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CAVE-DWELLING INVERTEBRATES IN MONTENEGRO

Božidar P. M. Ćurčić[1], **Vasile Decu**[2] and **Christian Juberthie**[3]

[1]*Institute of Zoology, Faculty of Biology, University of Belgrade,* 11000 Belgrade, Serbia
[2]*Institutul de Speologie, Romanian Academy of Sciences,* 010985 Bucharest, Romania
[3]09100 Saint-Lizier, France

Abstract — The paper presents the geotectonic structure and other features of Montenegro. Tables give lists of the country's currently known cave dwelling invertebrates.

Key words: Balkan Peninsula, Montenegro, cave invertebrates

GEOTECTONIC STRUCTURE

It is possible to isolate six larger geotectonic units as primary forms on the territory of Montenegro from the sea to the Durmitor dislocation in the northeast. They are: a. The coastal anticline, a zone built of rudist limestones and dolomites; b. the coastal syncline, a zone of schist–chert strata with eruptives and their tuffs; c. the Old Montengrin anticline, built of Mesozoic limestones and dolomites; d. the synclinal zone of the Zeta Plain, valley of the Zeta, Nikšić Polje, and Duga Gorge, which is built of rudist limestones and Paleogenic flysch; e. the anticline of Vojnik, Prekornica, and Zijovo, built of Mesozoic limestones and dolomites; and f. the synclinal zone of Durmitor flysch. Then there are the anticline of Volujak, Durmitor, and Sinjajevina; and the synclinal zone of the Ćehotina valley, which is completely unclear and will possibly drop out as a tectonic unit. Such distinct tectonic units in Montenegro are expressed only on the territory of karst, as we shall see later.

Stratigraphically, facially, and tectonically, the synclinal zones are more complex than the anticlinal zones, and they are also narrower. From analysis and examination of their mutual disposition, it is easy to discern that all of these units are areas of old embryonic forms of anticlines and synclines, so that a knowledge of the ancient Cordilleran era can be gained from the terrain.

Initially simple arches and dolines, the indicated units underwent great complication, until they gained their present–day thrust structure, in which it is nevertheless possible to distinguish the old anticlines and synclines.

With Triassic limestones and dolomites in their core, the anticlines behaved rigidly in the course of folding, but are usually gathered in small folds on the wings.

The synclines are characterized by numerous now in–thrusted strata, including many young ones (Upper Cretaceous and Paleogenic). These strata are greatly folded, and the synclines have lost their original appearance to a greater extent than the anticlines, since they are still thrusted out and enter the composition of those great thrusts as their inner side.

Such geotectonic discontinuity had a greater effect on areas of old (embryonic) synclines to a greater extent than anticlinal areas. Dislocation planes, as the boundary lines along which the anticlines settled on the previous adjacent unit, often are not simple: small thrusts and recumbent folds appear in those boundary synclinal zones, with consequent tectonic complication of the original synclinal form of the zones in question. These small thrusts in synclinal zones are especially noticeable when they are developed in diverse sediments, clastic and carbonate, but are harder to detect in an area of anticlines, which are usually built of Mesozoic limestones and dolomites. Thus, simple and extended dislocation planes do not always exist between these anticlinal units, which instead are separated by synclinal thrust depressions. However, accessory forms — folds and thrusts — are also developed in areas of anticlines, and their presence to date has been established especially in the Old Montenegrin anticlinal region. All old synclinal units have through constant and increasingly powerful folding passed over into larger units, which today make up a constituent part of the indicated thrusts. Thus, the Durmitor flysch has now been incorporated into the Kuči thrust, while the synclinal zone of the Zeta Plain, valley of the Zeta, Nikšić Polje, and Duga Gorge are part of the Old Montenegrin thrust.

Present throughout Dinarids, a relatively shallow sea existed in Montenegro before the main orogenies. There were also larger and smaller reefs together with other areas in their immediate vicinity that were suitable for formation of plastic clayey and sandy sediments. These areas of sedimentation were not precisely in any strict series, but a certain order in the direction of the geosynclinal axis nevertheless existed between them.

The first movements were manifested in the formation of anticlines and synclines. The hard parts of reefs at that time tended toward the anticlinal form, while their soft parts gravitated toward the synclinal one. However, there also could have existed certain regions of solid rocks (limestones, dolomites, and eruptives) in synclinal areas that sank deeply during those movements of the Dinaric marine space. In the course of sedimentation (and geotectonic movement), younger clastic sediments, usually of a flyshoid nature (Upper Cretaceous and Paleogenic), were formed over them. These younger sediments (and the orogenic formations themselves) underwent further folding as expressions of embryonic anticlines to form increasingly complex structures that finally passed over into the present–day extremely complex folds and even more often into thrusts.

Montenegro has Paleozoic strata that are of a distinctly clastic nature, being formations of a shallow sea and coastal environments. Carboniferous, Permian, and Devonian (uncertain) strata have been established. In their facial development, it is first of all evident that the Devonian strata are formations of a relatively deeper sea, and that absent among them are ones that would mark continental structures or signify influence of the proximity of dry land.

MESOZOIC PALEOGEOGRAPHY

The region of Montenegro in the Mesozoic was part of the broad Dinaric geosyncline. However, this area of Montenegro was not completely quiet tectonically throughout that long time period. Due to the movements that occurred, circumstances were altered in the marine environment, and sedimentation changed accordingly. Thus, the Mesozoic Era on the territory of Montenegro left many data from which we can fairly reliably reconstruct paleogeographic changes. These data are primarily in the nature of sediments, which are quite diverse and often vary in the same place; numerous fossil remains; and occurrences of eruptive rocks, with evidence of their influence on sedimentary rocks formed during their consolidation. Hiatuses have been established in the stratigraphic column, and data have been obtained on geotectonic movements. Strata of all three Mesozoic formations — Triassic, Jurassic, and Cretaceous — have been discovered and studied fairly thoroughly, with the result that paleogeographic data are both numerous and certain. Sediments of the Mesozoic Era include ones that are terrestrial, but marine sediments are much more widespread, thicker, and more diverse.

EROSION AND HOW IT AFFECTED RELIEF

Processes of erosion exerted significant influence on relief formation. Their intensity depended on strength of the agent in question, on the lithological base, i.e., on the susceptibility of certain rocks to mechanical and chemical decomposition, on the duration of phases of terrain resting, on climatic conditions and their changes during individual periods, etc.

The climate in this part of the world during the Tertiary was fairly uniform over longer periods of time, with higher temperatures and copious precipitation, which dictated the existence of a wealth of organic life. After the Savic Orogeny (during the Miocene), as well as in the middle and at the end of the Pliocene, there was a longer phase of relative peacefulness of terrains. Strong fluvial erosion and denudation acted on clastic rocks and fluviokarst, while corrosion acted on limestones. The corrosive process was especially intensive during longer phases of terrain resting in places of contact between limestones and clastic rocks (flysch, schists, and to some extent dolomites). Spacious plateaus were created in this way on limestones during the Oligocene and Miocene, for example the Katun karst and the plateaus of Rudine and Banjani in lower regions; and the rubbly Jezerska Visoravan, the plateau of the Pivska Planina Mountains, and others in higher regions. The indicated plateaus were uplifted and denivellated in the Lower Pliocene and later phases of land uplifting. The movements strengthened river erosion, which created canyon valleys in limestones. In phases of terrain resting during the Middle and Upper Pliocene, younger plateaus were formed by means of corrosion (it alone could cut limestone strata horizontally), denudation, and fluvial erosion — in the presence of rivers, which created flood plains — in suitable regions of contact between limestones and less permeable dolomites or flyschoid rocks, and these younger plateaus today form the floor of karst poljes. The corrosive plateau is covered by fluvioglacial deposits 15 m thick in the Nikšić Polje, 10 m thick in the Grahovo Polje, 8 m thick in the Dragulj Polje, 7 m thick in the Cetinjsko Polje, and 3 m thick in the Njeguši Polje.

Strong downcutting of rivers, eluviation of impermeable rocks, and mechanical weathering of bedrocks preceded the Pleistocene cooling. These processes were amplified by land movement and destruction of vegetation caused by climatic change. During the Pleistocene (the Ice Age), the high mountains and plateaus of Montenegro were subject to glaciation. Even today, these mountains on average receive 2500 to 5000 mm of precipitation annually, while in the Pleistocene the amount was the same or 20% less in some phases, but all in the form of snow. The average annual temperature was 10 to 12°C lower than today. The snowline was at 1300 m on Mts. Orjen and Lovćen, and between 1400 and 1500 m on the interior mountains. Glaciation on the high plateaus had a plateau character. The glacial cover had an area of 250 km^2 on Mt. Durmitor and the surrounding plateaus, about 200 km^2 on Mt. Lukavica and the surrounding plateaus, and about 250 km^2 in the Prokletije Mountains. Broken–up mountain glaciers formed many cirques, vals, morainal ramparts, and other forms of glacial erosion. Glacial tongues descended very far down valleys: from the Prokletije Mountains to Plav (907 m); from Mts. Maganik and Prekornica into the Nikšićska Župa region (with elevation of up to 800 m); from Mt. Orjen to Poljice (510 m); etc. The periglacial process involving freezing and thawing of soil and solifluction was strong during the Pleistocene in regions around the glacial covers, even as far as today's coastal regions.

More than of any other region, krš is characteristic of the relief of Montenegro. Krš (a rocky region) is a concept for which we also use the terms karst and kras, meaning an aggregation of relief forms composed of carbonate rocks with characteristic movement of water in them. The carbonate rocks are limestone, with more than 50% calcium carbonate ($CaCO_3$); dolomite, $CaMg(CO_3)_2$, with less than 50% calcium carbonate; chalk (fine–grained friable limestone with admixtures of clay, flint, etc.); travertine (porous limestone formed by sedimentation from hard water containing calcium bicarbonate); and many forms and types transitional between them. For more than a hundred years, the specific characteristics of karst have contributed to make it an outstanding scientific problem throughout the whole world. For Montenegro, karst is not only a general geographic and geological phenomenon characterized by a rocky landscape and harsh living conditions, but also a true symbol of the fate of the Montenegrin people. It covers almost all of Montenegro and is a factor of great significance for the republic's overall development. The formulation and resolution of problems connected with karst requires the cooperation of different specialties and specialists. The need to found a special institute for karst studies in Montenegro has been stressed with justification, but this project unfortunately has not yet been realized.

Extremely complex morphogenetic processes transpire in karst. The extent of karst development is dictated by the lithological base. Carbonate rocks, especially limestones, are subject to dissolution (melting). The inflow of acid–rich aggressive water widens fissures, of which there are many in limestones because pure limestone cracks readily. An insignificant quantity of insoluble components remains in pure limestones, and underground cracks are rarely closed. Predominantly barren rocks remain on the surface, and hence the name krš (rocky terrain). Analyzing 35 specimens of limestones from different regions of deep karst in Montenegro, investigators have concluded that the limestone contains 86 to 98% calcium carbonate ($CaCO_3$), which means that it is very pure. All of the most typical forms of karst relief — karrens, clefts, sinkholes (dolines), uvalas, poljes, pits, and caves — are developed in such karst.

MAIN UNITS OF RELIEF

In keeping with the lithological base, geotectonic structure, and erosive action of external forces, individual relief units were formed on the territory of Montenegro that differ fairly markedly among themselves, viz.: 1. The Montenegrin Coast; 2. the plateau of deep karst (the Katun karst, Grahovo region, and regions of Rudine and Banjani); 3. the Central Montenegrin depression; 4. the region of high mountains and plateaus; and 5. the region of Northeast Montenegro.

THE PLATEAU OF DEEP KARST

The given plateau is one of the most typical karst regions in the world. The thickness of carbonate rocks (predominantly limestones) comprises 4230 meters, and the karst process is active to the deepest layers. As Cvijić (1926, p. 434) states, "There is no deeper or more entire karst in the world than the Herzegovinian–Montenegrin karst between the valley of the Neretva, the Skadar mud flats, and the Adriatic Sea. Not a drop of water drains off from its surface, all water instead sinking into pits, ponors, blowholes, and fissures."

Composed of Mts. Orjen (1895 m), Lovćen (1749 m), Sutorman (1180 m), and Rumija (1595), a chain of mountains extends along the boundary with the coastal region, while Mts. Somina (1586 m), Njegoš (1761 m), Zla Gora (1459 m), Pusti Lisac (1476 m), Budoš (1217 m), and Garac (1436 m) face the central depression.

It is to the point to mention here that studies of limestone dissolution in different regions of the world have indicated that this process depends to a fairly great extent on climatic conditions. A climate characterized by high temperature and much precipitation in conjunction with a rich plant cover is especially favorable for limestone dissolution. Such a climate prevailed in our part of the world during the Pliocene. Melting of limestone comprises 1.51 cm in 1000 years on open horizontal surfaces in the Alps, while limestone melting on an open surface amounts to 1.4 cm. The process of limestone dissolution is accelerated under a loose cover overgrown with rich vegetation, so that melting comprises 2.5 cm in 100 years. In keeping with this

Fig. 1. Montenegrin Karst.

view, 250 meters of limestone could melt in a million years during periods characterized by a warm and damp climate in conjunction with a rich plant cover.

Mount Lovćen's central peaks — Štirovnik (1749 m) and Jezerski Vrh (1657 m), on which the mausoleum of P. Petrović Njegoš is located — are surrounded by many spacious uvalas and dales (Kuk, Bizaljevac, Vuči Do, Veliki and Mali Bostur, etc.). They are kettle–shaped and usually with one side open toward the lower parts. South of the highest peaks is the uvala Ivanova Korita (at an elevation of 1200 m), formed in marly lithiotic limestones. The longer axis of the uvala in an east–west direction measures about 2 km. The floor of the uvala is perforated by many small shallow dolines with low hillocks between them. It is rolling and opens gradually toward the lower parts, a direction used by the Cetinje–Budva road.

The plateau of deep karst is separated from the central depression by an inner mountain chain that begins with Mt. Somina and continues on to Mts. Njegoš and Zla Gora. These mountains are predominantly built of Upper Cretaceous limestones and dolomites. Lower Cretaceous sediments occur in the western part of Mt. Somina, and Jurassic limestones are present on the northern and northeastern slopes of Mt. Njegoš. The limestones on a great part of Mts. Somina and Njegoš are marly and thinly bedded, and this affected the relief, which exhibits gentler forms and has richer vegetation. Arranged in the Dinaric direction, the mountain ridges are usually of bedded limestones. Level floors are present on the mountain tops, but deep dolines are also found there. The sunny sides of Mts. Somina and Njegoš are forested only in the upper parts and over a large sector drop gently toward the karst plateau of Banjani and Rudine, while the shady sides are more thickly forested and descend more steeply into the Duga and Golija depression. The mountain Zla Gora (Bad Mountain) is built predominantly of pure Upper Cretaceous limestones and (as its name implies) is very impassable, rich with karrens, clefts, pits, and caves.

Running between Mts. Budoš and Garac are mountain ridges oriented in the Dinaric direction. These ridges drop steeply toward the Donja Zeta, but pass gently over into the plateau of the Katun karst in the southwest. Along this ridge are found the peaks Lisičke Glave (1154 m), Gola Brda (1185 m), Tisovi Kom (1139 m), Stolački Vrh (1134 m), Lupoglav (1102 m), and Bukove Glave (1048 m).

There are a number of uvalas in the wide depression that follows the zone of limestones and dolomites from Velimlje to Petrovići and beyond into the valley of the Trebišnjica. Spacious plateaus and uvalas are present around Bročanac and Petrovići. North of Petrovići are many uvalas in stepped belts constituting a continuation of the ones north of Velimlje. They include the uvalas Knez Do, Počekovići, Vraćenovići, Pilatovci, Vučji Do, Gornja Vrbica, Ubla, and Donje and Gornje Crkvice.

HIGH MOUNTAINS AND PLATEAUS

The region of high mountains and plateaus as a geomorphological unit dominates in the relief of Montenegro. It is made up of a number of mountain chains running in the Dinaric direction, between which are mountain plateaus and deep canyons. In the extreme southeastern part, the mountains turn from the Dinaric direction and extend in a northeast–southwest direction.

Characteristics of the lithological base and tectonic structure dictated the formation of mountain chains with fairly different composition from southwest to northeast. The content of limestones decreases toward the northeast, while that of clastic rocks increases. The first chain is made up of the mountains Golija, Vojnik, Maganik, Prekornica, and Zijovo, together with the mountains and plateaus between them.

The region of Mt. Durmitor is built of Paleozoic, Triassic, Jurassic, and Cretaceous marine sediments, as well as terrestrial deposits of Quaternary age. Paleozoic rocks — sandy and marly schists and conglomerates — occur around Tusina and in the valley of the Bukovica. Werfenian deposits occur in the canyons (Šćepan Polje, Jasena, Liječevina, Tepca, Djurdjevića Tara, and Lever Tara) and at the foot of the eastern slopes of the Durmitor massif, from the brook Mlinski Potok to the mouth of the Tusina in the Bukovica. Werfenian flysch deposits are often breached by eruptives (diabase–porphyrites). These deposits are covered first by Triassic limestones, often up to 800 m thick, then by Jurassic limestones and dolomites and schistose deposits of Durmitor flysch.

Mount Durmitor is characterized by diverse and very complex geological composition and structure, as well as by extremely varied foundation of terrains. This dictated pronounced dynamism of the relief, in which larger and smaller units can be singled out. There are three main relief units in the Durmitor region, namely Pivska Planina, the Durmitor massif, and Jezera Drobnjačka.

As for the Durmitor massif, it is made up of a group of mountain crests separated by deep dolines, uvalas, and valleys. Although the mountain has a reticulate morphological structure, it is possible to discern three series of crests that are still basically oriented in the Dinaric direction. The first series is made up of Ružica (2092 m), Lojanik (2027 m), and Boljske Grede (2066 m); the second of Rake (2160 m), Prutaš (2393 m), Uvita Greda (2159 m), and Sedlo (2226 m); and the third of Suva Rtina (2284 m), Bobotov Kuk (2523 m), and Sjeme (2477 m). Crests in the north and northeast — Štuoc (2103 m) and Pasina Gomila (2196 m) — and east — Medjed (2280 m) and Savin Kuk (2312 m) — are more weakly connected.

Together with certain others as well, the above-indicated crests are more than 2000 m high, and many investigators considered that they represent the remains of an uplifted plateau of which the Pivska Planina and Jezera Drobnjačka are parts.

The Durmitor massif rises from high plateaus with average elevation of 1450 m that are crossed by many roads. Moreover, the massif is broken up into numerous crests. These circumstances make Mt. Durmitor accessible to the highest peaks, which is a specific feature of it. Outstanding for their attractiveness and beauty are Bobotov Kuk, Medjed, and Savin Kuk. These peaks afford an impressive view of neighboring canyons, plateaus, and mountain peaks on a very wide horizon.

In the relief of Mt. Durmitor, valleys and uvalas are of special significance. Located on the Žabljak–Trsa road is the spacious uvala Dobri Do (1547 m), which is formed at contact between limestone and flysch. It is elongated in a northwest–southeast direction and descends in steps toward the middle, where a periodic stream flows that sinks into the limestone rim. On the hills Vjetrena Brda to the north, there is a pit 898 m deep, the deepest in the Balkans. Across the saddle of Prijespa (1962 m), Dobri Do passes over into the uvala Todorov Do, in which tracks of glacial erosion are very well preserved. From the middle of this uvala, the land rises in steps toward Prutas and passes over into Bljušturni Do in the southwest and farther on into the mountain Pivska Planina, where the Žabljak–Trsa road continues.

Many investigators have pondered the morphological evolution of the very complex forms of relief on Mt. Durmitor. There are numerous contradicting opinions on this complex question. Certain parts of the terrain have been greatly and fairly unequally dislocated by tectonic movements, especially along faults and lines of thrusting and nappe formation. Through the action of long–term exogenous modeling, thick deposits were eroded whose decomposed part was carried off into lower regions. The relief inheritance and agreement of younger forms and the lithological substrate support the conclusion that processes of relief formation were different in the recent geological past, and that Mt. Durmitor was affected by younger movements, which uplifted different parts unequally. Such flexures successively repeated after shorter or longer periods of terrain resting activated erosion, which acted differently on various kinds of rocks, with the result that very different kinds of relief were formed, depending on the lithological base.

Despite the fact that thick series of Mesozoic sediments were eroded during the long period of dry–land relief modeling, a difference stubbornly persisted between limestone blocks resistant to mechanical action and other rocks susceptible to decomposition and eluviation. Limestones are modeled underground: on the surface, they change more slowly and in a specific way. A strong process of eluviation and dispersive sinking took place on terrains built of dolomite and flysch. Landscapes of floors and flats typical of fluviokarst relief were formed in this way. Together with tectonic predisposition, selective erosion dictated that the high crests of Mt. Durmitor built of limestone remained high above less resistant deposits. Layers of limestone also remained in more thinly stratified deposits of Durmitor flysch, which often rise above more strongly eluviated strata of schists and sandstones. Unique examples of relief such as are present on Mt. Prutaš, Šareni Pasovi, etc., arose in this way.

The Prokletije Range is composed of several mountain chains in the border region between Yugoslavia and Albania and between the Podgorica–Skadar basin in the southwest and Metohija in the northeast. They are formed where the Dinarids are in contact with the Šar Mountains. Their basic direction of orientation is northeast– southwest. The relief is dominated by a long mountainous entity whose parts are fairly often separated by deep valleys. The main mountain chain is 70 km long. In it are the peaks Mali Jezerces (2694 m) in Albania, Mali Kolac (2542 m) in Montenegro, and Djeravica (2656 m) in Serbia. In the broader sense, the Prokletije Mountains include Bogićevica (2502 m), Koprivnik (2460 m), Čakor (2046 m), Mokra Planina (2110 m), Hajla (2400 m), etc.

The Prokletije Mountains have a fairly complex geological composition. Parts of these mountains from the Gusinje basin to the Albanian border are largely built of dark–blue and schistose limestones of the Lower and Middle Triassic, more rarely of lumpy Jurassic limestones and Upper Cretaceous desposits of Durmitor flysch, which are present throughout most of this part of the mountains. East of Višnjev and the sources of the river Jošenička Rijeka between the Lim and Metohija, as well as northward to Mokra Planina, the terrain is built of Paleozoic deposits: schists and sandstones with lenses of conglomerates and quartzites. Southwest of Mokra Planina in the region called Piševo are extensive outflows of volcanic rocks: andesites, karatophites, and tuffs. North of these regions, between the Lim and Ibar valleys and Metohija, the mountain landscapes are again predominantly built of Triassic clayey limestones, cherts, and dolomites, rarely of Jurassic limestones and dolomites as well.

CLIMATE

The part of Montenegro that is influenced by the Adriatic has very mild winters, which are especially characteristic of the seaside towns of Kumbor, Budva, and Ulcinj. The average January air temperature varies from 8.5 to 8.9° here, but is considerably lower at the extreme end of Boka Kotorska — 7.6° in Skaljari (20 m). However, it is typical that Ulcinj in the winter months has an air temperature 0.4° lower than in Kumbor, even though it is much farther south. During the winter, Kumbor (or Herceg–Novi) experiences cold buras, i.e., northeast winds, much more rarely than does Ulcinj, and this is reflected in lower winter air temperature in Ulcinj. Podgorica also has a fairly high air temperature of 5.7° in January, even though it is 37 km away from the Adriatic Coast. Comparison of Cetinje and Nikšić indicates different conditions. Both towns are at the same absolute altitude and both are on the floors of surrounding poljes. However, Cetinje is about four times closer to the Adriatic Coast than Nikšić, and — what is even more important — is separated from the coast by the 1749 m high Mt. Lovćen, whereas no such mountain exists between Nikšić and the Adriatic. For the latter reason, Cetinje has an air temperature in January that is even as much as 0.2° lower and an annual temperature that is 0.3° lower than in Nikšić.

Strange as it may seem, the Adriatic Sea in summer has no cooling effect on its surroundings such as that observed in the case of ocean coasts in temperate latitudes. On the contrary, the Adriatic Sea in its surface layer has a high temperature at the end of summer, as has already been mentioned, and this is reflected in high summer air temperatures. Summers are warm in the entire region near the Adriatic, especially in lower places. Most of them have an average air temperature in July higher than 25°: 25.9° in Danilovgrad (55 m) and even higher in Podgorica, as much as 26.7°. Not even the Mostar Polje or lower Vardar region have a July as warm as that, and Podgorica can be considered the warmest place in former Yugoslavia.

After air temperature, precipitation is the most important climatic element, since it — together with other influential factors — determines living conditions on the Earth. However, the distribution of annual amounts of precipitation in Montenegro is very complex due to the highly complicated nature of relief of the land. Relief exerts much greater influence on precipitation than on cloudiness. A damp wind blowing toward a mountain is forced to move upward along its slopes, but is thereby cooled, with the result that condensation of water vapor occurs at a certain altitude and rain or snow begins to fall at a higher elevation. Mountains thereby affect both the frequency and the amount of precipitation. High places are for this reason rainier than low ones. Mountain slopes exposed to the wind have more precipitation than the opposite leeward slopes at the same altitude. On the other hand, the annual amount of precipitation for the most part also declines from the Adriatic Coast toward the interior due to the large number of lower and medium–sized mountains. Forced upward movement of damp air occurs on each of their windward sides, and the air carries with it ever smaller amounts of water vapor as it penetrates the interior due to condensation on the westward slopes of these mountains. For this reason, the amount of possible rainfall grows constantly smaller with movement from west to east.

The most precipitation falls in the coastal mountains, especially in the Krivošije region and vicinity of Mt. Lovćen (5155 mm in Crkvice, 3927 mm in Cetinje). Precipitation declines fairly sharply toward the northeast, so that Andrijevica (near Mt. Maganik) has 1650 mm of precipitation annually, Žabljak (near Mt. Durmitor) 1943 mm, and Kolašin (near Mt. Bjelasica) 1842 mm. With elevations ranging from 586 to 880 m, lower valley weather stations in the northeast, Pljevlja, Bijelo Polje, Berane, and Gusinje have average annual precipitation of from 731 to 1181 mm. It increases toward the south due to shrinking distance away from the Adriatic Coast and partly due to increase of altitude in this direction. On the seacoast, annual rainfall on average is about twice as great as in the four indicated towns in the northeast, but it declines toward the south, Kumbor having 1892 mm, Budva 1614 mm, and Ulcinj 1290 mm.

HYDROLOGY

An abundance of diverse hydrological forms and phenomena can be found in Montenegro. This is a consequence of the complexity of geological composition and structure of the land, relief features, and climatic conditions. The chief geotectonic structures are oriented in the Dinaric (northwest–southeast) direction, and their disposition dictated the direction in which the main water courses flow. Moreover, great differences in the lithological base of separate parts of Montenegro caused differences in the wealth of underground and surface waters. Eruptives, crystalline schists, flysch deposits, and (to some extent) dolomites retain water, whereas limestones allow water to pass through fissures and channels in them until it reaches their lower limit.

The territory of Montenegro (13,812 km^2) on average receives 1798 mm of precipitation annually: of this amount, 1223 mm (68.0%) falls during the winter half of the year (October–March), while 575 mm (32.0%) falls in the summer half. Only Pljevlja and its surroundings have maximal precipitation in June: in all other places, the maximum occurs in November. Belonging to the watershed of the Adriatic Sea, the southwest part of Montenegro with an area of 6556 km^2 (the Montenegrin Coast, the region of deep karst, and the central Montenegrin depression) on average receives 2332 mm of precipitation annually, while the northeast part of the republic (which has an area of 7256 km^2 and belongs to the watershed of the Black Sea) on average receives 1315 mm. The average amount of water falling annually on the territory of Montenegro comprises $24{,}834\times10^6\ m^3$. Of this amount, the southwest part of Montenegro receives $15{,}289\times10^6\ m^3$, the northeast part $9542\times10^6\ m^3$. In view of the area of land involved, this is one of the greatest amounts of water received by any region in Europe. How much of this amount flows off on the surface and how much is absorbed by the land and drained underground depends primarily on the lithological base.

The presence of enormous areas of karst makes Montenegro unique. Geologo–lithological analyses indicate that 82% of its territory is built of limestones and dolomites. On this territory (the most typical karst region in the world), karst hydrological phenomena and landforms occur in all of their manifestations.

Scientists have argued about the behavior of water in karst, for more than a century now. Even today, many investigators adhere to the theory of Grund (1903) as to the existence of a united body of base water in karst and the theory of hydrographic zones of Cvijić (1926). On the basis of extensive research, today it can be accepted that ground water only exists above clastic rocks, and such rocks in Montenegro are usually very deep or encompass small areas. Capillary movement and drainage of normal base water is accomplished through permeable soil above an impervious layer, the lowest point of such outflow being sea level or the floor of endorheic depressions. In limestone rocks (in the region of deep karst in Montenegro, their thickness attains more than 4000 m), movement of water occurs through fissures and channels and under pressure. Underwater currents flow independent of each other, often in opposite directions, irrespective of surface relief. The end of water–permeable fissures, the impervious layer under limestones or "niveau de base karstique," represents the lower boundary of drainage of water under pressure. Circulation of water and development of underground cavities in limestones thus occur down to their lower boundary, often several hundreds of meters below sea level.

PEDOLOGY

It cannot be denied that soil is a basic factor for life on Earth. There would be no plant, animal, or human life on Earth without soil. Man has increasingly reclaimed naturally formed soil and significantly modified it in recent years in an attempt to achieve its better use. It is now becoming increasingly clear that a shortage of soil capable of producing food for people will impose a significant limit on further increase of the world's rapidly growing human population. As evidence of this growth, we note that that there were 745 million people on Earth in 1750, 1235 million in 1900, but 6400 million today.

Different pedogenetic factors and processes that took part in formation of the soil contribute to its quality. Soil formation is a long process. Many soils that we count as typical can be considered relict pedogenetic creations. On the other hand, the process of degradation or complete destruction of the pedological cover can in certain regions take place in a very short period of time.

Montenegro does not have very much soil suitable for cultivation. This is above all a consequence of the geologo–lithological composition of the land, especially its relief. Accordingly, enormous efforts to increase the area of land available for cultivation have been made in the past in the rocky republic of Montenegro and throughout the entire territory of the Dinarids. Terracing has been conducted on rocky slopes (this involves the building of embankments and throwing of soil on the floor of the steps that are formed). The process of deagrarization and urbanization has led to abandonment of rural land and expansion of central settlements in flat regions, while the construction of industrial installations has caused considerable shrinkage of arable land.

An indirect contribution to change in the quality of soils (and often to their complete degradation) has also been made by human activity, above all by the cutting down of forests. As in other regions, the land of Montenegro has its own age and history, laws of genesis and evolution, and its own morphology and geography.

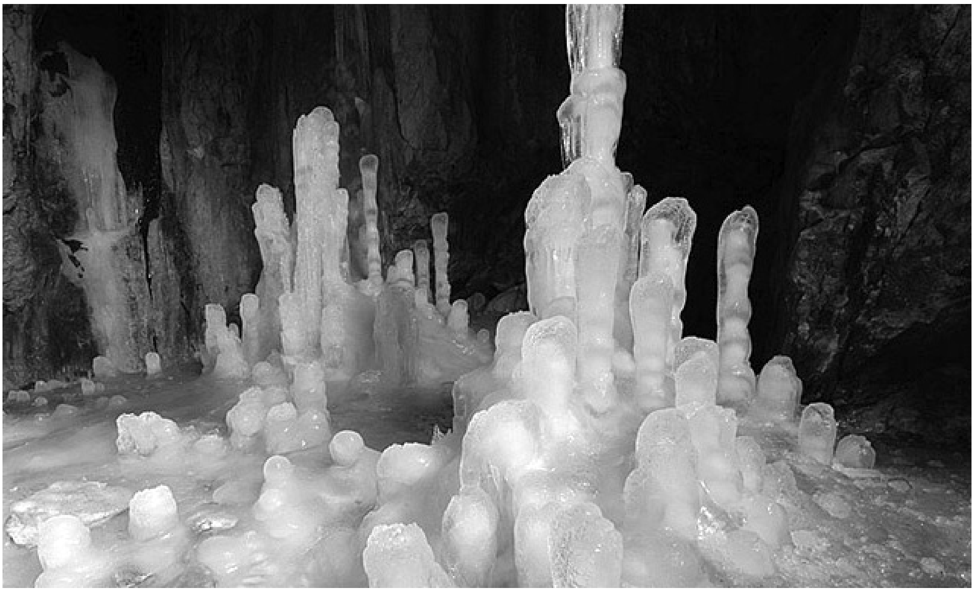

Fig. 2. The Ledena Pećina Cave in Montenegro.

Owing to its very complex geological composition, lithological base, relief, and climate, Montenegro represents a real mosaic of different types and kinds of soils.

THE HYPOGEAN AND SUBTERRANEAN FAUNA

The countries of the Balkans and Eastern Mediterranean (including Montenegro), located at the junction of three continental regions, are found in a climatically diverse region that has had a profound effect of the development of the fauna there. Zolitschka et al. (2000) stress that paleoecological research in Montenegro is important for three reasons, these being the potential of obtaining very long records of environmental change from basins that have not been overidden by extensive glaciations (unlike Northern Europe); the fact that the region is a frontier zone where the tropical climatic system of North Africa meets and interacts with the North Atlantic climate system; and the long history of human occupation and civilization in this region.

The diversity of the soil fauna is enormous in the area studied (Nouveiller, 1983). Virtually all animal phyla (with the exception of the echinoderms) are represented in the given region or soil horizons. Even in an extremely small part of some soil layer or in the limited soil zone, the diversity of life exceeds the biodiversity of coral reefs. Most soil animals are microscopic and must be separated from the substrate in which they are found before they can be studied in any way (Ćurčić and Radović, 1988).

For terrestrial cave organisms in Montenegrin caves, the general consensus (Barr, 1968; Peck, 1981) is that their immediate ancestors are forest-, soil-, and litter-

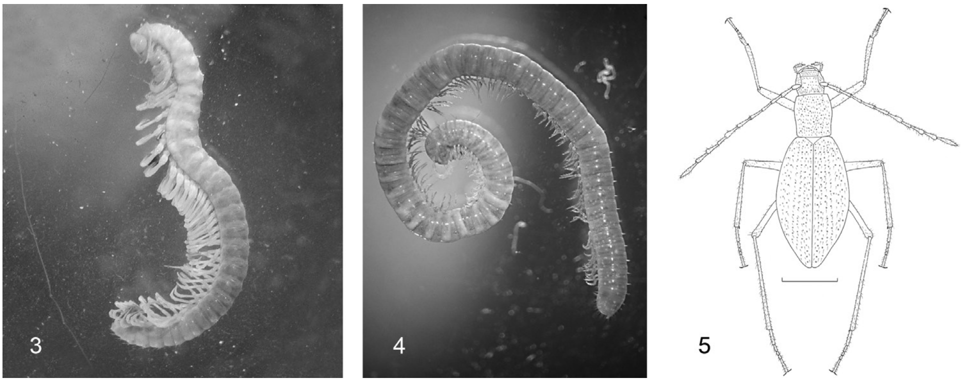

Fig. 3-5. The cave arthropods *Macrochaetosoma troglomontanum* Absolon et Lang from Western Montenegro (3); *Typhloiulus* sp. from Western Montenegro (4); and *Rozajella jovanvladimiri* S. Ćurčić, B. Ćurčić & Waitzbauer from Northern Montenegro (5).

dwelling invertebrates that invaded caves and were isolated there during Pleistocene interglacials. Although there is no direct fossil proof of this, there exists strong indirect evidence. First, caves in glaciated areas have a very depauperate or non-existent terrestrial fauna. Second, the closest surface relatives of many cave-limited species are found in the leaf-litter of boreal forests. Third, the regions most affected by Pleistocene climate, short of actually being ice-covered, have the largest number of terrestrial troglobites. Fourth, regions lacking forests through the Pleistocene have a very depauperate terrestrial cave fauna. Fifth, estimates of time since the divergence of closely related species, using Nei's (1975) formula and based on electrophoretic data, are consistent with isolation in the Pleistocene (Delay et al. 1980).

Isolation in subsurface waters is not the same as an isolation in caves. Although

Fig. 6. *Proteus anguineus* Laurenti from a spring nr. Nikšić, Western Montenegro.

there are a variety of subsurface habitats, it is convenient to distinguish interstitial and karstic habitats (Henry, 1978); the former consist of tiny water-filled spaces in habitats such as the underflow of rivers, and the latter consist of cave waters and associated niches. The colonization of karstic waters from interstitial waters and the colonization of cave waters from other karstic waters may be considerably more recent than the original isolation in phreatic waters. Our ignorance about the times of colonization of cave waters is complete. In that sense, Juberthie et al. (1980) introduced the term «superficial underground compartment» which, as a separate habitat, may have enormous importance in dispersal of cave species because it makes habitable areas more continuous. Its extent is unknown, and while most of the troglobitic species known from nearby caves have been found in the superficial underground compartment, some groups appear to be relatively abundant and others relatively scarce compared to cave populations (Pljakić, 1968; Juberthie, 1980).

Protozoa. Although free-living protozoans have not been investigated, a number of cilliates have been found on some cave specimens of *Niphargus*.

Turbellaria. Tricladids are present in some Montenegrin caves, but are far from being investigated. In addition, some undetermined ectoparasitic temnocephalids have been noted on rare specimens of four *Niphargus* species.

Gastropoda. Hydrobiid, orientalid, and emmericiid snails are often found in spring or cave waters in Montenegro, the majority of these being old and endemic forms (Table 1). Much more remains to be done before this faunistic group can be considered as adequately investigated.

Oligochaeta and **Hirudinea.** The former group is presently known from a number of undetermined specimens from different caves; while the latter is represented by some predatory depigmented species not studied in detail.

Cladocera, Copepoda, and **Ostracoda.** Cladocera, Copepoda, and Ostracoda are common in both underground lakes and streams, although they have received very little attention so far.

Isopoda. Terrestrial forms of several isopod families are represented in Montenegrin caves by a number of endemic species and genera. Aquatic isopods are also known from the area studied, although their systematic zoology is far from being complete.

Amphipoda. Amphipods include a high number of endemic lacustrine and brackish *Niphargus* species, as well as some relict interstitial forms.

Aranea. The entire spider fauna of Montenegro is very rich, contrary to its cave component, which includes several genera and species of great age and different origin (Table 2).

Pseudoscorpiones. Representatives of false scorpions are found in many Montenegrin caves. These belong to the genera *Chthonius, Neobisium,* and *Roncus* (Table 3).

Palpigradi. A number of undetermined *Eukenenia* and *Pauropus* species are

Table 1. List of cave hydrobiid snails inhabiting Montenegro. Abbreviations: N- Northern, S – Southern, W – Western, C – Central, Mo – Montenegro, Cro – Croatia.

Taxa	Distribution
HYDROBIIDAE	
HYDROBIINAE	
Adriohydrobia gagatinella (Küster)	S
ORIENTALIDAE	
ORIENTALINAE	
Orientalina curta curta (Küster)	S
Orientalina curta anagastica Radoman	Mo
Orientalina curta pivensis Radoman	N
Orientalina elongata Radoman	S
Orientalina lacustris Radoman	S
Orientalina montana Radoman	S
Anagastina vidrovani (Radoman)	W
Anagastina zetaevallis (Radoman)	S
Anagastina scutarica (Radoman)	S
Anagastina gluhodolica (Radoman)	C
Anagastina matjasici (Bole)	S
Antibaria notata (Frauenfeld)	S
Bracenica spiridoni Radoman	S
Plagigeyeiaria montenegrina Bole	C
EMMERICIIDAE	
Emmerici expansilabris Bourguinat	S/Cro

occasionally found in cave habitats, mostly under rotten wood or under litter of organic origin.

Opiliones. Apart from a number of presently known troglophilous species, it is possible that some Montenegrin caves are inhabited by several species from the neighboring Herzegovina (like the travuniids).

Chilopoda. These cave-dwellers include three species distributed in Central, Western, and Northern Montenegro (Table 4).

Diplopoda. This faunistic group is well represented in Montenegro (Table 5). It is probable that the diplopods of the area studied are much more varied than presently known.

Collembola. Presently, seven species of springtails are known to occur in Montenegrin caves. These belong to five genera and three families (Table 6).

Coleoptera. Coleopterans are the most important terrestrial group in the caves of Montenegro. Table 7 summarizes our present knowledge of this old, geographi-

Table 2. List of cave spiders inhabiting Montenegro. Abbreviations: SW – Southwestern, E – Eastern, W – Western.

Taxa	Distribution
DYSDERIDAE	
Folkia mrazeki (Nosek)	SW
Stalagtia hercegovinensis (Nosek)	W
Stalitella noseki Absolon & Kratochvíl	W
LINYPHIIDAE	
Troglohyphantes lesserti Kratochvíl	W
Troglohyphantes pretneri Deeleman-Reinhold	E
NESTICIDAE	
Typhlonesticus absoloni (Kratochvíl)	SW

Table 3. List of cave pseudoscorpions inhabiting Montenegro. Abbreviations: N – Northern, S – Southern, E – Eastern, W – Western, BH – Bosnia and Herzegovina..

Taxa	Distribution
CHTONIIDAE	
Chthonius (Chthonius) exarmatus Beier	W
Chthonius (Chthonius) globocicae Ćurčić	S
Chthonius (Chthonius) porevidi Ćurčić, Makarov & Lučić	W
Chthonius (Chthonius) prove Ćurčić, Dimitrijević & Makarov	W
NEOBISIIDAE	
Neobisium absoloni grande Beier	W/BH
Neobisium davidbengurioni Ćurčić & Dimitrijević	N
Neobisium dinaricum caligatum Beier	S
Neobisium dinaricum dinaricum Hadži	S
Neobisium dinaricum tartareum Beier	S
Neobisium goldameirae Ćurčić & Dimitrijević	N
Neobisium heros Beier	W
*Neobisium marcchagalli*Ćurčić & Ćurčić	W
Neobisium mendelssohni Ćurčić & Ćurčić	N
Neobisium montenegrense (Ellingsen)	S
Neobisium ninae Ćurčić & Dimitrijević	E
Neobisium temniskovae Ćurčić	W
Neobisium umbratile Beier	S
Roncus belbogi Ćurčić, Makarov & Lučić	W
Roncus davor Ćurčić, Dimitrijević & Makarov	N
Roncus golemanskyi Ćurčić	S
Roncus hors Ćurčić, Dimitrijević & Makarov	W
Roncus orao Ćurčić	S
Roncus orjensis Ćurčić & Dimitrijević	S
Roncus yaginumai Ćurčić, Ćurčić & Dimitrijević	S

Table 4. List of cave chilopods inhabiting Montenegro. Abbreviations: N – Northern, W – Western, C – Central.

Taxa	Distribution
LITHOBIIDAE	
Eupolybothrus (Eupolybothrus) gloriastygis (Absolon)	C
Lithobius (Lithobius) sketi Matic & Dărăbanțu	W
Lithobius (Thracolithobius) remyi Jawlowski	N

Table 5. List of cave diplopods inhabiting Montenegro. Abbreviations: N – Northern, S – Southern, W – Western, C – Central, Mo –Montenegro.

Taxa	Distribution
ANTHOGONIDAE	
Macrochaetosoma bifurcata Ćurčić & Makarov	W
Macrochaetosoma troglomontanum Absolon & Lang	W
HETEROLATZELIIDAE	
Heterolatzelia nivalis Verhoeff	Mo
GLOMERIDELLIDAE	
Typhloglomeris coeca Verhoeff	N
Typhloglomeris seuti Makarov	S
POLYDESMIDAE	
Polydesmus (Polydesmus) gradjensis (Jawlowski)	N
Polydesmus (Polydesmus) jugoslavicus Jawlowski	N
Brachydesmus (Brachydesmus) herzegowinensis Verhoeff	C
Brachydesmus (Brachydesmus) stygivagus Verhoeff	Mo
Brachydesmus (Brachydesmus) subterraneus Heller	C

Table 6. List of cave collembolans inhabiting Montenegro. Abbreviations: S – Southern, E – Eastern, W – Western.

Taxa	Distribution
ENTOMOBRYIDAE	
Heteromurus gradgensis Denis	E
Heteromurus absoloni Kseneman	S
Heteromurus anagastumensis Lučić & Ćurčić	W
Lepidocyrtus serbicus Denis	E
Pseudosinella joupani Denis	E
TOMOCERIDAE	
Tomocerus gradjackae Denis	E
ONCOPODURIDAE	
Oncopodura jugoslavica Absolon & Kseneman	E

Table 7. List of cave coleopterans inhabiting Montenegro. Abbreviations: N – Northern, NE – Northeastern, NW – Northwestern, S – Southern, SE – Southeastern, SW – Southwestern, E – Eastern, W – Western, C – Central.

Taxa	Distribution
CARABIDAE	
TRECHINI	
Neotrechus hilfi hilfi (Reitter)	S/SW
Neotrechus hilfi brevipennis Winkler	W
Neotrechus hilfi grossi Jeannel	N/C
Neotrechus hilfi jeanneli Winkler	W
Neotrechus hilfi schuleri Jeannel	W
Neotrechus lonai atavus Müller	SE
Neotrechus noesskei noesskei (Apfelbeck)	SW
Neotrechus noesskei troglomontanus Absolon & Mařan	SW
Neotrechus ottonis ottonis (Reitter)	W
Neotrechus paganettii matchai Breit	SW
Neotrechus paganettii paganettii (Ganglbauer)	S
Neotrechus setniki setniki (Reitter)	W
Neotrechus suturalis amplipennis (Müller)	SW/W
Neotrechus suturalis pretneri Scheibel	SE
Neotrechus suturalis suturalis (Schaufuss)	S
Aphaenops (*Adriaphaenops*) *staudacheri* Scheibel	S
Aphaenops (*Adriaphaenops*) *stirni* Pretner	C
Aphaenops (*Adriaphaenops*) *zupcense zupcense* Pavićević	N
Aphaenops (*Adriaphaenops*) *zupcense tartariense* Pavićević	N
PTEROSTICHINI	
Speluncarius anophthalmus Reitter	SW
Speluncarius setipennis Apfelbeck	S/SW
LEIODIDAE	
LEPTODIRINI	
Anthroherpon matulici (Reitter)	S
Anthroherpon matzenaueri augustae (Zariquiey)	SW
Anthroherpon matzenaueri matzenaueri (Apfelbeck)	SW
Anthroherpon matzenaueri taliensis (Zariquiey)	SW
Anthroherpon matzenaueri udrzali Giachino & Vailati	SW
Anthroherpon absoloni (Guéorguiev)	So
Anthroherpon apfelbecki lahneri (Matcha)	S
Anthroherpon gueorguievi Giachino & Vailati	W
Anthroherpon hoermanni orlovacensis (Guéorguiev)	SW
Anthroherpon latipenne attenuatum (Jeannel)	S
Anthroherpon latipenne gottli (Zariquiey)	SW
Anthroherpon latipenne latipenne (Apfelbeck)	S
Anthroherpon latipenne punctipennis (Jeannel)	SW
Anthroherpon piesbergeni (Zariquiey)	So
Anthroherpon taxi boschi (Zariquiey)	E
Anthroherpon taxi lemur (Knirsch)	SW
Anthroherpon taxi muelleri (Zariquiey)	Eo
Anthroherpon taxi pretneri Giachino & Vailati	W
Anthroherpon taxi remyi (Jeannel)	E
Anthroherpon taxi sydowi (Zariquiey)	C
Anthroherpon taxi taxi (Müller)	S
Anthroherpon taxi winkleri (Zariquiey)	E
Anthroherpon zariquieyi (Jeannel)	N
Hadesia vasiceki weiratheri Zariquiey	S
Remyella scaphoides borensis (Winkler)	N
Anillocharis stenopterus stenopterus Formánek	N

Table 7. Continued.

Taxa	Distribution
Anillocharis tenuilimbatus Jeannel	N
Blattochaeta hawelkai Knirsch	W
Blattochaeta marianii brevipennis Jeannel	SW
Blattochaeta marianii marianii (Reitter)	SW
Blattochaeta marianii paganettii Jeannel	SW
Blattochaeta matchai Jeannel	SW
Blattochaeta montenegrina Jeannel	S
Blattochaeta remyi Jeannel	E
Leonhardella (*Leonhardella*) *montenegrina* Jeannel	NW
Leonhardella (*Leonhardellina*) *antennaria acutangula* Jeannel	N
Leonhardella (*Leonhardellina*) *antennaria antennaria* Apfelbeck	N
Leonhardella (*Leonhardellina*) *antennaria brevis* Jeannel	N
Leonhardella (*Leonhardellina*) *roseni* Müller	N
Leonhardella (*Leonhardellina*) *setniki setniki* Reitter	N
Pholeuonopsis (*Scotosites*) *spaethi* Knirsch	N
Tartariella durmitorensis durmitorensis Nonveiller & Pavićević	N
Tartariella durmitorensis zephyrensis Nonveiller & Pavićević	N
Weiratheria bocki Zariquiey	S
Bathyscidius remyi Jeannel	E
Speonesiotes (*Albanella*) *lonae zoufali* (Reitter)	S
Speonesiotes (*Albanella*) *reissi* (Zariquiey)	SE
Speonesiotes (*Albanella*) *scutariensis* Müller	S
Speonesiotes (*Crivosiella*) *montenegrinus* Karaman	S
Speonesiotes (*Kulzeria*) *dorotkanus dorotkanus* (Reitter)	S
Speonesiotes (*Kulzeria*) *dorotkanus noesskei* Zariquiey	E
Speonesiotes (*Kulzeria*) *laticollis* Müller	S
Speonesiotes (*Kulzeria*) *matchai* Fagniez	SW
Speonesiotes (*Speonesiotes*) *narentinus narentinus* (Müller)	SW
Speonesiotes (*Speonesiotes*) *pretneri* Müller	S
Laneyriella matchai (Jeannel)	SW
Laneyriella scutariensis (Müller)	S
STAPHYLINIDAE	
PSELAPHINAE	
Bryaxis tuberculiceps Nonveiller, Pavićević & Besuchet	E
Nonveilleria lepida Pavićević & Besuchet	C
Pseudamaurops calcaratus Nonveiller & Pavićević	S
Seracamaurops fodori Szekessy	C
Seracamaurops grandis Winkler	SW

cally limited, and varied fauna, including representatives of carabids, leiodids, and staphylinids in particular.

*

In several areas of evolutionary biology, the study of caves can play an increasingly important role. There is, it seems to us, an important question that has received less attention. Are complex systems such as the tropics or organisms with complex life histories appropriate situations in which to test the models? In retrospect, the answer is no. A more appropriate plan is to test ecological models in relatively simple situations like caves. To reiterate, cave communities are simple, allowing more detailed examination of interactions; there are many replicate communities and natural occurences of species additions and removals; and at least some assumptions of the models, such as near equilibrium conditions, are more likely to be satisified in caves than in more complex systems. It seems highly probable that adequate experimental studies on cave species (due to their specific population structure and the degree of polymorphism) may greatly contribute to the elucidation of fundamental problems in the genetic aspects of their speciation in underground habitats (Kosswig, 1948, 1955, 1965; Poulson, 1963; Christiansen, 1961; Ćurčić, 1988).

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