Bison priscus*, *Capra* cf. *ibex* and *Rupicapra rupicapra* (NADACHOWSKi 1982; WOJTAL 2007; RZEBIK-KOWALSKA 2009; VALDE-NOWAK et al. 2014; NADACHOWSKI et al. 2015; POPOVIĆ et al. 2015). Some of the taxa were identificated by E. NIEZABITOWSKI from the old excavations done by CZARNOWSKI (1924) and KRUKOWSKI (1939-1948). Now it is impossible to verify the original identifications, because unfortunately the fossil material collected by KRUKOWSKI was lost during World War 2 (VALDE-NOWAK et al. 2014). Besides, also rather few remains of insectivores or bats, as well as fishes, amphibians and birds, were found, especially during washing of the sediments. However, identification of this material is still underway and no detailed information can be given (VALDE-NOWAK et al. 2014).

The faunal assemblage is dominated by carnivores, among which ursids are the best represented. Among them the speleoid bears heavily outnumber other carnivores, and represent almost 90% of the whole material (WOJTAL 2007; VALDE-NOWAK et al. 2014), while bears from the arctoid lineage, represented by large, massive forms, are much less numerous. Also canids are well represented, with all three Late Pleistocene species: wolf, red fox and polar fox. Members of the two remaining families: mustelids and felids, are quite scanty. Cats are mainly represented by isolated teeth and some small, postcranial bones, while only cranial remains of mustelids are present.

II. MATERIAL AND METHODS

Methods

Measurements were taken point to point, with an electronic calliper, to the nearest 0.01 mm. Each value given here is the mean of three measurements. Additionally some measurements were taken using a set for image analysis Olympus (Olympus stereo microscope ZSX 12, camera Olympus DP 71, programme Cell D). This set, together with camera Canon EOS 5D, was also used to take photographs. Osteological and dental terminology follows Anderson (1970). The measurements are shown in Figs 2-3.

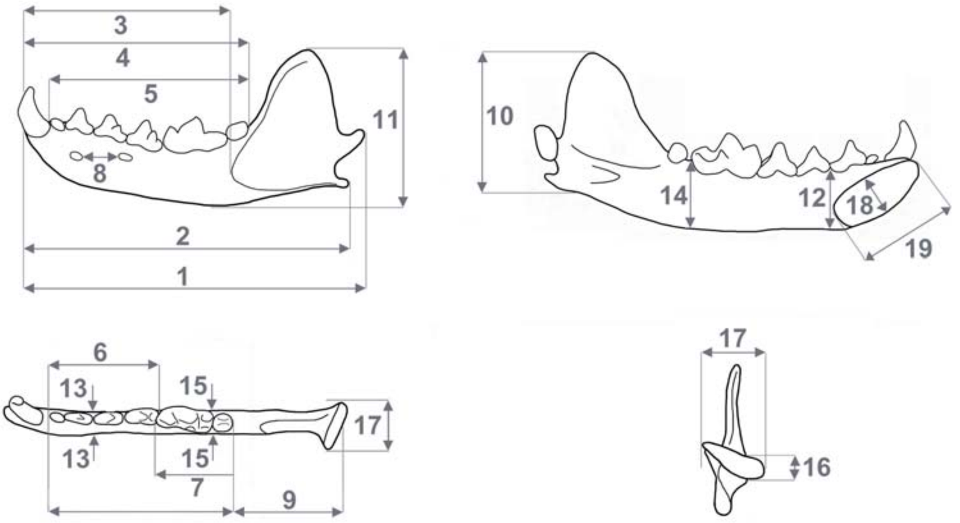

Fig. 2. Scheme of measurements of mustelid mandible: 1 – total length (condyle to infradentale), 2 – distance: angular process to infradentale, 3 – distance: infradentale to anterior margin of masseter fossa, 4 – distance: anterior margin of c1 to posterior margin of m2, 5 – cheek teeth row length (anterior margin of p1 to posterior margin of m2), 6 – premolar row length (anterior margin of p1 to posterior margin of p4), 7 – molar row length (anterior margin of m1 to posterior margin of m2), 8 – distance between mental foramina, 9 – distance: posterior margin of m2 to condyle, 10 – distance: angular process to coronoid process, 11– mandible maximum height, 12 – mandible body height between p3 and p4, 13 – mandible body thickness between p3 and p4, 14 – mandible body height between m1 and m2, 15 – mandible body thickness between m1 and m2, 16 – condyle height, 17 – condyle breadth, 18 – symphysis maximum diameter, 19 – symphysis minimum diameter.

Material

The studied material comes from the excavations conducted by Stanisław Kowalski in the 1960s outside the main chamber, at Oborzysko Wielkie, and from the studies started in 2007 in the main chamber (Wojtal 2007; Valde-Nowak et al. 2014). During the new excavations the position of bone and teeth fragments exceeding 2 cm in size was recorded in 3D. All the sediments from the new excavations were wet-sieved using nesting screens of different mesh size to recover the smallest lithic finds and the remains of smaller animals. All the material is stored at Institute of Systematics and Evolution of Animals, Polish Academy of Sciences in Kraków.

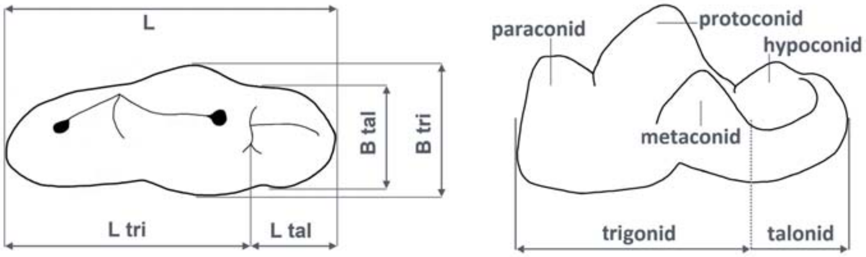

Fig. 3. Lower carnassial (m1) measurements (left) and cusps terminology (right). L – total length, L tri – trigonid length, L tal – talonid length, B tri – trigonid breadth, B tal – talonid breadth.

Among the 5 mustelids from the Ciemna Cave, two largest species are represented by very few remains: *Gulo gulo* by a damaged calcaneus (Fig. 4) and *Meles meles* by an isolated premolar and a single phalanx 2 (Table 1).

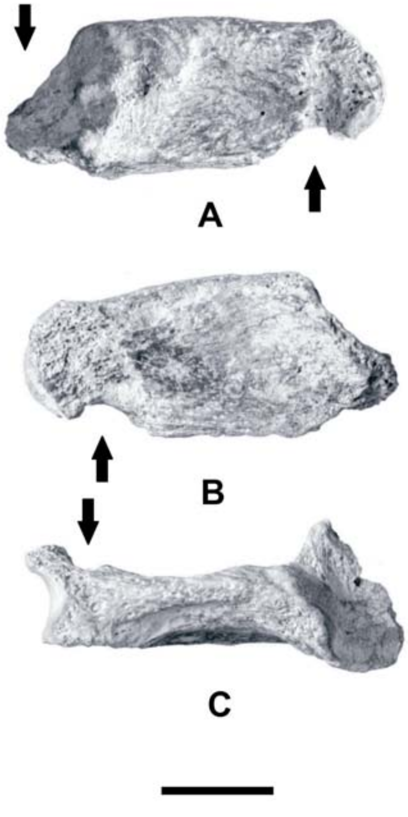

Fig. 4. Left calcaneus of *Gulo gulo* (MF/6841) from layer 6 of the Ciemna Cave, A – lateral external view, B – lateral internal view, C – dorsal view. Arrows indicate deep bite marks on both bone epiphyses, left most probably by *Canis lupus* or *Crocuta crocuta spelaea*. Scale bar 10 mm.

The best represented species is *Martes martes*, with the remains mainly in the form of isolated teeth (Fig. 5), but also a few well preserved mandibles (Fig. 6/1ac-3ac, Table 1).

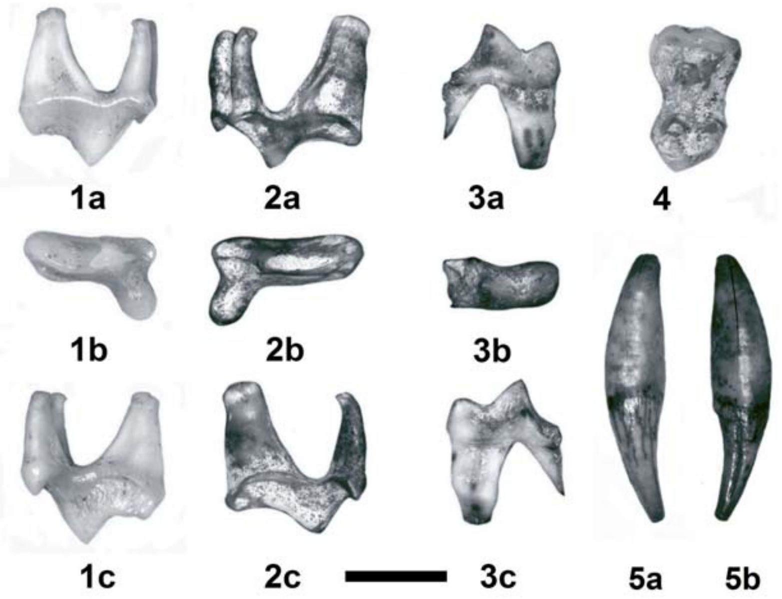

Fig. 5. Isolated teeth of *Martes martes* from the Ciemna Cave: right P4 MF/6889 (1a-c), left P4 MF/6896 (2a-c), right m1 MF/6897 (3a-c) (a – buccal view, b – occlusal view, c – lingual view), right M1 MF/6890 (4) and left C1 MF/6891 (5a-b), a – buccal view, b – lingual view. All specimens shown to scale, scale bar 5 mm.

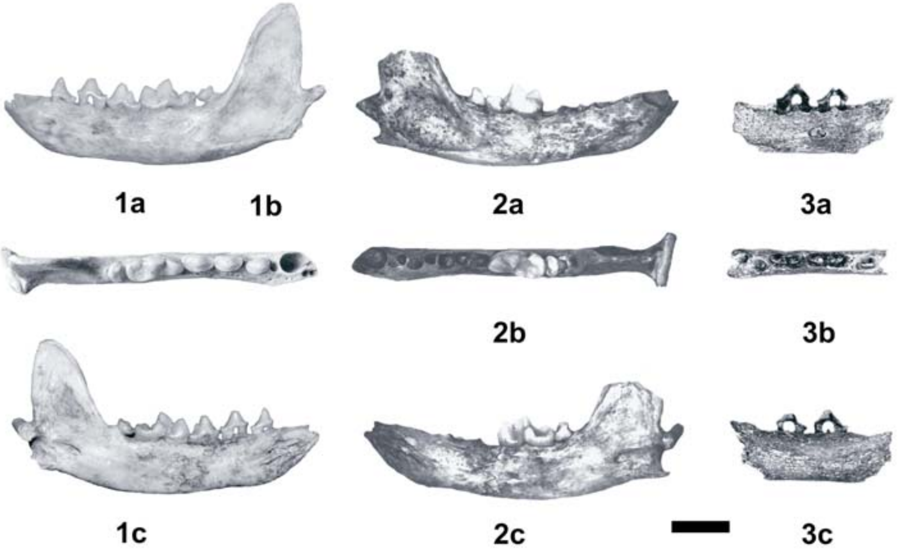

Fig. 6. Mandibles of *Martes martes* from the Ciemna Cave: left mandible MF/6886 (1a-c), right MF/6885 (2a-c) and right MF/6895 (3a-c), a – buccal view, b – occlusal view, c – lingual view. All individuals shown to the same scale, scale bar 10 mm.

Also all two smallest species of the genus *Mustela*: *M. ermine*a and *M. nivalis* are represented only by cranial material, mandibles and isolated teeth (Table 1).

The mustelid material is fairly well preserved and represents only adult individuals (Table 1). Quite surprising is the relatively high number of teeth or mandibles with traces of digestion (Table 2).

Table 1

Inventory calatogue of mustelids from the Ciemna Cave (age of layers according to VALDE-NOWAK et al. 2014)

Ord. no	Species	ISEZ coll. no	Field coll. no	Layer	MIS	Material	Digestion
1.	*Gulo gulo*	MF/6841			3	damaged, right calcaneus without proximal epiphysis	yes
2.	*Meles meles*	MF/6883	JC/7075	13	5	left p2	yes
3.	*Meles meles*	MF/6884	JC/6603	11	5	phalanx I	no
4.	*Martes martes*	MF/6904	JC/7403	13	5	talonid of right m1	no
5.	*Martes martes*	MF/6903	JC/16605	10	5	right c1	no
6.	*Martes martes*	MF/6902	JC/16503	10	5	left c1	no
7.	*Martes martes*	MF/6901	JC/16325	10	5	trigonid of left m1	no
8.	*Martes martes*	MF/6900	JC/15962	9	5	posterior half of left m1	no
9.	*Martes martes*	MF/6899	JC/4733	8	4	left P3	no
10.	*Martes martes*	MF/6898	JC/4203	7	4	right I2	no
11.	*Martes martes*	MF/6897	JC/4448	7	4	trigonid of right, damaged m1	yes
12.	*Martes martes*	MF/6896	JC/3717	7	4	left, heavily worn P4	yes
13.	*Martes martes*	MF/6895	JC/3301	6	4	fragment of right mandible body with much worn p3-p4	yes
14.	*Martes martes*	MF/6892	JC/13531	3/4	3	crown of right c1	yes
15.	*Martes martes*	MF/6891	JC/13350	3/4	3	right C1	no
16.	*Martes martes*	MF/6890	JC/10835	1.14	1	right, worn M1	yes
17.	*Martes martes*	MF/6889	JC/12416	1.14/2.11	1	right P4	no
18.	*Martes martes*	MF/6888	JC/12561	2.2	1	caudal	no
19.	*Martes martes*	MF/6887	JC/12561	2.2	1	left m1	no
20.	*Martes martes*	MF/6886	JC/23192	1	1	left hemimandible with p2-m2	no
21.	*Martes martes*	MF/6885	JC/23051	1	1	right mandible with damaged ramus and m1-m2	no
22.	*Mustela erminea*	MF/6894	JC/5555	10	5	right C1	no
23.	*Mustela erminea*	MF/6893	JC/15724	9	5	left mandible without sympysis and with much worn m1	yes
24.	*Mustela nivalis*	MF/1022/1			1	right C1	no
25.	*Mustela nivalis*	MF/1022/2			4	right P4	no
26.	*Mustela nivalis*	MF/1022/3			4	left c1	no
27.	*Mustela nivalis*	MF/1022/4			4	fragment of left mandible body with m1-m2	no

Table 2

Mustelid assemblage from the Ciemna Cave

Species	NISP/MNI	No. of digested bones
Gulo gulo	1/1	1
Meles meles	2/2	1
Martes martes	18/7	5
Mustela erminea	2/2	1
Mustela nivalis	4/2	–

Table 3

Mandible and teeth dimensions of mustelids from the Ciemna Cave (mm). For measurements scheme see Fig. 2 (for mandible) and Fig. 3 (for teeth)

Measurements		*Martes martes*			*Mustela erminea*	*Mustela nivalis*
		MF/6885	MF/6886	MF/6895	MF/6893	MF/1022/4
Mandible	1	53.47	52.69			
	2	51.68	51.47			
	3	34.53	34.72			
	4	34.47	34.75			
	5	28.97	29.07			
	6	17.23	16.78	15.66		
	7	13.48	12.62		7.97	4.97
	8	6.64	7.82	6.96		
	9	17.04	17.62		4.42	
	10		22.83		2.28	
	11		28.39			
	12	9.04	9.29			
	13	4.39	4.31			
	14	10.32	8.84			3.46
	15	4.54	4.35			1.78
	16	3.24	3.38			
	17	9.67				
	18	14.47	12.55			
	19	7.46	7.59			
p2	L		4.47			
	B		2.53			
p3	L		4.99	[5.30]		
	B		2.76			
p4	L		6.09	[6.00]		
	B		3.04			
m1	L	9.87	9.68		[6.60]	3.96
	L tri	6.49	6.44		[5.10]	2.84
	L tal	2.96	2.86		[1.50]	1.12
	B tri	4.02	3.91			1.42
	B tal	4.19	4.04			1.33
m2	L	3.68	3.47			0.94
	B	3.45	3.45			0.96

Table 4

Dimensions of isolated upper teeth of mustelids from the Ciemna Cave (mm)

Species	Coll. no	Layer	MIS	Tooth	1	2	3
Martes martes	MF/6896	7	4	P4	[8.80]	[3.20]	[5.50]
Martes martes	MF/6899	8	4	P3	5.78	3.02	
Martes martes	MF/6890	1.14	1	M1	9.64	6.38	4.12
Martes martes	MF/6898	7	4	I2	2.53	1.54	
Martes martes	MF/6891	3-4	3	C1	5.93	3.97	
Martes martes	MF/6889	1.14/2.11	1	P4	8.47	3.14	5.27
Mustela erminea	MF/6894	10	5	C1	3.08	2.04	
Mustela nivalis	MF/1022/1	4	3	C1	1.94	1.26	
Mustela nivalis	MF/1022/2	3	3	P4	3.16	1.55	1.12

Table 5

Dimensions of isolated lower teeth of mustelids from the Ciemna Cave (mm)

Species	Coll. no	Layer	MIS	Tooth	1	2	3	4	5
Meles meles	MF/6883	13	5	p2	6.24	3.86			
Martes martes	MF/6897	7	4	m1		6.75		3.38	
Martes martes	MF/6900	9	5	m1			3.74	4.08	4.19
Martes martes	MF/6903	10	5	c1	6.63	4.28			
Martes martes	MF/6902	10	5	c1	6.51	4.22			
Martes martes	MF/6904	13	5	m1			4.12		4.23
Martes martes	MF/6901	10	5	m1		7.56		4.64	
Martes martes	MF/6887	2.2	1	m1	9.64	6.53	3.17	4.02	4.17

III. TAXONOMIC PART

Among the five mustelids from the Ciemna Cave only the material of *Martes martes* is more abundant, while the remaining species are represented only by few skeletal elements, mainly isolated teeth and mandibles. In the past only *Mustela nivalis* was studied in detail (WÓJCIK 1974), while other species were only briefly mentioned. All the analysed individuals are adult animals, with dentition showing a certain degree of wear (Figs 5-7).

The single bone of *Gulo gulo* is too damaged to take exact measurements. However the shape and size confirm its earlier interpretation as a moderately large specimen and justify its inclusion in the faunal list from the Ciemna Cave. The bone bears some traces of gnawing and digestion, suggesting that the animal was killed or scavenged by another carnivore.

The most informative material is that of *Martes martes*; it is dominated by moderately large and quite gracile individuals, typical of the warmer periods and postglacial/Holocene sediments. The elongated mandible with proportionally slender body and with less pronounced curvature of the lower margin under m1, more widely open angle between ante-

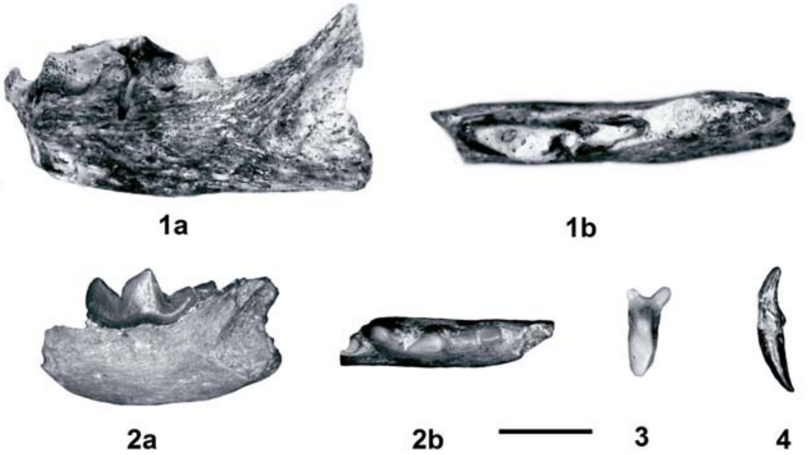

Fig. 7. Small members of the genus *Mustela* from the Ciemna Cave. *M. erminea*: left mandible MF/6893 (1a-b); *M. nivalis*: left mandible MF/1022/4 (2a-b), right P4 MF/1022/2 (3) and left c1 MF/1022/3 (4), a – buccal view, b – occlusal view. All specimens shown to the same scale, scale bar 1 mm.

rior and posterior ramus margin, point to *M. martes* and exclude *Martes foina*. *M. martes* is characterised by pronounced sexual dimorphism. On average males are by 6-9% larger than females, even if the size ranges overlap slightly (ANDERSON 1970). Fossil and recent material of males is also characterised by a robust build, more massive than in the females, which is manifested in a relatively high mandible body or in massive canines. The males have better developed muscle insertions, crest and sutures (MARCISZAK 2012).

M. martes is a classical example of Bergmann's rule, whereby larger individuals are found in colder climates, and those of smaller size are found in warmer regions or during warmer periods. One of the best bases for the reconstruction of mustelid size inferred from fossil material is m1. ANDERSON (1970) reported the values of m1 length in individuals from recent Central European populations: mean for males 9.75 mm (9.20-10.4 mm, n=19), mean for females 8.74 mm (8.2-9.3 mm, n=11). Based on a much more numerous, homogenous sample from the Polish population, MARCISZAK (2012) reported the following results: mean for males 10.64 mm (9.27-11.16 mm, n=169), and mean for females 9.04 mm (8.11-9.97 mm, n=111). Plotting the total length against the talonid breadth of m1 for the recent Polish *M. martes* (both sexes) and for the specimens from the Ciemna Cave suggests that the latter are females rather than males, with m1 not exceeding 10.0 mm: 9.87 mm (MF/6885), 9.68 mm (MF/6886) and 9.64 mm (MF/6887) (Fig. 8). Considering other teeth and skeletal elements, the individuals from the Ciemna Cave can be characterised as moderately large (Table 3). There are almost no large-sized specimens which were characteristic of the Late Pleistocene. Only the trigonid of right m1 MF/6901 and the isolated MF/6897, based on their great size and robust build, can be assigned to the Late Pleistocene *M. martes*. It is obviously not a distinct form; being morphologically almost identical, metrically it greatly exceeds even the largest Holocene or recent specimens (Table 4). Their immense size and massive build are usually correlated with cooler phases of the Late Pleistocene (ANDERSON 1970; MARCISZAK 2012).

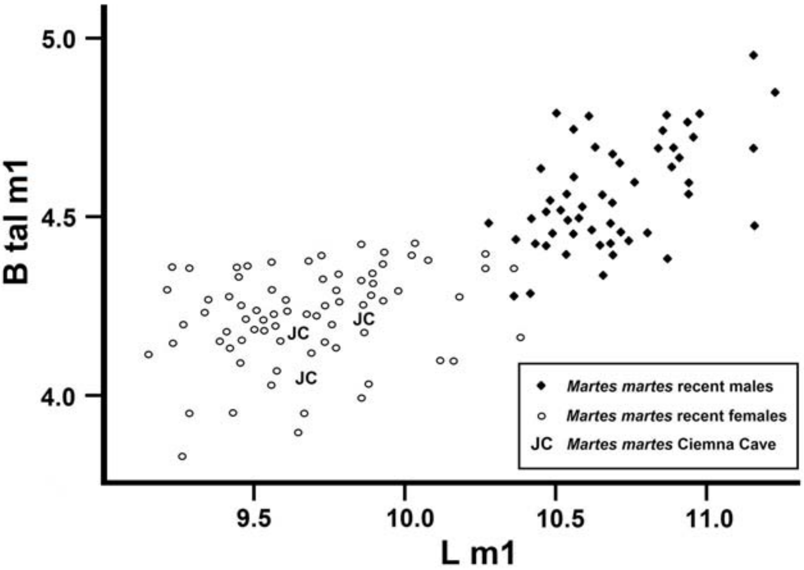

Fig. 8. Total length of m1 (L m1) plotted against talonid breadth (B tal) in recent *Martes martes* from Poland and *M. martes* from the Ciemna Cave. Measurements in mm.

The most valuable feature to distinguish between the two marten species is, however, the distance between mental foramina. JÁNOSSY (1963) found that its values did not overlap between the two species. In *M. foina* the distance is short (2.0-3.4 mm), while in *M. martes* it is much longer (5.9-9.6). Later the character was tested and positively verified by ANDERSON (1970), and subsequently used by many authors (e.g. LOY et al. 2004; RICHTER 2005; BACHANEK & WOŁOSZYN 2006) as a reliable taxonomic criterion. MARCISZAK (2012) confirmed its reliability once more, based on large samples from Central Europe. The mean for the recent Polish *M. martes* was 5.84 mm, while the mean for the recent Polish *M. foina* was 2.98 mm. In the indidviduals from the Ciemna Cave the values were 6.64 mm (MF/6885), 7.82 mm (MF/6886) and 6.96 mm (MF/6895), which also unambiguously confirmed their classification to *M. martes*. The character is so distinctive that even the heavily digested mandible fragment JC/12824, with much worn teeth, can be easily assigned as *M. martes* (Tables 3, 5).

Likewise, the lower dentition shows features typical of *M. martes*. The alveole of p1 is larger while the premolars are slightly narrower and higher than in *M. foina*. Morphologically m1 of the analysed specimens are much closer to *M. martes* than to *M. foina*, which has a proportionally shorter and broader trigonid. The mean talonid:trigonid length ratio is 43.5 for *M. martes* and 34.2 for *M. foina*. In the martens from the Ciemna Cave the ratio is 45.6 mm for MF/6885, 44.7 mm for MF/6886 and 48.6 mm for MF/6887. Another characteristic feature is that on average the talonid of m1 is slightly broader than the trigonid in *M. martes*, with the mean talonid: trigonid breadth ratio of 104.9, while in *M. foina* the corresponding value is 95.8. For the individuals from the Ciemna Cave the values correspond well with the mean for *M. martes*: 104.2 mm for MF/6885, 103.3 mm for MF/6886 and 103.7 mm for MF/6887. Also the morphology of the teeth agrees with those of *M. martes*, with a relatively poorly expressed notch located on the trigonid-talonid transition on the buccal side. The same pertains to the large, conical and high metaconid of m1. Finally, the two m2 from the Ciemna Cave are rounded and broad, with quite well developed, thin cingular ridge, collaring the whole crown. On average in *M. martes* m2 has its crown almost as long as wide, and the length:width ratio is 97.1, while in *M. foina* the breadth usually slightly exceeds the length and the mean ratio is 105.2. For two m2 from the Ciemna Cave the values are 93.8 for MF/6885 and 99.4 for MF/6886 (Table 5).

Also the upper teeth agree with the characteristic morphology of *M. martes*. The few canines have their crowns proportionally longer and less curved than in *M. foina*. The single P3 (MF/6899) has its crown noticeably expanded lingually and concave bucally in the middle part, a feature particularly characteristic of *M. martes*. In the moderately large and narrowly built P4 the two main cusps, the paracon and the metacon, form a slightly arched line, with the posterior part of the crown distalo-bucally oriented. The tooth has three roots and the external median rootlet is absent. Its rounded, well developed protocon is long and high and projecting anterio-ligually at about 60° to the rest of the crown. It has a centrally placed and sharply definied top. Its length is equal to the metacon breadth and the means of the ratio of paracon length to posterior crown breadth of both P4 from the Ciemna Cave are ca. 107.0 for MF/6896 and 104.0 for MF/6889, thus corresponding well with the mean for *M. martes* 95.5, but noticeably departing from the mean for *M. foina* 68.5 (Fig. 9) (MARCISZAK 2012). The high, strong paracon has a convex, sharpe cutting edge extending posteriorly to the metacon. The anterior paracon border is rounded and oriented slightly anterio-buccally. From the paracon top three long, thin crests run anteriorly, with one of them connected with the protocon apex. The metacon is high and elongated, with rounded posterior edge. The cingulum is well developed only on the lingual margin of the metacon.

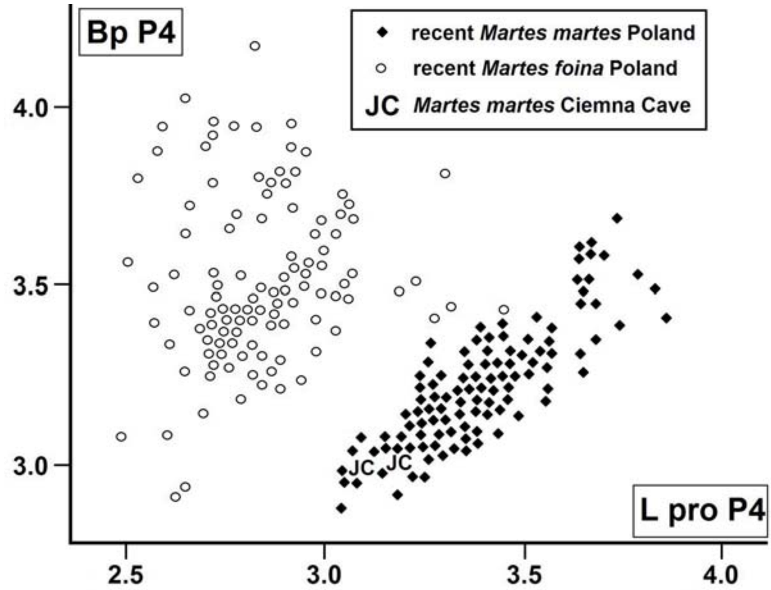

Fig. 9. Protocon length of P4 (L pro P4) plotted against posterior breadth of P4 (Bp P4) in recent *Martes martes* and *Martes foina* from Poland and in *M. martes* from the Ciemna Cave. Measurements in mm.

The isolated M1 (MF/6890) from the Ciemna Cave is very large and robust, even though it is much worn. Its external lobe is laterally broadely expanded and noticeably wider that the internal lobe. Both lobes are separated by a deep and broad depression running through the middle crown part. The tooth micro-relief is more complicated than that in *M. foina*. The lingual lobe is moderately expanded, while the asymmetrical, external one is proportionally broad and a well developed notch occurs on the labial margin, between the paracon and the metacon. The vestibular outline on the labial cingulum is similar as in *M. martes*, with a strongly incised concavity of the contour. Both main labial cusps, paracon and metacon, are elongated and high, but the well developed paracon is larger than the somewhat reduced metacon. They are well separated by a deep, narrow, V-shaped valley, while the tops of both cusps are linked by a thin, long crest. The protocon is quite low and long, divided into two portions of similar length and height. On the lingual lobe a long, thin crest forms the external cingulum margin running parallel through the whole length. The well-developed lingual cingulum forms a thick crest.

Remains of the two smallest mustelids, *Mustela erminea* and *Mustela nivalis*, are scarce in the Ciemna Cave (Table 1). According to WÓJCIK (1974) who was the only author who studied mustelid material in detail, *M. erminea* was not present at that time in the carnivore assemblage. He found three bones of *M. nivalis* (both canines and mandible) from the Ciemna Cave and compared them with the fossil material of *M. nivalis* from other Late Pleistocene sites as well as with the recent Polish specimens. He concluded that Late Pleistocene weasels were on average smaller than the nominate subspecies *M. nivalis nivalis* LINNAEUS, 1766, recently inhabiting Central Europe (ABRAMOV & BARYSHNIKOV 2000). In his opinion (WÓJCIK 1974) these small weasels from the last glacial were metrically and morphologically indistinguishable from modern dwarf individuals of *M. nivalis pygmaea* (ALLEN, 1903), which occur in Arctic regions (ABRAMOV & BARYSHNIKOV 2000).

Distinguishing small members of the genus *Mustela* is not an easy task, especially when the material is scarce or incomplete. The features which allow to separate them pertain mainly to calvarium; some characters of mandible, mostly dentition, are also useful. The most valuable criterion is the larger size of *M. erminea*, though it is not always reliable because of the pronounced sexual dimorphism (males of smaller species are sometimes larger than females of larger species), the effects of geographical distribution, altitude and local envinronmental conditions. Late Pleistocene members of *Mustela*, especially those from cooler periods, were on average smaller than the recent individuals (WÓJCIK 1974; MARCISZAK 2012). With the estimated length of m1 of ca. 6.60 mm, one specimen from the Ciemna Cave (MF/6893) represents *M. erminea*, while another mandible from the same cave (MF/1022/4), with m1 less than 4.00 mm long, was determined as *M. nivalis*.

Also other metric values proved to be reliable diagnostic criteria. *M. erminea* has proportionally broader posterior part of the p4 crown, but the features of m1 are the most distinctive features (Fig. 10). *M. erminea* has a longer trigonid, with the mean length ratio of talonid to trigonid of 23.4, while for *M. nivalis* the mean is 41.2. This ratio for the specimens from the Ciemna Cave is 29.5 (MF/6893) (*M. erminea*) and 39.4 (MF/1022/4; *M. nivalis*). The talonid in *M. erminea* is much more reduced, narrower and shorter, and the mean breadth ratio of talonid to trigonid is 76.0 for *M. erminea* and 92.1 for *M. nivalis*. The mandible of *M. nivalis* from the Ciemna Cave (MF/1022/4) has the ratio of 93.7. Another

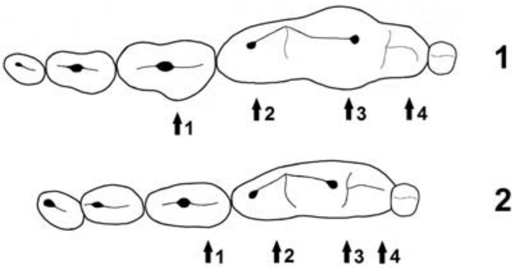

Fig. 10. Lower dentition features distinguishing *Mustela erminea* (1) and *Mustela nivalis* (2), arrows with numbers indicate differences in teeth morphology. *M. erminea* differs from *M. nivalis* in: breadth of posterior part of p4 crown (1), longer, higher and more massive trigonid (2), much more pronounced broadening of m1 crown at the base of protoconid (3) more reduced, shorter and narrower talonid (4). Diagrammatic, based on RABEDER (1976), MARCISZAK (2012) and MARCISZAK & SOCHA (2014).

significant feature is the presence of a very pronounced broadening of m1 crown situated at the protoconid level in *M. erminea*, which expands significantly the trigonid breadth (Fig. 11; Table 3). It should be borne in mind however, that all the above features, values and ratios, are mean values which were based on the Central European subspecies. The specific morphology of local populations, age, sex and geographical variation can successfully obscure the results (KING & POWELL 2007; MARCISZAK 2012).

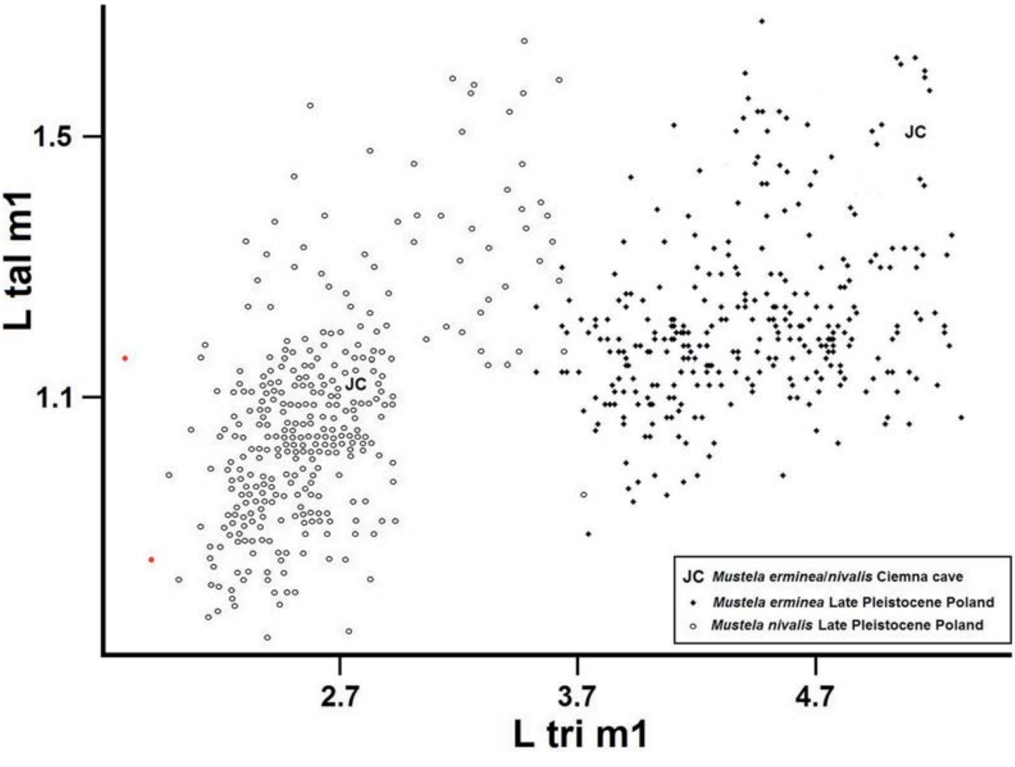

Fig. 11. Talonid length of m1 (Ltal m1) plotted against trigonid length of m1 (L tri m1) in *Mustela erminea* and *Mustela nivalis* from the Late Pleistocene of Poland. Data from MARCISZAK (2012) and references therein, measurements in mm.

IV. DISCUSSION

The examined mustelid material from the Ciemna Cave represents five species: *Gulo gulo*, *Meles meles*, *Martes martes*, *Mustela erminea* and *Mustela nivalis*. These species are widespread throughout the European Pleistocene and known from numerous palaeontological sites (SOMMER & BENECKE 2004; MARCISZAK 2012). Also archaeological excavations yielded many single records of mustelid species of different age (WYROST 1994; SOMMER & BENECKE 2004; MARCISZAK 2012). However, despite their relative abundance in faunal assemblages, these carnivores are usually respresented by a limited number of individuals and remains, for a few reasons. First of all, during earlier excavations (especially those done by archaeologists) sediments were either not sieved or washed at all or only to a very limited extent (WOJTAL 2007). Another reason is the small size of mustelids and the high probability of mistaking their remains, especially postcranial elements, for rodents, bats or even insectivores. They are often simply overlooked during taxonomic analysis, or mislabelled. The third reason is that they are too small to be a valuable prey for humans and were usually taken only accidentally (SOMMER & BENECKE 2004; WOJTAL 2007; MARCISZAK 2012). Birds of prey, owls and larger carnivores, e.g. *Vulpes vulpes* or even larger mustelids rather than humans are responsible for the accumulation of mustelid remains. Despite their agility and ferocious defensive behaviour, these small carnivores are relatively vulnerable to attacks by their larger counterparts (KING 1989; KING & POWELL 2007).

Martes martes, together with *Meles meles*, is the most common mustelid in the Late Pleistocene and Holocene European assemblages; it occurred in colder and warmer periods (WOLSAN 1989; SOMMER & BENECKE 2004; MARCISZAK 2012). Most individuals of *Martes martes* from the Ciemna Cave represent moderately large and small animals, of size and shape comparable to the modern or Holocene specimens. Only single teeth, like isolated M1 (MF/6890), may represent the great, robust *Martes martes*, a characteristic element of cooler phases of the Late Pleistocene, still present in the beginning of Holocene.

So far, in the Ciemna Cave as in other Polish Late Pleistocene caves *Martes foina* was not found in Pleistocene sediments; all the single finds, like the three mandibles from layer 1a-b of Biśnik Cave, are not older than a few hundred, maybe a few thousand years BC (MARCISZAK 2012). The possibility of confusing the two marten species is rather small. A thorough revision of mustelid material from Polish archaeological and palaeontological sites showed that *Martes foina* was absent in the fossil material (SOMMER & BENECKE 2004; MARCISZAK 2012). KOWALSKI (1959) listed two Pleistocene sites with the probable occurrence of *Martes foina*. Both were cited after different researchers, and the material was not seen by the author himself. The accurancy of identification and geological age was questioned already by ANDERSON (1970). A revision showed that a few long bones from caves Maszycka (OSSOWSKI 1885) and Wschodnia (ZOTZ 1939), classified and labelled as *Martes foina*, were actually *Martes martes*. *Martes foina* appeared not earlier than in the Neolithic period, which was most probably correlated with human colonisation (ANDERSON 1970).

Large accumulations of marten remains in sediments, like those in the Ciemna Cave, often representing numerous individuals including juveniles, are mainly due to the animals penetrating caves in search of food, especially bats. Finding a bat colony, the marten could use this source of food for a long time (STUBBE 1993). Caves and rock shelters are sometimes used by *Martes martes* as temporary places to rest or, less often, to rear offspring. Accidents and water can play a role in accumulation of the species remains. Due to their well-developed senses, alertness and ability to quick escape to heights inaccessible to the attacker, *Martes martes* rarely falls prey to other carnivorous mammals (JĘDRZEJEWSKA & JĘDRZEJEWSKI 2001). Because of its quite large size and fierce defensive behaviour, its only enemies among birds are the largest species, like *Bubo bubo* and *Aquila chrysaetos* (HEPTNER & NAUMOV 1967; STUBBE 1993). An important role was also played by humans who used martens as providers of valuable furs, and the phenomenon sometimes took on a mass character. There are sites, for example in Denmark, with large accumulation of remains of *Martes martes* with traces of human activity (DEGERBØL 1933; GRUNDBACHER 1992; STUBBE 1993; RICHTER 2005; AARIS-SØRENSEN 2009).

Gulo gulo is a permanent component of Late Pleistocene faunal assemblages, but its remains are quite rare in European cave localities. Even when present, the species is usually represented by few bones and heavily outnumbered by other carnivores (DÖPPES 2001; MARCISZAK et al. 2017). The wolverine is not regarded as a typical cave dweller and the almost complete absence of juveniles indicates that caves were not used to raise cubs (DIEDRICH 2008). The main reason for accumulation of wolverine remains in caves seems to be predation. Among the Late Pleistocene carnivores *Crocuta crocuta spelaea* seems to be the major predator responsible for that (DIEDRICH & COPELAND 2010). As remarked by DIEDRICH (2008: 128): "Carnivores were the last prey to be eaten and scavenged", so it is more likely that the wolverine was killed and brought into caves but in most cases not scavenged. In case of the wolverine remains left in the Ciemna Cave, the hyena is probably a likely but not the only possible predator. Some deep bite marks indicate that the bone was bitten off by a large carnivore, most probably *Canis lupus*. Today the wolf is the most important natural enemy of *Gulo gulo* (PASITSCHNIAK-ARTS & LARIVIÈRE 1995). In spite of that, the wolverine risks active scavenging on carcasses left by the wolf (PASITSCHNIAK-ARTS & LARIVIÈRE 1995; PERSSON et al. 2003). Based on this, the predators which killed or scavenged on *Gulo gulo* from the Ciemna Cave were *Canis lupus* or *Crocuta crocuta spelaea*.

V. CONCLUSIONS

The mustelids from the Ciemna Cave represent a typical assemblage of this family from European sites, dated at the Late Pleistocene and postglacial periods. Due to a limited number of species and remains they cannot provide detailed biostratigraphical or palaeoecological data, but still provide useful taxonomical information. The sediments from the Ciemna Cave were quite thoroughly sieved, so it is rather unlikely that some remains could have escaped identification. This makes any attempts at reconstructing the depositional history and the possible factors responsible for accumulation of wolverine bones rather limited. The bones bear no signs of burning, cutting or crushing which could be interpreted as traces of human activity. At the same time, many bones bear traces of digestion, which can be interpated as carnivore activity. Other mammals from the Ciemna Cave heavily outnumbered the mustelids, which is typical of most archaeological localities. The absence of intensive human activity and the limited number of bones suggest that the remains belonged to animals which died naturally or fell prey to predators and were not culture-related. The animals may have found their death at the locality during the depositional phase, or might be also post-dated, transported e.g. by water.

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