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SOME REMARKS ON THE EVOLUTION OF DINARIC CAVE PSEUDOSCORPIONS

The terrestrial troglobites of the Dinaric Karst are usually descendants of a tropical epigeous fauna living in Eurasia and North America at the beginning of the Tertiary period. Tropical fauna has subsequently disappeared from these regions. The species changed, were destroyed or emigrated towards the present-day tropics. Only in caves have some species survived. Simultaneous karstification provided a wide variety of niches underground, resulting in many refuges for originally epigeous species.

Underground pseudoscorpions are characteristic of regions with a Mediterranean climate. These species have maintained their habitat by penetrating deeper underground and colonizing caves, fissures in the soil, or the soil itself. The adaptive strategy in each case was different, as illustrated by the small size and flattened body of the inhabitants of fissures (some members of the pseudoscorpion genera **Chthonius** C.L.Koch and **Neobisium** Chamberlin), or by the elongated appendages and the development of numerous setae in cave species (e.g., representatives of **Chthonius, Neobisium, Roncus** L.Koch, **Insulocreagris** Ćurčić, and other genera).

Strict adaptation to life in deep soil is an adaptive response of the epigeous or humicolous species of many taxonomic groups (coleopterans, spiders, pseudoscorpions) in order to survive in Mediterranean climates since these species originated in some regions or periods with a more constant climate as regards humidity.

Hadži (1941) found that some representatives of **Chthonius** (**C. raridentatus** Hadži and **C. ellingseni** Beier) are found deeper in soil as the climate becomes more arid. In Carniola and in NW Croatia, they live therefore in humus, in leaf-litter and under stones, but to the south, these species also inhabit caves which usually have a relatively constant temperature and humidity. A similar phenomenon has been observed in **C. bogovinae** Ćurčić from E Serbia (Ćurčić 1988). This shows the fundamental importance that water has in the environment when changing from adaptation to life in soil to a more cryptic way of life -

in caves.

Some other genera of pseudoscorpions also have this feature. Within the Chthoniidae family, the species of **Tyrannochthonius** Chamberlin-related pseudoscorpions exhibit endogeous characteristics in Mediterranean climates and epigeous characteristics in other climates. For example, the troglobitic form **Troglochthonius** Beier is found in the caves of Herzegovina, Istria and Carso Triestino, while its epigeous relative, **Paraliochthonius** Beier, has a broad tropical and subtropical distribution. A newly described troglophilic **Tyrannochthonius** from E Serbia (Ćurčić, in press) has been established in the continental belt of the Balkan Peninsula, while its close relatives, **Paraliochthonius** and **Troglochthonius,** populate the northwestern and western areas of the peninsula. This is sound biogeographical evidence of the continuous evolution of this group of pseudoscorpions in the Proto-Balkans since the remote past, as well as of their subsequent divergent differentiation into different taxa in the same geographic area. Their present range, great disjunctions in the distribution areas as well as some morphological traits suggest that representatives of this group are probably from the Gondwanian age.

There are disjunctive distribution patterns in all major pseudoscorpion groups. Representatives of the recently discovered **Neobisium(Pennobisium** Ćurčić n. subgen.) in Central Dalmatia and in Istria exhibit similar distribution patterns. However, the biogeographical status of another new Neobisiid genus, **Protoneobisium** Ćurčić (which inhabits a few caves in Dalmatia) still remains enigmatic. Some groups of troglobitic pseudoscorpions pertaining to **Chthonius, Neobisium,** and to **Microcreagris** Balzan-related genera (**Insulocreagris, Acanthocreagris** Mahnert and **Balkanoroncus** Ćurčić), also have disjunctive distributions, with centres in Slovenia and further south (Central Dalmatia, Herzegovina and Montenegro) or east (E Serbia, W Bulgaria). In between are usually other, related species, but sometimes, there are overlapping distributions of species in Central Dalmatia, southern Croatia, Bosnia or western Serbia.

Deeleman-Reinhold (1978) has postulated a plausible explanation for this interrupted distribution. During the Tertiary period, the Proto-Balkan lands are believed to have had long periods of equatorial climate and to have been covered with tropical and subtropical forests. The large, probably rapid subversion of climate at the end of the Miocene (Hsü 1972) must have brought aridity to SW Yugoslavia, rendering it uninhabitable to humidity-dependent species. The large stretches of limestone bedrock, that are bare today, were then covered with impermeable sediments, obstructing escape to moisture-retaining limestone. These impermeable strata persisted much longer in the middle Dinarides than to

the north or south where they eroded. This was probably responsible for the distribution gaps in cave invertebrates including pseudoscorpions.

In a few places in the north and south a free passage was soon possible to the underlying limestone. This system offered suitable shelter for at least part of the retreating, hygrophilic fauna. This hypothesis can explain the concentration of relicts in Middle and South Dalmatia, in Herzegovina, and Montenegro, such as the genera **Insulocreagris, Troglochthonius, Microchthonius** Hadži, **Protoneobisium,** and some spiders (Deeleman-Reinhold 1978), coleopterans, molluscs, etc.

On the other hand, the eastern part of the peninsula was not exposed to such a degree of aridity, hence pseudoscorpions could have survived under more favourable conditions, where sufficient moisture could have been preserved even in the dryest periods. Let us mention here the genera **Acanthocreagris, Balkanoroncus, Tyrannochthonius,** and many species of **Chthonius, Neobisium** and **Roncus** which today live in caves situated on the edges of the former Tertiary lacustrine basins.

The analysis of pseudoscorpions given here helps interpret the origin and history of the Dinaric troglobitic pseudoscorpions. The primordial population colonized the Proto-Balkans at the very beginning of its existence. Subsequently, it gave birth to a number of phyletic lineages. First there are the relict species whose interrelationships with Pre-Tertiary pseudoscorpions have been established. These species, or stem forms, inhabited the leaf-litter and humus of the Dinaric forests during or even before the Tertiary. One can give numerous examples of discontinuous Eurasian and Euro-American distributions among both cave and epigeous forms (Vitali-di Castri 1973). Evidently, there was an abundance of epigeous Paleogene and Neogene fauna in Eurasia, and its disappearance from some parts is due not only to unfavourable changes of climate, but also to the lack of ways of migration or possibilities of shelter (Vučinić 1965).

The composition of early thermophilous fauna was not uniform , and regional differences no doubt existed. With the Ice Age, its distribution changed. Many species disappeared in Central and Northern Europe, Siberia and North America, mostly driven south, into refuges where climatic and other changes were less unfavourable. This process must have been complicated and cannot be explained only by climatic changes. It must have taken place with an uneven intensity in various parts of the northern hemisphere and must have extended over different groups of organisms (Stanković 1932). The disappearance of pseudoscorpion species and genera was least intense in shelters where the fauna was

able to maintain itself. We recognize three main shelter zones: the Mediterranean, East Asia and North America. It is certainly in the first that there are the most relicts of Tertiary epigeous fauna.

The Pannonian and Ponto-Caspian zones were refuges to the Tertiary elements of Central Europe which migrated southwards owing to climatic and other changes. However, the Mediterranean was populated by more thermophilous fauna (Kosswig & Battalgil 1943), whose living remains have been preserved in more isolated places. The discontinuous ranges of these remnants clearly indicate that Tertiary pseudoscorpion fauna was locally exposed more or less to destruction, under the influence of geotectonic events, climatic changes, competition with immigrants, etc. (Kosswig & Battalgil 1943, Ćurčić 1986).

It is not easy to analyse the origin and history of the endemic pseudoscorpions of the Dinaric underground, because they represent an adaptive and selected fauna. In spite of the fact that the Dinaric region was colonized at the beginning of its existence by pseudoscorpions, the question of the direct provenance of Dinaric cave pseudoscorpions still remains open. We have every reason to assume that this fauna evolved from ancient circum-Mediterranean fauna, its origin to be sought in the Proto-Balkans. Underground habitats succeeded one other in a continuous manner to our times. More ancient caves disappeared, whilst new ones were formed, thus permitting the survival of their fauna. This continuity of their habitats has certainly played an outstanding role in the preservation of old pseudoscorpion elements.

Among the main causes which have affected the evolutionary history of the Dinaric cave pseudoscorpions, one should emphasize the effects of the karstification process. This process is very little known as yet, hence its interpretation is more or less hypothetical. It is evident that the Dinaric Karst was not developed at one time, hence its colonization by pseudoscorpions must have occurred progressively throughout its life span.

The survival of numerous relict pseudoscorpions has been sustained by the continuity of the continental phase, by the relative constancy of living conditions in caves, as well as by the isolation of underground habitats. The occurrence of relict forms in caves (e.g., **Protoneobisium, Insulocreagris, Microchthonius, Troglochthonius,** many species of **Chthonius, Neobisium** and **Roncus**) supports the view that the subterranean milieux have existed without interruption (Beier 1963, Ćurčić 1975, 1986, 1988).

It is pertinent to note that faunal exchange between Dinaric and

other caves has been very limited, especially in the advanced phases of karstic evolution. This is due to their geographical position and to the adaptation of their inhabitants to specific living conditions. Cave pseudoscorpions were thus enabled to compete successfully with new immigrants. Living conditions in caves have certainly changed during the existence of caves, but not in a manner to have caused the disappearance of the majority of relicts. In addition, such changes have favoured the autochthonic evolution of cave inhabitants.

In conclusion, the period of formation for each endemic pseudoscorpion from the Dinaric Karst is difficult to ascertain with precision. One can only speculate in that respect by utilizing the sound criteria of taxonomy, comparative morphology and biogeography. Relicts with no close relatives, or with an isolated position in recent fauna, represent the most ancient cave relicts. Furthermore, relicts whose relatives occur in the Balkans are remnants of some ancient faunal complex, whose primordial distribution has often been drastically reduced to the Dinaric caves, representing their last refuge. In addition, there are relict pseudoscorpions whose related species are distributed elsewhere, these forms being descendants of a broadly distributed ancestor.

Thus, the Dinaric region is populated by a great number of endemic and relict cave pseudoscorpions, belonging mostly to the Chthoniidae and Neobisiidae families. These forms belong to different phyletic series, from the Gondwanian and Laurasian, on the one hand, to the North or South Aegean (or Proto-Balkan), on the other. These species and genera are vestiges of old faunae, which found their ultimate shelter below ground in the Dinaric Karst and the adjoining regions.

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