LJUBLJANA, JUNE 2004 Vol. 12, No. 1: 35–56

XVII. SIEEC, Radenci, 2001

THE CAVE-DWELLING FAUNA OF THE BALKAN PENINSULA: ITS ORIGIN AND DIVERSIFICATION

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Abstract The karst of the Balkan Peninsula is inhabited by a great number of endemic and relict cave animals pertaining to the Paleo-Mediterranean, Laurasian, Paleo-Aegean, and South- or North-Aegean (or Proto-Balkan) phyletic series of species and higher taxa. The major causes of the extraordinary variety of the troglobitic fauna of this region include: (1) the varied epigean fauna populating the Proto-Balkans in the remote past; (2) continuity of continental phases in different areas of the Balkans; (3) presence of mighty limestone beds and the subsequent evolution of the underground karst relief; (4) succession of suitable climatic conditions favouring the colonisation of subterranean habitats; and (5) divergent differentiation of different lower and higher taxa in numerous isolated niches underground. Study of the cave inhabitants of the Balkan karst has offered further proof of their great age and different origin. These species and genera represent the last vestiges of an old fauna, which found their ultimate shelter in the underground domain of the Balkans and its adjoining regions. Apart from this, it is apparent that specific aspects of geomorphological and climatic events in the Balkans, together with peculiarities in the historical development of the fauna there, caused the peninsula to become the main centre of dispersion and colonisation of species and groups of species, i. e., the main source for the revitalisation and genesis of biological diversity, not just in the Mediterranean region, but throughout all of Southeast Europe.

KEY WORDS: cave fauna, Balkan peninsula, biodiversity

Izvleček – JAMSKA FAVNA BALKANSKEGA POLOTOKA: NJEN IZVOR IN RAZNOVRSTNOST

Kras Balkanskega polotoka naseljuje veliko število endemičnih in reliktnih jamskih živali, ki pripadajo paleomediteranskim, lavrazijskim, paleoegejskim, južno- in severnoegejskim (protobalkanskim) filetičnim skupinam vrst in višjih taksonov. Glavni vzroki izjemne raznovrstnosti troglobiotične favne tega območja so: (1) raznovrstna nadzemna favna, ki je naseljevala proto-Balkan v daljni preteklosti, (2) trajnost kopnih obdobij v različnih predelih Balkana, (3) prisotnost mogočnih apnenčastih slojev in posledičen razvoj podzemnega kraškega reliefa, (4) vrstenje ugodnih klimatskih razmer, ki so spodbujale kolonizacijo podzemnih življenjskih prostorov, in (5) raznovrstne prilagoditve različnih nižjih in višjih taksonov v številnih izoliranih podzemnih nišah. Raziskave jamskih prebivalcev balkanskega krasa so dale dodatne dokaze njihove velike starosti in različnih izvorov. Te vrste in rodovi so zadnji predstavniki stare favne, ki je svoje zadnje zatočišče našla v podzemlju Balkana in sosednjih območij. Poleg tega je očitno, da so posebne geomorfološke in klimatske razmere na Balkanu, skupaj s posebnostmi v zgodovinskem razvoju tukajšnje favne, naredile Balkan za glavno središče razselitve in kolonizacije vrst in skupin vrst, torej glavni vir obnove in nastanka biotične raznovrstnosti, ne le v Mediteranu, temveč v vsej jugovzhodni Evropi.

KLJUČNE BESEDE: jamska favna, Balkanski polotok, biodiverziteta

The Balkan Landscape

Situated in the eastern part of the Mediterranean region and occupying the area between the Adriatic Sea to the west and the Black Sea to the east, the Balkan Peninsula (Fig. 1) faces Asia Minor, with which it formed, until sometime in the Pleistocene, an uninterrupted continental mass (the ancient Aegeis). As a consequence of later radial movements and especially of the breaking-down of the Aegean land mass, the bridge linking the Peninsula with Asia Minor was submerged, its last remnants being numerous extant islands (Dietz and Holden, 1970; Eldredge and Stanley, 1984).

Nowhere else in the Mediterranean region is the relief of land more complicated than in the Balkan Peninsula (Cvijič, 1904). Several great geotectonic units exist: first, the great Rhodopes mass should be distinguished as the ancient crystalline nucleus of the Hercynian age, which occupies the central part of the Balkan Peninsula. This resistant nucleus of the Peninsula, formed mainly of crystalline schists with intrusions of eruptive rocks, has been greatly broken and disrupted by faultings in a number of depressions and isolated blocks, some of which reach more than 2,800 m in elevation and represent the highest summits of the Peninsula. The Rhodopes range is succeeded in the north by the great Pannonian mass, deeply subsided, and covered with Neogene marine and lacustrine sediments (Laskarev, 1924).

Fig. 1: The Balkan Peninsula (Stanković, 1960).

All these ancient blocks played the part of an intermediary mass during the evolution of the Alpine orogeny (Kober, 1952). In fact, two branches of this great orogeny run around the ancient mass of the Peninsula: the Carpatho-Balkan Arch in the north and the Dinarides in the west and south (Fig. 2). The Southern Carpathians (the mountains of Transylvania) advanced in great overthrusts towards the south beyond the Danube penetrating the Peninsula (Eastern Serbia), to be continued in the east by the Balkan Range (or Mt. Stara Planina) in northern Bulgaria. This mountain chain, stretching from west to east for some 550 km to the Black Sea, represents a kind of backbone of the Peninsula and borders, to the north, the great Danubian Platform. It is after Mt. Balkan that the Peninsula has been named. South of this mountain chain lies a long series of tectonic depressions.

The whole western part of the Peninsula is occupied by the mighty folds of the Dinarides, which run parallel with and along the Adriatic and Ionian Seas, from the Eastern Alps in the north to Greece and the island of Crete in the south, where they change direction and continue to the east, passing by the Aegean islands of the Cyclades and Sporades and joining the Taurid Chain in Asia Minor. They form the great southern branch of the Alpine orogeny, which borders, in the west and south, the ancient intermediary mass of the Peninsula and constitutes a powerful tectonic

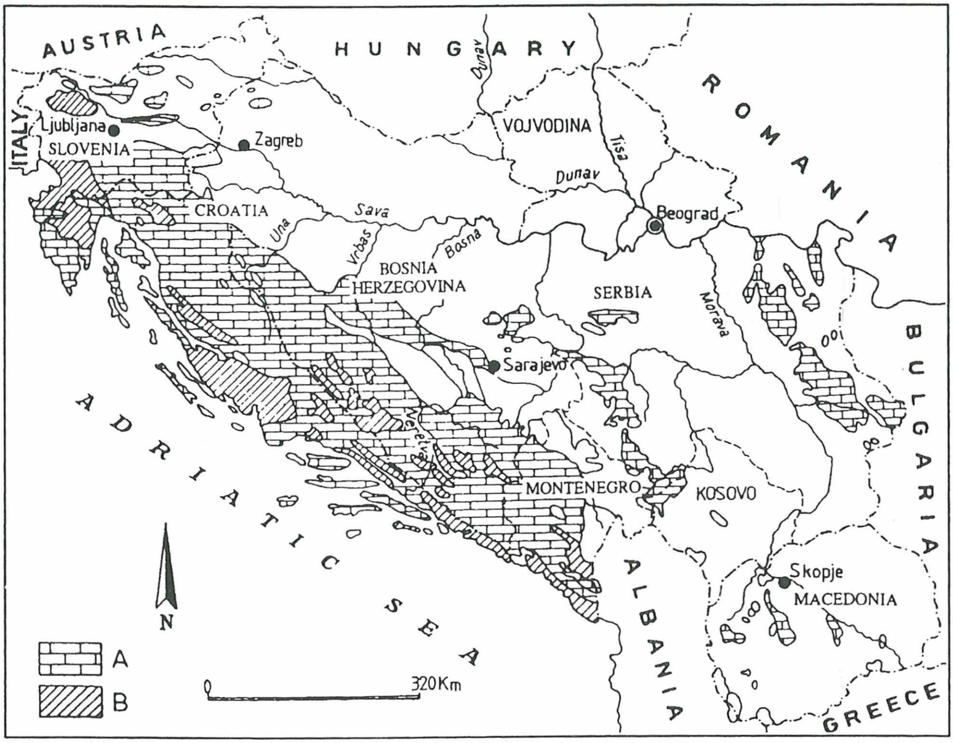

Fig. 2: Distribution of main karstic regions in western and central parts of the Balkan Peninsula. A - epigean karst, B - karst covered by the Tertiary and Paleozoic clastics (Juberthie and Decu, 1994).

unity. It is a series of parallel and close chains which occupies the western part of the former Yugoslavia (as well as of Western Serbia), the whole of Albania, western Macedonia, and Greece, and whose highest summits rise beyond 2,500 m.

The northern and central parts of the Balkan Peninsula are essentially mountainous areas. With the exception of the great Pannonian Plain and the Danubian Platform in the north, flat ground is mainly limited to the numerous great tectonic depressions observed in most of the Peninsula. They bear witness to violent tectonic activity, particularly during the Neogene and the Pleistocene epochs. The relief of Serbia is in fact extremely broken by numerous fractures. A set of basins run along the central axis of Serbia, from the Danube in the north to Macedonia in the south. There exists the great longitudinal depression, now followed by the Morava and Vardar rivers. Another series of basins more to the east is found in east Serbia. Most of the time these are ancient lacustrine basins. Similar tectonic depressions can be also observed in the western part of Serbia, but it is mostly in the Aegean region that the breaking-up of the relief due to radial movements reaches its extreme (Cvijić, 1906, 1911, 1924, 1928).

The tormented relief influences the climate of the Balkan Peninsula, much more than its geographical position in the south of Europe. The Mediterranean climate is felt along the Adriatic, Ionian and Aegean Seas, as well as in some regions in the continental area. The mountain ranges of the interior of the country prevent further penetration of this climate. However, in summer, the anticyclone of the Azores in the west, the overheated depressionary area over the Arab-Syrian desert in the east, and that over the African desert in the south-east provoke a strong barometric gradient, followed by the northern sector winds which prevail in the Eastern Mediterranean. In winter, however, the Mediterranean zone is between two areas of high pressure in the north and south, and the sea remains warmer than the continental masses around it. This causes the formation of depressionary areas over different regions of the Mediterranean zone, the existence of an autonomous current of perturbation and changeable weather characterized by frequent precipitation (Biel, 1944). According to Vujević (1953), most of the northern part of the peninsula is largely open to the influence of the Central European climate, while its eastern part is under the influence of the Pontic climate.

Karst of the Peninsula

The Dinaric karst is composed predominantly of limestones and dolostones of the Cretaceous and Jurassic ages (Fig. 3). It consists of a coastal zone (the Outer Dinarides) and the more inland Inner Dinarides, where the underlying Paleozoic strata emerge locally. These limestone masses are strongly faulted and fractured, their total thickness varying between 1,000 and 5,000 m (Cvijić, 1893). The whole area is littered with caves, and the enormous quantity of precipitation is mostly drained underground. The Dinaric Mountains are of fairly recent age. During the Paleocene and the first part of the Eocene epochs, flysch was deposited over large areas on top of the limestone. Only after marine regression had set in around the mid-Eocene could karstification begin locally. But most of this process could set in only after denudation of flysch. This process is estimated to have begun in the younger Tertiary period at the earliest. Most of the orogenetic activity took place during the Pliocene and the Quaternary periods. Both the rising of the Dinarides and the karstification process are still present today.

The karst regions of the Carpatho-Balkan Arch in Eastern Serbia and Western Bulgaria resemble the typical (Dinaric) karst. The karstic terrains of these areas are thus characterized by an extremely complex and variable relief. Cretaceous limestones are more abundant, while Triassic limestones are less frequent. Cenozoic formations, however, are also widely distributed; they are represented mainly by Oligocene and Neogene lacustrine sediments.

The mountains of Eastern Serbia represent a direct continuation of the Southern Carpathians extending from Romania, which do not merge directly with the Balkanides; rather, they deviate or diverge to bypass the "resistant" basin of the Crnorečka Kotlina in Eastern Serbia.

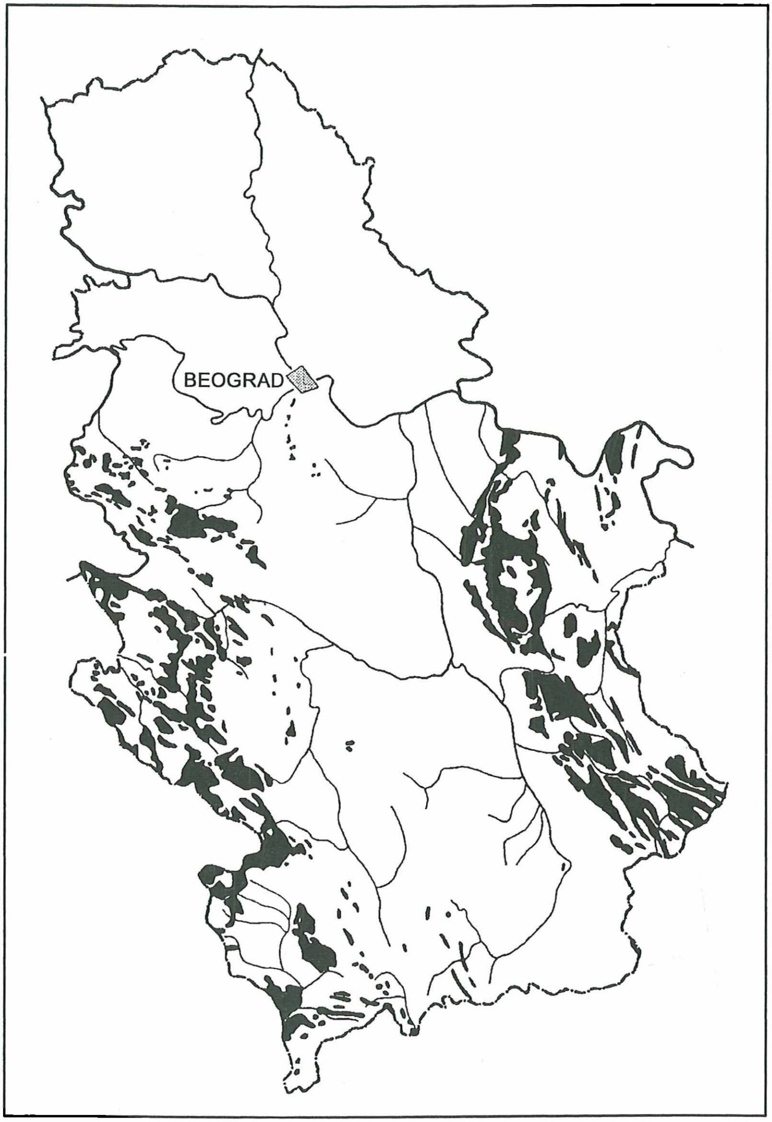

Fig. 3: Distribution of karst in Serbia (Gavrilović, 1976).

The general geotectonic structure of both the Dinarides and Carpatho-Balkanides was changed by powerful movements; by the process of folding and faulting; and by epeirogenetic movements (Fig. 4). As a result, numerous fissures and channels appeared, deeply penetrating the limestone beds. These fissures and crevices formed a dense reticulum, thus permitting both free circulation of groundwater and intensification of the karst process in superficial and deep parts of the limestone masses.

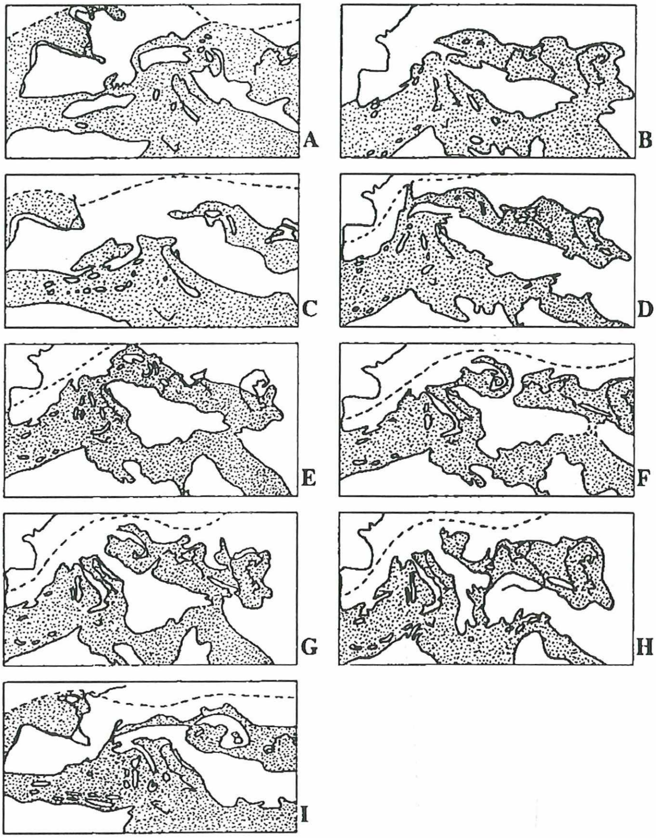

Fig. 4: Evolution of dry land in South Europe during the Tertiary. A - Oligocene; B - Lower Oligocene; C - Upper Miocene; D - Upper Miocene; E - Middle Miocene; F - Middle Miocene; G - Middle Miocene; H - Lower Miocene; I - Lower Miocene (Mršić, 1997).

Cave Fauna in The Balkans: Its Origin and Historical Development

The terrestrial cave-dwellers in Serbia are usually the descendants of a tropical epigean fauna living in Europe and North America at the beginning of the Tertiary. The tropical fauna subsequently disappeared from these regions (Camacho, 1992). The species changed, were destroyed, or migrated towards the modern tropics. Only in caves have some species survived, since simultaneous karstification provided a wide variety of niches underground, which resulted in a huge new refugial zone for originally epigean species.

Most systematic zoologists have reported a north-south or east-west polarization in the distribution of true cave animals. Thus, clusters of related taxa are found in Eastern (or Northern Serbia), while a different set of taxa occur in Western (or Southern) Serbia. This was clearly shown by Deeleman-Reinhold (1978) and by Ćurčić (1975, 1988a). Examples of this type of distribution are numerous (Fig. 5), and the phenomenon occurs in most terrestrial members of those orders present in Balkan caves (Jeannel, 1942; Guéorguiev, 1973, 1977; Kratochvíl, 1978; Polenec, 1969).

Biogeographically, some genera and species of the Balkan terrestrial and aquatic troglobites are characterized by a disjunctive distribution. This type of partition can be attributed to successive paleogeographical and climatic changes, since the distributions of these troglobitic animals and their closest epigean relatives correspond to

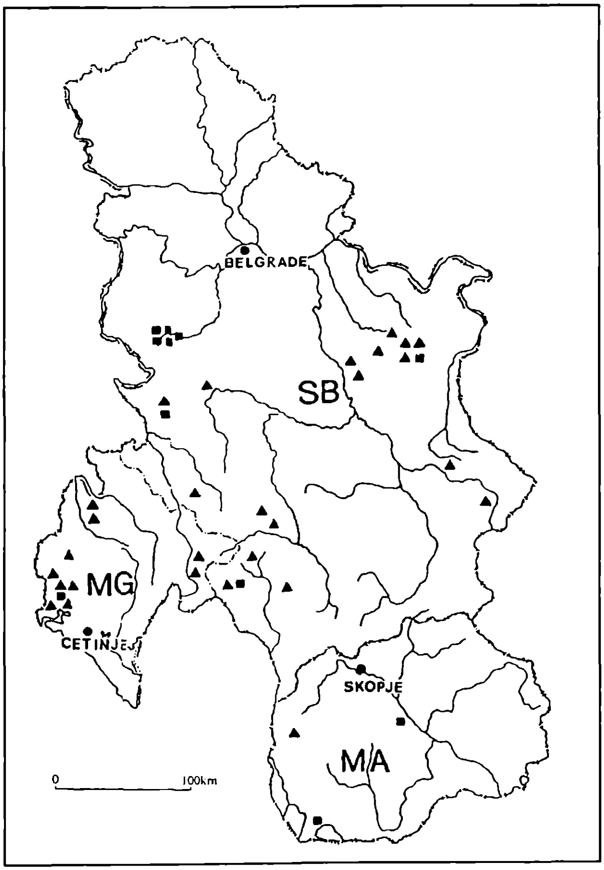

Fig. 5: Distribution of cave diplopods in Serbia (SB), Montenegro (MG), and Macedonia (MA): troglobitic (solid triangles) and troglophilic and trogloxenic forms (solid squares) (Ćurčić and Makarov, 1998).

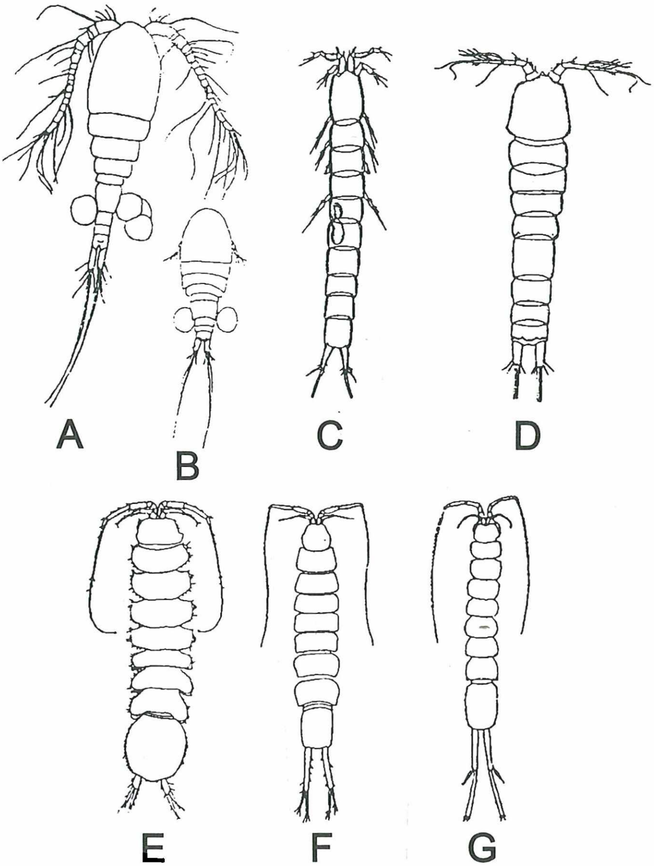

Fig. 6: Cave aquatic copepod crustaceans: *Kieferiella delamarei* Lescher-Moutone (A), *Speocyclops gallicus* Chappuis & Kiefer (B), *Parastenocaris dianae* Chappuis (C), *Parapseudoleptomesochra subterranea* (Chappuis) (D); and cave aquatic isopod crustaceans *Proasellus valdensis* (Chappuis) (E), *Synasellus brigantinus* Braga (F), and *Phreatoasellus joianus* Henry & Magniez (G) (Juberthie and Decu, 1994).

the distribution within the old Mediterranean dry land which existed at the very beginning of the Tertiary period; despite the fragmentation of this land mass since the Eocene epoch, the long continuity of the continental phase in areas inhabited both by epigean ancestors and their hypogean descendants has been preserved up to the present time. Consequently, the present localities of these genera are probably remnants of their primordial distribution areas (Figs. 6 and 7) (Ćurčić and Dimitrijević, 1998,1996; Ćurčić *et al.* 1997).

There are disjunct distribution patterns in all major terrestrial cave invertebrates, with centers in different areas of the peninsula. Inbetween are areas of some other, related species, but sometimes there are overlapping species distributions

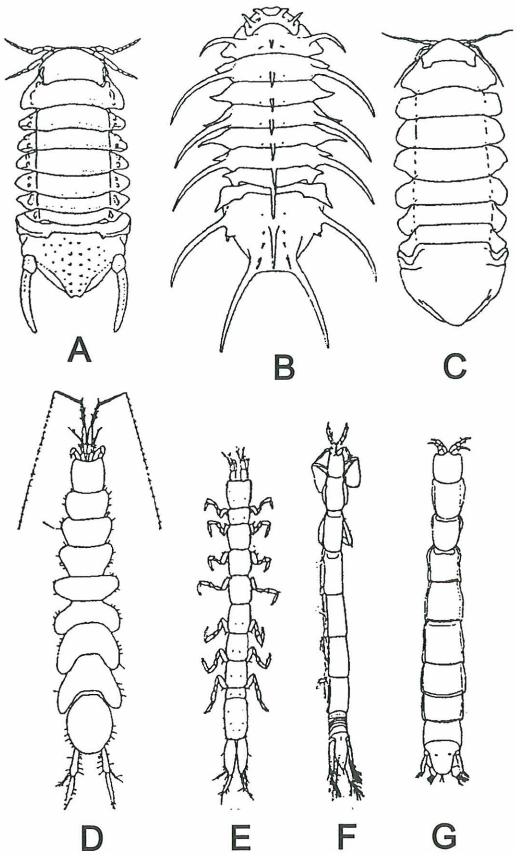

Fig. 7: Cave aquatic isopod crustaceans *Monolistra caeca absoloni* Racovitza (A), *Monolistra spinosissima* Racovitza (B), *Coecospheroma burgundum* Dollfus (C), *Mackinia continentalis* Birstein & Ljovuschkin (D), *Microcharon marinus* Chappuis & Delamare-Debouteville (E), *Cruregens fontanus* Chilton (F) and *Stygocyathura orghidani* Negoescu-Vladescu (G) (Juberthie and Decu, 1994).

(Deeleman-Reinhold, 1978; Ćurčić,1988a, 1988b; Ćurčić and Lučić, 1998; Ćurčić and Makarov, 1998; Radoman, 1981, 1985; Pljakić, 1977). The same applies to some lacustrine forms, which are of ancient (marine) origin (Pljakić, 1977; Radoman, 1985).

Both Deeleman-Reinhold (1978) and Ćurčić (1988a) have postulated a plausible explanation for this interrupted distribution. During the Tertiary period, the Proto-Balkan land is believed to have had long periods of equatorial climate and to have been covered by tropical and subtropical forests (Stevanović, 1951, 1967). Early strains of photophobic, hygrophilic, and humicolous animals proliferated there in moist detritus. The large, probably rapid, climatic subversion at the end of the

Miocene epoch (Hsü, 1972, 1978) must have brought aridity to the Balkan Peninsula, rendering it uninhabitable to the majority of humidity-dependent species (Nonveiller, 1983). Large stretches of limestone bedrock which are bare today were then covered by impermeable sediments, obstructing escape to moisture-retaining limestone. These impermeable strata persisted much longer in the middle Dinarides than to the north, east, or south, where they eroded (Luković, 1935). This was probably responsible for the distribution gaps in most cave invertebrates. Subsequently, with decreasing aridity, the Balkans became the main center of dispersion of different faunistic groups to the east and west, as well as to the north and south. This fact explains some close interrelationships between many local faunal elements inhabiting the Iberian Peninsula, the Apennines, the Crimea, and the Caucasus, on the one hand, and elements inhabiting the Balkan Peninsula on the other (Fig. 8).

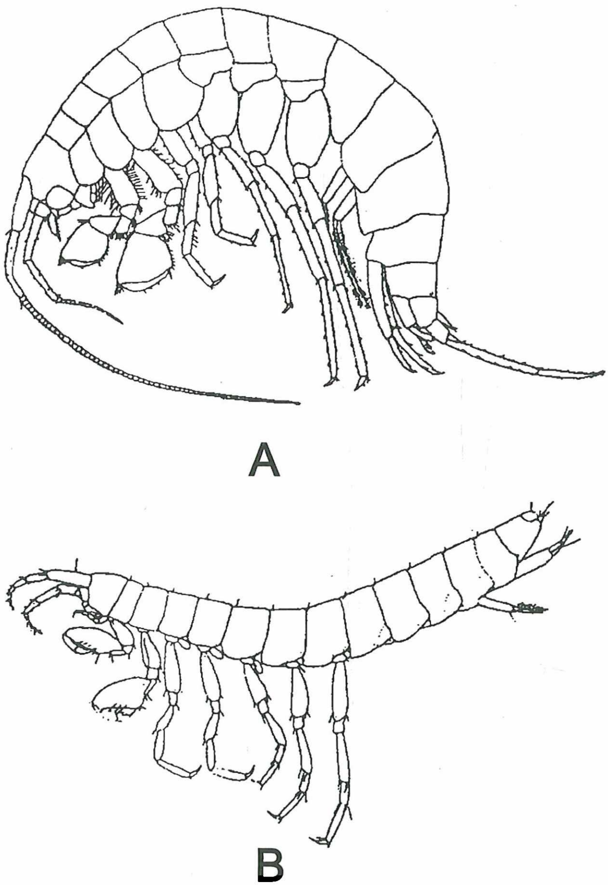

Fig. 8: Cave aquatic amphipod crustaceans *Niphargus virei* Dollfus (A) and *Ingolfiellla cottarellii* Ruffo & Vigna-Taglianti (B) (Juberthie and Decu, 1994).

In a few places, free passage was possible early to the underlying limestone; this system could have preserved sufficient moisture even in the driest period to offer shelter to at least a part of the retreating, humidity-seeking fauna. This hypothesis can explain the concentration of relicts in Dalmatia, Herzegovina, and Montenegro, as well as in both Western and Eastern Serbia.

Study of the evolution of numerous cave autochthones leads us to reconsider the origin and history of life underground in Serbia. Usually, these concepts were one-sided and concerned with whether different endemic species are relicts (Culver, 1970; Wallwork, 1972; Juberthie and Decu, 1994) or else attempted to elucidate their origins, ages, and the ways in which they have survived without taking into account their subsequent evolution. In their works on some Balkan arthropods, Ćurčić (1972, 1974, 1976, 1983, 1986, 1987, 1988a, 1988b, 1988c), Ćurćić and Makarov (1988), Ćurčić *et al.* (1997), Pljakić (1977), and Radoman (1985) concluded that some Tertiary (and even pre-Tertiary) arthropods and other invertebrates have survived there almost intact.

Thus, some scientists were preoccupied with one issue only: the origin of the diverse species which lived underground in the Balkan Peninsula at the beginning of its existence. These animals presumably lived on the floors of ancient tropical or subtropical forests, which existed before the origin of caves. But the present cave animals must have gone through a long evolutionary history, which resulted in the current composition of the Balkan cave fauna (Figs. 9 and 10). During that time, certain species disappeared, others evolved at different geological times, and many species underwent evolution underground, giving birth to new autochthones (both species and genera). In order to understand the way in which the present composition of such cave fauna has evolved, it is not enough only to seek the origin and the age of relicts, or those of the ancestors of the autochthone taxa. Just as important is their history in relation to that of their subterranean habitats. There is also a danger of attributing too great an importance only to autochthones in interpreting the origin of the Balkan cave-inhabiting fauna. It is certainly wrong to hold with Vandel (1964) who claims that some arachnid families are "almost entirely young" This opinion is based on the unproven hypothesis that changes in the conditions of life underground have been so important that they were followed by the disappearance of almost all primary representatives of many families, with the exception of a few stem forms which gave birth to a new autochthonous or endemic fauna; this is definitely not true!

The opinion of Beier (1940, 1966, 1969) is more likely. He thought that the Balkan cave forms were of two groups. The first consists of relicts from the Paleogene and Neogene periods which used to be more thermophilous than the current fauna. The remains of this fauna have been preserved, outside the Dinarides, in the Carpathians and Balkan Mountains, the Crimea, the Caucasus, the Pyrenees, the Apennines and elsewhere (Birstein, 1947,1947; Birstein and Ljovushkin, 1967; Jeannel, 1943, 1965; Jeanel and Leleup, 1952,1965; Stanković, 1932; Stanković and Pljakić, 1958; Radoman, 1985; Ćurčić, 1988b). The second group includes autochthones which developed in caves during their geomorphological evolution.

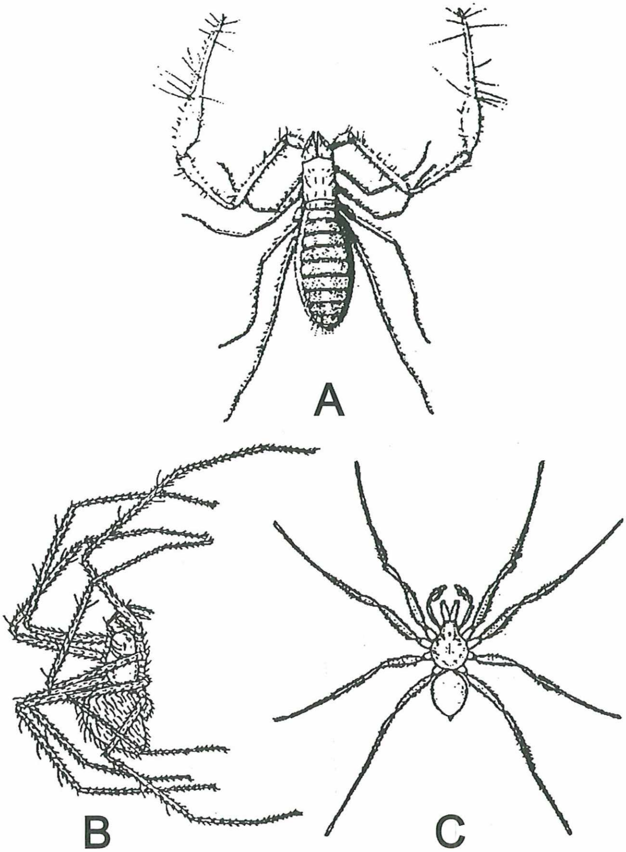

Fig. 9: Cave pseudoscorpion *Neobisium tuzetae* Vachon (A) and cave spiders *Troglohyphantes orghidani* Dumitrescu & Georgescu (B) and *Stalita taenaria* Schiødte (C) (Juberthie and Decu, 1994).

Both Beier (1966) and Ćurčić (1988a) therefore consider both the autochthones and their relictual nature in interpreting the origin and degree of endemism in some Serbian cave-dwelling faunistic groups (Hadži, 1965).

Analysis of the once existing fauna helps in interpreting the origin and history of some Balkan troglobites. 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 come the relict species, whose interrelationship with the Paleogene and Neogene (and even the pre-Tertiary) faunistic elements has already been noticed (Ćurčić, 1975, 1988a). These species, or their stem forms, inhabited leaf-litter and humus of the Dinaric and Carpatho-Balkan forests during or even before the Tertiary period. One can give numerous examples of discontinuous Eurasian distributions

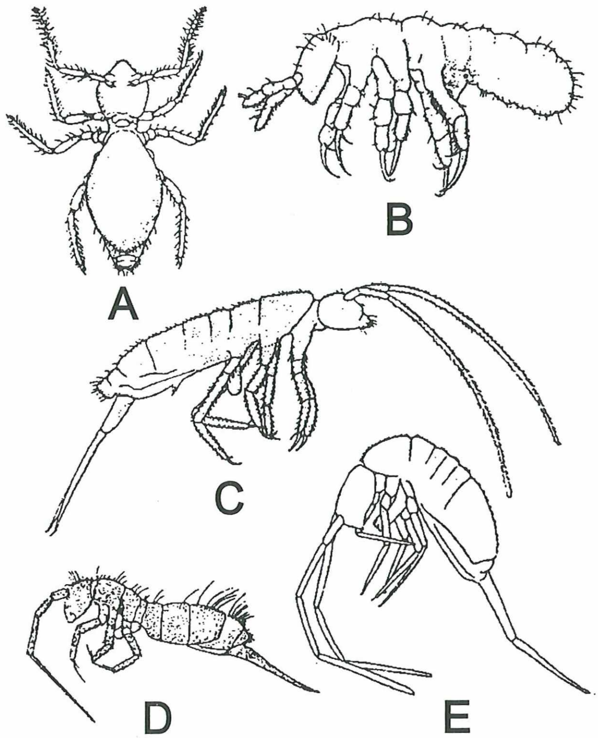

Fig. 10: Cave wingless insects *Arrhopalites pygmaeus* (Wankel) (A), *Ongulorychiurus colpus* Thibaud & Massoud (B), *Tritomurus falcier* Cassagnau (C), *Bessoniella procela* Deharveng & Thibaud (D) and *Troglopedetes delamarei* Massaoud & Gruia (E) (Juberthie and Decu).

among both cave and epigean species (Stanković, 1932; Vitali Di Castri, 1973). Evidently, there existed rich epigean Paleogene and Neogene faunae in Eurasia, and their disappearance from some parts is due not only to unfavorable changes in climate, but also to the lack of migration routes or possibilities of finding shelter (Tollmann, 1968).

Differentiation of cave animals in the peninsula

The composition of the old thermophilous fauna was not uniform, and regional differences no doubt existed (Juberthie and Decu, 1994). With the Ice Age, its distribution changed. Many species that disappeared in Central and Northern Europe, Siberia, and North America for the most part were pushed south, into refugial zones where climatic and other changes were less unfavorable. This process must have been complicated and cannot be explained only by climatic changes. It must have taken place with uneven intensity in various parts of the northern hemisphere and must have extended to different groups of organisms. The disappearance of some arthropod species and genera was the least intense in shelters where the fauna was able to maintain itself. We recognize three main refugial zones: the Mediterranean area, East Asia, and North America. It is certainly the first that has the most relicts from the Tertiary epigean fauna (Ćurčić, 1988a).

From the biogeographical point of view, the Mediterranean and the Pannonian and Ponto-Caspian regions are the two main refugial zones in Europe. The Pannonian and the Ponto-Caspian zones were refugia for Tertiary elements of Central Europe which migrated southwards due to the climatic and other changes. On the other hand, the Mediterranean area was populated by a more thermophilous fauna (Kosswig, 1955; Kosswig and Battalgil, 1943), whose living remains have been preserved in more isolated places. Furthermore, the discontinuous ranges of

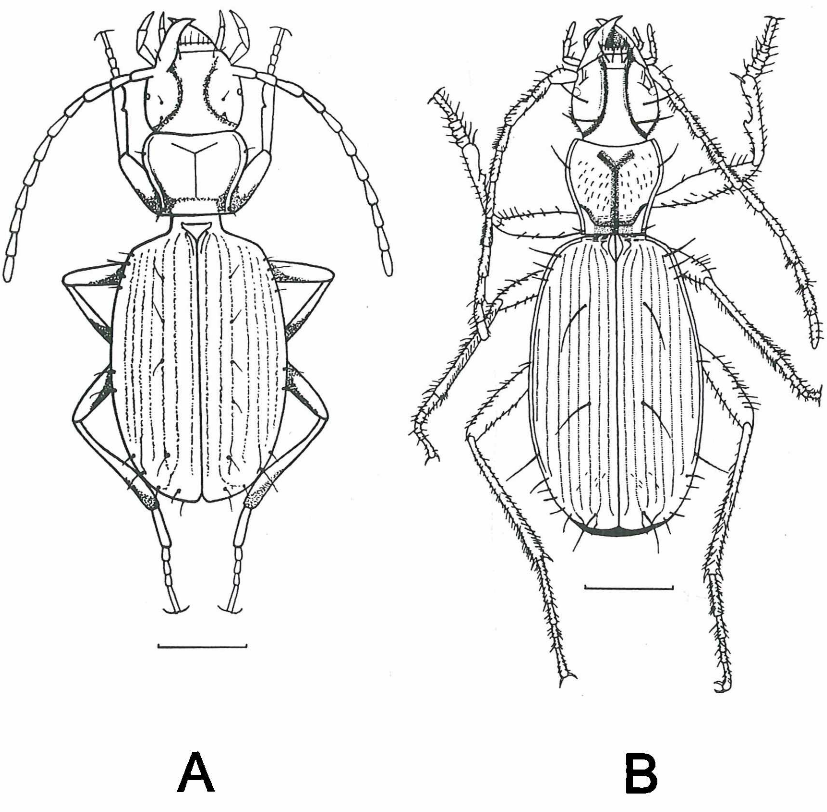

Fig. 11: Cave coleopterans *Duvalius (Neoduvalius) starivlahi* B. Guéorguiev, S. B. Ćurčić & B. P. M. Ćurčić (A), and *Duvalius (Paraduvalius) stankovitchi georgevitchi* Jeannel (B) (Guéorguiev *et al.* 2000; Ćurčić, S. B. 2001).

these remnants (or "living fossils") clearly indicate that the Tertiary invertebrate fauna was locally exposed more or less to destruction, under the influence of different geotectonic events, climatic changes, competition with immigrants (Kosswig and Battalgil, 1943; Stanković, 1960; Ćurčič, 1986), etc. The better an area was sheltered, the richer it is in relicts (Mayr, 1969, 1970). This is indeed the case with the fauna of the Balkan karst whose wealth of relicts inhabiting caves is impressive. Similar cases are encountered in other adjoining regions, for instance Serbia, Montenegro, Slovenia, Croatia, Macedonia, Bulgaria and Greece (Ćurčić, 1987; Beron, 1994; Buresch, 1924).

It is not easy to analyze the origin and history of endemic forms in Dinaric and Carpatho-Balkan subterranean habitats, because they represent an adaptive and selected fauna. The colonization of their underground milieux must have begun a long time ago, and passed through successive stages during different geological times (Fig. 11), together with the development of different karstic phenomena. It is therefore possible to distinguish in each faunistic group several historical lineages, their exact ages being difficult to establish (Guéorguiev, 1977; Jeannel, 1943; Ćurčić, 1986). We have every reason to assume that the fauna evolved from ancient circum-Mediterranean fauna, and its origin should be sought in the Balkan Peninsula. There the underground milieux have succeeded each other in a continuous manner up to the present time. More ancient caves disappeared, while new caves formed, thus favoring the survival of their fauna. This continuity of subterranean habitats has certainly played an outstanding part in the preservation of some ancient faunistic elements.

However, the large and rapid climatic subversion at the end of Miocene epoch (Ćurčić, 1988a), which had brought aridity to the Mediterranean area, rendered it uninhabitable by humidity-dependent species. Furthermore, the Balkan Peninsula, where sufficient moisture could have been preserved, offered a shelter for the retreating and hygrophilic fauna. Among the main causes which have affected the history of cave invertebrates in the Balkan Peninsula, one should emphasize the effects of the karstification process (Krešič, 1988). This process is very little known as yet, hence its interpretation must be more or less hypothetical. It is evident that the Balkan karst was not developed at one time, hence its colonization had to have occurred progressively thoughout its life span (Gavrilović, 1976, 1989; Ćurčić and Makarov, 1988).

It is pertinent to note that faunal exchange between different caves and those found elsewhere has been very limited, especially in the advanced phases of karstic evolution (Hadži, 1941). This is due to their geographical position, and to the adaptation of their inhabitants to specific life conditions. Thus, cave invertebrates have evolved to compete successfully with new immigrants. However, the living conditions in caves must be considered as relative. These conditions have certainly changed during the existence of the caves, but not in a manner to have provoked disappearance of the majority of relicts. In addition, such changes have favored the divergent differentiation of cave inhabitants.

The epoch of its formation for each endemic cave species in the Balkans is difficult to ascertain with precision. It is possible to speculate in this regard only for taxa with more primitive traits and disjunctive areas. Relatives of these forms are distributed elsewhere. Relicts whose relatives still occur in the Balkans therefore represent the remnants of some less ancient faunal complex. The geographical distribution of these animals is more reduced than that of the former faunistic group and is confined to certain caves, which represent their last refugia. Relicts with no close relatives include groups with an isolated position in the recent fauna, their origin being difficult to establish precisely; their closely related species are to be sought among extinct or fossil forms. Thus, these animals represent the most ancient cave relicts.

In conclusion, the Balkan karst is inhabited by a great number of endemic and relict cave animals pertaining to the Paleo-Mediterranean, Laurasian, Paleo-Aegean, and South- or North-Aegean (or Proto-Balkan) phyletic series (Furon, 1950, 1959). The major causes of the extraordinary variety of the troglobitic fauna of this region include: (1) the varied epigean fauna populating the Proto-Balkans in the remote past; (2) continuity of continental phases in different areas of the Balkans; (3) presence of mighty limestone beds and the subsequent evolution of the underground karst relief; (4) succession of suitable climatic conditions favoring the colonization of subterranean habitats; and (5) divergent differentiation of different lower and higher taxa in numerous isolated niches underground.

Study of the cave inhabitants of the Balkan karst has offered further proof of their great ages and different origins. These species and genera represent the last vestiges of an old fauna, which found shelter in the underground domain of the Balkans and its adjoining regions.

Apart from this, it is apparent that specific aspects of geomorphological and climatic events in the Balkans, together with peculiarities in the historical development of the fauna there, caused the Peninsula to become the main center of dispersion and colonization of species and groups of species, i. e., the main source for the revitalization and genesis of biological diversity, not just in the Mediterranean region, but throughout all of Southeast Europe.

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Zeitschrift/Journal: Acta Entomologica Slovenica

Jahr/Year: 2004

Band/Volume: 12

Autor(en)/Author(s): Curcic B.P.M., FRES , Jovanovic Mladen

Artikel/Article: The cave-dwelling fauna of the Balkan peninsula: its origin and diversification Jamska favna Balkanskega polotoka: njen izvor in raznovrstnost 35-56