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First record of the root vole *Microtus oeconomus* (PALLAS, 1776) (Arvicolidae, Rodentia, Mammalia) in Croatia – fossil remains from the Late Pleistocene of Vindija Cave

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ABSTRACT

Late Pleistocene remains of *Microtus oeconomus* (PALLAS, 1776), a species that is not any more a member of the extant fauna of Croatia, have been recently found in Vindija Cave sediments. The sample of 21 teeth shows a slight increase of M_1 length and decrease of A/L ratio within the cave sequence from older (G complex; 32 to 42 ka) towards younger strata (E+F complex; layer E is dated at ca. 18.5 ka). The most frequent morphotype is type B sensu NADACHOWSKI (1982). The new record does not allow further detailed ecological implications than what is already known about the Late Pleistocene habitats in this region.

Keywords: root vole, *Microtus oeconomus*, teeth, morphometric analyses, Late Pleistocene, Vindija Cave, Croatia

1. INTRODUCTION

Vindija Cave is a well known Pleistocene locality in Croatia. Its Pleistocene sediments (MIS 6 – MIS 2) (Figs. 1 & 2), contain numerous small mammal remains and other faunal representatives. During more than a decade of continuous excavations at the site (1974–1986 conducted by Mirko MALEZ), these discoveries were collected with variable care and/or appropriate methods (MIRACLE et al., 2010, and references therein). More accurate collecting has been performed during excavation of complex G (32–>42 ka /HIGHAM et al., 2006; WILD et al., 2001/), containing Neanderthal remains and of complex E+F (18.5–30 ka /WILD et al., 2001/), with remains of modern humans (Fig. 2). The majority of the dental and other skeletal microvertebrate remains including *Microtus oeconomus* (MAUCH LENARDIĆ, 2004, 2005), originates from the sediments of these strata, while one M_1 originates from older sediments of the layer I (ca. 88 ka; WILD et al., 2001).

Microtus oeconomus is the only extant *Microtus* species with a holarctic distribution and ranges from northwest Europe, eastward through north and central Asia to Alaska and northwest Canada (BRUNHOFF et al., 2003). Four phylogeographical groups have been identified and traced back to several glacial periods. They reflect late glacial and postglacial range expansions and shifts as well as fragmentation of populations (*idem*).

2. GEOLOGICAL SETTINGS

The geographic position of the cave is 46° 18’ 12’’ N, 16° 14’ 38’’ E, and the entrance is 275 m a.s.l. (PAUNOVIĆ et al., 2001; WILD et al., 2001, and references therein). The cave consists of a single, funnel-shaped chamber over 50 m long, 28 m wide and 20 m high, although prior to excavation, the cave roof was less than 3 m above the surface (MIRACLE et al., 2010).

Figure 1: Location map of Vindija Cave.

Thirteen layers (from the youngest A /Holocene/ to the oldest M /MIS 6 or older/) show different sedimentation cycles, and comprise faunas of different composition. *Microtus oeconomus* teeth have been uncovered from stratigraphic units I, G lower, G upper (inclusive signature G2), complex E+F and layer E (after original signature; see Fig. 2).

3. MATERIAL AND METHODS

The determinations, terminology and metrical methods were used after VAN DER MEULEN (1973), RABEDER (1981) and NADACHOWSKI (1982).

Measurements:

The overall tooth length (L), the length of anteroconid complex (a) and width (W) have been measured and A/L index was calculated (according to VAN DER MEULEN, 1973). All measurements are in millimetres (mm). The parameters have been statistically calculated with STATISTICA 6.0

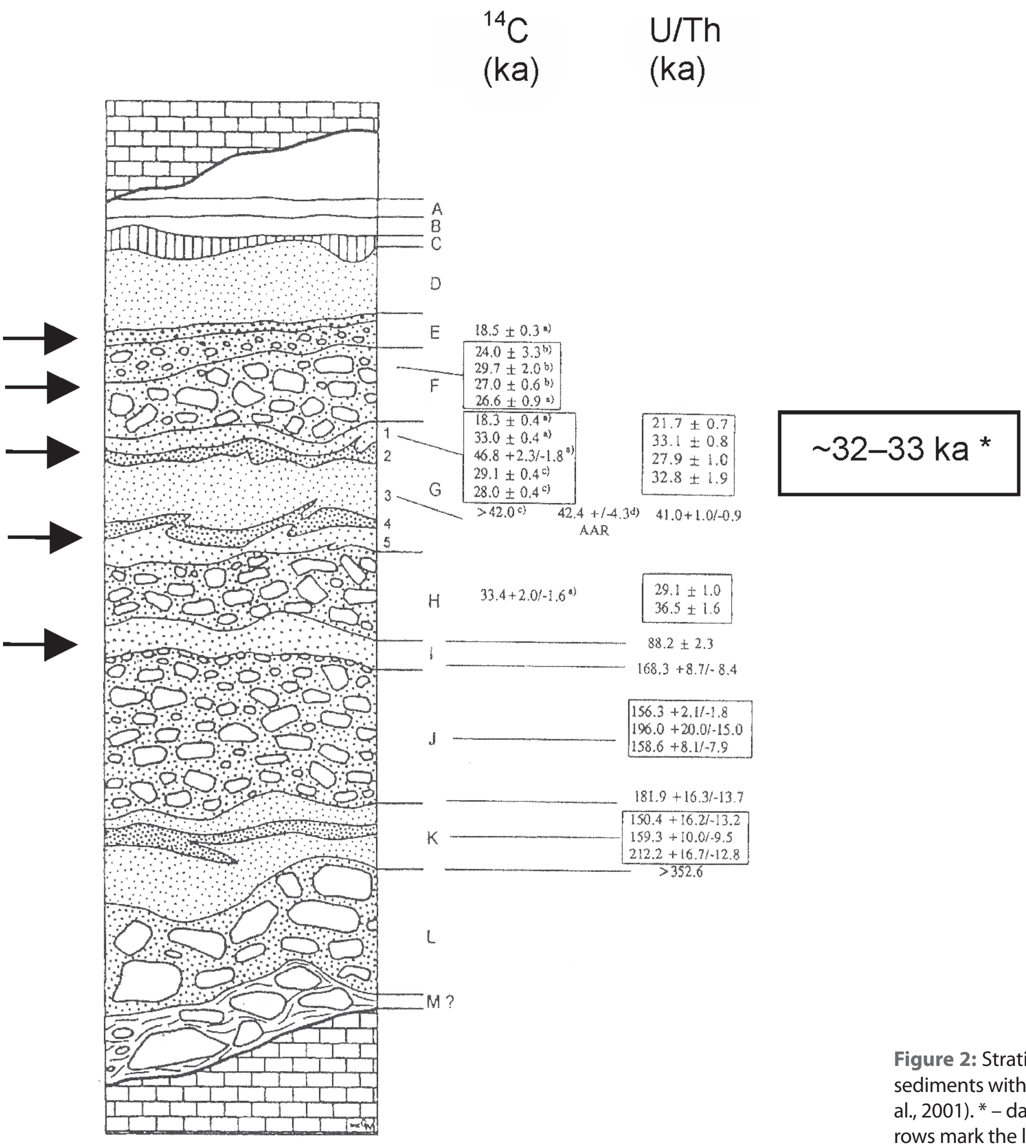

Figure 2: Stratigraphic column of Vindija Cave sediments with ^{14}C and U/Th data (after WILD et al., 2001). * – data after HIGHAM et al. (2006); arrows mark the layers with *Microtus oeconomus*.

(StatSoft.Inc., 1994–2001 for Windows). On graphs standard deviation (SD), standard error of the mean (SE) and mean values are indicated.

Morphotypes:

Morphotypes of M_1 have been determined and named after NADACHOWSKI (1982) (Fig. 3).

Morphotype B: with pronounced LSA5.

Morphotype C: with smooth BSA4 and BRA4 of varying size (example **a** – lesser distinct, example **b** – more distinct). Width between T5 and T6 (confluence) varies.

Morphotype D: with BSA4 very well developed, connection between T5 and T6 is very narrow (not confluent).

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), M_1 (first lower molar), M_2 (second lower molar), LSA5 (fifth lingual salient angle), BSA4 (fourth buccal salient angle), BRA4 (fourth buccal re-entrant angle), T5, T6 (fifth, sixth triangle), ka (thousands of years), n (number of specimens), min. (minimal value), max. (maximal value), MIS (Marine Isotope Stage), LG (Last Glacial).

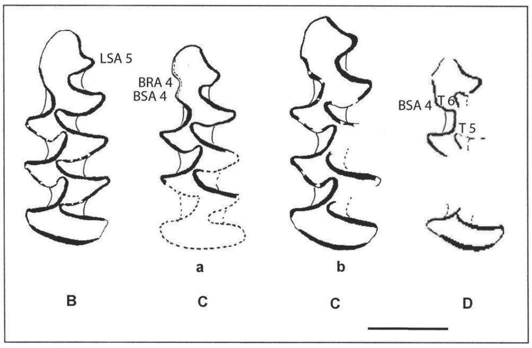

Figure 3: Morphotypes of *Microtus oeconomus* first lower molars (M_1) from Vindija Cave: B (layer E, Inv. No. 207; inverted image), C (**a** – layer G2, Inv. No. 70; **b** – layer I, Inv. No. 419), and D (layer G2, Inv. No. 40; inverted image). Bar scale is 1 mm.

4. RESULTS

Order Rodentia BOWDICH, 1821
Suborder Myomorpha BRANDT, 1855
Superfamily Muroidea, ILLIGER, 1811
Family Cricetidae FISCHER VON WALDHEIM, 1817
Subfamily Arvicolinae GRAY, 1821
Tribe Arvicolini GRAY, 1821
Genus *Microtus* SCHRANK, 1798
Microtus oeconomus (PALLAS, 1776)

1982 *Microtus oeconomus* – NADACHOWSKI, p. 74–81, figs. 20, 21, 22;

Material: 7 M_1 sin. (Inv. numbers: 23-1, 32-1, 70-1, 164-1, 202-1, 213-1 and 419-2), 12 M_1 dext. (Inv. numbers: 20-1, 39-1, 40-1, 45-1, 50-1, 73-1, 77-1, 160-1, 206-1, 207-1, 45-proba III and 46-proba III), and 2 M_2 sin. (Inv. numbers: 23-1 and 70-1).

Description: M_1 with four, rarely with five closed triangles; with weakly developed T6; BSA4 sometimes present; specifically shaped anterior cap (lobus) with flattened buccal side. T5 is mostly broadly confluent with T6 and anterior lobus on the occlusal surface (Fig. 3).

Measurements:

First lower molars (M_1):

L, a, W and A/L values are given in Figs. 4 and 5, and Tab. 1. Measured parameters were grouped and compared for two complexes – E+F and G. Mean values for L, a and W are greater for the samples from the E+F complex than for the G complex (Figs. 4 and 5), while for the A/L index is opposite.

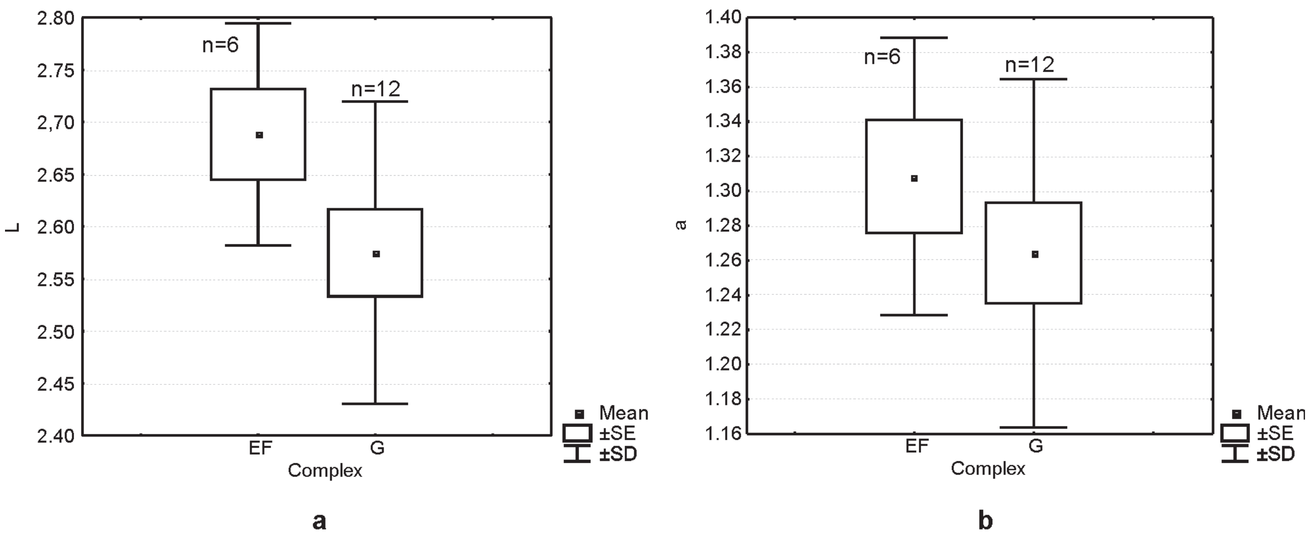

Figure 4: Graph of mean values, standard error of the mean values (SE) and standard deviation (SD) for length L (**a**) and length of anteroconid complex a (**b**) of *Microtus oeconomus* M_1 for the Vindija Cave E+F and G complexes.

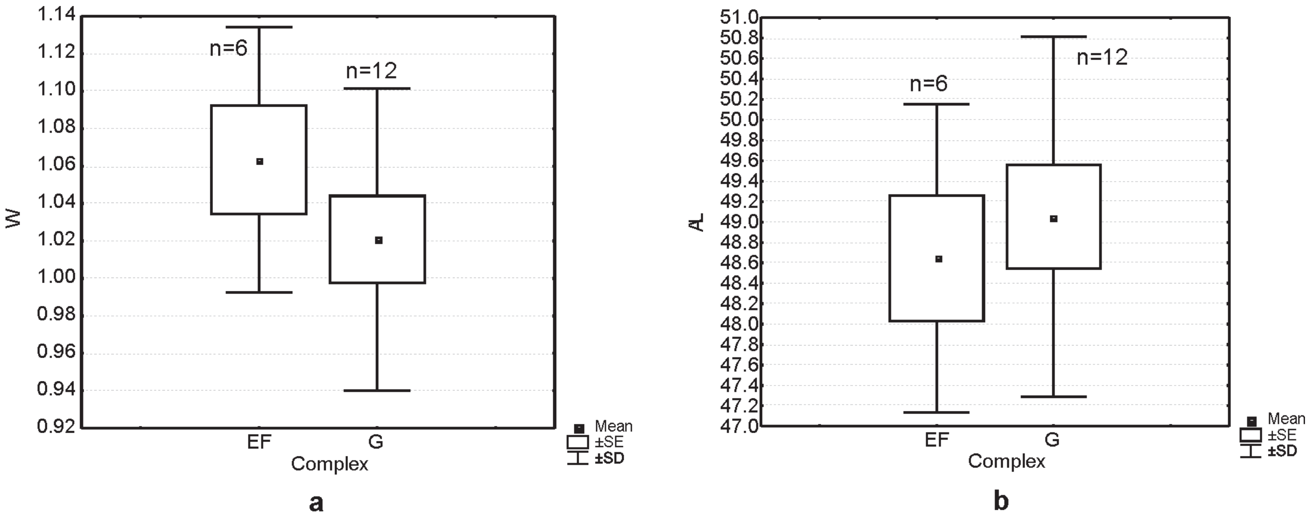

Figure 5: Graph of mean values, standard error of the mean values (SE) and standard deviation (SD) for width W (**a**) and A/L index (**b**) of *Microtus oeconomus* M_1 for the Vindija Cave E+F and G complexes.

Table 1: Minimum (min.), mean and maximum (max.) values of L and A/L for *Microtus oeconomus* M_1 from Vindija Cave.

Layer/ complex	L				A/L			
	n	min.	mean	max.	n	min.	mean	max.
E	4	2.57	**2.69**	2.83	4	40.13	**48.01**	50.18
E+F	2	2.61	**2.70**	2.78	2	49.64	**49.92**	50.19
Gupper	10	2.29	**2.56**	2.76	10	47.16	**48.87**	52.90
Glower	2	2.57	**2.66**	2.75	2	49.42	**49.99**	50.55
I	1		**2.94**		1		**47.96**	

Table 2: Measurements (L and W) for *Microtus oeconomus* M_2 from Vindija Cave.

Inv. no.	Layer/complex	L	W
23-3 (sin.)	E+F	1.48	0.87
70-1 (sin.)	G2	1.54	0.96

Table 3: Morphotype frequencies for *Microtus oeconomus* M_1 from different layers/complexes of Vindija Cave.

Layer/ complex	MORPHOTYPES							
	B		C		D		TOTAL	
	n	%	n	%	n	%	n	%
E+F	4	66.7	2	33.3			**6**	**31.6**
Gupper	6	60.0	3	30.0	1	10.0	**10**	**52.6**
Glower			2	100			**2**	**10.5**
I			1	100			**1**	**5.3**
TOTAL	**10**	**52.6**	**8**	**42.1**	**1**	**5.3**	**19**	**100**

Second lower molars (M_2):

Only two M_2 (Tab. 2) with values of L and W enable no morphometrical analysis.

Morphotypes:

On 19 M_1 of *Microtus oeconomus,* (12 of them are from the G complex), morphotypes B, C and D sensu NADACHOWSKI (1982) have been identified (Fig. 3; Tab. 3), while morphotype A is completely absent. In the small sample, the most abundant morphotype is B (10 teeth or 52.6 %).

5. DISCUSSION

Based on M_1 morphology alone, a specific determination between *Microtus oeconomus* and *Chionomys nivalis* might be in some cases problematic, since (as shown by ANGERMANN, 1971) that both species share common M_1 morphotypes. In his paper about Late Quaternary rodents of Poland, NADACHOWSKI (1982) elaborated this problem in fossil material. The „oeconomus« morphotype is the most frequent in the Polish Late Pleistocene samples, but decreases during the Late Glacial. NADACHOWSKI (1982) assumes that at the margin of the species range, non-typical morphological features occur more frequently, which parallels the situation during the last glaciation when under the influence of ameliorating climate the root vole retreat to the north, and the frequency of the „alien« morphotypes increased to 36 %. Also the extreme frequency of the nivalid morphotype (35 %) is observed in recent populations inhabiting the tundra zone (NADACHOWSKI, 1982). The comparison between the frequency of *Microtus oeconomus* of various Polish sites shows even greater differences (from 2–5 % to 46 %), but up from the Upper Pleniglacial a gradual decrease is observed: from 10–30 % in the Upper Pleniglacial, to 4–17 % in the Late Glacial and eventually to 1–8 % during the Holocene (NADACHOWSKI, 1982). However, analysing the vole dentition from Bacho Kiro cave (Bulgaria) NADACHOWSKI (1984) corrected the previous determination of M_1 of *Microtus* cf. *oeconomus* to extreme variants (morphotype A) of the snow vole *Chionomys nivalis* (MARTINS,

1842) based on data of fossil and recent samples from Switzerland, the Tyrol, Murańska cave and other localities in the Tatras, Greece, Romania, Bulgaria etc.

In the M_1 of Vindija Cave, the most frequent morphotype is B (52.6 %; four closed triangles), morphotype C is less abundant, morphotype D is represented by one tooth only, and morphotype A is completely lacking. These data would fit roughly between the values of the Late Glacial and recent condition in Polish samples, documented by NADACHOWSKI (1982): Lower Pleniglacial (LP) – 61.7 %, Upper Pleniglacial (UP) – 60.9 %, Late Glacial (LG) – 46.8 %, recent (R) – 59.2 %.

The metrical analysis of M_1 of *Microtus oeconomus* shows an increase of the length and a decrease of the A/L index from the older G to the younger E+F complex. Also NADACHOWSKI (1982) observed a distinctive increase of M_1 length during the Late Quaternary of Poland (with the smallest specimens in the Lower Pleniglacial, and the biggest in the extant fauna – *idem*). The mean A/L values from Poland fluctuate between 48 and 49 but the differences between the groups are not statistically significant. In the Vindija sample, the maximal values are somewhat smaller, and minimal values are slightly bigger compared to the Polish samples, whereas the mean values remain more or less similar. However, L and A/L are smaller in the Croatian samples compared to the Polish ones (Tab. 4) (NADACHOWSKI, 1982; MAUCH LENARDIĆ, 2005). Comparison of M_1 length gives similar mean values for the Vindija E+F complex sample and recent German specimens (Tab. 4; TAST, 1982).

According to SPITZENBERGER & BAUER (2001), a morphological rather similar ancestor of *Microtus oeconomus* first appeared in the Lower Pleistocene, and specimens of the present shape during the Middle Pleistocene respectively. They quote the oldest 'true' *M. oeconomus* as being from the volcanic ash in the open-site Miesenheim near Koblenz (Rheinland-Pfalz, Germany), dated at 612 ka. *Microtus oeconomus* belongs to the Holarctic Pleistocene tundra-steppe fauna, which existed during the LG (more than 55 ka), and therefore also occurred on the North American continent. The species also occurs in some Late Pleistocene Austrian localities (Gamssultzenhöhle, Grossen Ofenberger-höhle: Upper Würmian, Nixloch: Dryas – 10.55 ka until Holocene) (SPITZENBERGER & BAUER, 2001). Within the Late Pleistocene and Holocene, several populations west and south of the recent main distribution of *M. oeconomus* became isolated. In southern Germany, the Czech Republic and Hungary, the species was still recorded in the Holocene, in Moldova until the Neolithic, and in southern France, as the last boreal element of Ice Age fauna, the species disappeared ca. 7000 years ago (SPITZENBERGER & BAUER, 2001). Recent investigations in Hungary have confirmed the presence of some isolated (sub)populations, one near Balaton lake (NE), and a second (Barcs), about 100 km east of the Vindija site (BIHARI et al., 2007).

Table 4: Tooth length (L) and A/L index for *Microtus oeconomus* samples: * – Germany (Fürstenwalde near Berlin; TAST, 1982); ** – Poland (different localities; NADACHOWSKI, 1982).

Age (in ka BP)	L			A/L		
	n	min.–max.	mean	n	min.–max.	mean
R (Germany)*	15	2.05–2.90	**2.71**	–	–	–
R (10 – 0)**	30	2.74–3.37	**2.98**	30	43–52	**48**
LG (16 – 10)**	16	2.64–2.96	**2.84**	16	46–51	**49**
UP (30 – 16)**	30	2.50–3.19	**2.77**	30	46–54	**48**
LP (62 – 52)**	30	2.47–2.89	**2.65**	30	45–52	**49**

The distribution is confirmed by NADACHOWSKI (1982) who mentions a Late Pleistocene expansion of the range of *Microtus oeconomus* further west than today: in Central Europe, England, France and Switzerland as well as further south in Hungary and Romania. The species survived here longer than many other tundra adapted species; e.g., in Hungary it still occurred during the Subboreal (Bükk Phase) in the Bükk mountains, and in the caves of the Aggtelek Karst (NADACHOWSKI, 1982). At the beginning of the Holocene, the distribution of this species was divided into two parts: a tundra range and a forest-tundra range of Europe, parts of Asia and North America, with isolated populations in the Netherlands, Austria and the Small Hungarian Lowland (NADACHOWSKI, 1982).

Microtus oeconomus is an indicator of a cold climate and tundra-forest environments with abundant water, respectively (NADACHOWSKI, 1982). Tundra (root) voles appear to have an extremely wide tolerance to different habitats, but may be locally restricted by competition with other microtines (GUTHRIE, 1968). In some regions, *Microtus oeconomus* could be restricted to low wetland communities, unforested areas, wet meadows, around lakes, streams or marshes (GUBÁNYI et al., 2007).

Microtus oeconomus has been determined for the first time in Croatia in the Late Pleistocene sediments of the Vindija Cave (MAUCH LENARDIĆ, 2004, 2005), and it is not part of the extant fauna in the vicinity of the cave (PETROV, 1992). Thus the findings from Vindija Cave imply a somewhat colder and more wet climate in this region during some phases of the Late Pleistocene than today. The youngest strata from which this species is determined in Vindija is the E+F complex (layer E is dated as ca. 18.5 ka). There are no records of this species in younger layers, neither are there in the faunal remains from other Croatian localities with contemporaneous strata, such as Marlera I (southern Istria), the Mujina pećina cave (middle Dalmatia; MAUCH LENARDIĆ, 2005, 2008) or Vela spila on Korčula island, respectively (MAUCH LENARDIĆ, in press).

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