

The fossil and recent malacofauna of the island of Susak (Croatia) (Gastropoda: Prosobranchia, Basommatophora, Stylommatophora)

With 4 Figures and 1 Table

VESNA ŠTAMOL & MARIJA POJE

Abstract. Field research into the recent and fossil malacofauna on the island of Susak (Croatia) discovered 45 species of land snails. Only 28 taxa had hitherto been recorded in the literature. We consider that the taxa *Paludina* spec., *Physa* spec., *Aplexa hypnorum*, *Planorbis* spec., *Pagodulina pagodula*, *Macrogastra ventricosa*, *Papillifera papillaris* should be deleted from the list either of the recent or the fossil malacofauna of Susak. As far as the taxa *Pomatias elegans*, *Rumina decollata*, *Delima bilabiata biasoletiana*, *Monacha cartusiana*, *Eobania vermiculata* are concerned, we would claim that they are recent on Susak and by no means fossil specimens, as has been suggested in the literature. *Truncatellina velkovrhi* was found among the recent snails, and this represents only its second known occurrence. - The malacofauna which has existed on Susak from the Upper Pleistocene till the present times is in its ecological features mainly steppe fauna adapted to a variety of climatic conditions; initially a warm and slightly humid climate, then cold and dry, and by the end of the ice age extremely humid and relatively warm, at present a eumediterranean climate. A consequence of such climatic changes was an almost total exchange of fauna, so that recent and fossil fauna have only one species in common. A zoogeographic analysis of recent and fossil malacofauna also shows that they differ significantly. In the case of the recent malacofauna, Mediterranean and east Adriatic elements predominate; amongst fossil malacofauna Holarctic, Palaearctic and European species are most prominent. - An analysis of fossil malacofauna has indicated the Upper Pleistocene origin of the sand deposits of the island of Susak, with stress on the fact that the youngest sequence belongs to the late ice age, i. e. the Dryas, which has not hitherto been demonstrated.

Kurzfassung. Die fossile und rezente Landschneckenfauna der Insel Susak (Kroatien) (Gastropoda: Prosobranchia, Basommatophora, Stylommatophora). - Im Laufe einer Untersuchung der rezenten und fossilen Malakofauna der Insel Susak (Kroatien) haben wir das Vorkommen von 45 Arten der Landschnecken festgestellt. In der Literatur sind bisher nur 28 Taxa angeführt. Wir sind der Meinung, daß die Taxa *Paludina* spec., *Physa* spec., *Aplexa hypnorum*, *Planorbis* spec., *Pagodulina pagodula*, *Macrogastra ventricosa*, *Papillifera papillaris* aus der Liste der rezenten Arten oder der Liste der fossilen Arten auf Susak gestrichen werden müssen. Was die Arten *Pomatias elegans*, *Rumina decollata*, *Delima bilabiata biasoletiana*, *Monacha cartusiana*, *Eobania vermiculata* betrifft, sind wir der Ansicht, daß diese zu den rezenten Arten auf Susak gehören und daß sie keineswegs fossil sind, wie in der Literatur behauptet wurde. Unter den rezenten Schnecken wurde auch *Truncatellina velkovrhi* gefunden, welches der zweite bisher bekannte Fundort ist. - Nach ihren ökologischen Merkmalen ist die Malakofauna, die seit dem Pleistozän auf Susak existiert, überwiegend eine Steppenfauna, die sich verschiedenen klimatischen Bedingungen angepaßt hat: zuerst an ein warmes und leicht feuchtes Klima, dann an ein kaltes

Addresses of the authors:

Vesna Štamol, mag. sci., Croatian Natural History Museum, Demetrova 1, 10000 Zagreb (Croatia)

Marija Poje, mag. sci., Institute of Paleontology and Quaternary Geology, Croatian Academy of Sciences and Arts, A. Kovačića 5, 10000 Zagreb (Croatia)

und trockenes Klima, am Ende des Eiszeitalters an ein extrem humides und relativ warmes Klima, und in der Gegenwart an ein eumediterranes Klima. Eine Folge solcher klimatischen Schwankungen war eine fast vollständige Umwandlung der Fauna, so daß die rezenten und die fossilen Arten nur ein einziges beiden gemeinsames Glied haben. Eine zoogeographische Analyse der rezenten und der fossilen Malakofauna zeigt, daß sie sich wesentlich voneinander unterscheiden. Bei der rezenten Fauna herrschen mediterrane und ostadriatische Elemente vor, wogegen die fossile Malakofauna vorwiegend holarktische, palaearktische und europäische Arten aufweist. - Die Analyse der Malakofauna deutet auf ein oberpleistozänes Alter der Sandschichten auf Susak hin, mit Betonung der Feststellung, daß die jüngste Sequenz in das späte Eiszeitalter gehört, d. h. in das Dryas, worauf bisher noch niemand hingewiesen hat.

Introduction

Pleistocene sandy strata facilitating research into Quarternary malacofauna are rare in the Adriatic region. Their presence on the island of Susak makes the island highly suitable for research into fossil fauna. On the other hand, these deposits give the island of Susak features that are remarkably different from those of the other Adriatic islands, and for this reason the island has long attracted the interest of naturalists. Research has been mainly directed to solving the problem of the origin of the sand on Susak and generally into the pedology and flora of Susak. Molluscs have been mentioned only incidentally as evidence of the presence of sand on Susak from fresh water, land or marine sources (FORTIS, 1771; LORENZ, 1859; TOMMASINI, 1862; MARCHESETTI, 1882; STACHE, 1888; KIŠPATIĆ, 1910; HOERNES, 1911; HIRC, 1914; BLAŠKOVIĆ, 1957; GRAČANIN, 1957; MARKOVIĆ-MARJANOVIĆ, 1966; BOGNAR et al., 1983, 1989). Very few studies of malacofauna mention Susak, and its malacofauna is recorded in a desultory fashion (STURANY, 1915; WAGNER, 1924, 1925; GRAACK, 1989). The fossil and recent malacofauna of Susak have hitherto not been investigated systematically.

In our research we have tried to define the compositions and the features of the recent and fossil land malacofauna of Susak, the succession of the palaeobiocoenoses features in the evolution of the Upper Pleistocene and the reasons which led to this.

A comparison of the recent land malacofauna of Susak with that of the nearest island, Lošinj, notes their similarities and differences and possible reasons are suggested. To the same end a comparison was made between the fossil malacofauna of Susak and fossil Pleistocene malacofauna of Savudrija in Istria.

The natural features of the island of Susak

The island of Susak (Sansego, Bodulei) belongs to the north-eastern Adriatic archipelago and is situated in the outer group of Kvarner islands (Fig. 1). It lies 7.4 kms west of the island of Lošinj. Its area is no more than 3.76 sq. kms. Its highest point is Garba (98 m above sea-level) (STRAŽIČIĆ, 1975). The island has the appearance of steps sloping down steeply to the shoreline, which is only slightly indented with an overall length of 11.25 kms (BLAŠKOVIĆ, 1957).

Although Susak does not have its own meteorological station, we may assume that the (macro)climatic conditions there resemble those on Lošinj - a typical Mediterranean climate with hot, dry summers and mild, rainy winters. The average annual temperature is about 15°C, with an average annual rainfall of 825 mm (BLAŠKOVIĆ, 1957).

Susak is built of sandy loess or loess-like deposits more than 30 m thick and sedimented on the Cretaceous limestones. These deposits are of aeolian origin and of Pleistocene age (ROGLIĆ, 1962; MARKOVIĆ-MARJANOVIĆ, 1966; WEIN, 1976; BOGNAR, 1983; BOGNAR et al., 1989; CREMASSI, 1990; BOGNAR et al., 1992).

The soils on Susak are yellowish-grey or brown colored carbonate in composition and differ from the cognate soils of the littoral Karst by a lighter mechanical constitution, with lower humus and nitrogen content and specific forms of limestone concretion (GRAČANIN, 1957).

There are no watercourses on Susak. There are three wells fed by precipitation, but which tend to dry up during the summer.

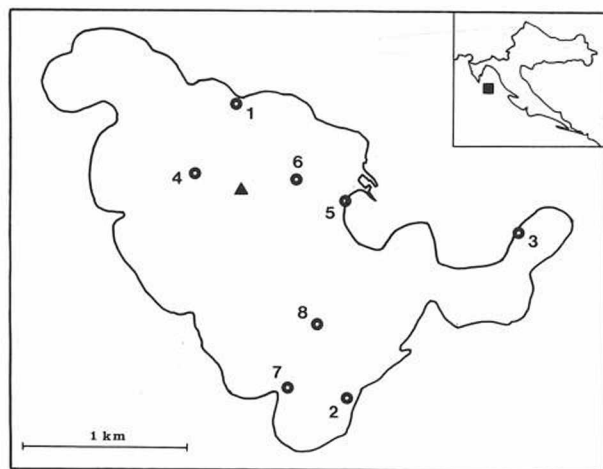


Fig. 1: A map of the island of Susak showing collection sites. Sites are denoted by numbering referring to the list of sites in the text.

A large part of Susak is covered by cultivated land in the form of vineyards. The margins of the cultivated land and of the intersecting paths have been planted with reeds (*Arundo donax*) to prevent erosion of the soil by wind and rainfall. Uncultivated land and abandoned vineyards are covered by grassland and increasingly dense bramble thickets (*Rubus spec.*). There are natural woods or macchia on Susak, and this is what gives the island the characteristic vegetational physiognomy. There are very few trees, and all of them have been deliberately planted. Black pine (*Pinus nigra*) has been planted to little effect, locust trees (*Robinia pseudacacia*) with rather more success.

List of sites

The sites are listed in alphabetical order, and their location, with the corresponding numbers may be seen in Fig. 1. The names of sites have been taken from the fundamental national map: the island of Susak, sheets 16, 17 and 26, scale 1:5000 (1988). In the case of each site the UTM notation of relevant sector measuring 10×10 kms has been quoted, along with the elevation above sea-level, the habitat and the collection date. The letter F has been used to mark sites where fossil samples were collected, and R is used to mark recent samples. The UTM designation of the sites has been worked out by reference to Sheet 252-D UTM on the world map 1:500000 (1970).

References to the literature with the author's name, year and page numbers have also been compiled. They cover the island a whole, either because authors have not given precise details of a site, or because it is difficult to identify the exact point of collection referred to in the article (Hirc, 1914). Thus, all the data in the literature refer to the island, denoted in the list by the letter S.

1. Grabrovica (bay), VK42, 2 m s. l., stony grassland, 19.10.1990: R.
2. Obis (bay), VK42, 20 m s. l., grassland, 21.10.1990: R.
3. Ogradica (region), VK42, 0-37 m s. l., landslide, 22.10.1990: F (see Fig. 2)
4. Plase (region), VK42, 83 m s. l., locust grove, 21.10.1990: R, F.
5. Susak (port), VK42, 5 m s. l., wayside vegetation, 22.10.1990: R.
6. Susak (port) - Garba (summit), VK42, 40 m s. l., grassland, 22.10.1990: R.
7. Susanka (region and bay), VK42, 30 m s. l., grassland, 21.10.1990: R, F.
8. Zamarišica (region), VK42, 45 m s. l., grassland, 20.10.1990: R.

S - Susak (island), VK42: LORENZ (1859: 90, 93); TOMMASINI (1862: 838); MARCHESSETTI (1882: 294, 301, 303); STACHE (1888: 258); HIRC (1914: 9, 10, 14, 15, 16); STURANY (1915: 400, 401); WAGNER (1924: 112, 1925: 68); MARKOVIĆ-MARJANOVIĆ (1966: 33, 35, 37, 41); BOGNAR et al. (1983: 10, 11; 1989: 11, 12); GRAACK (1989: 10, 11, 13, 14, 15, 16, 17).

Material and methods

Fossil fauna was collected on vertical profiles where sampling was possible continuously from the bottom to the top of the profile. Samples were taken at each change in sediment,

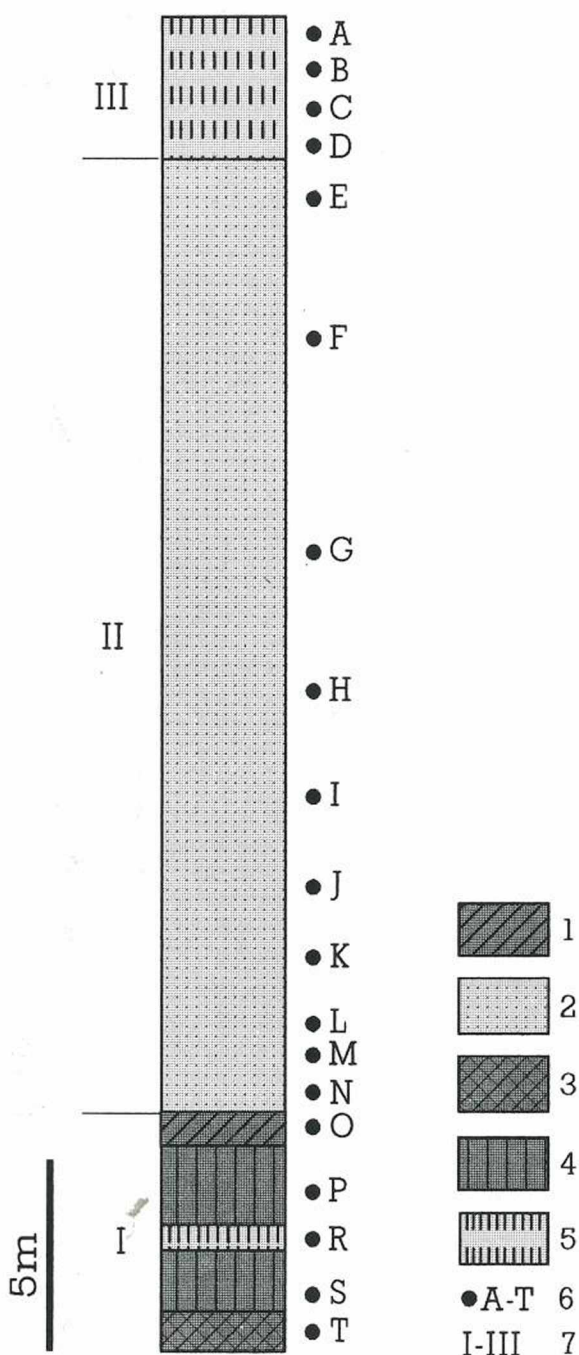


Fig. 2: Schematic sedimentary log of the profile Ogradica (site no. 3): 1 - dark-brown fossil soil; 2 - aeolian sands; 3 - basic red fossil soil („terra rossa“); 4 - brown fossil soils; 5 - loess/loess-like deposits; 6 - A-T samples; 7 - I-III = sequences.

in quantities between 2 and 3 kgs. In the laboratory procedure the sediment was mixed with water and passed through filters with mesh sizes declining to a minimal diameter of 0.9 mm.

Recent fauna was collected by taking individual specimens of the larger snails, and also through soil samples of ca. 2 dm³. Care was taken to ensure that all the typical biotopes were

included as well as the microhabitats of the snails. After drying and passing through a series of sieves with decreasing mesh down to 1×1 mm the snails were picked out from the samples.

Identification was carried out on the basis of conchological features as in BOLE (1969), KERNEY et al. (1983), LOZEK (1964), NORDSIECK (1969), SUBAI (1980). Taxonomical names were quoted according to KERNEY et al. (1983), and taxa not included in that work were classified according to JAECKEL et al. (1958). Ecological classification of species was carried out according to LOZEK (1964), and identification of the zoogeographical elements according to KERNEY et al. (1983).

Results and discussion

In 32 samples from four sites 1,957 specimens of fossil snails were collected and 23 species were identified. 20 samples from 7 sites yielded 4,069 specimens, and 23 recent species were identified. The material collected was housed in the General collection of recent malacofauna in the Croatian Natural History Museum (Zagreb, Croatia), in the Institute of Paleontology and Quaternary Geology in the Croatian Academy of Sciences and Arts (Zagreb, Croatia), and in Staatliches Museum für Tierkunde Dresden (Dresden, Germany).

1. List of snails

This list includes both recent and fossil malacofauna. In the case of each taxon, literature data on the area investigated are given (if they exist). Data extracted from the literature include the names (synonyms) by which taxon is referred in the relevant work, the author's name, the year of publication, and the page reference where the taxon is related to Susak. As with the data taken from the literature and quoted above, these references cannot always be linked with particular sites on Susak. Data relating to our field research of fossil fauna are marked by the letters TF, recent fauna are identified under TR. The data include the enumeration of sites identified from the list of sites and from the Fig. 1. Occasionally, fossil specimens were discovered during the search for recent malacofauna, and vice versa, such finds are marked in the list by a star (*).

1. ?*Viviparus* spec.

Paludina: LORENZ (1859: 90).

2. *Pomatias elegans* (O. F. MÜLLER, 1774)

Cyclostoma: LORENZ (1859: 90): VK42 - S;

Cyclostoma elegans: LORENZ (1859: 93): VK42 - S;

Cyclostomus reflexus: HIRC (1914: 9): VK42 - S;

Cyclostomus elegans: HIRC (1914: 10): VK42 - S;

Cyclostomus: HIRC (1914: 15): VK42 - S;

Pomatia elegans: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37): VK42 - S;

Pomatias elegans: GRAACK (1989: 10): VK42 - S;

TR: VK42 - 2, 4, 6, 7, 8;

TF: VK42 - 4*, 7*.

3. *Physa* spec.

Physa: HIRC (1914: 16): VK42 - S.

4. *Aplexa hypnorum* (LINNAEUS, 1758)

Aplexa hypnorum: MARCHESETTI (1882: 294, 301): VK42 - S;

Aplexa hypnorum: HIRC (1914: 10): VK42 - S.

5. *Planorbis* spec.

Planorbis: MARCHESETTI (1882: 294, 301): VK42 - S;

Planorbis: STACHE (1888: 258): VK42 - S;

Planorbis: HIRC (1914: 10, 16): VK42 - S.

6. *Succinea oblonga* DRAPARNAUD, 1801
Limnaeus: LORENZ (1859: 90): VK42 - S;
Succinea: LORENZ (1859: 90): VK42 -S;
Limnaeus minutus: LORENZ (1859: 93): VK42 -S;
Limnaeus minutus: HIRC (1914: 10): VK42 - S;
Limnaeus: HIRC (1914: 14): VK42 - S;
Succinea spec.: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37, 41): VK42 - S;
Succinea spec.: BOGNAR et al. (1983: 10): VK42 - S;
Succinea spec.: BOGNAR et al. (1989: 11): VK42 - S;
Succinea oblonga: GRAACK (1989: 11): VK42 - S;
 TR: VK42 - 4*, 6*, 7*, 8*;
 TF: VK42 - 3, 4, 6, 7.
7. *Truncatellina callicratis* (SCACHI, 1833)
 TR: VK42 - 2, 4, 6, 7, 8.
8. *Truncatellina velkovrhi* (ŠTAMOL, 1995)
 TR: VK42 - 4.
9. *Vertigo angustior* JEFFREYS, 1830
 TF: VK42 - 7.
10. *Pagodulina pagodula* (DES MOULINS, 1830)
Pupa pagodula: MARCHESETTI (1882: 294): VK42 - S;
Pupa pagodula: HIRC (1914: 10): VK42 - S.
11. *Pupilla muscorum* (LINNAEUS, 1758)
 TR: VK42 - 4*, 6*, 7*, 8*;
 TF: VK42 - 4, 6, 7.
12. *Pupilla triplicata* (STUDER, 1820)
 TF: VK42 - 3, 4, 6, 7.
13. *Lauria cylindracea* (DA COSTA, 1778)
 TR: VK42 - 4, 6.
14. *Vallonia costata* (O. F. MÜLLER, 1774)
Vallonia spec.: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37, 41): VK42 - S;
Vallonia spec.: BOGNAR et al. (1983: 10): VK42 - S;
Vallonia spec.: BOGNAR et al. (1989: 11): VK42 - S;
 TR: VK42 - 2, 4, 6, 7, 8;
 TF: VK42 - 3, 4, 6, 7.
15. *Vallonia pulchella* (O. F. MÜLLER, 1774)
 TF: VK42 - 3.
16. *Chondrula tridens eximia* (ROSSMÄSSLER, 1837)
Pupa quinquedentata: LORENZ (1859: 93): VK42 - S;
Pupa quinquedentata: HIRC (1914: 10): VK42 - S;
Chondrula tridens eximia: STURANY (1915: 400): VK42 - S;
 TR: VK42 - 2, 6, 7, 8.
17. *Punctum pygmaeum* (DRAPARNAUD, 1801)
 TR: VK42 - 4*, 6*, 7*, 8*;
 TF: VK42 - 3, 4, 6, 7.
18. *Discus ruderatus* (FÉRUSAC, 1821)
 TR: VK42 - 6*, 7*, 8*;
 TF: VK42 - 3, 4, 6, 7.
19. *Vitrinidae* fam.
 TF: VK42 - 3.
20. *Vitrea subrimata* (REINHARDT, 1871)
 TR: VK42 - 2, 4, 6, 7, 8.

21. *Vitrea* spec.
TF: VK42 - 4.
22. *Nesovitrea hammonis* (STRÖM, 1765)
TR: VK42 - 4*, 7*, 8*;
TF: VK42 - 3, 4, 6, 7.
23. *Oxychilus cellarius* (O. F. MÜLLER, 1774)
Oxychilus cellarium austriacus: MARKOVIĆ-MARJANOVIĆ (1966: 33, 35, 37): VK42 - S;
Oxychilus cellarium austriacus: BOGNAR et al. (1983: 10, 11): VK42 - S;
Oxychilus cellarium austriacus: BOGNAR et al. (1989: 11, 12): VK42 - S;
TR: VK42 - 8.
24. *Oxychilus draparnaudi* (BECK, 1837)
TR: VK42 - 4, 8.
25. *Oxychilus inopinatus* (ULIČNÝ, 1887)
TR: VK42 - 6, 8.
26. *Oxychilus* spec.
TF: VK42 - 4.
27. *Limax* spec. (large)
TF: VK42 - 6.
28. *Limax* spec. (small)
TF: VK42 - 4, 7.
29. *Euconulus fulvus* (O. F. MÜLLER, 1774)
TR: VK42 - 4*, 6*;
TF: VK42 - 3, 4, 6, 7.
30. *Ceciloides aciculoides* (WESTERLUND, 1887)
TR: VK42 - 4, 6, 7, 8;
TF: VK42 - 3*, 4*.
31. *Rumina decollata* (LINNAEUS, 1758)
Bulimus decollatus: LORENZ (1859: 93): VK42 - S;
Bulimus decollatus: HIRC (1914: 10): VK42 - S;
Stenogyra decollata: HIRC (1914: 14, 15): VK42 - S;
Rumina decollata: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37): VK42 - S;
Rumina decollata: GRAACK (1989: 13): VK42 - S;
TR: VK42 - 1, 2, 4, 6, 7, 8.
32. *Poiretia cornea* (BRUMATI, 1838)
Poiretia cornea: GRAACK (1989: 15): VK42 - S;
TR: VK42 - 1, 4, 6, 8.
33. *Cochlodina laminata* (MONTAGU, 1803)
TF: VK42 - 6, 7.
34. *Delima bilabiata biasoletiana* (CHARPENTIER, 1852)
Clausilia semirugata: LORENZ (1859: 93): VK42 - S;
Clausilia semirugata: HIRC (1914: 10): VK42 - S;
Clausilia biasoletiana: STURANY (1915: 401): VK42 - S;
Delima alschingeri biasoletiana: WAGNER (1924: 112): VK42 - S;
Delima alschingeri biasoletiana: WAGNER (1925: 68): VK42 - S;
Delima gibbula: MARKOVIĆ-MARJANOVIĆ (1966: 35, 37): VK42 - S;
Delima gibbula: BOGNAR et al. (1983: 11): VK42 - S;
Delima globbula: BOGNAR et al. (1989: 12): VK42 - S;
Delima semirugata semirugata: GRAACK (1989: 14): VK42 - S;
TR: VK42 - 2, 4, 6, 7, 8.
35. *Delima conspurcata blanda* (ROSSMÄSSLER, 1836)
Clausilia plauda: LORENZ (1859: 93): VK42 - S;
Clausilia plauda: HIRC (1914: 10): VK42 - S.

36. *Papillifera papillaris* (O. F. MÜLLER, 1774)
Pupa papillaris: LORENZ (1859: 93): VK42 - S;
Pupa papillaris: HIRC (1914: 10): VK42 - S.
37. *Macrogastra plicatula* (DRAPARNAUD, 1801)
Clausilia plicatula: MARCHESETTI (1882: 294, 303): VK42 - S;
Clausilia plicatula: HIRC (1914: 10): VK42 - S;
 TF: VK42 - 6, 7.
38. *Macrogastra ventricosa* (DRAPARNAUD, 1801)
Clausilia ventricosa: MARCHESETTI (1882: 294): VK42 - S;
Clausilia ventricosa: HIRC (1914: 10): VK42 - S.
39. *Clausilia parvula* FÉRUSAC, 1807
Clausilia dubia: MARCHESETTI (1882: 294, 303): VK42 - S;
Clausilia dubia: HIRC (1914: 10): VK42 - S;
 TF: VK42 - 3.
40. *Bradybaena fruticum* (O. F. MÜLLER, 1774)
 TR: VK42 - 4*;
 TF: VK42 - 3, 4, 6, 7.
41. *Cernuella virgata* (DA COSTA, 1778)
Helix variabilis: MARCHESETTI (1882: 294): VK42 - S;
Helix variabilis: LORENZ (1859: 93): VK42 - S;
Helix variabilis: HIRC (1914: 10): VK42 - S;
Cernuella virgata: GRAACK (1989: 15): VK42 - S;
 TR: VK42 - 6, 8.
42. *Cernuella jonica* (MOUSSON, 1854)
Helix profuga: MARCHESETTI (1882: 294): VK42 - S;
Helix profuga: HIRC (1914: 10): VK42 - S;
 TR: VK42 - 1, 5.
43. *Helicella obvia* (MENKE, 1828)
 TR: VK42 - 2, 6.
44. *Trochoidea pyramidata* (DRAPARNAUD, 1805)
Helix pyramidata: LORENZ (1859: 93): VK42 - S;
Helix conica: MARCHESETTI (1882: 294): VK42 - S;
Helix conica: HIRC (1914: 10): VK42 - S;
Helix pyramidata: HIRC (1914: 10): VK42 - S;
Trochoidea pyramidata: GRAACK (1989: 15): VK42 - S;
 TR: VK42 - 1, 2, 6, 7.
45. *Helicopsis* cf. *striata* (O. F. MÜLLER, 1774)
Helix striata: LORENZ (1859: 93): VK42 - S;
Helix striata: HIRC (1914: 10): VK42 - S;
 TF: VK42 - 3.
46. *Monacha cartusiana* (O. F. MÜLLER, 1774)
Helix cartusianella: LORENZ (1859: 93): VK42 - S;
Helix cartusianella: HIRC (1914: 10): VK42 - S;
Monacha cartusiana: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37): VK42 - S;
Monacha cartusiana: BOGNAR et al. (1983: 10): VK42 - S;
Monacha cartusiana: BOGNAR et al. (1989: 11): VK42 - S;
Monacha cartusiana: GRAACK (1989: 15): VK42 - S;
 TR: VK42 - 1, 2, 4, 6, 7, 8.
47. *Monacha parumcincta* (L. PFEIFFER, 1848)
Monacha parumcincta: GRAACK (1989: 15): VK42 - S;
 TR: VK42 - 2, 4, 6, 7, 8.

48. *Hygromia cinctella* (DRAPARNAUD, 1801)
TR: VK42 - 8.
49. *Trichia hispida* (LINNAEUS, 1758)
Trichia hispida: GRAACK (1989: 15): VK42 - S;
TR: VK42 - 4*, 6*, 7*, 8*;
TF: VK42 - 3, 4, 6, 7.
50. *Helicodonta obvoluta* (O. F. MÜLLER, 1774)
Helix obvoluta: MARCHESETTI (1882: 294): VK42 - S;
Helix obvoluta: HIRC (1914: 10): VK42 - S.
51. *Arianta arbustorum* (LINNAEUS, 1758)
TR: VK42 - 1*, 4*, 6*;
TF: VK42 - 3.
52. *Eobania vermiculata* (O. F. MÜLLER, 1774)
Helix vermicularis: LORENZ (1859: 93): VK42 - S;
Helix vermiculata: TOMMASINI (1862: 838): VK42 - S;
Helix vermiculata: MARCHESETTI (1882: 294): VK42 - S;
Helix vermicularis: HIRC (1914: 10): VK42 - S;
Eobania vermiculata: MARKOVIĆ-MARJANOVIĆ (1966: 33, 37): VK42 - S;
Eobania vermiculata: GRAACK (1989: 16): VK42 - S;
TR: VK42 - 1, 2, 6, 7, 8.
53. *Cepaea* spec.
TF: VK42 - 3.
54. *Helix aspersa* O. F. MÜLLER, 1774
Helix aspersa: LORENZ (1859: 93): VK42 - S;
Helix adpersa: TOMMASINI (1862: 838): VK42 - S;
Helix adpersa: HIRC (1914: 10, 14, 15): VK42 - S;
Helix aspersa: GRAACK (1989: 16): VK42 - S;
TR: VK42 - 1, 4, 6, 8.

According to data published hitherto, the malacofauna of the island of Susak includes 28 land and fresh-water species. In the course of our research we were able to confirm the existence of 19 species. As may be observed from the list of snails, we believe that, in certain cases from the literature, what we have are incorrect identifications (*Limnaeus minutus*, *Pupa quinqueidentata*, *Delima semirugata*, *D. gibbula*, *Clausilia dubia*, *Helix conica*), and such data have been assigned to the relevant taxa. It is difficult to explain certain references in the literature to easily identifiable species which we failed to find in the course of our research (*Paludina* spec. [= *Viviparus* spec.], *Physa* spec., *Aplexa hypnorum*, *Planorbis* spec., *Pagodulina pagodula*, *Macrogastra ventricosa*, *Papillifera papillaris*), and we are inclined to doubt their presence on Susak. As far as two species which remain are concerned, what we have seem to be imprecise identification, or actual indigenous species from Susak's past (*Helicodonta obvoluta*) or the present day (*Delima conspurcata blanda*). Authors rarely mention the particular strata in which fossil molluscs were discovered. And then there are members of recent fauna which have found their way in various ways into lower strata attributed to fossil fauna. Such species *Monacha cartusiana*, *Delima gibbula* (MARKOVIĆ-MARJANOVIĆ, 1966; BOGNAR et al., 1983, 1989), and *Pomatias elegans*, *Rumina decollata*, *Eobania vermiculata* (MARKOVIĆ-MARJANOVIĆ, 1966) we regard as recent species.

In the course of our research on Susak we found a total of 45 species of snails, thus almost doubling the number of species recorded for the island. They included 23 recent and 23 fossil species. All the species belong to land mollusca. Only one species, i. e. *Vallonia costata* featured in the recent as well as the fossil malacofauna. This suggests that major changes in ecological conditions took place between the Pleistocene and the present day, bring about the almost total exchange of land malacofauna.

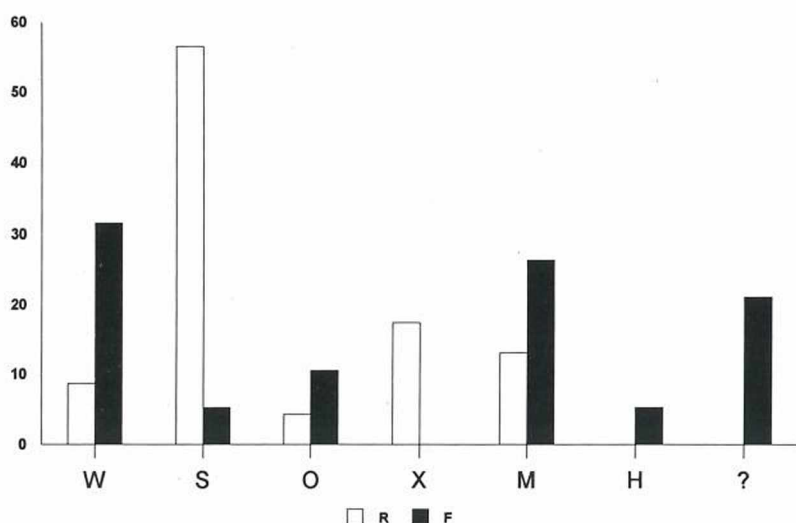


Fig. 3: Ecological spectra of fossil and recent snails: W - species of woodlands; S - steppe species; O - species of open habitats; X - species of dry habitats; M - species of semi-moist habitats; H - species of very moist habitats; R - recent malacofauna; F - fossil malacofauna.

2. Ecological spectra

The ecological features of the malacocoenoses during a period of some 120,000 years suggest the climatic changes of a mainly steppe-like landscape. The climate changed from warm and slightly humid to cool and dry, and ultimately to a distinctly humid and relatively warm climate by the end of the Ice Age and finally changing to the present eumediterranean climate (Fig. 3).

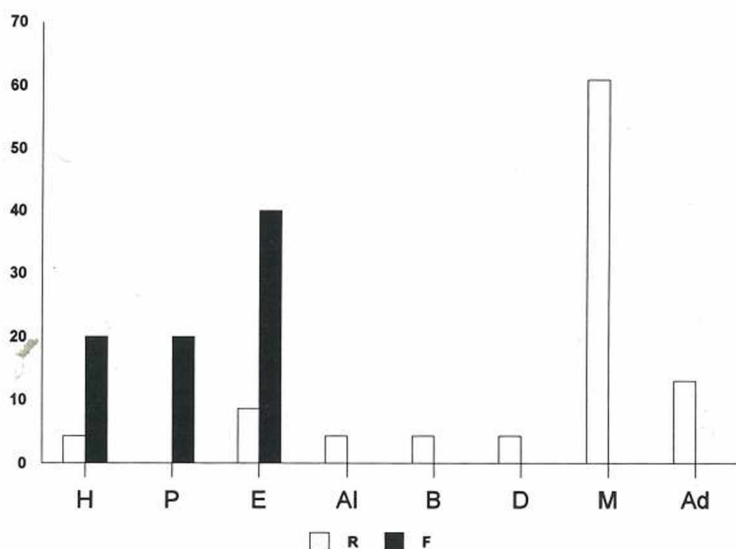


Fig. 4: Zoogeographical spectra of fossil and recent snails: H - Holarctic, P - Palaeartic, E - European, Al - Alpine, B - Balkan, D - Dinaric, M - Mediterranean, Ad - Adriatic elements; R - recent malacofauna; F - fossil malacofauna.

3. Zoogeographical spectra

In the fossil fauna of Susak Holarctic, Palaearctic and European species predominate (Fig. 4). Southern and Mediterranean species are confined to the oldest strata, and even there only a small percentage occurs. The fauna of the glacial periods is as a rule monotonous and represented in its geographical distribution by Holarctic, Palaearctic and European elements, while towards the interglacial and interstadial phases and the Holocene period a number of species with restricted distribution make their appearance. Thus, in the recent malacofauna of Susak Mediterranean and eastern Adriatic elements predominate, but there are also Alpine, Dinaric and Balkan elements, together with the Holarctic and European elements that still persist (Fig. 4).

4. Recent malacofauna

The species *Truncatellina velkovrhi* features prominently in our list of snails. Hitherto, it had been found only on the island of Grgur (Croatia) (ŠTAMOL, 1995). On Susak it was found on one site only (Plase, site no.4) in a grove of locust trees. It occurs together with *Truncatellina callicratis*, as is also the case with the locus typicus (ŠTAMOL, 1995). It is interesting that *T. callicratis* is represented on other sites on Susak, whereas the *T. velkovrhi* does not occur.

5. A comparison of the recent malacofauna of the islands of Susak and Lošinj

The fauna of the islands as a rule represents an attenuated version of the fauna on the nearby mainland. Small islands have a reduced version of the fauna of adjacent larger islands, and the smaller the area of the island, the poorer its fauna. Thus it was to be expected that the island of Susak would have a poorer fauna than the island of Lošinj, which is twenty times larger.

A comparison of the fauna of Susak with that of Lošinj (ŠTAMOL & VELKOVHRH, 1995) revealed the expected great affinity of 75% according to Sørensen, but also a surprisingly large number of species, no fewer than 8, which are found on Susak but not on Lošinj. There are *Truncatellina velkovrhi*, *Chondrula tridens eximia*, *Oxychilus inopinatus*, *Rumina decollata*, *Cernuella virgata*, *Cernuella jonica*, *Helicella obvia* and *Trochoidea pyramidata*. It is possible that species found on Susak but not on Lošinj inhabit Lošinj as well, but research to date has not revealed them. Alternatively it may be that species that inhabit Susak do not live on Lošinj because of the specific consistency and composition of the soil and the nature of the habitats (on Susak sandy soils and open grassland habitats, on Lošinj woodland biotops, scrub and tilth). Further research may provide an answer.

6. Fossil fauna

The geological vertical profiles on which Pleistocene malacofauna were gathered at sites 4 (Plase), 6 (Susak-Garba) and 7 (Susanka) are 5-6 meters high. Only at site no. 3 (Ogradica) is the profile 37 meters thick (0-37 m above sea level) (Fig. 2).

On the basis of analysis in the field and the composition of the malacofauna, the deposits at profile Ogradica may be divided into three characteristic sequences: I - lower, II - middle and III - upper. The deposits exposed on the profiles Susanka, Plase, Susak-Garba belong to sequence III of profile Ogradica.

Sequence I - lower section of profile Ogradica, 6-7 thick (samples T-O). It includes basic red fossil soil (T), above which there is brown fossil soil (S), then a yellowish loess-like sediment (R), and brown (P) and dark brown (O) fossil soils. The basic red fossil soil (T) lies

Species	ecotype	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	R	S
<i>Discus ruderatus</i>	1W	4	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Vitrinidae indet.		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3
<i>Bradybaena fruticum</i>	2W(M)	1	.	1	.	.	.	1	.	.	.	.	1	.	.	.	.	1	.
<i>Bradybaena</i> sp.		.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
<i>Limax</i> sp. (big)	2W(M)!	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Arianta arbustorum</i>	2W(M)(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.
<i>Arianta</i> sp.		.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
<i>Cepaea</i> sp.		.	.	.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.
<i>Pupilla triplicata</i>	4S(+)	.	1	.	.	4	.	7	5	.	.	3	5	.	.	.	.	23	6
<i>Pupilla</i> sp.		.	.	.	1	.	.	1	.	.	3	1	4	4	2	.	.	4	.
<i>Helicopsis striata</i>	4S+	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.
<i>Helicopsis</i> sp.		.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.
<i>Vallonia pulchella</i>	5O	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.
<i>Vallonia costata</i>	5O(W)(+)	53	23	60	4	6	3	10	.	.	.	2	15	6	2	.	.	93	7
<i>Vallonia</i> sp.		.	.	.	.	.	.	.	1	1	2	2	.	4	.	.	.	.	.
<i>Nesovitrea hammonis</i>	7M(+)	14	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	6	.
<i>Euconulus fulvus</i>	7M(+)	14	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Punctum pygmaeum</i>	7M(+)	.	.	1	.	1	.	3	.	.	.	.	.	.	.	.	.	7	.
<i>Limax</i> sp. (small)	7M(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	1
<i>Trichia hispida</i>	7M+	27	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
<i>Trichia</i> sp.		.	.	1	.	1	1	1	1	1	.	1	1	.	.	.	.	2	.
<i>Clausilia</i> cf. <i>parvula</i>	7Mf(+)	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.
Clausiliidae indet.		1	.	1	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.
<i>Succinea oblonga</i>	8H+	25	60	30	8	.	.	.	.	.	.	.	.	.	.	.	.	4	.
<i>Vertigo angustior</i>	8H	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Helicidae indet.		.	.	.	.	1	.	1	1	.	.	.	1	.	.	.	1	.	.
Σ		141	108	94	13	15	5	26	9	3	6	9	28	15	6	0	5	148	17

Tab. 1 (a)

directly on the Cretaceous limestones. It is very similar to „terra rossa“ and suggests a warm Mediterranean climate during its formation. Apart from the present era, conditions for the formation of this kind of soil have existed during the Riss/Würm (Eemian) interglacial period, and we assume that it is of corresponding age. The fossil soils above (S, P, O) are the brown woodland and brown woodland-steppe soils of a warm and moist climate which supervened during interstadials. As a rule they do not contain carbonates, so that they are sterile as far as malacofauna is concerned; it is hard to define their chronostratigraphic position. Interval R is a greenish-yellow loess-like sediment which suggests an interruption of the pedological processes and the beginning of loess accumulation with cooling of the climate. The malacofauna of this stratum is associated with a warm, most steppe biotope, while the superimposed stratum in relation to the basic red soil probably belongs to the first Würm stadial.

Sequence II - the middle section of profile Ogradica, approx. 25 m thick (samples N-E). This is a thick complex of aeolian sand. On the greater part of the profile there is distinct

Taxa	ecotype	A	B	C	D	E	F
<i>Discus rudieratus</i>	1W	-	7	13	2	-	-
<i>Macrogastra cf. plicatula</i>	1W!	-	-	4	14	-	-
<i>Macrogastra</i> sp.	-	-	1	-	-	-	-
<i>Cochlodina cf. laminata</i>	1W!	-	-	1	-	-	-
<i>Cochlodina</i> sp.	-	-	1	-	-	-	-
Clausiliidae indet.	-	-	-	-	-	1	1
<i>Bradybaena fruticum</i>	2W(M)	-	-	-	-	-	1
<i>Arianta arbustorum</i>	2W(M)(+)	-	-	1	-	-	-
<i>Pupilla triplicata</i>	4S(+)	19	-	-	8	-	2
<i>Vallonia costata</i>	5OW(+)	55	40	52	60	17	48
<i>Pupilla muscorum</i>	5O+	10	-	3	-	-	-
<i>Pupilla</i> sp.	-	-	5	-	-	-	-
<i>Nesovitrea hammonis</i>	7M(+)	-	5	36	6	2	10
<i>Eucomulus fulvus</i>	7M(+)	-	3	12	7	6	9
<i>Punctum pygmaeum</i>	7M(+)	-	20	47	94	-	11
<i>Limax</i> sp. (small)	7M(+)	-	1	24	-	-	2
<i>Trichia hispida</i>	7M+	-	12	9	19	3	16
<i>Succinea oblonga</i>	8H+	-	19	12	60	20	31
Σ		84	114	214	270	49	131

Taxa	ecotype	A
<i>Discus rudieratus</i>	1W	1
<i>Cochlodina cf. laminata</i>	1W!	1
<i>Macrogastra cf. plicatula</i>	1W!	1
<i>Bradybaena fruticum</i>	2W(M)	2
<i>Limax</i> sp. (big)	2W(M)!	1
<i>Pupilla triplicata</i>	4S(+)	8
<i>Vallonia costata</i>	5OW(+)	80
<i>Pupilla muscorum</i>	5O+	5
<i>Punctum pygmaeum</i>	7M(+)	90
<i>Eucomulus fulvus</i>	7M(+)	10
<i>Trichia cf. hispida</i>	7M+	4
<i>Nesovitrea hammonis</i>	7M(+)	8
<i>Succinea oblonga</i>	8H+	24
<i>Pupilla</i> sp.	-	17
Σ		252

Tab. 1 (d)

Tab. 1 (b)

Taxa	ecotype	A	B	C	D	E
<i>Discus rudieratus</i>	1W	-	-	1	2	2
<i>Bradybaena fruticum</i>	2W(M)	-	-	1	-	-
<i>Pupilla cf. triplicata</i>	4S(+)	-	-	-	-	7
<i>Pupilla</i> sp.	-	-	-	1	-	-
<i>Pupilla cf. muscorum</i>	5O+	-	-	-	5	-
<i>Vallonia costata</i>	5OW(+)	-	-	7	60	40
<i>Vallonia</i> sp.	-	-	1	-	-	-
<i>Trichia hispida</i>	7M+	-	-	-	-	5
<i>Trichia</i> sp.	-	-	1	1	-	-
<i>Eucomulus fulvus</i>	7M(+)	-	-	-	7	4
<i>Eucomulus</i> sp.	-	-	1	1	-	-
<i>Nesovitrea hammonis</i>	7M(+)	-	-	-	2	-
<i>Limax</i> sp. (small)	7M(+)	-	1	-	1	-
<i>Punctum pygmaeum</i>	7M(+)	-	-	4	-	-
<i>Succinea oblonga</i>	8H+	-	-	2	4	13
<i>Vitrea</i> sp.	-	2	-	-	-	7
<i>Oxychilus</i> sp.	-	1	-	-	-	5
Clausiliidae indet.	-	-	-	-	-	3
Helicidae indet.	-	-	1	-	-	-
Σ		3	5	18	81	86

Tab. 1 (c)

Table 1 (a-d): Specimen numbers of fossil snails on the site: a) Ogradica; b) Susanka; c) Plase; d) Svjetionik-Garba; A-S: samples of the deposits (A = youngest). Ecotype according to LOŽEK (1964): 1W - species of woodlands; 2W/M - species of semi-moist woodlands; 4S - steppe species; 5O - species of open habitats; 7M - species of semi-moist habitats; 8H - species of very moist habitats; ! - important species of moist/warm climatic periods; + - species mainly appearing in loess deposits, but found also in other sediments; (+) - species appearing locally in loess deposits.

lamination. It may be assumed that it belongs to phase 4 ¹⁸O isotopic chronology (CREMASCHI, 1990).

Malacofauna of the sequence II (samples N-E) is deficient. We would ascribe this deficiency to the fact that the sandy, more or less silicate substrate is not frequently inhabited by snails, while probably also due to unfavorable sedimentary conditions and climate. We were able to identify species that are associated with barren, steppe-like biotops, while the presence of species favouring damp habitats was negligible. Judging by the malacofauna of this

kind, we may conclude that at the time when sedimentation took place in the middle zone a relatively cool and dry climate prevailed.

Sequence III - the upper part of profile Ogradica (samples D-A), or the whole profile in sites Susanka and Plase, and profile Susak-Garba 40 m above sea-level. This sequence consists of yellowish-greenish dust most closely resembling typical loess. Thickness of these youngest strata on the island of Susak is some 4-6 m.

The malacofauna of all four profiles is exceptionally rich (Tab. 1) (especially in the case of profile Susanka), with species from open, bare and unwooded surfaces, along with a large proportion of species from damp habitats. Woodland species represent no more than a low percentage. Some of them are index molluscs for woodlands of warm interglacials as e. g. *Cochlodina laminata*, *Macrogastra plicatula* and *Limax* spec. (large). During deposition of the youngest strata on the Susak island relatively warm and humid climate prevailed.

A comparison of the malacofauna of the youngest strata on Susak with that of Savudrija (north-west Istria) (MALEZ et al., 1976) showed, in terms of Sørensen's coefficient, a coincidence of 60%. Given this similarity, we may regard the youngest strata on Susak as being the same age as those of Savudrija. As the upper stratigraphic sequence of Savudrija (samples a-f) on the basis of ^{14}C analysis (11000 BP) and the finding of Tardigravettian culture is to be attributed to Dryas period, i. e. to the final phase of loess accumulation in Würm glaciation, so we would assign the upper layers on Susak to the late glacial (Dryas) period. Differences in the malacofauna of these two areas indicate a cooler and dry climate, with the more pronounced steppe-like character of Savudrija opposed to Susak. This may be explained by the more mainland situation of Savudrija in that period which was governed by a sea-level 30 m lower than it is today (ŠEGOTA, 1991).

It is hard to determine the chronostratigraphy of the Pleistocene strata of Susak in the absence of radiometric dating. An attempt by palaeomagnetic analysis merely showed that the sand sediment on Susak is no more than 700,000 years old (BOGNAR et al., 1992). WEIN (1976) and CREMASCI (1990) assigned the sand deposits on Susak to the Würm glacial period. Our researches indicate that sequence III, i. e. the youngest strata on Susak might be assigned to the late glacial period, i. e. to the Dryas.

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Autor(en)/Author(s): Stamol Vesna, Poje Marija

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