

First record of *Dicrostonyx* (Rodentia, Mammalia) in the Late Pleistocene/?Holocene sediments of Croatia



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ABSTRACT

The fossil remains of lemmings (*Dicrostonyx* sp.) have been discovered for the first time in Croatia. The small sample of 11 teeth (M_{1-3} and M^1) originate from the Late Pleistocene/?Holocene sediments from the Romualdova pećina site (Western Istria). The resemblance has been observed in morphological data, while some metrical parameters differ slightly in comparison to the findings from some other European localities, for example from Poland, Austria and France. The mean length value of M_{1s} from the Croatian sample is higher than the Austrian (Nixloch and Merkenstein Caves), and French (Bois Roche site) ones, while it is the same for similar specimens from the Polish Late Glacial, but smaller than the Polish Holocene findings, respectively. The differences in A/L and C/W1 indices have also been observed between samples from the Romualdova pećina and Polish samples of Late Glacial and Holocene age. As a good indicator of a cold and dry climate, the lemmings from the Romualdova pećina give support to the conclusion that this part of Europe was a refugial region for this and some other small mammal species during the expansions of the ice cover, and reflect Quaternary environmental fluctuations, which were frequent and pronounced at the end of this period.

Keywords: lemming, *Dicrostonyx*, teeth, morphometric analyses, Late Pleistocene, Romualdova pećina, cave, Croatia

1. INTRODUCTION

In many areas of the European continent, lemmings (*Dicrostonyx* sp.), as extremely boreal taxa, had disappeared during the last interglacial (Riss-Würm) period, and in two waves recolonized central and southern Europe from the Scandinavian region. The first recolonization occurred around 40 ka BP, when they reached the Alps, Carpathians and Caucasus Mts., while during the second widening of their areas (cca. 20 ka BP), lemmings migrated farther south, in the Carpathian basin and southern parts of western Europe, respectively (KORDOS, 1990). During these areal expansions, *Dicrostonyx* also inhabited the region of present day western Croatia.

Results of morphometric analyses of *Dicrostonyx* teeth are presented here. This taxon is determined in the Late Pleis-

tocene sediments of the Romualdova pećina (Romualdo's or Lomardo's Cave, in further text Romualdova) locality for the first time. The cave is situated on the southern side of the Limski (Lim) Channel near Rovinj in western Istria (Fig. 1), and has been an interesting palaeontological site since the 1960s (MALEZ, 1962, 1968, 1978; KOMŠO, 2011). The cave is formed in the Upper Jurassic limestones, with the entrance at 120 m a. s. l. It is more than 100 m long, and has the shape of underground corridor which is in some places widened into elongated halls (MALEZ, 1962). During field work in 1961, 1962, and 1973, when MALEZ and his team made probe excavations (Fig. 2a, b), very abundant fossil material was collected, in which bear (*Ursus spelaeus* and *U. arctos*) remains were the most numerous, in addition to other taxa listed in Figure 2c (after Malez's original deter-

mination; MALEZ, 1968). The results of geometric-morphometric analyses of the Romualdova bear molars were presented by SEETAH et al. (2012), where the authors quoted the similarities/differences of bear populations (beside Romualdova, the Vindija sample has also been investigated) through time and space. Detailed revision of the macrofaunal remains is now in progress (MIRACLE et al., in preparation).

Molars have been separated recently from the small mammal sample and prepared for preliminary analyses by the present author. In this material, the arvicolines prevail, among which voles are the most abundant: *Arvicola amphibius* (=terrestris), *Myodes* (=Clethrionomys) *glareolus*, *Microtus* ex gr. *arvalis/agrestis*, *M. ex gr. subterraneus/multiplex*, *M. oeconomus*, and *Chionomys nivalis*, but other „micromammals“ such as Chiroptera and Eulipotyphla (=Insectivora; genera *Erinaceus* and *Talpa*, Fig. 2c) are also represented. As previously mentioned, one of the most interesting discoveries is lemming teeth (*Dicrostonyx* sp.) recorded for the first time from the Late Pleistocene and perhaps Holocene sediments of Croatia. In 2007 and 2008, KOMŠO and his team started systematic excavations in the cave (KOMŠO, 2011), and abundant fossil material, collected during these field-campaigns, still waits to be palaeontologically analysed.

The lemmings are small arvicoline rodents represented by 12 living species, adapted to cold and dry habitats, having a holarctic distribution today. Recent DNA techniques and analyses allow different phylogenetic studies on the contemporary lemming populations (e. g. FEDOROV, 1999; PROST et al., 2010; and references therein), that provide new data on the evolutionary rates and phylogenetic relationships of this taxa. The results of mtDNA analyses for the populations from the Canadian Arctic, Greenland and eastern Beringia have been presented by FEDOROV & STENSETH (2002). The authors argued about the division of different phylogroups (Canadian Arctic and eastern Beringia), and gave the possible time of their divergence at 115 – 10 ka. The hypothesis of ice-free areas during the last glaciation, beside the data of the *Dicrostonyx* findings, is also supported by the fossil specimens of other good indicators of the tundra environments such as saiga (*Saiga tatarica*) and muskoxen (*Ovibos moschatus*; FEDOROV & STENSETH, 2002). The climatic changes at the end of the Pleistocene and beginning of Holocene also favoured possible habitat changes, which had a direct influence on the distribution and hence on the evolutionary rates in many small mammal taxa, including lemmings. During the Pleistocene, especially the Late Pleistocene, alternation of glacial and interglacial periods resulted with restricted areas of the particular species into refugial

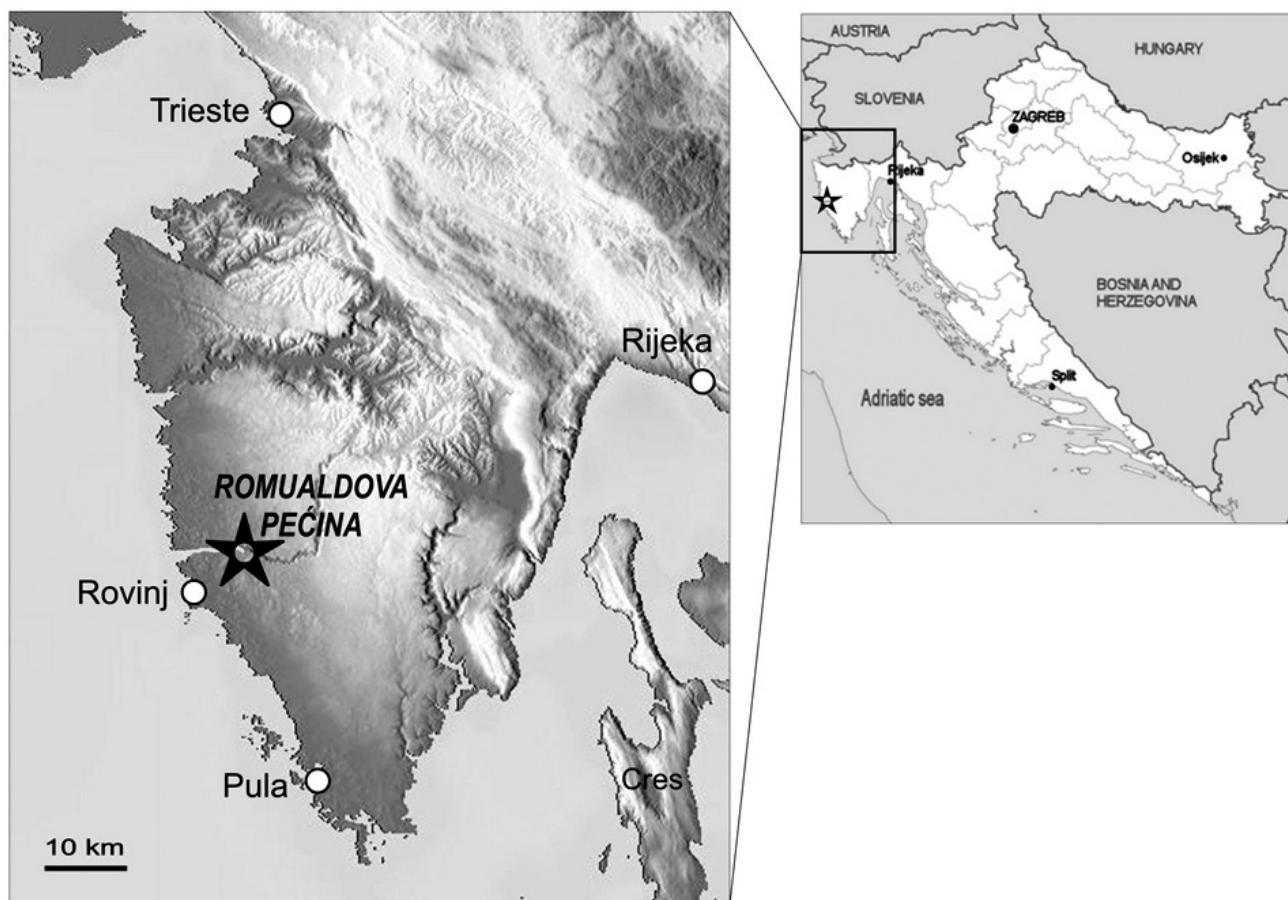


Figure 1: Geographical location of Romualdova pećina (western Istria) ; internet source: <http://www.maps-for-free.com/>

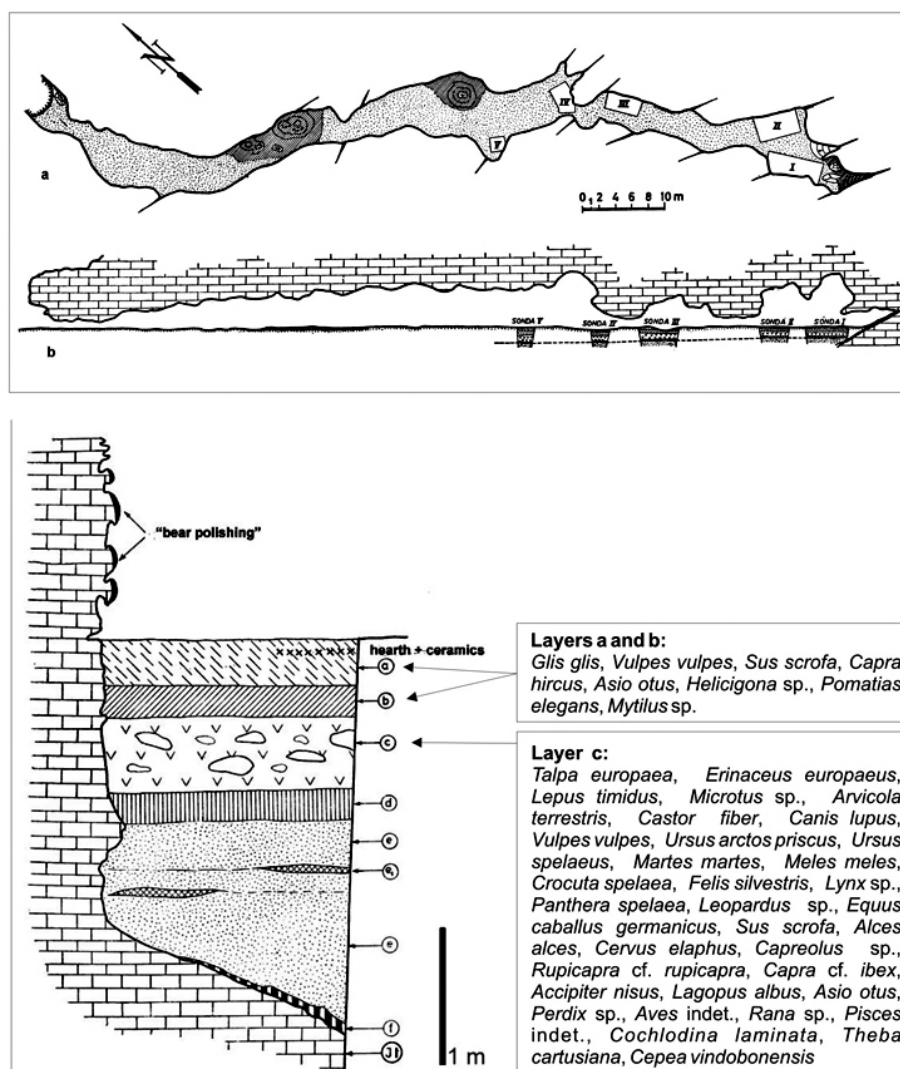


Figure 2: Romualdova pećina: a – ground-plan; b – profile; c – stratigraphic profile/layers with determined fauna. **LEGEND:** layer *a* – dark reddish-brown compact clay with small limestone particles, layer *b* – dark yellow-brown compact clay, layer *c* – dark brown clay with limestone debris, human traces, and abundant fossil remains, layer *d* – yellow-reddish fat clay without limestone debris, layer *e* – brownish-yellow fine-grained sand with inclusions of reddish clay, layer *f* – sinter deposit, J1 – Jurassic limestone (after: MALEZ, 1968).

ones (FEDOROV & STENSETH, 2002). The Balkan peninsula is one of the regions of interest for such research (MIRACLE et al., 2010), while migrations of various large and small mammals were defined by the particular geographic position of this part of Europe. In his work MALEZ (1986, p. 106) wrote that the most southern locality of *Dicrostonyx torquatus* (arctic or collared lemming) on the territory of the former Yugoslavia was Babja jama Cave near Dob at Domžale in Slovenia (46°03' N and 14°30' E). The new discoveries from the Croatian Romualdova site (45° 7' 44" N and 13°14' 17" E) move this line farther south. The species of the genus *Dicrostonyx* are not the members of the present day fauna of Croatia.

2. GEOLOGICAL SETTINGS

MALEZ (1962, 1968, 1978) provided sedimentary and stratigraphic sequences for Romualdova (Fig. 2), and wrote that fossil remains, including abundant small mammal findings, appeared at layer *c* in the test-pits made in 1961 and 1962. This layer was most probably sedimented during the Würm III Stadial (MALEZ, 1968). Furthermore, beside animal remains, stone artefacts, traces of hearths, one human

tooth has also been discovered proving the presence of Palaeolithic men in the cave (MALEZ, 1968, 1978). The most complex profile of the Quaternary layers was discovered in test-pit I (Fig. 2). After recent investigations conducted by KOMŠO (2011), and palaeontological analyses in progress, a more precise stratigraphic position of the particular layers will be soon defined.

3. MATERIAL AND METHODS

A small sample of 153 upper and lower arvicoline teeth, separated from other faunal remains which comprise several hundreds of specimens, has been morphometrically analysed. In this collection 11 molars (mainly M_{1-3} , and M^1 ; Fig. 3b, c) belong to the genus *Dicrostonyx*. Unfortunately we do not know the exact stratigraphic position of these fossil remains, and worse still, it is not known from which excavation campaign year they come from. Therefore, it is assumed that they belong to the faunal sample from layer *c*, not only because the majority of the specimens which are stored at the Institute's collections were found in the 1960's, but also because MALEZ (1978) emphasized that this is the Pleistocene layer with abundant fossil findings. Furthermore,

all collection/inventory numbers contain only locality abbreviations and the ordinal number. Taxonomic determinations, molar terminology and metrical methods were used after RABEDER (1981), NADACHOWSKI (1982) and NAGEL (1992).

Measurements:

The overall tooth length (L), the length of the anteroconid complex (a), width of the posterior lobe (W), c (distance between LRA5 and BRA5 inside the enamel wall), w1 (width of anterior part between LSA6 and BSA5) have been measured (Fig. 3a), and A/L and C/W1 (ratios were multiplied by 100) indices were calculated (according to NADACHOWSKI, 1982). All measurements are in millimetres (mm).

Morphotypes:

Morphotypes of M₁ have been determined and named after NADACHOWSKI (1982, p. 26–27) for the species *Dicrostonyx gulielmi*.

The fossil material is stored at the Institute for Quaternary palaeontology and geology of the Croatian Academy of Sciences and Arts in Zagreb.

Abbreviations:

Used abbreviations are: sin. (sinister = left), dext. (dexter = right), M₁, M₂, M₃ (first, second, third lower molar), M¹ (first upper molar), BSA5 (fifth buccal salient angle), LSA6 (sixth lingual salient angle), BRA5 (fifth buccal re-entrant angle), LRA5 (fifth lingual re-entrant angle), T5, T7 (fifth, seventh triangle), luv-side (anterior side of a salient angle), lee-side (posterior side of a salient angle), ka (thousands of years), n (number of specimens), min. (minimum value), max. (maximum value), χ (mean value), Rp (Romualdova pećina).

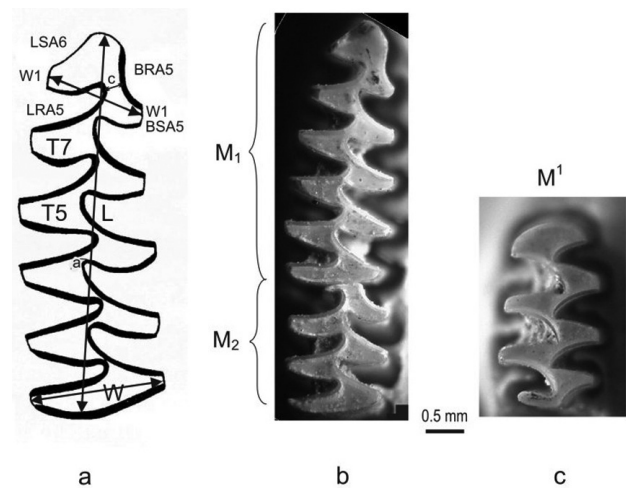


Figure 3: Molars of *Dicrostonyx* sp. from the Romualdova pećina Late Pleistocene layers: a – measurement points on the first lower molar (not to scale; drawing partly after: NADACHOWSKI, 1982, Fig. 2/3); b – mandible with M₁ and M₂ dext. (collection number: Rp/21); c – first upper right molar (M¹ dext.; collection number: Rp/23).

4. RESULTS

Order Rodentia BOWDICH, 1821

Superfamily Muroidea, ILLIGER, 1811

Family Cricetidae FISCHER VON WALDHEIM, 1817

Subfamily Arvicolinae GRAY, 1821

Tribe Dicrostonychini KRETZOI, 1955

Genus *Dicrostonyx* GLOGER, 1841

Dicrostonyx sp.

(Figs. 3a, b, c)

Material: 11 molars (3 M₁ sin.; collection numbers: Rp/118, 124 and 125), 2 M₁ dext. (collection numbers: Rp/21

Table 1: Metrical values (L, a, W, c, w1, A/L, C/W1) for the *Dicrostonyx* sp. molars from Romualdova pećina, Late Glacial and Holocene Polish samples of *D. gulielmi* (NADACHOWSKI, 1982), and Late Pleistocene *D. torquatus* sample from Bois Roche site in France (SESE & VILLA, 2008). For abbreviations see the text.

Measurements and indices (M ₁)	Romualdova pećina <i>Dicrostonyx</i> sp.		Poland (Holocene) <i>D. gulielmi</i>		Poland (Late Glacial) <i>D. gulielmi</i>		Bois Roche, France (Late Pleistocene) <i>D. torquatus</i>	
	n	min.-max. (χ)	n	min.-max. (χ)	n	min.-max. (χ)	n	min.-max. (χ)
L	5	3.37–3.91 (3.63)	10	3.76–4.06 (3.89)	9	3.43–3.81 (3.63)	7	3.17–3.83 (3.55)
a	5	1.97–2.4 (2.17)	–	–	–	–	–	–
W	4	1.24–1.42 (1.31)	–	–	–	–	7	1.18–1.52 (1.34)
c	5	0.19–0.25 (0.22)	–	–	–	–	–	–
w1	3	0.95–1.07 (0.99)	–	–	–	–	–	–
A/L	5	57.43–62.31 (59.75)	10	55–61 (58)	9	56–61 (58)	–	–
C/W1	3	20–23.36 (21.4)	10	10–30 (23)	9	10–36 (21)	–	–

Table 2: Minimum, maximum and mean values for M_{1-3} and M^1 length of *Dicrostonyx* sp. from Romualdova pećina in comparison to the Austrian samples (NAGEL, 1992, 1997).

Locality	Length (L)		
	n	min.-max.	χ
		M_1	
Romualdova pećina	5	3.37–3.91	3.63
Nixloch cave	10	3.17–3.73	3.5
Merkenstein cave	50	2.25–3.63	3.15
		M_2	
Romualdova pećina	4	1.71–1.93	1.81
Nixloch cave	23	1.6–2	1.8
		M_3	
Romualdova pećina	1	1.92	-
Nixloch cave	11	1.45–2.32	1.71
		M^1	
Romualdova pećina	2	2.64–2.67	2.66
Nixloch cave	16	2.2–2.78	2.42
Merkenstein cave	50	2.03–2.65	2.42

and 22), 3 M_2 sin. (collection numbers: Rp/118, 124 and 125), 1 M_3 sin. (collection number: Rp/125), 1 M^1 sin., and 1 M^1 dext. (part of the skull; collection number: Rp/23).

Description: The molars of *Dicrostonyx* are rootless, without cement, with leptoknem enamel band (luv-side /concave/ is thicker than the lee-side /convex/; see the Abbreviations) which is on all anticlines and apices discontinuous (so called enamel-free areas; Fig. 3). The first lower molars (M_1) from the Croatian sample consists of posterior lobus, eight triangles and anterior cap. On the basis of number and shape of the anteroconid complex AGADJANIAN (1976) proposed four morphotypes (I – IV) for the known *Dicrostonyx* species, which were also presented in the Austrian locality Nixloch (cave near Losenstein-Ternberg in Upper Austria; age: 18.310 ± 580 y BP ^{14}C ; NAGEL, 1992). In the small sample of five M_1 s from Romualdova the morphotypes have been determined after NADACHOWSKI (1982; for the species *D. gulielmi*). Significant variations of the anteroconid complex could not be observed, and all five molars have been determined as pertaining to the morphotype E.

The results of the metrical analyses are presented in Tables 1 and 2.

5. DISCUSSION

The dentitions of lemmings show great individual variations (especially on M_1 s and M^1 s) on which basis some authors differentiated two species (*Dicrostonyx gulielmi* and *D. henseli*; HINTON, 1910, 1926; cited in: NADACHOWSKI, 1982). JÁNOSSY (1954) wrote that these two species represent only variations of the species *D. torquatus*.

The evolution of the upper teeth of *Dicrostonyx* from the Middle Pleistocene to recent was presented by AGAD-

JANIAN & KOENIGSWALD (1977), and from the aforementioned Nixloch Cave, a smaller sample of this genus has also been morphometrically analysed (NAGEL, 1992). In the same article NAGEL gave the data (so called morphodynamic index) for other Austrian sites: Kemathenhöhle (30 ka BP), Geißenklösterle (31 ka BP) and Kleine Scheuer (13.25 ka BP). The latter author analysed the *D. gulielmi* findings (NAGEL, 1997) from the Merkenstein Cave (Lower Austria) as well, quoting the possibility that the findings belong to the subspecies *D. gulielmi gulielmi*. The length of M_1 s from this site shows that they are somewhat smaller than those from Nixloch (Tab. 2). The age of the Merkenstein locality is the same as for Nixloch, or even younger. The Romualdova teeth show greater length values for the first upper and first lower molars than the aforementioned Austrian ones. From the Würmian/Late Glacial faunal list of the Knochenhöhle site near Kapellen in southeastern Austria (~14 – 10 ka BP; FLADERER, 2000) *Dicrostonyx* (i. e. *D. torquatus* f. *gulielmi*) is also known.

After NADACHOWSKI (1982) there is a great morphological variability on M_1 s (in species *D. gulielmi*), from more primitive morphotypes (e. g. A) with less in number and more confluent triangles to progressive types (G, H, I) with less confluent and up to eight, even nine triangles. Other parts of M_1 s also show some variations, such as connections between two triangles etc. In the Croatian sample, variations of the anteroconid complex have not been observed, due to the low number of discovered M_1 s, and all teeth have eight closed triangles (not confluent).

NADACHOWSKI (1982, p. 31) discovered decreasing length values of M_1 s (for the species *D. gulielmi*, from the Lower to Upper Pleniglacial, and to the Late Glacial, respectively). In the samples from the Holocene (e. g. Niedostepna, Tunel Wielki, Ciasna, etc.) the M_1 length increases again. Furthermore, in the Polish sample A/L indices fluctuate between 56 and 58 (original values are 0.56 and 0.58, because they were not multiplied by 100; author's remark), and significant differences occur between Upper Pleniglacial and Holocene. C/W1 (NADACHOWSKI originally signed this ratio as C3/W3; author's remark) the coefficient also differs statistically (*idem*, p. 33). The Romualdova sample shows the highest A/L values, while the C/W1 index is the same as in the Late Glacial Polish sample (Tab. 1). Furthermore, *Dicrostonyx* molar length from Romualdova has a higher mean value in comparison to the early Late Pleistocene *D. torquatus* sample from Bois Roche (France; SESÉ & VILLA, 2008), while for the width it is just the opposite (Tab. 1).

The record of *D. torquatus* from Hungary (e. g. in Jankovich Cave, western Hungary; JÁNOSSY, 1986) is of Late Glacial age, while it lacks in Holocene layers completely. The same author gives detailed faunal lists for other Hungarian Late Pleistocene localities (e. g. Pilisszántó /10 km NNE from Budapest/, Remete Cave /NW from Budapest/, Bivak Cave /W Hungary/, Tokod-Nagyberek /W from Tokod village/, Gencsapáti /N from Szombathely/, Süttö locality no. 6 /~120 km NW from Budapest/), where the lemmings were present in different stages and substages. No morphometric data are available in the work of JÁNOSSY (1986). The

southernmost locality with lemming remains is near Veszprem (about 47° N).

GUILDAY (1963) wrote about two species of collared lemmings from the palearctic Pleistocene sites, and as the common Eurasian fossils, he stressed *D. gulielmi* (localities: Hutton Cave, Somersetshire, England) as the Late Pleistocene form of the recent *D. torquatus*. The same author also mentioned some other Old World Pleistocene *Dicrostonyx* sites in England, Ireland, France, Germany, Poland, and former Czechoslovakia.

As previously mentioned, the lemmings had a wide distribution in Eurasia during the Late Pleistocene. The southernmost localities have been discovered in the southwestern part of France, Switzerland, Hungary and Ukraine (JÁNOSSY, 1954, VILLA et al., 2010), and on the North American continent these animals were distributed from Alaska to the Great Lakes (GUILDAY, 1963; REPENNING et al., 1964, cited from: NADACHOWSKI, 1982). On the North American continent, the most southern localities have been recorded in Pennsylvania (from ~40° to ~42° N). Contemporaneous areas of the lemmings are in the arctic and sub-arctic tundra and forest-tundra in the palearctic (circumpolar), from the White Sea, western Russia, to the Chukotski Peninsula, north-east Siberia, and Kamchatka; including Novaya Zemlya and the New Siberian islands, Arctic Ocean (WILSON & REEDER, 2005), but excluding Wrangel Island (GROMOV & ERBAEVA, 1995; PAVLINOV et al., 2002). TSYTSULINA et al. (2008) quoted the fact that once it was believed that *Dicrostonyx torquatus* „encompass most or all New World populations, but karyotypic and breeding evidence supports the strict application of *D. torquatus* for only Eurasian populations“ (see also: WILSON & REEDER, 2005, and references therein).

The habitat that *Dicrostonyx* prefers is dry and stony tundra. It is sympatric with another lemming vole, *Lemmus*, which occupies the same ecological niches.

The impact of the herbivorous mammals, including *Dicrostonyx*, on the arctic vegetation as an important lemming-plant interaction was emphasized by OKSANEN et al. (2008). The lemmings feed on grasses, sedges and other green vegetation in summer, and twigs of willow, aspen and birches in winter, as mentioned for one representative of the genus, *Dicrostonyx groenlandicus* (so called northern collared lemming) which lives in the tundra regions of northern Canada, Alaska and Greenland. The most common lemming predators are snowy owls (*Bubo scandiacus*), gulls, wolverines, the Arctic foxes and the polar bears (http://en.wikipedia.org/wiki/Northern_collared_lemming).

Further detailed studies of the faunal remains from Romualdova will provide the answers as to which layers/age the *Dicrostonyx* discoveries on this site originate, and the specific determinations will be possible on the larger sample as the result of the systematic excavations which have been performed in previous years. Furthermore, it will be determined whether the Romualdova lemmings are more similar to the representatives of the recent species *D. torquatus*, or more probably, that they belong to *D. gulielmi*.

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