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Pollen analyses of Pleistocene hyaena coprolites from Montenegro and Serbia

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Abstract. The results of pollen analyses of hyaena coprolites from the Early Pleistocene cave of Trlica in northern Montenegro and the Late Pleistocene cave of Baranica in southeast Serbia are described. The Early Pleistocene *Pachycrocuta brevirostris*, and the Late Pleistocene *Crocuta spelaea* are coprolite-producing species. Although the pollen concentration was rather low, the presented analyses add considerably to the much-needed knowledge of the vegetation of the central Balkans during the Pleistocene. Pollen extracted from a coprolite from the Baranica cave indicates an open landscape with the presence of steppe taxa, which is in accordance with the recorded conditions and faunal remains. Pollen analysis of the Early Pleistocene samples from Trlica indicate fresh and temperate humid climatic conditions, as well as the co-existence of several biotopes which formed a mosaic landscape in the vicinity of the cave.

Key words: pollen, coprolites, Pleistocene, cave, Serbia, Montenegro.

Апстракт. У раду су приказани резултати анализе полена екстрахованог из копролита фосилних хијена из раног плеистоцена карстне шупљине Трлица у северној Црној Гори и касног плеистоцена пећине Бараница у југоисточној Србији. Копролити потичу од две различите врсте хијена, раноплеистоценске врсте *Pachycrocuta brevirostris*, и касноплеистоценске врсте *Crocuta spelaea*. Мада је број екстрахованих поленових зрна мали, резултати анализе полена из ових узорака дају значајан допринос познавању плеистоценске вегетације централног Балкана, за које иначе постоји врло мало података.

Кључне речи: полен, копролити, плеистоцен, пећина, Србија, Црна Гора.

Introduction

Pleistocene pollen data from the central Balkans are very scanty (Janković *et al*. 1984; Nikolić 1992). The Early Holocene is somewhat better covered. Data on the history of Postglacial vegetation come from the Vlasina peat-bog in south-eastern Serbia (Černjavski, 1938) and the Jelica Mountain in western Serbia (Šercelj & Culiberg 1992). Important information about the Early Holocene vegetation comes from the Vlasac archaeological site found in the Iron Gates sector of the Danube Gorge. It is a Lepenski Vir culture site, excavated in the 1970s (Garašanin 1978; Srejović & Letica 1978). Pollen analysis has been performed on human coprolites (Carciumaru 1978), and gave a rather large number of pollen grains. Findings of coprolites at Pleistocene sites in Montenegro and Serbia gave hope about the potential of palynology in these food stuffs, and provide previously missing data concerning the vegetation.

Localities

Baranica. It is a cave in eastern Serbia, situated on the right bank of the Trgoviški Timok River, approximately 5 km south-east of the town Knjaževac. It is a composite cave consisting of many narrow cave passages. There are several entrances into the cave system; one positioned 15 m above the river bed (260 m altitude) opens into an entrance chamber 5 m wide. This part of the cave is named Baranica I. The other entrance

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is located about 20 m above the first (280 m-asl), and is named Baranica II.

Archaeological excavations were first performed in 1994 in Baranica I. The site became renowned because many bones were found that "looked like" bone implements, which were later recognized in further research as hyaena-made. Nevertheless, archaeological implements were found during the continuation of the excavations between 1995 and 1997. Upper Palaeolithic artifacts were found in Baranica I (MIHAILOVIĆ *et al*. 1997) and numerous faunal remains in both Baranica I and Baranica II (DIMITRIJEVIĆ 1997, 1998).

The accumulation of faunal remains is mostly due to the scavenger activity of cave hyenas (DIMITRIJEVIĆ 2004), which produced a very rich vertebrate assemblage. The list of large mammals found gives a good representation of the fauna in the region at this period, with more taxa being found than in any other cave locality in Serbia (Table 1). The regional importance of Baranica is accentuated by the fact that it is the first locality in the region with fauna reflecting the conditions of the Last Glacial Maximum. As opposed to other excavated sites in Serbia, Baranica also shows cold fauna, including the wolverine, *Gulo gulo* and the wooly rhino, *Coelodonta antiquitatis*. It is also worth stressing the absence of warm temperate species such as the roe deer and the wild boar.

Table 1. List of the large mammals found in the caves Baranica I and II, Late Pleistocene, eastern Serbia.

Order	Species
Lagomorpha	*Lepus* sp.
	Ochotona pusilla (PALLAS)
Carnivora	*Canis lupus* LINNAEUS
	Vulpes vulpes (LINNAEUS)
	Ursus spelaeus ROSSENMÜLLER
	Gulo gulo (LINNAEUS)
	Martes martes LINNAEUS
	Meles meles (LINNAEUS)
	Mustela nivalis LINNAEUS
	Crocuta spelaea (GOLDFUSS)
	Panthera spelaea (GOLDFUSS)
	Panthera pardus (LINNAEUS)
	Felis silvestris SCHREBER
Proboscidea	*Mammuthus primigenius* (BLUMENBACH)
Perissodactyla	*Coelodonta antiquitatis* (BLUMENBACH)
	Equus ferus BODDAERT
	Equus hydruntinus REGALIA
Artiodactyla	*Megaloceros giganteus* (BLUMENBACH)
	Cervus elaphus LINNAEUS
	Bos primigenius BOJANUS
	Bison priscus (BOJANUS)
	Capra ibex LINNAEUS
	Rupicapra rupicapra (LINNAEUS)

Besides large mammal bones, remains of small mammals, birds, herpetofauna and fish are also found. Nineteen species of rodents have been identified (Table 2). Similar to large mammals, the small mammal remains indicate the cold conditions of the Last Glacial period, especially boreal and arctic species such as *Microtus gregalis* and *Dicrostonyx* (BOGIĆEVIĆ 2005).

Table 2. List of the rodent fauna found in the caves Baranica I and II, Late Pleistocene, eastern Serbia.

Family	Species
Sciuridae	*Spermophilus* cf. *citellus* (LINNAEUS)
Castoridae	*Castor fiber* LINNAEUS
Dipodidae	*Sicista subtilis* (PALLAS)
Cricetidae	*Cricetulus migratorius* (PALLAS)
	Cricetus cricetus LINNAEUS
	Mesocricetus newtoni NEHRING
	Arvicola terrestris (LINNAEUS)
	Chionomys nivalis (MARTINS)
	Microtus arvalis (PALLAS)
	Microtus agrestis (LINNAEUS)
	Microtus gregalis (PALLAS)
	Terricolla subterraneus (DE SÉLYS-LONGCHAMPS)
	Clethrionomys glareolus (SCHREBER)
	Dicrostonyx sp.
	Lagurus lagurus (PALLAS)
Muridae	*Apodemus sylvaticus* (LINNAEUS)
Spalacidae	*Spalax leucodon* (NORDMANN)
Gliridae	*Dryomys nitedula* (PALLAS)
	Muscardinus avellanarius (LINNAEUS)

Trlica. It is a karstic cavern which opens at 770 m-asl in Triassic limestones, located on the slope of the so-called Trlica Hill, near the city of Pljevlja in northern Montenegro. The Trlica Hill surmounts a Tertiary coal basin and the valley of the Ćehotina River. Palaeontological excavations were performed in three short campaigns (1988, 1990, and 2001). Abundant remains of mammals were found embedded in clastic deposits infilling the karstic cavern (Table 3) (DIMITRIJEVIĆ 1991, 1997, 2004; FORSTEN & DIMITRIJEVIĆ 1995; CRÉGUT & DIMITRIJEVIĆ 2006). Large herbivores, particularly ruminants, are numerous, while carnivores and rodents are each represented by a few bones and/or teeth. Several layers are distinguished in the cave profile (layers I–V), showing that the conditions were changing during deposition, although probably not during a long time span. The stratigraphic age has been correlated to the upper part of the Early Pleistocene (DIMITRIJEVIĆ 1990) and more precisely defined by *Stephanorhinus* cf. *hundsheimensis* (CODREA & DIMITRIJEVIĆ 1997), which correlates the fauna with biozones 20–22 (GUÉRIN 1980) and MQ3 (late Early Pleistocene)

Table 3. List of the mammal fauna found in the Trlica Cave, Early Pleistocene, Montenegro.

Order	Species
Rodentia	*Dolomys dalmatinus* KORMOS
	Hystrix sp.
Carnivora	*Canis etruscus* MAJOR
	Canis falconeri FORSYTH MAJOR
	Vulpes sp.
	Ursus etruscus CUVIER
	Gulo schloseri KORMOS
	Mustelidae gen. et sp. indet.
	Homotherium cf. *crenatidens* FABRINI
	Panthera cf. *gombaszoegensis* KRETZOI
	Lynx sp.
	Pachycrocuta brevirostris (AYMARD)
Proboscidea	*Palaeoloxodon antiquus* (FALCONER & CAUTLEY)
Perissodactyla	*Stephanorhinus* cf. *hundsheimensis* (TOULA)
	Equus stenonis COCCHI
	Equus cf. *major* BOULE
Artiodactyla	*Alces* cf. *carnutorum* (LAUGEL)
	Eucladoceros giulii KAHLKE
	Cervus elaphus LINNAEUS
	Megalovis balcanicus CRÉGUT-BONNOUIRE & DIMITRIJEVIĆ
	Soergelia intermedia CRÉGUT-BONNOUIRE & DIMITRIJEVIĆ
	cf. Rupicaprinae
	Bison (*Eobison*) sp.

(AGUSTI *et al*. 1987). The presence of *Hystrix* indicates a temperate climate.

Samples

Two coprolites, one from the Baranica Cave, and another one from the site of Trlica were extracted for pollen analysis in 2004. The number of pollen grains was low, especially in the Trlica sample. For this reason, five more coprolites were analysed in 2005, which gave better results (Fig. 1). Their dimensions and mass are given in Table 4.

The specimen from Baranica comes from the part of the cave named Baranica II. Specimens from Trlica originate from the layers I, sublayer Ia (TRL 90/10/19, TRL 90/10/21, and TRL 90/34/7) and IV (TRL 90/80/2, TRL 90/82/2, and TRL 90/84/4).

By their shape, dimensions and texture, all specimens resemble hyena coprolites, especially those specimens from Trlica which are complete. The specimen from Baranica is a broken half, showing a compact structure and homogeneous composition on the breakage, which is essentially calcium phosphate originating from the bones consumed by this animal. It is known that pollen is incorporated into coprolites in different ways: absorbed with food (meat and stomach contents of the prey), with water, by the licking of fur or paws and, in some cases, even by ingesting vegetable matter. Taphonomic observations on fresh hyaena dung show that the pollen spectra obtained from coprolites gave relatively unbiased pictures of the landscape (SCOTT *et al*. 2003). Thus, fossil coprolites can provide available palaeoenvironmental information (LEROI-GOURHAN 1966; MOE 1983; SCOTT 1987; ARGANT 1990, 2004; CARRIÓN *et al*. 2001; YLL *et al*. 2006). As they generally correspond to a very short period of time, they should also be indicators of the season when the coprolites were produced (ARGANT 1990, 2004; TOMESCU 2006).

According to the faunal list from the two localities, these coprolites might originate from two different hyena species, Early Pleistocene *Pachycrocuta brevirostris*, and Late Pleistocene *Crocuta spelaea* (ERXLEBEN). Even if the feeding habits of these two species could slightly differ, the chemical composition and morphology of their coprolites look similar. Their life habits and territorial range should be reasonably similar to those of the recent species *Crocuta crocuta*, mostly a scavenger. Since it is considered that members of the latest species cover a territory with-

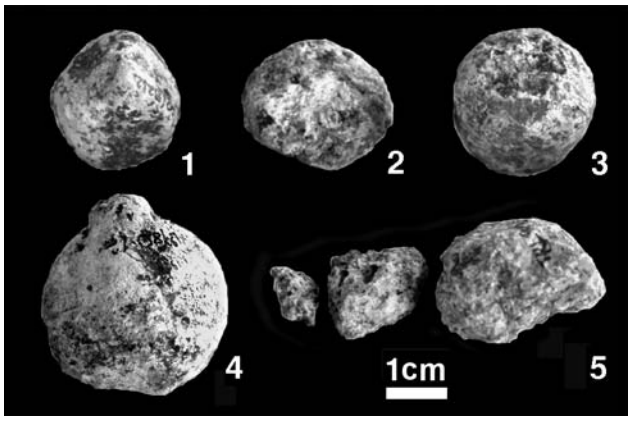

Fig. 1. Five analyzed coprolites from the Early Pleistocene of Trlica, Montenegro. **1,** TRL 90/82/2; **2,** TRL 90/34/7; **3,** TRL 90/84/4; **4,** TRL 90/80/2; **5,** TRL 90/10/19.

Table 4. Dimensions and masses of the coprolites from Trlica, Early Pleistocene, Montenegro. * measurement was impossible because the coprolite was broken

	Length (mm)	Width (mm)	Thickness (mm)	Mass (g)
TRL90/8012	32.3	30.0	32.1	24.2
TRL90/10119	27.0	17.2	*	6.7
TRL90/3417	24.2	22.0	25.0	13.6
TRL90/8212	21.2	20.0	27.1	13.5
TRL90/8414	25.0	*	*	6.1

in a distance up to 4 km (ARGANT 2004), the pollen analyses from coprolites are expected to give data on climatic and edaphic conditions in the near vicinity of the sites.

Sample preparation

The surface was first very precisely cleaned, by intensive brushing under a jet of water, in order to remove potentially polluted material and to ensure that only the content of the coprolite was treated.

The content of the coprolite was then prepared by concentration in a dense liquid, comprising the following principal stages:

- Decarbonatation with hydrochloric acid, desilicification with hydrofluoric acid (concentration 40%, cold test).
- Removal of the organic matter by heating in potassium hydroxide solution for 10 minutes.
- Concentration in a dense solution (Thoulet solution, potassium iodomercurate d = 2)
- Mounting in glycerin.
- Washing out with distilled water after each operation.

Results of the pollen analysis, Baranica II Cave (Table 5)

The sample from the Baranica Cave came from half of the coprolite (inventory number BAR II 97/12/3).

Altogether it yielded 13 pollen grains and only 7 taxons. Trees were mostly represented by *Pinus* and *Juniperus*, both genera heliophilous and pioneers. A single deciduous tree was present: *Fraxinus*, a tree demanding moist soil and good exposure to sunlight. Its presence most probably depicting a gallery forest. Among herbs, the genus *Artemisia* was the best represented. It was accompanied by an Asteraceae of the *Carduus* type, one Poaceae and one pollen grain of Scrophulariaceae.

According to these results, it is obviously not possible to precisely reconstruct the past vegetation. Yet, some information can be given: a very open landscape with the presence of steppe taxa related to rather rigorous climatic conditions. Together with the fauna, this is in accordance with the conditions of the Last Glacial. It is not possible to be more precise because of the small number of pollen grains and the isolated character of the sample.

Results of the pollen analysis, Trlica Cave (Table 5, Fig. 2)

Only three pollen grains were extracted out of the first sample from Trlica, (TRL 90/1021), two originating from trees, and one from grass. Nevertheless, even this small number of pollen grains showed the absence

Table 5. Content of pollen and spores from the Late Pleistocene *Crocuta spelaea* coprolite from Baranica II Cave, and Early Pleistocene *Pachycrocuta brevirostris* coprolites from the Trlica Cave. AP, arboreal pollen; NAP, nonboreal pollen.

TAXA \ SAMPLE	BAR II 97/1213	TRL 90/1021	TRL 8012	TRL 8414	TRL 3417	TRL 8212	TRL 10119
Alnus			11		1		
Quercus		1	7				
Corylus		1	6				1
Pinus	2		5				
Fagus			4				
Abies			2				
Betula			2				
Carpinus			1				
Buxus			1				
Juniperus	1		1				
Fraxinus	2						
AP	**5**		**40**	**0**	**1**	**0**	**1**
NAP	**8**		**16**	**0**	**0**	**0**	**0**
POACEAE	1		2				
Artemisia	3						
CYPERACEAE			2				
RANUNCULACEAE		1					
SCROPHULARIACEAE	1						
Carduus type	1						
Plantago			1				
Calluna			6				
Typha latifolia			1				
Indeterminate	2		4				
Total	**13**		**56**	**0**	**1**	**0**	**1**
Spores de *Sphagnum*			18				
Phytoliths			2				
Ind. Microfossils		3					
Indet. Sporange		1					

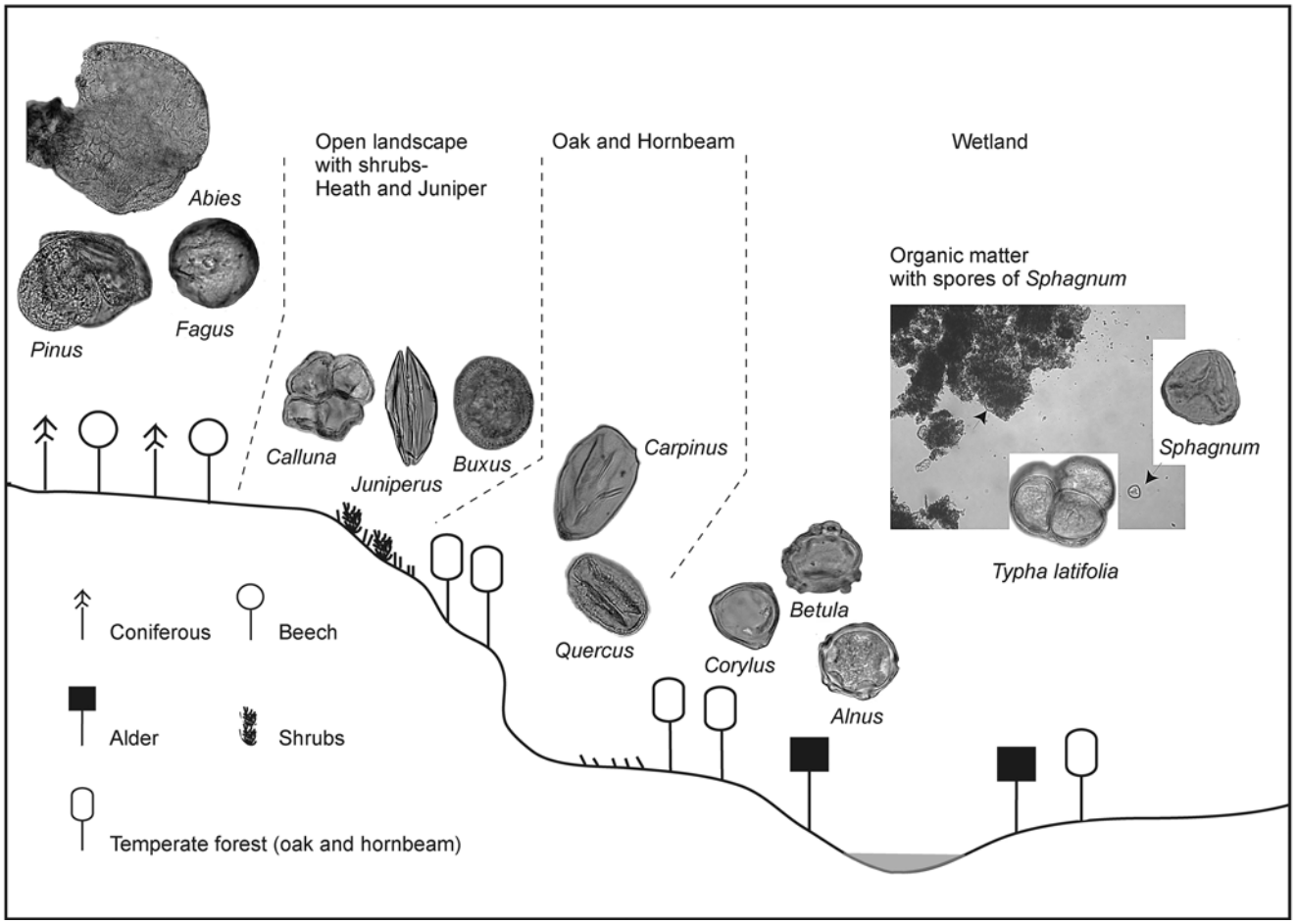

Fig. 2. Pollen extracted from the coprolite TRL 90/80/2 from Trlica, Early Pleistocene, Montenegro. Hypothetical distribution of the taxa along an imaginary profile.

of a steppe environment. *Quercus* and *Corylus* are mesothermophilous trees, demanding temperate and humid conditions.

Due to the small number of grains in this sample, five more coprolites were analysed. All of them were completely searched under the microscope.

Two coprolites were completely sterile: TRL 90/84/4 and TRL 90/82/2. Two others contained a single grain each: TRL 90/34/7 (*Alnus*) and TRL 90/10/19 (*Corylus*). Only the largest and best preserved coprolite, TRL 90/80/2 showed a relatively rich content, with a total of 56 pollen grains (Table 5).

All of the latter were very well preserved, and in some of them the cell structure is still observable. Fifteen different taxons were identified. Tree pollen grains dominated with 40 grains out of the total of 56. Although the sum of pollen grains was not sufficient to calculate percentages, they were sufficient to suggest that wooded areas existed in the animal habitat, and that they occupied an important portion of the region.

A quarter of the tree pollen grains originated from alder (*Alnus*), a tree demanding soil humidity. The animal probably visited an alder forest and, consequently a field in the vicinity of a stream and/or a swamp. This was confirmed by observing moss fibres together with 18 spores of *Sphagnum* cf. *fallax*, a species which is characteristic of swampy fields, peat bogs, alder fields or humid and sour prairies (JAHNS 1989). *Sphagnum* spores do not disperse widely; consequently in this case they could have been absorbed by an animal only at the place at which they developed. Some of them were still sealed in an organic fibrous matter (Fig. 2), which could originate only from swampy alder terrains. A humid environment where animals were coming to drink is also illustrated by a tetrad of club grass (*Typha latifolia*), a species which grows on low elevations, and, in this case, was probably not very far from the cave. Birch undoubtedly represented a part of this humid formation. Oak (*Quercus*) and hazel (*Corylus*) seem to have been quite abundant. Hornbeam (*Carpinus*) and ground box (*Buxus*) were also observed, which can grow in low humid places, but also on more arid slopes, while on higher elevations there were fir (*Abies*) and beech (*Fagus*), although, the presence of fir and beech in a valley cannot be excluded. Finally, the presence of *Juniperus*, heliophilous taxon signalling the presence of openings in the tree cover occupied also by grasses (Poaceae, plantain) and *Calluna* (Ericacae), was also registered.

The complete pollen content from the coprolites of Trlica enables a tentative reconstruction of the environment in which the Trlica fauna existed. A summary of this reconstruction is given in Fig. 2, illustrating a possible distribution of the identified vegetation, as well as providing photographs of some of the pollen grains extracted from the coprolite TRL 90/80/2.

The reconstruction is, of course, hypothetical, and should be taken with caution. The coexistence of several biotopes is suggested, forming a mosaic landscape where trees occupied an important place. At the bottom of the valley, the humid bank of a stream or a pond was mostly occupied by alder, at the foot of which a moss (*Sphagnum*) carpet had developed. Mesothermophilous trees (oak, hornbeam, hazelnut), as well as shrubs (juniper, ground box and broom) were growing on the slopes, while at higher levels there were fir-beech forests. Throughout this area, open spaces were interspersed. The observed combination of species indicates temperate climatic conditions, fresh and humid, which enabled development of different biotopes dependent on the altitude and on edaphic conditions.

Conclusion

The number of pollen grains extracted from the coprolites from the two cave localities, Late Pleistocene Baranica in Serbia and Early Pleistocene Trlica in Montenegro, was rather low and gave only modest possibilities for the reconstruction of the vegetation milieu of the surroundings of the two caves. Yet, for those two localities, coprolite analyses gave the only data on the vegetation. This may also be the case for other cave localities in which coprolites are found, since cave sediments are often unsuitable for fossilisation of plant remains, and pollen grains particularly. Since it is well known that important faunal remains, sometimes only available for certain regions or time spans, are often related to caves, the instances of pollen preservation in coprolites are even more valuable. Pollen is not always present in coprolites but encompassed in their mass, pollen grains are sometimes safe from digestive processes and oxygen impact and are, therefore, well preserved. When coprolites are numerous, and their stratigraphical position well-defined, they should be regarded as important for pollen sampling. On the basis of the analyses of pollen extracted from the coprolite from the Baranica Cave an open landscape with the presence of steppe taxons related to rather rigorous climatic conditions is assumed, which is in accordance with the conditions of the Last Glacial and faunal remains recorded. The pollen content from the coprolites of Trlica enabled a tentative reconstruction of the environment. Temperate climatic conditions were indicated, fresh and humid, as well as the co-existence of several biotopes which formed a mosaic landscape, depending on the altitude and edaphic conditions.

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Резиме

Анализа полена из фосилних копролита хијена из плеистоцена Србије и Црне Горе

Мало има података о плеистоценској вегетацији централног Балкана, док је, захваљујући анализама полена, ранохолоценска вегетација нешто боље позната. Један од примера реконструкције ранохолоценске вегетације је полен анализа из хуманог копролита са археолошког налазишта Власац. Када смо на плеистоценским налазиштима Бараница у Србији, и Трлица у Црној Гори, поред фосилних костију и зуба, открили и копролите хијена, понадали смо се да се у њима сачувао полен, јер су седименти са истих налазишта, пећински кластити, неповољни за очување полена и биљних остатака уопште.

Узорци копролита, један из горњоплеистоценских слојева пећине Бараница у Србији, и шест из доњоплеистоценских слојева Трлице у Црној Гори (табела 1), послати су у лабораторију у Француску, где су, уобичајеним лабораторијским методама, поленова зрна издвојена из копролита и направљени танки пресеци.

Узорак из Баранице садржао је свега 13 поленових зрна, односно 7 таксона (табела 2). Дрвеће је углавном представљено хелиофилним, пионирским родовима бором (*Pinus*) и клеком (*Juniperus*). Од листопадног дрвећа заступљен је само јасен (*Fraxinus*), дрво коме је потребно влажно земљиште и осветљеност, и чије је присуство вероватно у вези са близином реке. Од трава и грмља, заступљен је пелен (*Artemisia*), затим Asteraceae типа *Carduus*, и по једно зрно Poaceae, Ranunculaceae и Scrophulariaceae. На основу овако малог броја поленових зрна, није, наравно, могуће реконструисати вегетацију, али је ипак очигледно да се ради о отвореним пределима са присуством степских елемената у оштрим климатским условима. То су услови који одговарају последњем глацијалу, односно у сагласности су са одредбом старости на основу фаунистичких остатака.

У узорцима из доњоплеистоценских наслага Трлице број очуваних поленових зрна био је разнолик: у једном се налазило свега три зрна, у два по

једно зрно, два узорка су била потпуно стерилна, а из једног је издвојено 56 зрна (сл. 1; табела 1 и 2).

Поленова зрна су веома добро очувана, и на некима се виде детаљи ћелијске структуре. Одређено је 15 различитих таксона. Доминира полен дрвећа. Добар део поленових зрна дрвећа потиче од јове, дрвета коме је неопходна влага, односно непосредна близина текуће или стајаће воде за преживљавање. Овакви услови одговарају и маховини тресетници (*Sphagnum* cf. *fallax*) од које је пронађено 18 спора. Неке од спора су још увек уклопљене у фиброзну органску материју (сл. 2). На влажну средину указују и рогоз (*Typha latifolia*) и бреза (*Betula*). Прилично бројни су храст (*Quercus*) и леска (*Corylus*). Граб (*Carpinus*) и шимшир (*Buxus*) могу да расту у хумидним низијама, али и на сувљим падинама, док су на вишим деловима терена расли јела (*Abies*) и буква (*Fagus*). Најзад, присуство хелиофилног рода *Juniperus* указује на постојање и отворених простора на којима су расле траве (Poaceae) и *Calluna* (Ericacae).

Покушај реконструкције вегетације у околини Трлице приказан је на сл. 2, на којој је могући распоред индентификованих таксона илустрован сликама појединачних поленових зрна, издвојених из најбогатијег узорка TRL 90/80/2. Реконструкција је, наравно, хипотетичка, и треба је опрезно узети у обзир. Претпоставља се коегзистенција неколико биотопа у мозаичном распореду. Дрвеће игра важну улогу. У долини, влажне обале речног тока, или баре, заузима углавном јова, испод које се развија тепих тресетнице (*Sphagnum*). Мезотермофилно дрвеће (храст, граб, леска), као и грмље (клека, врес и рогоз) расли су на падинама, док су се на узвишењима простирале јелово-букове шуме, испрекидане пропланцима. Асоцијација указује на умерене климатске услове, свеже и влажне, који су омогућили развој различитих биотопа, зависно од висинских и едафских услова.

Полен није увек присутан у копролитима, али, уклопљена у масу копролита, поленова зрна понекад буду сачувана од дигестивних процеса и дејства кисеоника. Када су копролити бројни, а њихова стратиграфска припадност дефинисана, могу бити важни извор узорака за полен анализу, нарочито на оним налазиштима, на којима недостају други материјали погодни за очување полена, као што је случај са пећинским наслагама.