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Origin and development of the mammalian fauna of the Julian Alps

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SUMMARY

In the Würm the Julian Alps (hereinafter JA) were almost entirely covered with a thick sheet of ice. In the Boreal at the latest, i.e. 9000 years ago, the climatic conditions in the JA became similar to those of the present day. Thus it seems that the recent mammalian fauna of the JA consists mostly of species that made their way to this territory only as late as the post-Glacial, i.e. less than 10.000 years ago.

At present the JA are populated by 24 species of insectivores, rodents and lagomorphs, which is not a small number in comparison with the 25 species living in the entire Alpine region of Yugoslavia. The only glacial relict is *Lepus timidus*, whereas the remaining species are post-Pleistocene arrivals. Of greatest importance in the colonization of the JA was the refuge to the south of the ice-bound territory. Two characteristic species which invaded the JA and the northwestern Dinaric Alps from this refuge were *Chionomys nivalis* and *Pitymys liechtensteini*. The post-Pleistocene arrivals from the east (e.g. *Pitymys subterraneus*) as well as the late post-Pleistocene invaders (e.g. *Apodemus agrarius*, *Micromys minutus*) no longer exerted an influence upon the formation of the recent JA fauna. The last group is represented by sinanthropic species which in the JA colonized human settlements (*Rattus*, *Mus*) and cultivated areas i.e. fields, meadows and pastures.

INTRODUCTION

The Julian Alps (hereinafter JA) represent the southwesternmost part of the Alpine mountain mass. In the Pleistocene the region of the present Alps was the greatest southern uninterrupted ice-bound territory. Thus also in the Würm the JA were almost entirely covered with a thick sheet of ice and were mainly devoid of fauna. However, in the glaciations themselves smaller areas in the ice-bound region were populated by mammals of northern origin (species of the tundra and the taiga). Most of the fauna presently populating this territory nevertheless found a refuge in the non-iced territory to the south of the present Alps. An important refuge of this type was also in the hills and the lowlands of northwestern Yugoslavia. As documented (Rakovec 1975), already in the Würm this territory was populated by a number of mammalian species now living here as well as in the JA: *Sorex minutus*, *S. araneus*, *S. alpinus*, *Crocidura* sp., *Talpa europaea*, *Muscardinus avellanarius*, *Glis glis*, *Clethrionomys glareolus*, *Microtus arvalis*, *M. agrestis*, *Chionomys nivalis*, *Pitymys* sp. (*subterraneus* group) and *Lepus europaeus*. This fauna undoubtedly formed a base which in the Holocene again populated the JA once the gla-

ciers retreated from there. In the Boreal at the latest, i.e. 9000 years ago, the conditions in the territory of the JA already resembled those reigning at present and which till the present day have undergone no essential changes. Thus it seems that the recent fauna of the JA represents mainly the species that invaded them only less than 10.000 years ago.

The object of this paper is to compare the recent fauna of three mammalia orders (Insectivora, Lagomorpha, Rodentia) of the JA with that of the surrounding regions in northwestern Yugoslavia and to explain the origin of the mammalia fauna of this region with respect to the resemblances and differences as well as by considering glacial and later events.

MATERIAL AND METHODS

Taken into account were three orders of mammals (Insectivora, Lagomorpha, Rodentia) including 35 species from the territory of northwestern Yugoslavia. The reason therefor was a fairly thorough research work done on their distribution areas and a relatively weak anthropogenic influence upon their distribution, otherwise quite powerful in carnivores (Carnivora) and even-toed ungulates (Artiodactyla).

The mammalian fauna of the JA was compared with faunas of eleven geographic regions in northwestern Yugoslavia, namely (Fig. 1):

The Alps:

1. the Julian Alps
2. the Karavanken Mountains
3. the Kamnik Alps
4. Pohorje

The Dinaric Alps:

5. Trnovski gozd and Čaven
6. Snežnik and Risnjak
7. Učka with Čičarija
8. the Velebit

Submediterranean region:

9. Karst
10. northwestern Istria

Hills and lowlands of the continental Slovenia:

11. pre-Alpine hills (western part)
12. subpannonic region

The data on the mammalian fauna are mostly results of recent field investigations and therefore as yet unpublished, whereas some of them have been taken from the following works: Dal Piaz 1927-1929, Dulić 1961, 1962 a, b, Dulić and Vidinić 1964, Kryštufek 1983 a, b, c, 1985, a, b, Kryštufek and Kovačić 1984, Petrov 1968, 1976, 1979, Petrov and Živković 1979, Tvrtković et al. 1979, 1985.

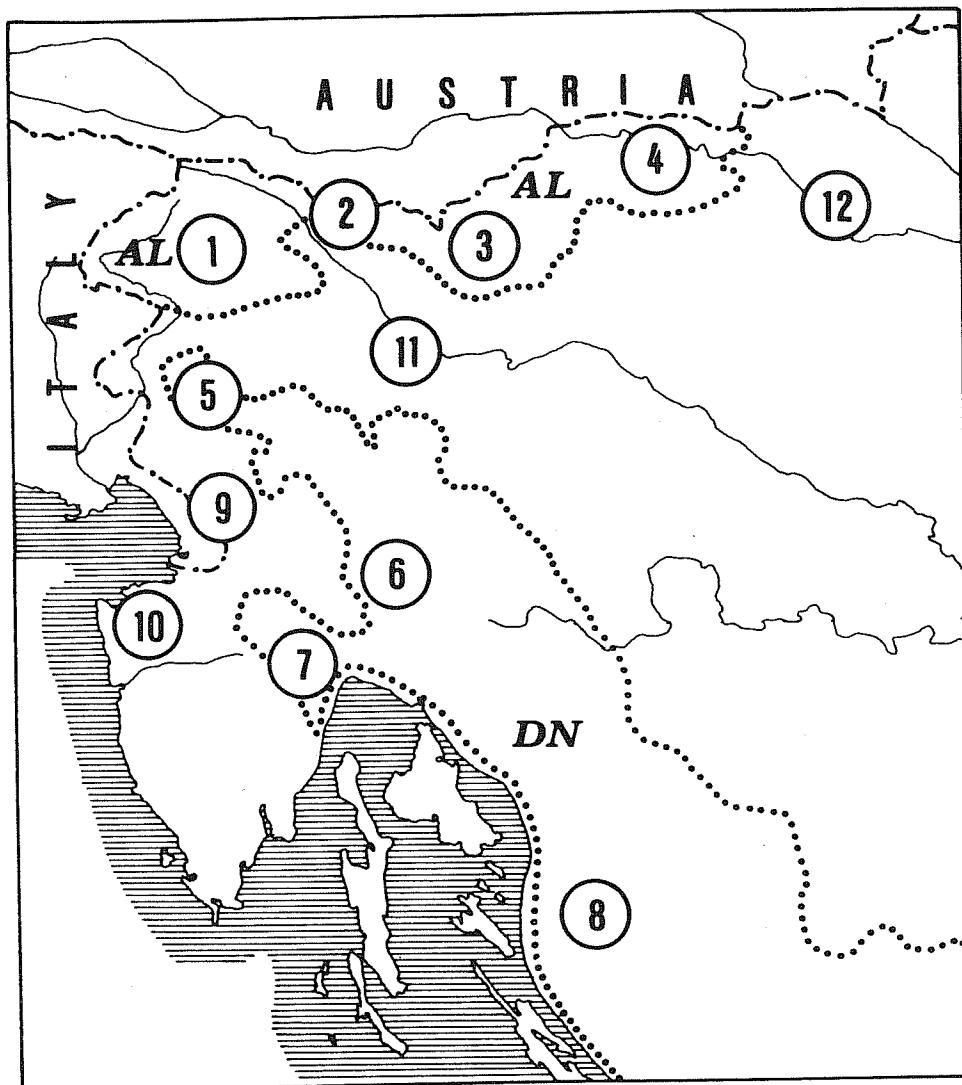


FIG. 1 - Geographic regions of Northwestern Yugoslavia. The pointed line separates and delimits the Alpine (AL) and the Dinaric (DN) mountain massives. See the text for the explanation.

In comparing the similarities among mammalian faunas of single regions the coefficient of community (CC) was calculated:

$$CC = 100 \times C / n_1 + n_2 - C$$

where C represents the number of species common to the two areas, n_1 is the number of species in the smaller fauna, and n_2 the number in the larger one.

Such an obvious synanthropic group as rats (*Rattus* spp.) was omitted from the calculation of CC.

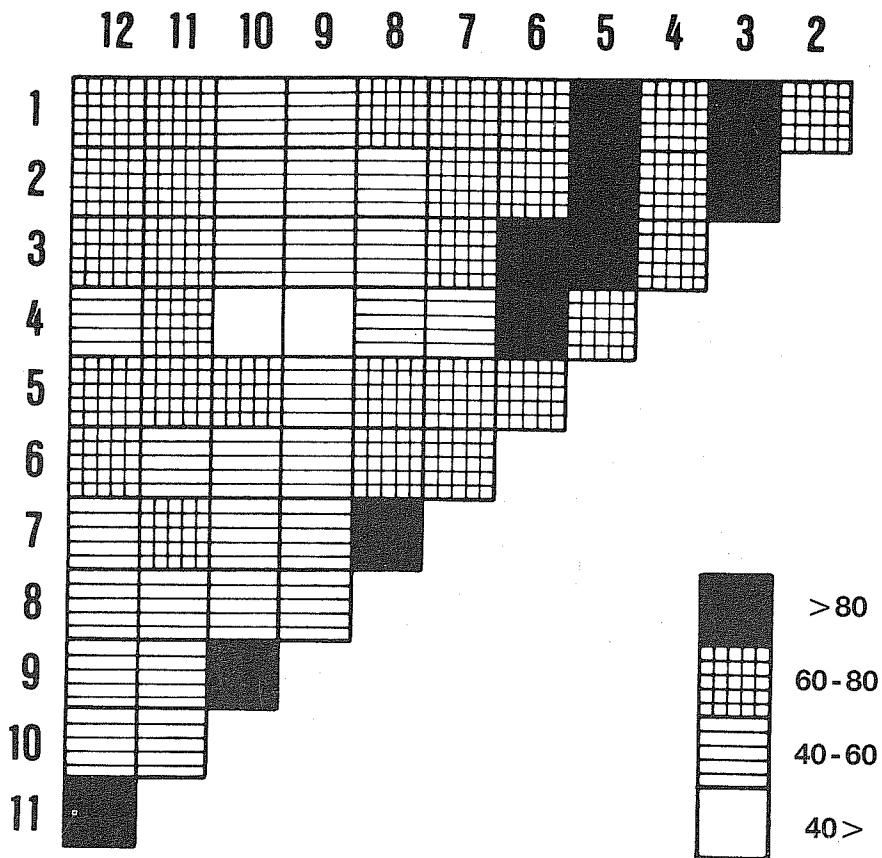


FIG. 2 - CC values between pairs of mammal faunas of single geographic regions. The regions are numbered as in Fig. 1.

RESULTS

Analysis of the Mammalian Fauna of the JA

The species that the JA have in common with other Alps are mostly those mammals present also in the hills and the lowlands of the continental Slovenia. The species concerned are those that in the Würm lived on the non-ice-bound territory wherefrom they spread, in the Boreal at the latest, to the JA.

The species living in northwestern Yugoslavia exclusively in the Alps (the JA included) is *Lepus timidus* the recent area of which reveals all the characteristics of a glacial relict.

Some species by which the JA differ from the eastern parts of the Alps (Pohorje) are characteristic of the northwestern Dinaric Alps. The question is above all of two zoogeographically interesting voles, namely: *Pityomys liechtensteini* and *Chionomys nivalis*. In the Würm they supposedly found a ref-

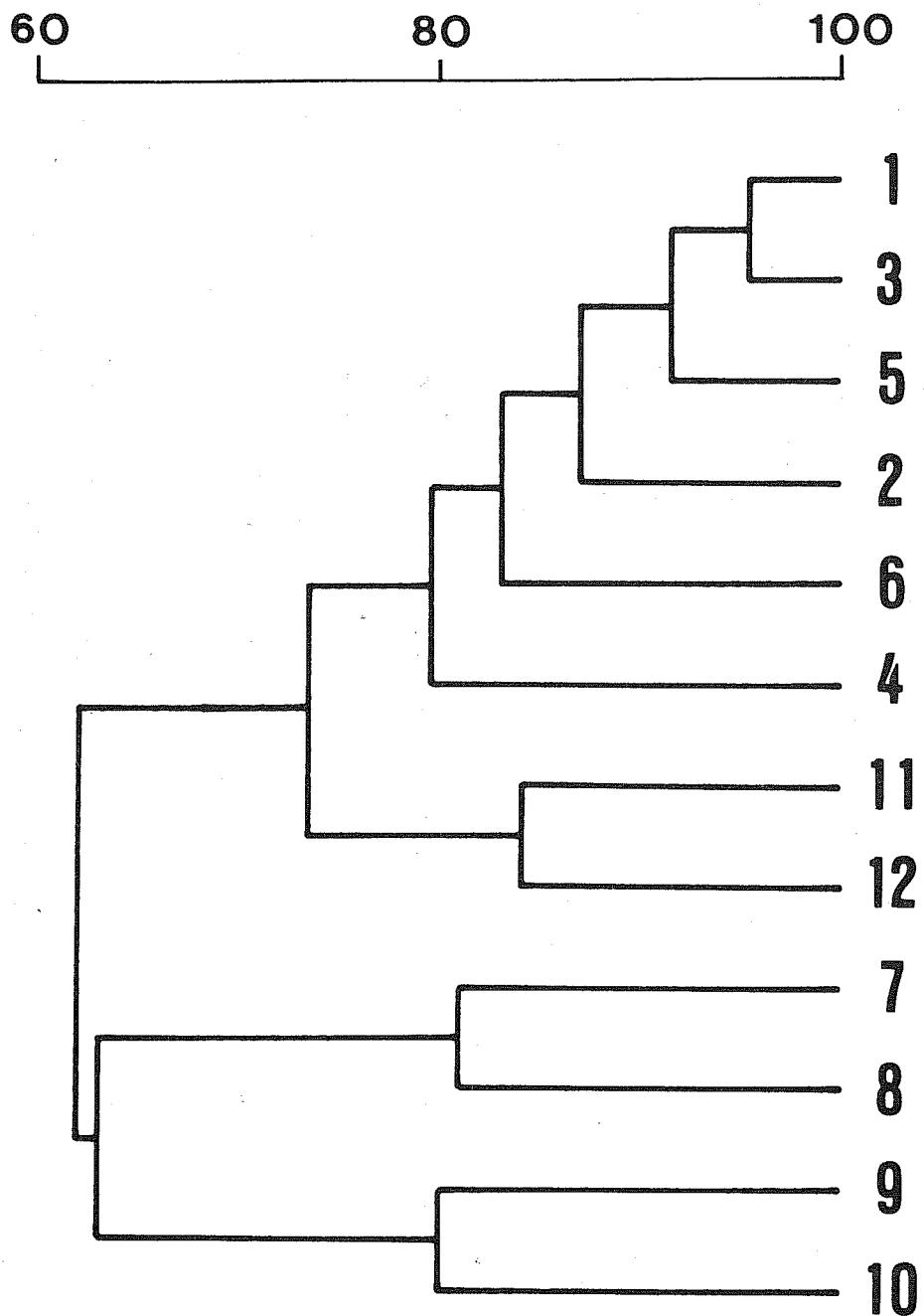


FIG. 3 - Dendrogram prepared by a cluster analysis of CC. The regions are numbered as in Fig. 1. See also Fig. 2.

uge to the south of the JA wherefrom they populated them in the Boreal at the latest. It is interesting to note the relationship between the areas of *Pitymys liechtensteini* and *P. subterraneus*. These congeneric species ecologically exclude each other while their areas are mainly allopatric. Where these areas join, the two species never live syntopically. We presume that *P. subterraneus* populated the Alps from the east and *P. liechtensteini* from the south (Fig. 5). Thus the latter sooner reached the JA (as well as the Kamnik Alps) and the former Pohorje and the Karavanken Mountains. This also explains the fact that *P. liechtensteini* alone lives in the lowlands to the west of the Dinaric mountain chain (i.e. in the submediterranean region) and *P. subterraneus* to the west of it.

The resemblance of the mammalian fauna of the JA to that of the Dinaric highland decreases from the north to the south, i.e. along with the increasing of the geographic distance. The value of CC between the JA and Trnovski

TABLE I - Presence of mammals in single geographical regions in NW Yugoslavia. The regions are numbered as in Fig. 1.

Geographic region	1	2	3	4	5	6	7	8	9	10	11	12
<i>Erinaceus concolor</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sorex minutus</i>	+	+	+	+	+	+	+	+	-	+	+	+
<i>Sorex araneus</i>	+	+	+	+	+	+	+	+	-	-	+	+
<i>Sorex alpinus</i>	+	+	+	+	+	+	+	+	-	-	+	-
<i>Neomys fodiens</i>	+	+	+	+	+	+	-	-	-	-	+	+
<i>Neomys anomalus</i>	+	+	+	-	+	-	+	-	+	+	+	+
<i>Crocidura suaveolens</i>	+	+	-	-	+	-	+	+	+	+	+	+
<i>Crocidura leucodon</i>	-	-	-	-	-	-	+	+	+	+	+	+
<i>Suncus etruscus</i>	-	-	-	-	-	-	-	-	-	+	-	-
<i>Talpa europaea</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Sciurus vulgaris</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Cricetus cricetus</i>	-	-	-	-	-	-	-	-	-	-	-	+
<i>Clethrionomys glareolus</i>	+	+	+	+	+	+	+	+	-	-	-	+
<i>Dinaromys bogdanovi</i>	-	-	-	-	-	-	-	+	-	-	-	-
<i>Arvicola terrestris</i>	+	+	+	+	+	+	-	-	+	-	+	+
<i>Microtus agrestis</i>	+	+	+	+	+	+	-	-	-	-	+	+
<i>Microtus arvalis</i>	+	+	+	-	+	-	-	-	-	+	+	+
<i>Chionomys nivalis</i>	+	+	+	-	+	+	+	+	+	+	-	-
<i>Pitymys subterraneus</i>	-	+	-	+	-	-	-	-	-	-	+	+
<i>Pitymys liechtensteini</i>	+	-	+	-	+	+	+	+	+	+	-	-
<i>Apodemus agrarius</i>	-	-	-	-	-	-	-	-	+	+	-	+
<i>Apodemus sylvaticus</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Apodemus flavicollis</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Apodemus mystacinus</i>	-	-	-	-	-	-	-	-	-	-	-	-
<i>Micromys minutus</i>	-	-	-	-	-	-	-	-	+	+	+	+
<i>Mus hortulanus</i>	+	+	+	-	+	-	-	-	-	-	+	+
<i>Mus domesticus</i>	-	-	-	-	-	-	-	-	+	+	+	-
<i>Rattus rattus</i>	+	+	+	+	+	+	-	-	+	+	+	+
<i>Rattus norvegicus</i>	-	-	-	-	-	-	-	-	+	+	+	+
<i>Glis glis</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Dryomys nitedula</i>	+	+	+	+	-	+	-	+	-	-	-	-
<i>Eliomys quercinus</i>	-	-	-	-	-	-	-	+	+	-	-	-
<i>Muscardinus avellanarius</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lepus europaeus</i>	+	+	+	+	+	+	+	+	+	+	+	+
<i>Lepus timidus</i>	+	+	+	+	-	-	-	-	-	-	-	-

gozd (point 5 in fig. 1) is 91.3, whereas between the JA and the Velebit (point 8 in Fig. 1) 61.5 only. Of the Dinaric highlands as researched (see the dendrogram in Fig. 3) localities 5 and 6 are grouped to the Alps while localities 7 and 8 form an independent cluster. The Dinaric highlands lying north-westernmost thus lose a considerable number of mammals otherwise characteristic of the Dinaric Alps as a whole (e.g. *Dinaromys bogdanovi*). The greatest concentration of mammals forming a specific part of the fauna of the southern European (Mediterranean) subregion in the Balcan Peninsula is between the rivers Neretva and Vardar (Petrov 1979). Even though in the Pleistocene a part of this fauna (e.g. *Dinaromys bogdanovi*) lived also at the roots of the extreme northwestern areas of the Dinaric Alps and in northern Italy (Petrov and Todorović 1982), southern European (Mediterranean) mammals (sensu Petrov 1979) exerted no influence on the recent fauna of the JA. This most probably results from the climatic factors (increased continentality of the climate; Petrov 1985) as in the Pleistocene the northern border of the Adriatic Sea was shifted for some 250 km towards the south.

Zoogeographic Categories

The following zoogeographic categories are distinguished among the JA mammals:

1. Glacial Relicts (Example: *Lepus timidus*; Fig. 4). This group of mammals is represented by northern elements which in the Pleistocene spread their distribution area towards the south. In the JA *L. timidus* is their sole representative, whereas they were much more numerous in the Slovene Pleistocene (see Rakovec 1975).

2. Post-Pleistocene Invaders

- 2.1. Invaders from the Refuge to the South of Glaciers (Examples: *Chionomys nivalis*, *Pitymys liechtensteini*; Fig. 5).

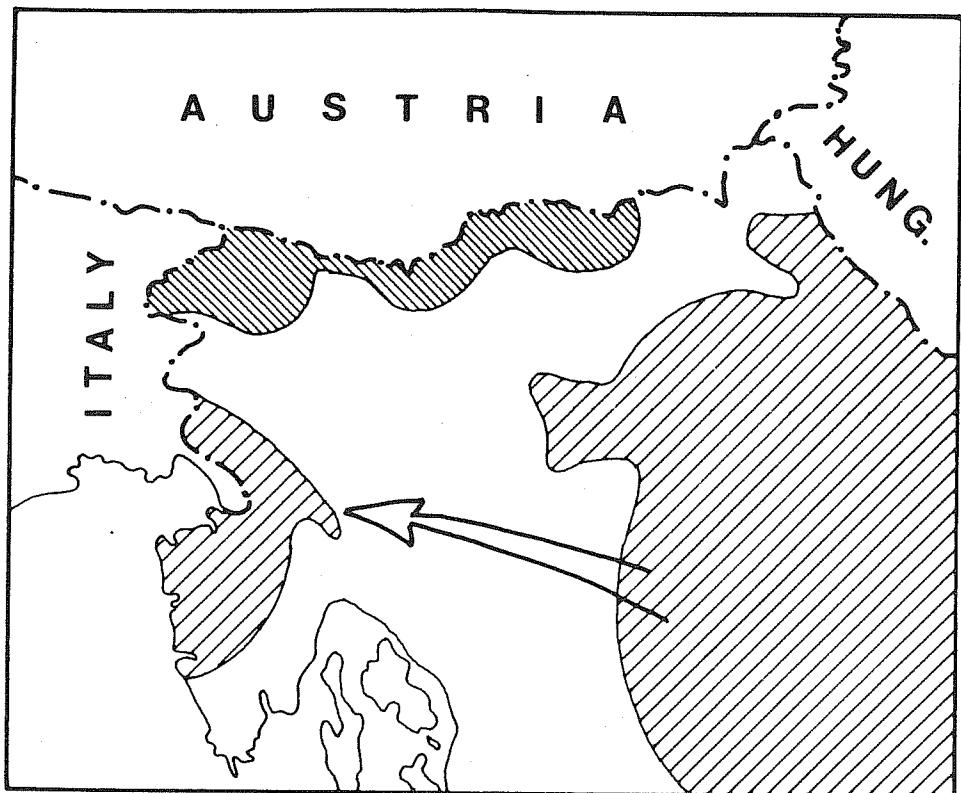
This type of mammalian fauna is spread in the JA, the Kamnik Alps, the Dinaric Alps and the Submediterranean but is not present in the subpannonic region, the hills of the continental Slovenia and the extreme eastern parts of the Alps.

- 2.2. Invaders from The East (Example: *Pitymys subterraneus*; Fig. 5).

The question regards those mammals that in the Holocene invaded towards the JA from the east. They populated the more eastern parts of the Alps (e.g. Pohorje) but most probably exerted no influence on the recent mammalian fauna of the JA.

- 2.3. Invaders from Both Sides (Examples: *Sorex araneus*, *Clethrionomys glareolus*).

The mammals represented in northwestern Yugoslavia by two subspecies are believed to originate from different ancestral Pleistocene populations. One of the subspecies probably originates from the refuge to the south of glaciers (as 2.1.) whereas the other is an invader from the east (as 2.2.). In the western part of northwestern Yugoslavia *Cl. glareo-*



a



b

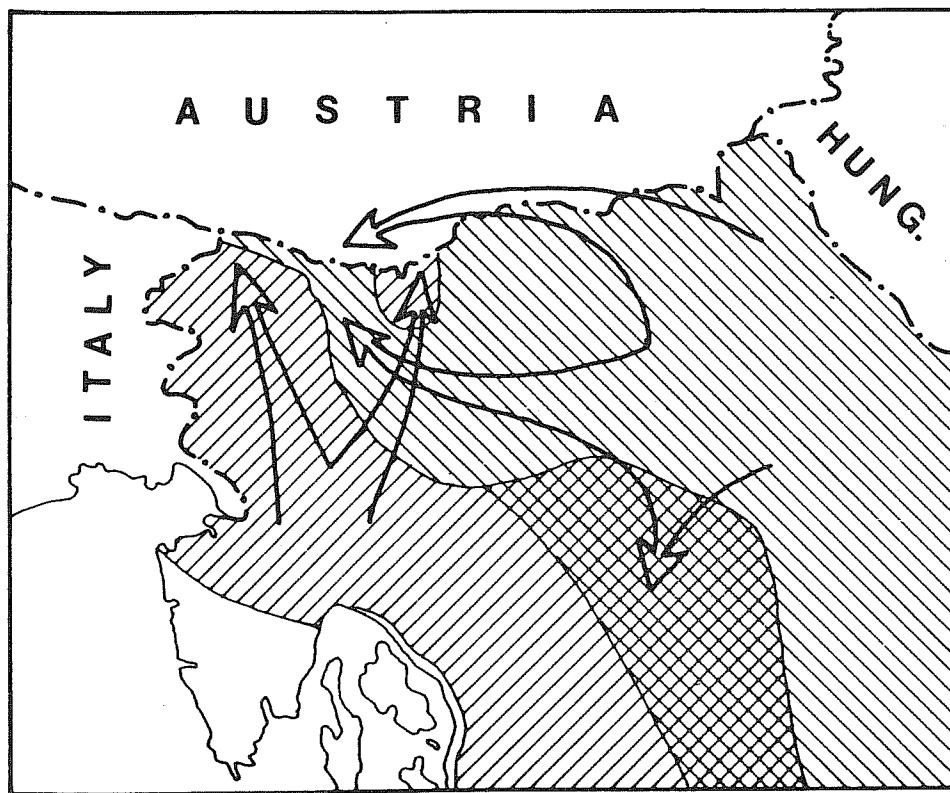
Fig. 4 - Distribution maps of some zoogeographically characteristic species of mammals in northwestern Yugoslavia.

a - *Lepus timidus* (glacial relict); b - *Apodemus agrarius* (late post-Pleistocene invader); the arrow indicate the hypothetical direction of invasion.

lus is represented by a large subspecies (*Cl. glareolus gorka*) and in the eastern part by a small one (*Cl. glareolus cf. isticus*). Similarly, a large subspecies of *Sorex araneus* lives in the western part of northwestern Yugoslavia (*S. araneus eleonorae*) and a small one (*S. araneus* ssp.) in the eastern part (Pohorje included).

In this case the JA would be populated from the refuge to the south of the ice-bound territory.

Late post-Pleistocene invaders, i.e. the species that invaded the territory of northwestern Yugoslavia relatively late in the Holocene when the recent mammalian fauna had been more or less definitively formed (Examples: *Micromys minutus*, *Apodemus agrarius*). These species are



a



b

FIG. 5 - Distribution maps of some zoogeographically characteristic species of mammals in northwestern Yugoslavia.

a - *Pitymys liechtensteini* (invader from the refuge to the south of glaciers); b - *Pitymys subterraneus* (invader from the east); the arrows indicate the hypothetical directions of invasion.

bound to interzonal, azonal and anthropogenic habitats (Kryštufek and Kovačić 1984) and did not invade the JA (Fig. 4).

3. Synanthropic Species

- 3.1. Commensal Species (Examples: *Rattus* spp., *Mus* spp.). In the region of the JA (as well as the Alps within the Yugoslav borders in general) there are known to exist no feral populations of house mice and rats.
- 3.2. Species Having Spread due to Deforestation and Agrarization (Examples: *Crocidura suaveolens*, *Talpa europaea*, *Microtus arvalis*, *Apodemus sylvaticus*). These species were enabled to invade the JA only as a result of deforestation (i.e. formation of open habitats) or else became more frequent or more generally spread. They are mostly bound to fields, meadows and pastures up to 1000 - 1500 m of above sea-level.

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