Paleoecological Analysis of the Early Pleistocene Vertebrate Fauna from Razvodje and Tatinja draga (Croatia)

by

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Abstract

In this paper are presented the results of paleoecological analysis of the vertebrate assemblages from bone-breccias found in Croatia along the Adriatic coast near Razvodje (Lower Early Pleistocene) and Tatinja draga (Middle Early Pleistocene). Because of the differences in the community structure and frequencies of registered taxa they are designed as "Lagurus-Podarcis sicula assemblage" (Tatinja draga) and "Allophaiomys-Microtus-Lacerta agilis assemblage" (Razvodje). Analysis also shows that at both localities the arid biocoenoses are accompanied with mesophyllous areas, bushes and open landscape biotopes developed under temperateound periodically humid climatic conditions, as well as similarity with contemporary faunas of Italy, Austria and southeastern Europe. Endemic small vertebrate taxa and the presence of species living today in the area indicate that the main features of the recent fauna were formed during the Early Pleistocene.

1. Introduction

Best known from the numerous localities of the bone-breccias along the Adriatic coast are Šandalja I near Pula (Istria), Podumci near Unešić (Dalmatia), as well as Tatinja draga near Karlobag and Razvodje near Knin, but until 1980 only faunal lists or paleontological descriptions of the skeletal remains have been published (Kormos 1918, 1931, Kowalski 1958, Malez 1971). Therefore the recent studies of the faunal assemblages, especially of the micromammals, include also biostratigraphical analyses: the Early Pleistocene age of the bone-breccias discovered at Tatinja draga,

Razvodje and Podumci was confirmed by the morphogenetic analyses of micromammals (MALEZ & RABEDER 1984, PAUNOVIĆ & RABEDER 1996), with reference to geochronologically important arvicolids. Metrical data and molar morphotypes of the genus Lagurus, as well as Pliomys indicate that the fauna from Razvodje (Lower Early Pleistocene) is older than the fauna from Tatinja draga (Middle Early Pleistocene), and Podumci (Late Early Pleistocene). At the same time, analyses of the lower vertebrates shows differences between Razvodje and Tatinja draga (PAUNOVIĆ & RABEDER 1996). Therefore using the results of paleontological and statistical analyses of all faunal remains, we have tried to reconstruct the ecological relationships in these two chronologically and geographically separated assemblages.

2. Localities

The studied Early Pleistocene bone-breccias were found in karstic fissures of Paleogene rocks at Tatinja draga near Karlobag on the foot of the Mt. Velebit and Razvodje near Knin on the slopes of Mt. Promina (Fig. 1). The bone-breccia matrix from Tatinja draga is reddish-brown in colour, reflecting a temperate climate during the deposition, while the yellowish-green sandy clay matrix from Razvodje was deposited under colder climatic conditions (MALEZ & RABEDER 1984, PAUNOVIĆ & RABEDER 1996). A small amount of large mammal remains in distinction from the small mammals and lower vertebrates is characteristic for both of the studied localities.

3. Large Mammals

After the first publication of some faunal remains from Tatinja draga (Kormos 1918), M. Malez (1960, 1968, 1971) also listed the large mammals in his papers (Table 1). The preliminary list of the macromammal remains from the bone-breccia at Razvodje was published in 1971 by M. Malez (Table 1).

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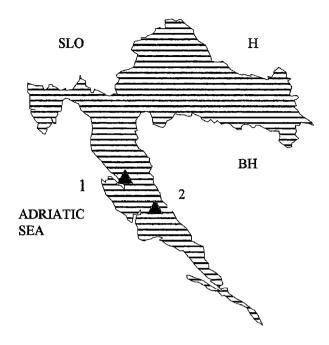


Figure 1. Map of Croatia and the situation of the localities.

According to the data from the literature (Table 1) the faunal assemblages are similar: in Tatinja draga Capreolus suessenbornensis is missing, while in Razvodje Vulpes has not been registered. Regretably, in both cases the number of remains and frequency of taxa is not listed. For the moment, the determination made by MALEZ (1971) must be accepted and the only conclusion is, that the listed large mammals are both forest- and open forest-dwelling taxa (except for Equus stenonis), which appear to have been sympatric in the Early Pleistocene faunas from Croatia. Thus, after the large mammals, the age of the faunas from Razvodje and Tatinja draga is Early Biharian (Villany-5), or due to the sedimentation processes (if determination of the large mammals is correct) the studied faunal assemblages are composed of the mixed remains belonging to the various stages of Early Pleistocene. Namely, Equus stenonis and Ursus arvernensis are no longer present in Tamanian (Betfian) assemblages of SE

Species	Razvodje	Tatinja draga
Canis sp.	Х	X
Vulpes sp.		Х
Ursus arvernensis	Х	Х
Mustela sp.	Х	Х
Equus stenonis	Х	Х
Cervus sp.	Х	Х
Capreolus sp.	Х	Х
Capreolus cf. suessenbornensis	X	

 $\begin{tabular}{ll} \textbf{Table 1}. Large mammals from Razvodje and Tatinja draga (after Malez, 1971). \end{tabular}$

Species	Razvodje	Tatinja draga
Talpa minor	x	х
Talpa europaea		X
Sorex runtonensis	х	X
Episoriculus thenii	Х	X
Beremendia fissidens	Х	X
Crocidura kornfeldi	X	X
Hypolagus brachygnathus	Х	X
Lepus sp.	Х	X
Marmota sp.		X
Sciurus sp.	Х	
Glis sackdillingensis	X	X
Allocricetus croaticus	Х	
Allocricetus bursae		X
Microtus praehintoni	Х	
Microtus ratticeps		X
Mimomys malezi	Х	X
Mimomys savini	Х	X
Mimomys pusillus	Х	X
Dinaromys dalmatinus	Х	X
Pliomys cf. schernfeldensis	Х	
Pliomys simplicior	X	
Pliomys bolkayi		Х
Pliomys cf. hollitzeri		X
Lagurus arankae	Х	Х
Apodemus cf. sylvaticus	Х	X
Apodemus mystacinus epimelas	Х	Х

Table 2. Small mammals from Razvodje and Tatinja draga.

Europe (Rekovets & Krakhmalnaya 1998). Also, after Alberdi, Caloi & Palombo (1998) the comparative analysis of large mammals from Italy (Farneta and Pirro faunal unit = Early Pleistocene = Biharian) shows a dominance of open enivronments-dwelling taxa, and U. arvernensis and E. stenonis were not found in these assemblages. In Farneta unit successive and rapid spreads of grazer elements took place interspersed with short phases of partial reforestation. The different types of large mammal assemblages may correspond to the more or less arid or forested phases. In the Pirro faunal unit the species adapted to the open environments reached their maximum, although some elements that inhabit environments with a more dense woodland are still present. This unit is probably corresponding to a climatic cooling of the Menapian stage in northern Europe.

Thus, the large mammal assemblages from Razvodje and Tatinja draga correspond probably to the Farneta unit and new evaluation of *U. arvernensis*, *E. stenonis* as well as *Capreolus suessenbornensis* remains must be preformed.

Taxa	Lower Early Pleistocene Razvodje	Middle Early Pleistocene Tatinja draga	Modern fauna
Episoriculus	thenii	thenii	_
Allocricetus	croaticus	(bursae)	_
Apodemus mystacinus	epimelas	epimelas	epimelas
Microtus	(cf. praehintoni)	eoratticeps	(div. sp.)
Mimomys	malezi	malezi	_
Dinaromys		dalmatinus	bogdanovi
Pliomys	(simplicior)	bolkayi	_

Table 3. Endemic small mammal taxa (non-endemic taxa in paenthesis).

4. Small Mammals

The taxonomic study of small mammal remains was published in 1996 (PAUNOVIĆ & RABEDER), and therefore only the results are discussed in the present study.

The fauna of Razvodje (Table 2, Fig. 2) contains arvicolids (Microtus cf. praehintoni, Pliomys simplicior / hollitzeri, Mimomys pusillus) which indicate an Early Pleistocene age. A new species of hamster (Allocricetus croaticus) has to be emphasized (Paunović & Rabeder 1996). The fauna of Tatinja draga (Table 2, Fig. 2) contains more individuals and is also dominated by arvicolids (Lagurus arankae, Pliomys bolkayi, P. hollitzeri, Dinaromys dalmatinus, Mimomys savini, M. pusillus). Among these remains Microtus eoratticeps was determined for the first time (Paunović & Rabeder 1996).

From the registered small mammals, Sciurus, Allocricetus croaticus, Microtus praehintoni, Pliomys schernfeldensis and Pliomys simplicior are missing in the assemblage from Tatinja draga, while in the assemblage from Razvodje Talpa europaea, Marmota sp., Pliomys bolkyai and P. hollitzeri are not determined (Table 2).

The faunal assemblage from Tatinja draga is strongly dominated by *Lagurus arankae* (76%), while in the assemblage from Razvodje *Allocricetus* and *Microtus* taxa were registered with the same frequency of 31%

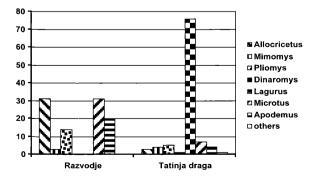


Figure 2. Frequencies of rodent taxa in % (after Paunović & RABEDER, 1996).

(PAUNOVIĆ & RABEDER 1996). So, considering the frequency of *Lagurus*, *Microtus* and *Allocricetus*, the assemblage from Razvodje can be designed as "*Microtus-Allocricetus* fauna" and the one from Tatinja draga as "*Lagurus*-fauna"

Species	Razvodje	Tatinja
•	J	draga
Phoxinus sp. (Ph.)		2 (50%)
Cypriniformes (Cyp)		2 (50%)
Σ		4
Bufo viridis (Bv)		2 (6%)
Rana latastei (Rl)		3 (9%)
Rana arvalis (Ra)		1(3%)
Rana sp. (R)		5 (15%)
Hyla arborea (Ha)		3 (9%)
Bombina bombina (Bb)		1 (3%)
Anura indet. (A)		19 (55%)
Σ		34
Lacerta viridis (Lv)	17 (12%)	7 (4%)
Lacerta agilis (La)	17 (12%)	5 (3%)
Lacerta oxycephala (Lo)	11 (8%)	3 (2%)
Lacerta lepida (Ll)	7 (5%)	5 (3%)
Lacerta vivipara (Lvi)	2 (1%)	
Lacerta sp. (L)	57 (41%)	84 (52%)
Podarcis muralis (Pm)	9 (6%)	9 (5%)
Podarcis sicula (Ps)	14 (10%)	22 (13%)
Podarcis sp. (P)		18 (11%)
Anguis fragilis (Af)	2 (1%)	1 (0,5%)
Ophisaurus pannonicus (O)	2 (1%)	7 (4%)
Anguinidae (An)		1 (0,5%)
Σ	138	162
Vipera ammodytes (Va)	4 (11%)	1 (8%)
Vipera berus (Vb)	2 (6%)	
Vipera sp. (V)	4 (11%)	1 (8%)
Coronella austriaca (Ca)	6 (17%)	6 (50%)
Coronella sp. (C)	3 (8%)	
Elaphe longissima (El)		3 (25%)
Elaphe sp. (E)	3 (8%)	
Natrix natrix (Nn)	2 (6%)	
Natrix sp. (N)	3 (8%)	
Coluber sp. (Cl)	2 (6%)	
Colubrinae (Col)	1 (3%)	1 (8%)
Serpentes indet. (S)	5 (14%)	. ,
Σ	35	12

Table 4. Number of determined skeletal remains of lower vertebrates from Razvodje and Tatinja draga (figs. -5).

Among the fauna a high amount of endemic taxa is remarkable: Episoriculus thenii, Allocricetus croaticus, Apodemus mystacinus epimelas, Microtus eoratticeps, Mimomys malezi, Dinaromys dalmatinus, Pliomys bolkayi (Table 3).

5. Lower Vertebrates

5.1. Material and Methods

The preliminary list of lower vertebrate taxa was published in 1996 (Paunović & Rabeder). Due to the high amount of well preserved and characteristic skeletal remains, the taxonomy of 214 bones from Tatinja draga, and 174 from Razvodje has been determined after the determination keys (Böhme 1977, Paunović 1984, Rauscher 1992, Szyndlar 1981) as well as in comparison with the skeletal collection of the recent taxa (Table 4).

The determination shows that in the assemblage from Razvodje the fish and frogs are not represented, while in the assemblage from Tatinja draga snakes are registered in small number (Table 5, Fig. 3). In the same time, both assemblages are dominated by lacertids, but with high percentage of only generically determined skeletal remains due to the number of strongly damaged bones and / or teeth (Table 4).

Therefore, due to the results of the taxonomy, for comparison and evaluation of these two assemblages, the statistical analysis of frogs, lizards and snakes remains was made separately.

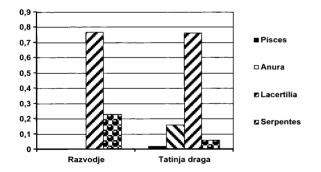


Figure 3. Frequencies of lower vertebrates from Razvodje and Tatinja draga.

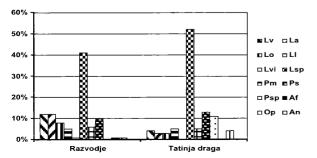


Figure 5. Frequencies of lacertid taxa from Razvodje and Tatinja draga (abbreviations in Table 4).

5.2. Statistical Analysis of Skeletal Remains

5.2.1. Pisces

The four bones found among the material from Tatinja draga obviously belong to the cyprinids, respectively to the genus *Phoxinus*.

5.2.2. Anura

From the 34 humeri or ilia 19 (or 55%) obviously belong to frogs, but they are damaged and therefore non-diagnostic. Determined taxa (Table 3) in amount of 45% belong mostly to ranids (27%), then to *Hyla arborea* (9%), *Bufo viridis* (6%), and *Bombina bombina* (3%) (Table 4, Fig 4).

5.2.3. Lacertilia

Among lizards from both localities the lacertids dominate in Razvodje with 96% and in Tatinja draga with 91%, while anguinids are registered with only 4% and 9% respectively. Differences between them are the appearance of *Lacerta vivipara* in the faunal assemblage from Razvodje, as well as different frequency of taxa (Table 3, Fig. 5).

5.2.4. Serpentes

Snakes are more common in the fauna from Razvodje than in Tatinja draga, and among determined taxa the species of Natricinae and Colubrinae are more frequent than those of Viperinae (Table 3, Fig 6). The most frequent species in both faunas is *Coronella austriaca* (6%). The difference between them is also a number

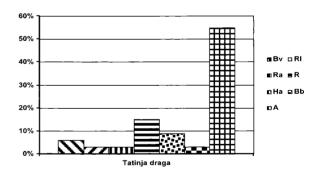


Figure 4. Frequencies of frog taxa from Tatinja draga (abbreviations in Table 4)

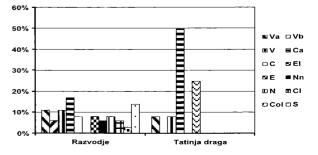


Figure 6. Frequencies of snake taxa from Razvodje and Tatinja draga (abbreviations in Table 4).

of determined taxa: among snakes from Tatinja draga only 4 species were determined, while the list of Razvodje consists of 7 (Table 3, Fig. 6).

5. 3. Community Structure

In the present study the changes in the community structure were analysed on the basis of frogs, lacertids and snakes of which the taxonomical position and the number of individual was estimated.

	Razvodje	Tatinja draga
Pisces		4 (2%)
Anura		34 (16%)
Lacertilia	138 (77%)	162 (76%)
Serpentes	35 (23%)	12 (6%)
Σ	173	212

Table 5. Frequencies of lower vertebrates from Razvodje and Tatinja draga.

Species	Razvodje	Tatinja draga
	MNI (P)	MNI (P)
Bufo viridis		9 (0,18)
Rana latastei		2 (0,04)
Rana arvalis		1 (0,02)
Hyla arborea		1 (0,02)
Bombina bombina		1 (0,02)
Lacerta viridis	6 (0,10)	3 (0,06)
Lacerta agilis	9 (0,16)	4 (0,08)
Lacerta oxycephala	6 (0,10)	2 (0,04)
Lacerta lepida	6 (0,10)	2 (0,04)
Lacerta vivipara	1 (0,01)	
Podarcis muralis	5 (0,09)	3 (0,06)
Podarcis sicula	5 (0,09)	9 (0,18)
Anguis fragilis	2 (0,03)	1 (0,02)
Ophisaurus pannonicus	1 (0,01)	3 (0,06)
Vipera ammodytes	4 (0,07)	1 (0,02)
Vipera berus	2 (0,03)	
Coronella austriaca	6 (0,10)	6 (0,12)
Elaphe longissima		1 (0,02)
Natrix natrix	2 (0,03)	
MNI	55	49
S (total number of species)	13	16
H (Shannon index)	3,64	3,90
d (species diversity)	4,007	3,89
e (equitability)	2,56	2,77

Table 6. Quantitative analysis of lower vertebrates from Razvodje and Tatinja draga.

The data were expressed in terms of community structure indices, and the results achieved by analysis of the relative frequency for each species (P = n / N), as well as of the number of species (species diversity) calculated from the equation: $d = S-1 / \ln N$ (S = number of species, N = number of individuals), while the degree to which individual species are evenly represented (dominance or equitability) was computed from the equation $e = H / \ln S$ (H = Shannon index calculated from equation after NADACHOWSKI 1998).

Biotop	Small vertebrates
forest	Sorex, Talpa, Lepus,
open forest	Sciurus, Glis, Apodemus,
	Rana latastei, Hyla arborea,
	Lacerta agilis, Vipera
	berus, Elaphe longissima,
	Coronella austriaca
open landscape	Crocidura, Lepus,
	Hypolagus, Talpa, Hyla
	arborea, Anguis fragilis,
	Lacerta agilis
steppe	Lagurus, Marmota,
	Allocricetus, Pliomys
stony landscape	Dinaromys, Lacerta viridis,
karst	Lacerta lepida, Podarcis
	muralis, Podarcis sicula,
	Ophisaurus pannonicus,
	Vipera ammodytes,
	Coronella austriaca
running water	Phoxinus, Natrix natrix
stagnant water	Bombina bombina, Lacerta
moor	vivipara, Vipera berus,
	Natrix natrix

 Table 7.
 Early Pleistocene Biotopes at Razvodje and Tatinja draga.

6. Discussion

Considering the ecology of the listed small vertebrates, six main biotopes which have probably existed in the surroundings of both localities can be distinguished (Table 7). *Bufo viridis* and *Microtus* taxa are ecologi-

cally non-diagnostic and therefore not listed in the table. Among other small vertebrates forest- and openforest, open landscape- and steppe-, stony landscape- and karst-dwelling taxa are represented. Also, some of them are water-dwelling. In both faunas thermophilous elements are Lacerta viridis, L. lepida, L.oxycephala, Podarcis sicula, P. muralis, Ophisaurus pannonicus, Elaphe longissima, Vipera ammodytes, Coluber, and Coronella austriaca.

Generally, at both localities the arid biocoenoses (steppe, stony landscape, karst) are accompanied with mesophilous areas, bushes and open landscape biotopes developed under temperate and periodically humid climatic conditions.

Yet, the differences between Razvodje and Tatinja draga are expressed in composition and frequency of taxa. For example, absence of amphibians in the fauna from Razvodje, presence of thermophilous Lacerta oxyce-phala in Tatinja draga with 2%, and in Razvodje or Lacerta vivipara found only in the assemblage from Razvodje. The "Allocricetus-Microtus-Lacerta agilis" assemblage from Razvodje is characterized by a high percentage of the steppeand open landscape-dwelling species, with 73% thermophilous elements among lower vertebrates (Tables 3, 7). Similarly, "Lagurus-Podarcis sicula" assemblage from Tatinja draga consists of 75% thermophilous elements among lower vertebrates (Table 3, 7) and 75% of steppe elements among small mammals. In the same time, the analysis of relative frequencies of lower vertebrate species (P) shows that in the assemblage of Razvodje among lacertids dominates the non-termophillous Lacerta agilis, probably indicating somewhat cooler climate conditions in this area than today. This can also be confirmed by the presence of Vipera berus and Lacerta vivipara (Table 6), and explained with different geographic positions of the localities. Namely, the bone breccia at Tatinja draga is found at the Adriatic coast at approximatelly 15 msl, and the same one at Razvodje at 300 msl on the slopes of Mt. Promina. For example, today the vertical distribution of reptile species on Mt. Velebit and surrounding areas (Mršić 1978, TVRTKOVIĆ & KLETEČKI 1993b) shows that Lacerta viridis is spread from 0-300 msl, Lacerta agilis from 850-1500 msl, Lacerta vivipara from 1100 - 1500 msl. and *Podarcis sicula* from 0-80 msl. Therefore, also the neotectonic movements must be considered: the most significant, about 1500m, vertical movements were registered on Mt. Velebit (PRELOGOVIĆ 1975). So, probably in the Early Pleistocene the altitude difference between the two studied localities was less expressed. At the same time, today's undersea springs along the Adriatic coast were probably surface running waters which were caused also by the changes of the sealevel. Thus, the running waters have been the source of the mosaic-like development of mesophyllous forests,

meadows and steppe environments under temperate climatic conditions. At the same time the connections and/or migrations of fauna between Central, SE and SW Europe must have been easier because of lack of the physiographic barriers. Namely, in comparison with other Early Pleistocene localities, the small vertebrate fauna is similar to the assemblage from Deutsch-Altenburg (RAUSCHER 1992) indicating a temperate climate and connection with Central European faunal assemblages. At the same time, faunal assemblages from Razvodje and Tatinja draga are similar to the faunal units of Italy in which forest species are almost equal in number to the open area taxa (Farneta faunal unit found at Pietrafitta: ALBERDI et al. 1998), as well as with SE European Tamanian faunas (REKOVETS & Krakhmalnaya 1998).

Considering also the fact that in the Early Pleistocene this region was far from the Adriatic (maximum regression was during the Late Biharian: NILSSON, 1983), stronger continental influences and different ecological relationships must have prevailed during the deposition of sediments on both localities. Such different relationships also explain the remains of Lacerta lepida whose characteristics are smaller dimensions than these of the recent specimens from the Iberian penninsula. Perhaps, it is question of a Pliocene relict population, which dissappeared from the eastern Adriatic coast during the transgression in Middle Pleistocene. Also, the presence of Lacerta oxycephala (in Tatinja draga 8%, in Razvodje 2%) speaks in favour of different ecological relationships: today L. oxycephala is an endemic species found among small vertebrates in Mediterranean beech forest at Mt. Biokovo near Cetina river, as well as in Konavle near Dubrovnik in Carpinetum orientalis-belt (TVRTKOVIĆ & KLETEČKI, 1993a). Thus, considering also small mammal taxa, today's fauna of the Adriatic coast was probably formed during the Early Pleistocene as a result of Pliocene migrations and endemism reflecting the influence of climate alterations caused by global changes as well as by the proximity of the Alps and the Dinarids on one side, and by Adriatic sea on the other. At the same time endemism can also be the result of the isolation of populations caused by sealevel changes as well as by neotectonic movements.

7. Conclusion

The study of vertebrate fauna from bone-breccias found at Razvodje and Tatinja draga has lead to the following conclusions:

• With reference to geochronologically important arvicolids, metrical data and molar morphotypes of the *Lagurus* and *Pliomys* taxa indicate that the fauna from Razvodje (Lower Early Pleistocene) is older than the fauna from Tatinja draga (Middle Early Pleistocene).

- The large mammals from Razvodje and Tatinja draga are both forest- and open forest- dwelling taxa (except *Equus stenonis*). The assemblages correspond probably to the Farneta unit of Italy and a new evaluation of the skeletal remains described as *Ursus arvernensis*, *Equus stenonis* and *Capreolus suessenbornensis* must be performed.
- The small mammal assemblage from Tatinja draga is strongly dominated by *Lagurus arankae*, while in the assemblage from Razvodje the *Microtus* and *Allocricetus* taxa dominate with the same frequency. Also, among the fauna a high amount of endemic taxa is remarkable.
- Among the lower vertebrates, relative frequency of the species shows that in the assemblage from Razvodje *Lacerta agilis* and in Tatinja draga *Podarcis* sicula are dominant. Fewer endemic taxa were registered.
- Combining the results of community structure analyses the studied faunas can be described as: "Microtus-Allocricetus-Lacerta agilis assemblage" (Razvodje) and "Lagurus-Podarcis sicula assemblage" (Tatinja draga).
- Generally, at both localities the arid biocoenoses (steppe, stony landscape) were accompanied with mesophyllous areas, bushes and open landscape

- biotopes developed under temperate and periodically humid climatic conditions. Also, the existence of some running and/or stagnant waters is provable in the surroundings of both localities.
- The "Allocricetus-Microtus-Lacerta agilis assemblage" from Razvodje, as well as "Lagurus-Podarcis sicula assemblage" from Tatinja draga are characterized by a high percentage of steppe- and open landscape-dwelling taxa among small vertebrates. For both assemblages a high amount of thermophilous elements are characteristic as well as the presence of water-dwelling taxa among lower vertebrates.
- The described assemblages are similar to the fauna from Deutsch-Altenburg indicating a temperate climate and connection with the Central European faunal assemblages. In the same time they are similar with the Farneta faunal unit of Italy, as well as with the Southeastern European Tamanian faunas.
- High amount of genera still living in this area speaks in favour of the idea, that the fauna of the Adriatic coast and islands was formed during the Early Pleistocene. At the same time the frequency of endemic taxa reflects evolutionary changes of isolated populations depending on specific geologic, geographic as well as climatic alterations which were registered for the Quaternary of the described area.

8. References

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