Cave pseudoscorpions of eastern Serbia : origin and biogeographical implications

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1. Geomorphology

The karst regions of Eastern Serbia are confined to the eastern zone of the younger fold mountains, composed mainly of limestones and dolostones. These areas are characterised by discontinuous distribution and shallower layers of limestones and dolostones, in contrast to the Dinaric Karst, although in some respects they resemble the typical western karst. Carbonate rock terrains account for approximately 3,320 sq. km., or 19.5 % of the territory of Eastern Serbia (Gavrilović 1965, 1989).

To the west and east, Eastern Serbia is bounded by the valleys of the Velika Morava and Timok rivers respectively. To the north, this area stretches as far as the Danube valley and to the south as far as the Nišava and Kutinska Reka valleys (Petrović 1974). The mountains of Eastern Serbia are fractured and intersected by numerous depressions. These masses are separated from one another by numerous basins and deep canyons. The karst terrains, then, which are confined predominantly to the mountain ranges, mountain tops and ridges, form isolated oases surrounded by impermeable rocks of a different age.

The karst terrains of Eastern Serbia are characterised by an extremely complex and variable surface relief. The landscape is dominated by typical karst phenomena as well as by the presence of polymorphic karstic elements. The karstic process took place in Mesozoic limestone and dolostone rocks. Cretaceous limestones are more abundant, Triassic limestones being less frequent. Cenozoic formations, however, are also widely distributed. These are represented mainly by Oligocene and Neogene lacustrine sediments.

Tectonic interrelationships in the varied geological structure in Eastern Serbia are highly intricate and are distinguished by their Alpine structure. The morphotectonic evolution of the region is closely correlated to the origin of the relief

and the successive formation of recumbent folds, thrust faults and other faulting phenomena (Petrović 1974).

It is thought (Gavrilović 1965) that the mountains of NE Serbia represent a direct continuation of the southern Carpathians extending from Romania and also that the mountains of SE Serbia merge directly with the Bulgarian Balkanides. However, there is still insufficient evidence to establish whether the Carpathians actually do continue into the Balkan mountains or not. Cvijić (1900) held that the Carpathian and the Balkan mountain systems do not merge; rather, according to him, they deviate or diverge to bypass the "resistant" basin (or depression) of the Crnorečka Kotlina. According to the same author, this fact is one of the main proofs that they are two entirely separate mountain masses. Actually, this whole problem has not been received enough attention, especially from the point of view of a morphological study (Grubić and Marković 1967).

Powerful tectonic movements over long periods of time and the processes of folding, faulting, tear faults formation, as well as epeirogenetic movements, have greatly influenced the general geotectonic structure of Eastern Serbia. These processes have strongly affected both the structure and form of the limestone masses. Numerous fissures and channels appeared as the result of these movements, penetrating the limestone mass down to base level. These fissures and crevices, as well as diastromes, formed a dense reticulum permitting the circulation of ground water and thus causing the continuation and intensification of the karst process in both superficial and deep parts of the limestone masses. In view of these factors, as well as the high degree of dissection and levels of precipitation, almost all the conditions for further development of the varied karst relief in Eastern Serbia were present.

Biospeleological considerations

The majority of cave pseudoscorpions in Eastern Serbia are the descendants of tropical epigean forms, which were widely distributed over the Laurasian land mass at the end of the Mesozoic and at the beginning of the Tertiary. However, the tropical fauna has successively disappeared from these areas. The primordial forms vanished, changed or migrated farther

The simultaneous karstification, however, yielded a wide range of niches underground, thus providing the indispensable conditions for the origin of refugial zones for the endangered and originally epigean species.

Cave-dwelling pseudoscorpion species are now found mainly in regions with a Mediterranean climate. These forms have remained mostly in their archetypal areas, colonizing the underground habitats (caves and potholes), but some of them continued to live either in the deep layers of humus and soil or under stones. Adaptive strategies in each case were different. This fact can be illustrated by the (small) body size and flattening of the body in some forms which inhabit crevices and small fissures in the soil (e.g., some forms belonging to the pseudoscorpion genus Chthonius C. L. Koch), and by the attenuated appendages and development of numerous elongated tactile setae in some cave inhabitants (representatives of the pseudoscorpion genera Chthonius, Neobisium Chamberlin, Roncus L. Koch, Acanthocreagris Mahnert). Adaptation to the life solely in deep soil and underground is not characteristic of a particular taxonomic or morphologic group of animals but rather represents an adaptive response of the epigean and humicolous species, including pseudoscorpions, in order to survive in the conditions of a typical or modified Mediterranean climate.

Since present-day cave species originated in regions (or geological epochs) with more constant climatic conditions, especially with regard to humidity, it should be pointed out that even today some representatives of the genus Chthonius inhabit the deeper soil layers or caves as the climate becomes more arid (Ćurčić 1988a, 1988c). Thus, for example, in Carniola and NW Croatia, such species inhabit humus and leaf-litter and are found also under big stones. To the south (in southern Croatia and in Herzegovina), the same species populate caves which, as a rule, have relatively constant temperature and humidity. In addition, C. bogovinae Ćurčić lives in caves on the slopes of the Kučaj Mts. in Eastern Serbia. But, at higher altitudes of the same mountain massif, this cavernicolous species occurs in deep soil and under stones. A similar phenomenon has also been noted in the case of C. troglobius Hadži from Macedonia (Ćurčić 1988a, 1988b). Analysis of this behaviour

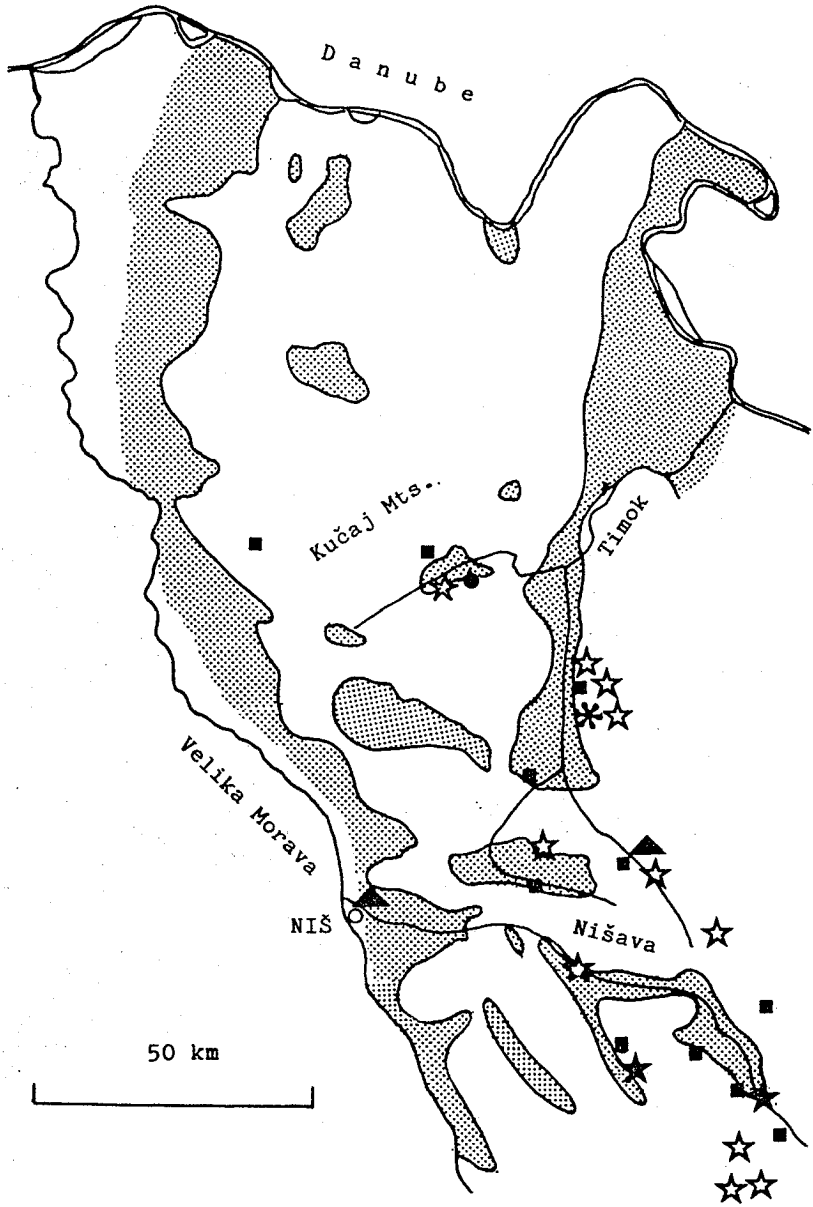

Fig. 1 Distribution of the Neogene sediments in Eastern Serbia (after Grubić and Marković 1967) and present areas of cave species of Chthonius (Chthonius) C. L. Koch (solid squares), Chthonius (Ephippiochthonius Beier)(solid triangles), Roncus L. Koch (open stars), Neobisium Chamberlin (solid stars), Acanthocreagris Mahnert (solid circle), and Tyrannochthonius Chamberlin (asterisk).

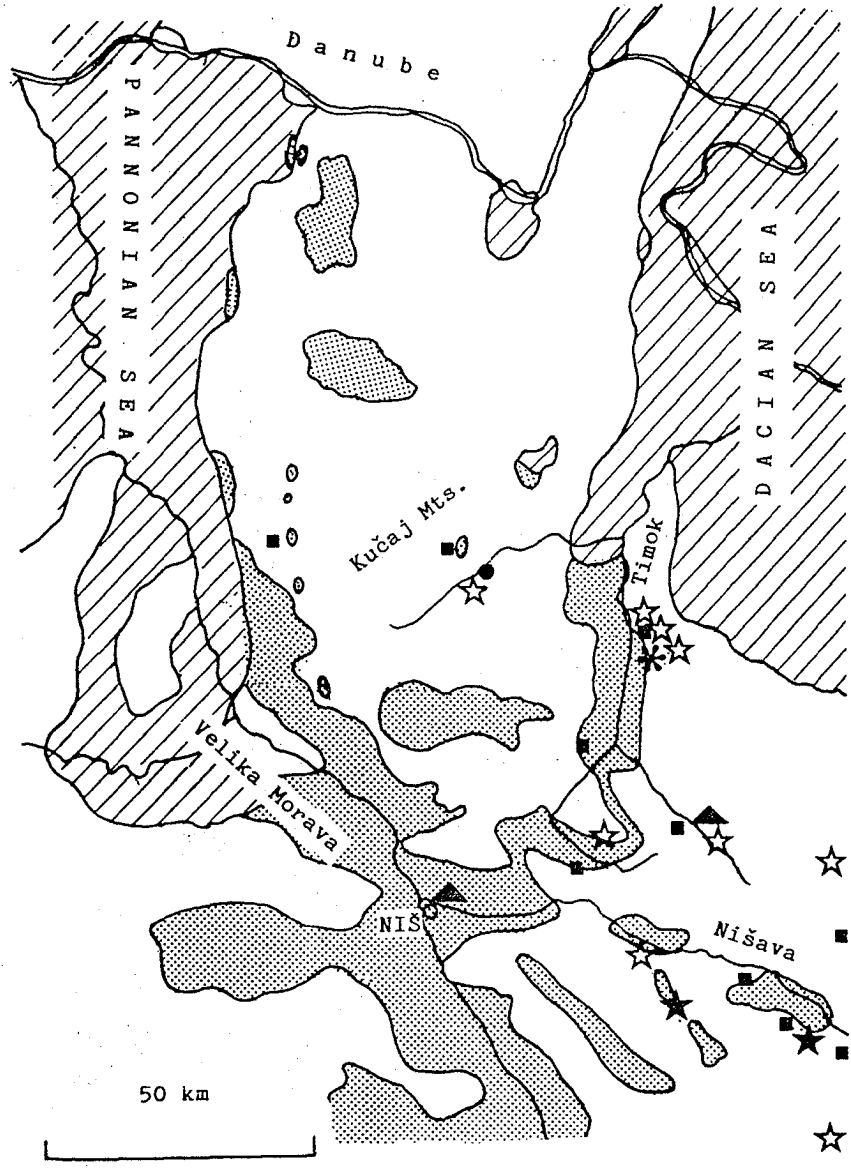

Fig. 2 Distribution of dry land and marine and lacustrine basins during the Tertiary in Eastern Serbia (after Stevanović 1967) and present areas of cave species of Chthonius (Chthonius) C. L. Koch (solid squares), Chthonius (Ephippiochthonius Beier)(solid triangles), Roncus L. Koch (open stars), **Neobisium** Chamberlin (solid stars), Acanthocreagris Mahnert (solid circle), and Tyrannochthonius Chamberlin (asterisk).

of these hypogean forms to life underground is more pronounced, the more arid the climate in the areas under study.

Relict and endemic pseudoscorpions of Eastern Serbia

The pattern of the relictual and autochthonous fauna of endogean pseudoscorpions of Eastern Serbia has been greatly influenced by the process of karstification as well as by the evolution of the ancient marine and lacustrine basins. The continuity of these basins has been affected by the different duration of marine transgressions and regressions (Stevanović 1951, 1967; Grubić and Marković 1967). It is also worth mentioning that there were three lacustrine phases in Eastern Serbia: the Upper Oligocene, Mio-Pliocene and Upper Oligocene phases (Luković 1935). The humidity in this area was probably high in these periods, especially if we remember that the level of ground water was at the time very close to the soil surface (Milojević 1951).

In view of these considerations, it is of particular interest to compare the distribution of Neogene sediments, as well as the distribution of marine and lacustrine Tertiary basins in Eastern Serbia with the present distribution areas of endemic and relictual pseudoscorpions in the caves of this region (Figs. 1 and 2). It is evident that the present distribution of endemic troglobitic pseudoscorpions from the subgenus Chthonius (Chthonius)(C. **bogovinae** Ćurčić, C. **latidentatus** Ćurčić, C. **olalija** Ćurčić, C. **german** Ćurčić, C. **zmaj** Ćurčić, C. **troglav** Ćurčić, C. **stevanovici** Ćurčić, C. **iugoslavicus** Ćurčić, and C. **lesnik** Ćurčić) in general coincides with the peripheral areas of the Neogene sediments, or with the fringe zones of either marine or lacustrine basins (Fig. 2). A similar situation is found in the case of the subgenus **Chthonius (Ephippiochthonius** Beier)(Figs. 1 and 2). Needless to say, the cavernicolous representatives of the latter subgenus (C. aff. **tetrachelatus** (Preyssler), C. **serbicus** Hadži) cover a considerably smaller area in Eastern Serbia than the same component of the nominal subgenus.

The present distribution of the endemic and relict troglobites belonging to the genus **Roncus** (R. **vada** Ćurčić, R. **remesianensis** Ćurčić, R. **timacensis** Ćurčić, R. **bauk** Ćurčić, R. **pljakici**

Hadži), compared with the distribution of Neogene sediments (Fig. 1) as well as with the distribution of dry land and marine and lacustrine basins during the Tertiary in Eastern Serbia (Fig. 2), suggests that the present localities of the species are dispersed in the vicinity of the ancient marine and (particularly) lacustrine basins. A significant finding was that the area of the cave inhabitants of **Roncus** is almost identical with the distribution area of the cavernicolous forms of **Chthonius** in this region (Fig. 2).

The repartition of the genera **Acanthocreagris** (**A. ludiviri** Ćurčić) and **Neobisium** (**N. babusnicae** Ćurčić and **N. stankovici** Ćurčić) corresponds to the distribution of dry land on the periphery of the Tertiary lacustrine basins in the area under study. Comparison of the distribution areas of cave **Acanthocreagris** and **Neobisium** in Eastern Serbia has also shown that the area of **Acanthocreagris** is found more to the north, and that of the cave **Neobisium** more to the south (Figs. 1 and 2).

The only locality of the genus **Tyrannochthonius** Chamberlin (**T. psoglavi** Ćurčić) known to date is situated in the vicinity of the seashore of the once existing Dacian Basin (Sea). The presence of this genus and species on the Balkan Peninsula supports the hypothesis of its autochthonous and residual origin (Ćurčić 1988a, 1988b, 1988c).

In lieu of a conclusion

Analysis of the paleobiogeographical, biogeographical and taxonomic features of the pseudoscorpions of Eastern Serbia which were studied, has provided clues about their probable origin and historical development in this region.

The geographic distribution and taxonomic features of this endemic and relictual fauna point to the different origin and age of its pseudoscorpion genera and species. For example, **Tyrannochthonius psoglavi** has its origin in common with other tyrannochthoniid forms, which are presently found in tropical and subtropical regions. Therefore, this pseudoscorpion should be considered as being of Gondwanian origin. It can also be assumed that **T. psoglavi** today populates the remains of its autochthonous area in Eastern Serbia.

Among the ancient relicts of Eastern Serbia, we should

Neobisium, which probably belong to the phyletic series of the Laurasian origin. A similar situation is encountered as regards the representatives of the genus Roncus (Ćurčić 1988). In addition, it should be emphasized that the divergent differentiation of species belonging to these genera has been taking place in the Balkan Peninsula. In the context of the Peninsula, Eastern Serbia should be considered one of the most important centres of the adaptive radiation of pseudoscorpion species.

The cave forms of Chthonius probably belong to the descendants of the "Meso-Aegean" phyletic series (Gueorguiev 1977) and these are probably either of the Paleogene or of the Neogene age (Ćurčić 1988). Their differentiation into endemic forms has been taking place in conditions of karstification which has been particularly intensive in Eastern Serbia. Therefore, these species belong to the residuary fauna once inhabiting the old Balkan dry land.

It is evident that the cave pseudoscorpions under study had lived or originated in areas or geological epochs with a humid climate. The modern subterrestrial forms, which are now adapted to life underground, are probably the descendants of the ancient epigean hygrophylic forms. With increasing aridity and the formation of different niches underground, these species evolved as cave inhabitants. In addition, all or the majority of the modern forms today populate the remains of their autochthonous areas.

The origin and development of the rich endemic and residuary fauna of cave pseudoscorpions in Eastern Serbia have been affected by several factors, most notably the outstanding variety of ancient epigean fauna once to be found in Eastern Serbia and the continuity of the continental phase which in this part of Serbia has been maintained since the end of the Paleozoic era. Furthermore, the presence of deep limestone sediments has made the development of underground karst relief possible, and the climatic conditions have been also suitable by enabling the survival of the endangered species. Finally, in the underground habitats the process of adaptive radiation of species has been taking place for a long time. Therefore, Eastern Serbia, and especially the underground habitats in this region, should be considered one of the most important centres of the endemic differentiation of relict pseudoscorpion fauna in the Mediterranean region.

Indeed, the variety and relictuary nature of the East Serbian pseudoscorpion fauna, as well as its interrelationships with forms in adjacent regions, indicate that the Balkan Peninsula (and therefore Eastern Serbia) is an important centre of the "evolutionary explosion" of species, as well as one of important centres of colonization of some pseudoscorpion groups, in the direction of both the western and eastern parts of the ancient Mediterranean dry land.

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Addendum

Grubić, A., M. Marković. 1967. Morfologija Istočne Srbije. VIII Karp.-Balk. Geol. Asoc., Geološki pregled Karpato-Balkanida Istočne Srbije (Stratigrafija, tektonika i magmatizam), 5-8, Beograd.

SUMMARY

The origin and development of the rich endemic and residuary fauna of cave pseudoscorpions in Eastern Serbia have been affected by several factors, most notably the variety of ancient epigean fauna once to be found in Eastern Serbia and the continuity of the continental phase which in this area has been maintained since the Paleozoic era. Furthermore, the presence of deep-lying limestone sediments has made the development of underground karst relief possible, and the climatic conditions have been also suitable by enabling the survival of the endangered species. Finally, in the underground habitats the process of adaptive radiation of species has been taking place for a long time. Therefore, Eastern Serbia, and especially the underground habitats in this region, should be considered one of the most important centres of the endemic differentiation of relict pseudoscorpion fauna in the Mediterranean region.

Indeed, the variety and relictuary nature of the East Serbian pseudoscorpion fauna, as well as its interrelationships with forms in adjacent regions, indicate that the Balkan Peninsula (and therefore Eastern Serbia) is an important centre of the "evolutionary explosion" of species, as well as one of important centres of colonization of some pseudoscorpion groups, in the direction of both the western and eastern parts of the ancient Mediterranean dry land.