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The world's deepest subterranean community - Krubera-Voronja Cave (Western Caucasus)

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Abstract:

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Subsurface biota extends over a wide variety of habitats that can be spatially interconnected. The largest communities of this subsurface biota inhabit cavities and are well known mainly in caves where biologists are able to have access. Data about deep subterranean communities and arthropods living under one thousand meters was unknown. An expedition to world's deepest cave, Krubera-Voronja in Western Caucasus, revealed an interesting subterranean community, living below 2000 meters and represented by more than 12 species of arthropods, including several new species for science. This deep cave biota is composed of troglobionts and also epigean species, that can penetrate until -2140 m. Deep subterranean ecosystems should not be seen only as an evolutionary dead end towards the troglomorphic syndrome, but also as a shelter for epigean species populations, especially during long periods of time when surface conditions are severe for their survival. Most of the subsurface biota depends on allochthonous sources of organic carbon coming from: water percolating from the surface, sinking streams that enter caves, and activities of animals moving in and out of caves. The biocoenosis and the vertical distribution of invertebrate fauna of Krubera-Voronja are provided, from its entrance to the remarkable depth of 2140 meters, including the discovery of world's deepest dwelling arthropod.

Keywords: deep subsurface biosphere; biospeleology; vertical distribution; Krubera-Voronja; Western Caucasus

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INTRODUCTION

Since Jules Verne wrote the Journey to the Center of the Earth (1864), the aim to discover and reach the deepest place below surface has been a challenge to generations of explorers. Nowadays, this is possible in the Arabika massif (Western Caucasus), inside the Krubera-Voronja cave that became in 2001 the deepest cave on Earth. The remarkable record of -2191 (±9) meters deep was possible due to explorations that began in the 1960's and resumed in the last years (Klimchouk et al., 2009).

Despite the large potential of Western Caucasus for caves, one of the largest karst massifs in the World, it has been little explored from a biospeleological point of view, especially the deepest cave systems. The main reasons were the political conflicts in the Caucasian area, combined with the difficulty of biological exploration in such deep and cold systems. Sampling is only possible within organized expeditions during warmer parts of the year.

Included in the West Transcaucasia Ecoregion (Abell et al., 2008: 409), biospeleological reasearch in Caucasus region began in 1929 in the south part, the Koutaia caves, and the first attempt to catalog the Caucasian cave fauna was made by Birstein (1950). After 1965, these studies gained a new impetus in the Western Caucasus, especially in the Alek massif near Sochi and in the Bzybski chain, the two contiguous massifs of Arabika (Gvozdetski et al., 1994). Several interesting cave-dwelling species have been recorded in this area, such as the leech *Erpobdella absoloni ratchaensis* Kob.; the slug *Troglolestes sokolovi* Ljovushkin & Matiokin, 1965; the harvestmen of the genus *Nemaspela* Šilhavý, 1966; the endemic millipede genera *Leucogeorgia* Verhoeff, 1930 and the

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Archileuco georgia Lohmander, 1939; the monospecific amphipod genus *Zenkevitchia* Birstein, 1940; the shrimp *Troglocaris schmidti fagei* Birstein, 1939; and the endemic ground-beetle species of the genera *Jeannelius* Kurnakov, 1959, *Meganophthalmus* Kurnakov, 1959 and *Duvalius* Delarouzee, 1859, among others (Birstein, 1939; Ljovuschkin, 1972; Stoch, 1972; Golovatch, 1985; Belousov, 1991; Belousov et al., 1995; Kryzhanovskij et al., 1995; Chemeris, 2009).

Since the description of the cave salamander *Proteus anguinus* by Laurenti in 1752, thousands of cave-dwelling animals (troglo- and stygobionts) have been recorded all over the world, except in Antarctica (Culver et al., 2006; Gibert & Culver, 2009). Many speculations about biodiversity patterns and species distributions, and the relationship between cave length and species numbers have been made by scientists in the last years (Culver et al., 2006; Schneider & Culver, 2004; Zagmajster et al., 2008), but the vertical limit of its distribution in function of cave's great depths remain unknown.

Only a few invertebrates have been recorded at great depths, such as the scorpion *Alacran tartarus* Francke, 1982 and the nicoletiid zygentoman *Anelpistina specusprofundis* Espinasa & Voung, 2008 which have been collected at -750 and -920 meters in the Huautla Plateau (Oaxaca, Mexico) (Espinasa & Voung, 2008; Prendinia et al., 2010); the springtail *Tritomurus veles* Lukić, Houssin & Deharveng, 2010 in Croatia found at -430 m (Lukić et al., 2010); and the troglobiotic pseudoescorpion *Neobisium (Blothrus) birsteini* Lapschoff, 1940 collected in 2009 in the Krubera-Voronja cave (Sánchez-Dehesa & Zarazoga, 2010). But no arthropods had ever been recorded living at a depth of 2000 m below surface (Borgonie et al., 2011).

In the summer of 2010 an Ibero-Russian speleological expedition to Krubera-Voronja cave initiated a biospeleological study in the cave. The results are presented providing the first data of biocoenosis and vertical distribution of invertebrate fauna of the deepest cave on Earth.

MATERIAL AND METHODS

Region of study

Krubera-Voronja cave is located in the Ortobalagan valley, a glaciokarst landscape, within the Arabika Massif, one of the largest limestone massifs of the Western Caucasus in Abkhazia (Fig. 1, 2). This massif, strongly pronounced at elevations ranging between 1900 and 2500 metres, is composed of lower Cretaceous and upper Jurassic limestone (Klimchouk et al., 2009). This cave received its first name Krubera through a dedication to Alexander Kruber, a founder of karst science in Russia, and the latter Voronja (=Crow's cave) due to the presence of crow nests at the cave entrance.

Krubera-Voronja cave is developed in the thickly bedded and massive upper Jurassic limestone. Its entrance is located at 2240 meters above sea level, at 15 km from the Black Sea, through an open-air pit of 60 m deep in the slope of the valley. The cave has two main branches of strictly vertical pits separated by short meanders. At the depth of 1400 meters, in the main branch of the cave, several siphons require cave-diving techniques to reach the actual terminus of the cave, a last siphon at -2140 m that has been dived to a depth of 2191 m below the surface (García-Dils, 2004, 2006; Klimchouk et al., 2009).

Fig. 1. Location of Arabika massif, Western Caucasus.

Fig. 2. View over the Ortobalagan Valley, with the location of Krubera-Voronja Cave and winter view over Arabika (Photo by S. Reboleira and D. Provalov).

The formation of the caves along the Ortobalagan valley was probably originated at 5.96 - 5.33 My in re- sponse to the Messinian salinity crisis, when the Black Sea was almost dry (Klimchouk et al., 2009). Evidence of this is the connection to submarine springs, proved by the use of dye tracing in Kujbyheskaja cave (Klim- chouk, 1990).

Sampling strategy

Field work was conducted in the Krubera-Voronja cave (Fig. 3) (UTM: 43° 24′ 35″ N, 40° 21′ 44″ E) until -2140 m deep by the Ibero-Russian CAVEX Team.

The cave was monitored from 27 July 2010 to 24 August 2010, from the base of the first shaft, in total darkness at -60 m, to the deepest part of the cave, the last siphon at -2140 meters.

Sets of pitfall traps (6 cm diameter and 7 cm deep, with a 1 cm diameter tube fixed inside at the centre) were used in the base of the first shafts and in each bivouac (-700 m, -1400 m and -1690 m). Traps were partially filled with 1.2-propanodiol, and Abkhazian cheese was used as bait. Monitoring of pitfalls was supplemented by one hour of active search during the visit to the cave. The stygofauna was sampled by direct collecting of the specimens from the final siphon.

Samples were sorted and specialists in each taxonomic group identified material.

RESULTS

Physical parameters

The temperature of the cave is very constant throughout the year and it was possible to record a vertical gradient in temperature, increasing with depth from 2 °C to 7.5 °C at the final siphon at -2140 meters (Fig. 3), during the sampling period.

The flow of water going down by gravity is constant along the cave, which allows movement of organic matter to the deepest parts of the cave in a short period of time. A small water flow (up to 1 l/s) appears in the cave at a depth of about -340 m, but it disappears in many sections, not varying significantly between the winter when all surface is covered by snow and the snow melting of spring and early summer. The rise in the level of the aquifer by autumn rains or during the spring may flood the cave to a depth of 1600 m, trapping stygofauna from the phreatic levels in the suspended siphons along the cave.

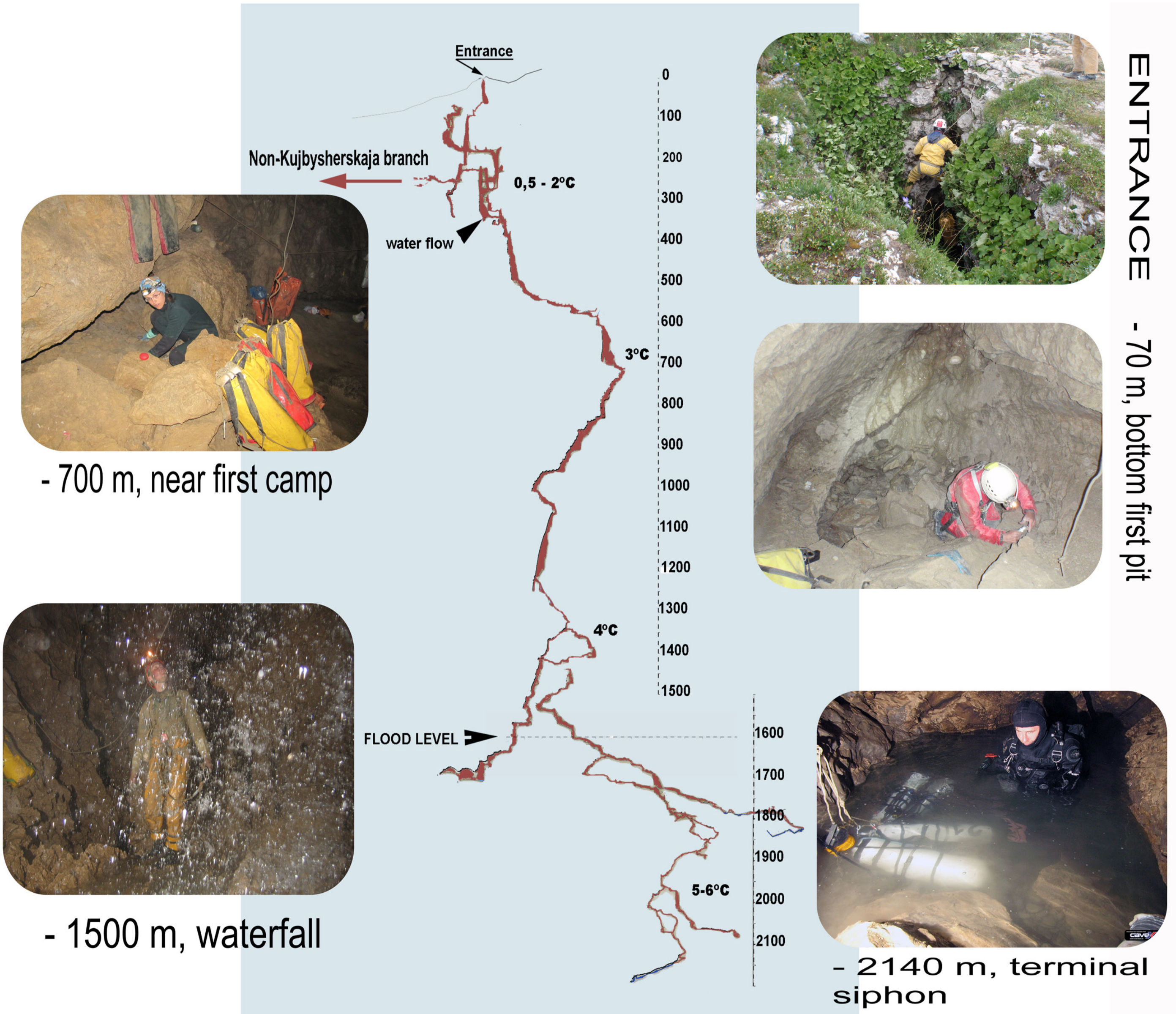

Fig. 3. Krubera-Voronja Cave habitats and temperature gradient. Cave map: adapted from Ukrainian Speleological Association 2010, compiled by A. Klimchouck (Photos by S. Reboleira, D. Provalov and S. García Dils).

The invertebrate fauna and its vertical distribution

Sixteen species of invertebrates were found living inside Krubera-Voronja cave during the sampling period (Table 1, Fig. 4, 5, 6). Eight species exhibit clear troglomorphic characters such as eye redution or absence and depigmentation. Six of them were classified as troglobionts and two aquatic species as stygobionts (*sensu* Schiner, 1854 & Racovitza, 1907).

Invertebrate fauna was found from the base of the entrance pit at -60 m up to the last siphon at -2140 m. The deepest troglobiotic species, the recently described springtail *Plutomurus ortobalaganensis* (Fig. 5A), was found at -1980 m (Jordana et al. 2012), and the deepest stygobiotic species (*Troglocaris* sp. *Fig. 6A* and *Zenkevitchia* sp. Fig. 6B) was found at the depth of -2140 m, and nowhere else in the cave (Fig. 6). The flying dipteran *Trichocera maculipennis* was the only invertebrate recorded at all depth levels, from the surface down to the deepest unflooded part of the cave. The recently described leiodid beetle *Catops cavicis* (Fig. 4D) was found in abundance down to -1600 m, which is a remarkable depth for a non-adapted cave animal (Giachino, 2011).

DISCUSSION

Vertical distribution of the fauna

The highest biodiversity (12 species) was found at the bottom of the entrance pit of Krubera-Voronja at a depth of -70 m. Entrance pits can be considered as "ecological traps" due to the higher number of epigean species than of species with clear adaptations to subterranean life (Turquin & Bouvet, 1977). In the case of Krubera-Voronja the bottom of the first pit at -60 m acts like a big pitfall trap for epigean fauna, represented by surface species of *Carabus* ground-beetles, Gnaphosidae spiders and abundant mites. The "pitfall effect" also provides a microhabitat rich in organic matter, like vegetal detritus and fungi from the surface. This specific border habitat allows the survival of a community of detritivore troglophiles composed by several acari, the springtails *Anurida stereoodorata* (Fig. 5B), *Deuteraphorura kruberaensis* and *Plutomurus ortobalaganensis*, the leiodid beetle *Catops cavicis*, and the flying dipteran *Trichocera maculipennis*. This area provides an important food source for detritivorous troglobionts like the large Chordeumatida millipede (Fig. 4E). This also provides

Table 1. Fauna of Krubera-Voronja cave. Sampling method: direct search (S), pitfalls (P), Ec: ecological classification.

Taxa	Depth (metres)	SM	Ec
Pseudoescorpiones, Neobisidae *Neobisium (Blothrus) birsteini* Lapschoff, 1940	60; 700; 1400	S	Troglobiont
Opiliones, Nemastomatidae *Nemaspela* sp	60	S	Troglobiont
Araneae, Linyphiidae *Troglohyphantes* sp.	10; 80	S	Troglophile
Araneae, Gnaphosidae Sp. indet	60	P	Trogloxene
Acari Sp. indet	60; 700; 1400; 1600; 1980	P	Troglophile
Diplopoda, Chordeumatida Sp. indet	60; 700; 1400; 1600; 1980	S	Troglobiont
Decapoda, Atyidae *Troglocaris* sp.	2140	S	Stygobiont
Amphipoda, Typhlogammaridae *Zenkevitchia* sp.	2140	S	Stygobiont
Collembola, Hypogastruridae *Schaefferia profundissima* Jordana & Baquero, 2012	1600	S, P	Troglobiont
Collembola, Neanuridae *Anurida stereoodorata* Jordana & Baquero, 2012	60	S, P	Troglophile
Collembola, Onychiuridae *Deuteraphorura kruberaensis* Jordana & Baquero, 2012	15; 60	S, P	Troglophile
Collembola, Tomoceridae *Plutomurus ortobalaganensis* Jordana & Baquero, 2012	60; 1980	S, P	Troglobiont
Coleoptera, Carabidae *Carabus* sp.	60	S	Trogloxene
Coleoptera, Carabidae *Duvalius* sp.	60	S	Troglobiont
Coleoptera, Leiodidae *Catops cavicis* Giachino, 2011	60; 700; 1400; 1600	S, P	Troglophile
Diptera, Trichoceridae *Trichocera (Saltrichocera) maculipennis* (Meigen 1818)	60; 700; 1400; 1600; 2140	S, P	Troglophile

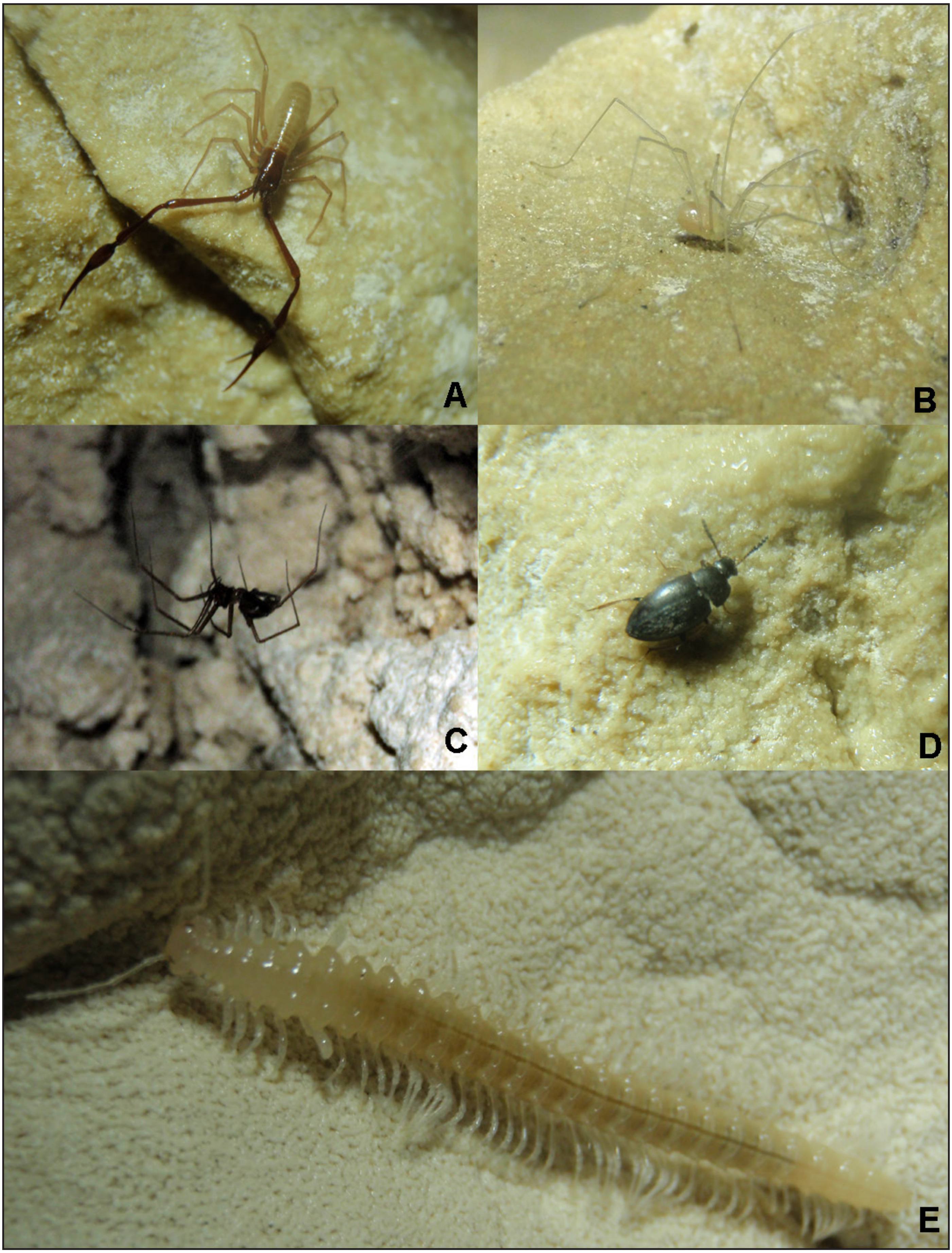

Fig. 4. Invertebrate fauna collected in Krubera-Voronja Cave. A – The troglobiont pseudoscorpion *Neobisium birsteini*. B– The troglobiont harvestman *Nemaspela* sp. C – The troglophile spider *Troglohyphantes* sp. D – The troglophile leiodid beetle *Catops cavicis*. E – The troglobiont diplopod (Photos by S. Reboleira).

a hunting area for four troglobiont predators, the pseudoescorpion *Neobisium birsteini* (Fig. 4A), the harvestman *Nemaspela* sp. (Fig. 4B), the ground-beetle *Duvalius* sp., and also for the troglophilic spider *Troglohyphantes* sp. (Fig. 4C), the latter only recorded at this depth (Table 1). In the pools, larvae of the dipteran *Trichocera maculipennis* can be observed in abundance, attesting to the importance of the subterranean environment in the reproductive cycle of this species where available water in the epigean environment is very scarce, as is usual at high altitude on karst massifs.

Several meters after the entrance pit and going down into the cave, the vegetal detritus disappears and the fauna became scarce. Below -70 m the community appears to be supported by the dissolved organic matter (DOM) as occurs in other subterranean environments as well (Culver & Pipan, 2009), by some suspended particles of organic matter including micro-invertebrates and larvae that are carried by the percolating water and mainly by the constant water flow that appears here and there along the cave. Neither the presence of bacterial biofilms nor the concentration of dissolved organic carbon (DOC) was investigated in epikarst water, but it may also provide a source of organic matter for hypogean invertebrates in deep parts of the cave.

Reaching major depths, the most abundant detritivorous animals are Acari, the two troglobiont springtails *Schaefferia profundissima* and *Plutomurus ortobalaganensis*, and the troglobiont chordeumatid millipede. The presence of the leiodid *Catops cavicis* down to -1600 meters is surprisingly deep for a non-troglomorphic beetle, which leads us think that it may be in an early stage of recent colonization of the subterranean environment in this area. The last two species were also recorded during our expedition in contiguous caves around Krubera cave, like in Berschilskaja cave at depths of -3 and - 15 meters. The only predator recorded at great depths in Krubera-Voronja cave was the pseudescorpion *Neobisium birsteini*. The springtail *Schaefferia profundissima* was only recorded at -1600m, while other troglobiont species were at different depths (see Table 1; Fig. 7).

The deepest troglobiont found was the springtail *Plutomurus ortobalaganensis*, recorded at -1980 m, but the deepest terrestrial invertebrate found inside Krubera-Voronja were females of the dipteran *Trichocera maculipennis* reaching the depth of -2140 m, unexpected for a flying epigean species. This species is well adapted to cold and its presence in the subterranean ecosystem at high altitudes is well documented in western European caves, and in surface habitats in northern Europe (Matile, 1994; Plachter, 1983). The ecological role of this dipteran is under appreciated in caves, and the presence of this species at -2000m in Krubera-Voronja has been observed in winter (García-Dils, pers. comm)., when the epigean conditions enable their survival in the surface for months. So, their larvae can be carried by hydrochoria through the entire cave, representing an important food source in such deep systems. Species of this family have been observed above -1000m in Berger cave in the Vercors massif, France (Reboleira, pers. obs)..

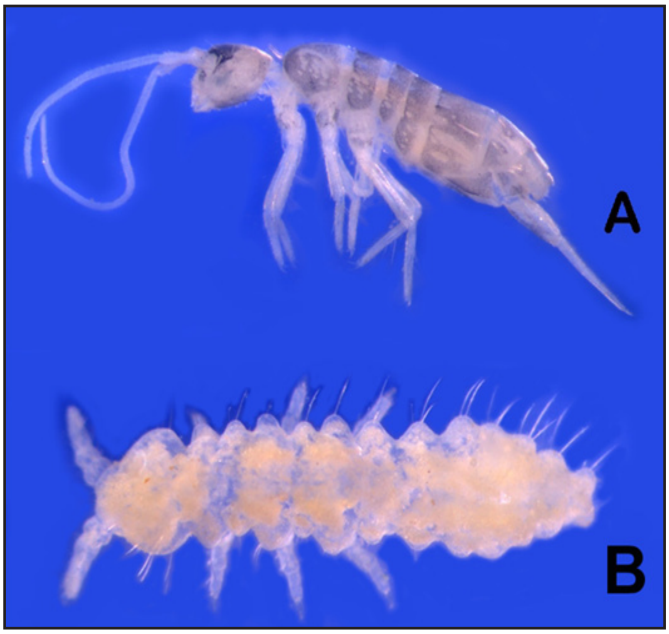

Fig. 5. Troglobiont fauna collected in Krubera-Voronja cave. A – The springtail *Plutomurus ortobalaganensis*. B – The springtail *Anurida stereoodorata* (Photo by S. Reboleira).

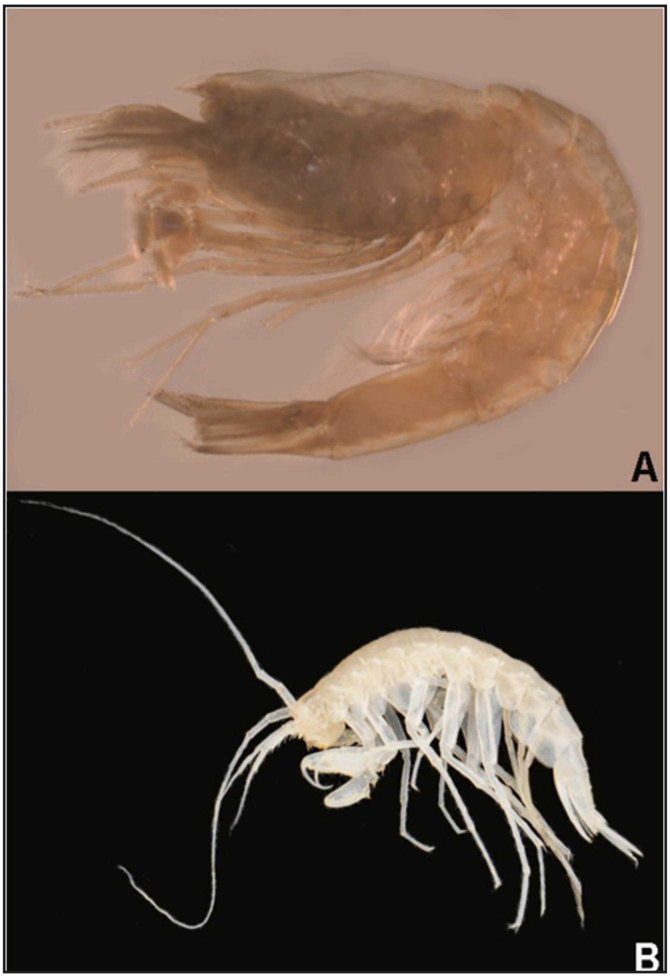

Fig. 6. Stygobiont fauna of Krubera-Voronja cave. A – The shrimp *Troglocaris* sp. B – The remarkably large amphipod *Zenkevitchia* sp. (Photo by S. Reboleira and S. García Dils).

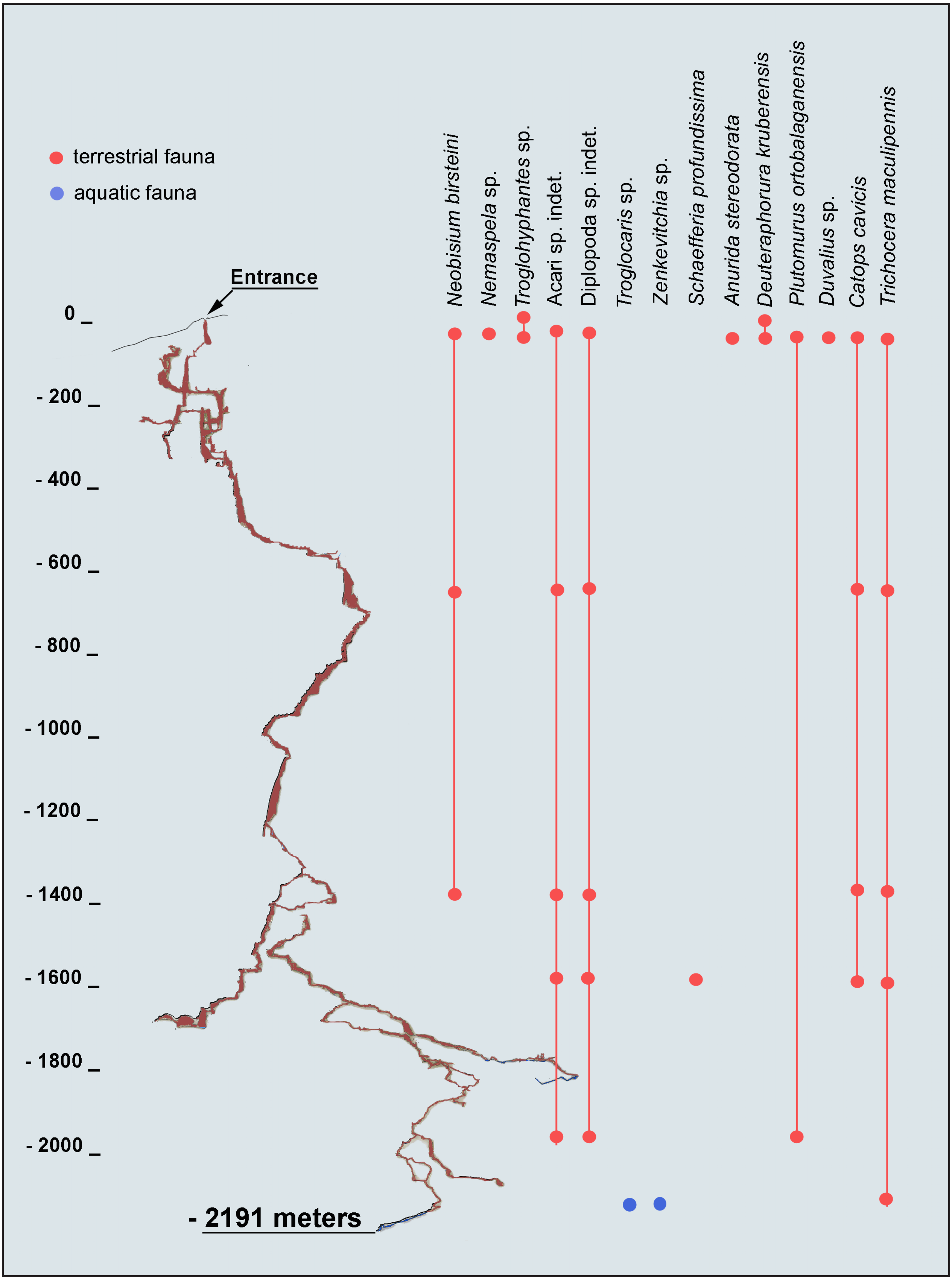

Fig. 7. Hypogean fauna recorded by depth in Krubera-Voronja cave. Cave map: adapted from Ukrainian Speleological Association 2010.

The troglobiotic fauna of Krubera-Voronja cave appears in areas of abundant air flow. The troglobiont millipede, that was also found in other caves around the Ortobalagan valley at small depths, was found in Krubera-Voronja at -1500m (García-Dils, pers. comm)., in a windy area under a water cascade, probably feeding on the bacterial biofilm of the walls.

The presence of macro-stygofauna is confined to the deepest siphons of the cave at -2140 m, represented by the giant gammarid amphipod *Zenkevitchia* sp. (~20 mm body size) and by the small shrimp *Troglocaris* sp. (~5 mm body size). The abundance of both stygobionts and the size of the amphipod suggests that the groundwater of Krubera-Voronja cave is rich in nutrients.

During the rainy seasons of spring and autumn, the cave floods up to -1600 meters depth (García-Dils, pers. comm).. This periodic flood that occurs several times along the year, can trap stygobiont fauna in the suspended pools and siphons (Hüppop, 2000). After succumbing with the decrease of the water level the corpses of this fauna can be a nutrient supply to troglobiont species at major depths in an upwelling effect from the rise of phreatic water (Fig. 3).

BIOGEOGRAPHY OF KRUBERA-VORONJA FAUNA

The community of Krubera-Voronja cave is composed of genera or species groups also known from other subterranean habitats in the Caucasus. Following the ridge of high troglobiont diversity of Europe through Asia, as suggested by Culver et al. (2006), the Caucasian area can be included in the potential subterranean hotspots of the karst regions around the world, argument that can explain the high biodiversity found in Krubera-Voronja cave.

Nemastela harvestmen include troglobiotic species inhabiting caves of Crimea and Caucasus (Chemeris, 2009). Ground-beetles of the genus *Duvalius* and the pseudescorpion *Neobisium birsteini* are also recorded from several caves on the Western Caucasus (Harvey, 2011; Kryzhanovskij et al., 1995). Studies on endogean and hypogean carabid beetles from the Caucasus region suggest the penetration of the hypothetical ancestor forms of the endogean beetles from the Boreal Egeida (Jeannel, 1930), while other groups came from the Hyrcanian Provinces and the Toros Mountains, a fauna derived from West Himalayan ancestors (Zamotajlov et al., 2010). The genus of the carabid beetle found on the cave has a wide distribution along the Mediterranean area expanding through Asia (Casale & Laneyrie, 1982).

It is well know the hydrological connection of Arabika massif groundwater with the Black sea (Klimchouk et al., 2009), but the stygobionts from Krubera-Voronja seem to have no relation with a thalassostygobiont ancestor. Recent molecular studies on sytgobiont species of the genus *Troglocaris* from West-Balkan lineages relate the split between the Caucasian and the Dinaric karst at 6 - 11 My, which allows the supposition of a common freshwater ancestor of cave shrimps during the Paratethys phase, in opposition to the marine relict hypothesis, preciously used to explain this biogeographical relation (Sket & Zakšek, 2009; Zakšek et al., 2010). The amphipod *Zenkevitchia* is a cave-dwelling endemic genus from the Caucasian caves (Holsinger, 1994).

FINAL REMARKS

The deepest troglobiont documented is the springtail *Plutomurus ortobalaganensis*, a small detritivorous invertebrate that inhabits Krubera-Voronja cave from -60 m to -1980 m. The amphipod *Zenkevitchia* sp. and the shrimp *Troglocaris* sp. are the first stygobiotic invertebrates ever recorded below -2000 meters.

The penetration of non-troglomorphic fauna until -2140 meters deep is remarkable, showing that there is not a direct relation between the degree of troglomorphism and the depth occupied in a cave, which leads new perspectives to the idea that only cave-dwelling fauna have their entire life cycle inside the subterranean environment. So, life in caves should not be seen only as an evolutionary dead end towards the troglomorphic syndrome, as it has been suggested before (Prendinia et al., 2010), but also as a shelter for epigean species populations, especially for long periods of time when surface conditions are severe for their survival, in case of extreme cold or heat.

With the evidence of how deep invertebrate life can be found inside Krubera-Voronja cave, registered until its major depth of 2140 m, several options may explain this fact: 1) food supply carried by water flow along the cave may support macro-invertebrate fauna in the deep parts of karst systems; 2) the presence of non-troglomorphic diptera may be a main support for such invertebrate biocoenosis; 3) some primary, chemolithotrophic production at microbiological level may be contributing to the survival of this biocoenosis in deep parts of subterranean environments. New biospeleological deep explorations will help us to understand the ecosystem of the deep subsurface biota.

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REFERENCES

Abell R., Thieme M. L., Revenga C., Bryer M., Kottelat M., Bogutskaya N., Coad B., Mandrak N., Contreras Balderas S., Bussing W., Stiassny M.L.J., Skelton P., Allen G.R., Unmack P., Naseka A., Ng R., Sindorf N., Robertson J., Armijo E., Higgins J.V., Heibel T.J., Wikramanayake E., Olson D., López H.L., Reis R.E., Lundberg J.G., Sabaj Pérez M.H. & Petry P., 2008 - *Freshwater Ecoregions of the World: A new map of biogeographic units for freshwater biodiversity conservation.* BioScience, **58**: 403–413. http://dx.doi.org/10.1641/B580507

Belousov I.-A., 1991 - *Nouveaux* Duvalius *Delarouzée du Caucase et de l'Asie Centrale soviétique (Col., Carabidae, Trechini).* Bulletin de la Société Entomologique de France, **96**: 283 - 287.

Belousov I.-A., Zamotajlov A.-S., & Alexander S., 1995 - *A new hypogean species of the genus Duvalius Delarouzée from the west Caucasus (Coleoptera, Carabidae, Trechini).* Entomol Basiliensia, **18**: 53–59.

Birstein J.A., 1939 - *On the cave shrimps of Abkhazia.* Zoologichesky Zhurnal, **18**: 960-975.

Birstein J.A., 1950 - *Zametka o bokoplavah Altaia.* Trudi Tomskogo Gosudarstvennogo Universiteta imeny V.V.Kuybisheva, **111**: 113-117.

Borgonie G., García-Moyano A., Litthauer D., Bert W., Bester A., van Heerden E., Möller C., Erasmus M. & Onstott T. C., 2011- *Nematoda from the terrestrial deep subsurface of South Africa.* Nature, **474**: 79–82. http://dx.doi.org/10.1038/nature09974

Casale A. & Laneyrie R. 1982 - *Trechodinae et Trechinae du monde. Tableau des sous- familles, tribus, séries phylétiques, genres, et catalogue général des espèces.* Mémoires de Biospéologie, **9**: 1-226.

Chemeris A.N., 2009 - *New data on the harvestman genus* Nemaspela *Silhavý, 1966 (Arachnida: Opiliones).* Bulletin of the British Arachnological Society, **14**: 286-296.

Culver D.C., Deharveng L., Bedos A., Lewis J.J., Madden M., Reddell J.R., Sket B., Trontelj P. & White D., 2006 - *The mid-latitude biodiversity ridge in terrestrial cave fauna.* Ecography, **29**: 120–128. http://dx.doi.org/10.1111/j.2005.0906-7590.04435.x

Culver D.C. & Pipan T., 2009 - *Biology of caves and other subterranean habitats.* Oxford University Press, Oxford, 256 p.

Espinasa L. & Voung N. H., 2008 - *A new species of cave adapted nicoletiid (Zygentoma: Insecta) from Sistema Huautla, Oaxaca, Mexico: The tenth deepest cave in the world.* Journal of Cave and Karst Studies, **70**: 73–77.

García-Dils S., 2004 - *Krúbera -2080 m. Primer -2000 del planeta.* Subterránea, **22**: 18-25.

García-Dils S., 2006 - *Krúbera-Voronya -2.170. Exploraciones 2005-2006.* Subterránea, **26**: 16-20.

Giachino P.M., 2011 - Catops cavicis *n. sp. from Krubera Cave (Abkhazia, Caucasus), an interesting species of the* C. alpinus *group (*sensu *Perrau, 2000) (Coleoptera, Cholevidae).* Boletín de la Sociedad Entomológica Aragonesa, **39**: 87-89. http://cholevidae.myspecies.info/content/catops-cavicis-n-sp-krubera-voronya-cave-abkhazia-caucasus-interesting-species-c-alpinus-gro

Gibert J. & Culver D.C., 2009 - *Assessing and conserving groundwater biodiversity: and introduction.* Freshwater Biology, **54**: 639-648. http://dx.doi.org/10.1111/j.1365-2427.2009.02202.x

Golovatch S., 1985 - *Two new genera of cave-dwelling millipedes (Diplopoda), with remarks on the millipede fauna of West Caucasian caves.* International Journal of Speleology, **14** (1): 39-50.

Gvozdetski N.A., Morozov S.A., Smirnov & Golovatch S.I., 1994 - *C.E.I., Bielorussie, Ukraine.* In: Juberthie C. & Decu V. (Eds). - *Encyclopaedia Biospeologica.* Moulins-Bucarest: Société de Biospéologie: 641-648.

Harvey M.S., 2011 - *Pseudoscorpions of the World, version 2.0.* Western Australian Museum, Perth. http://www.museum.wa.gov.au/catalogues/pseudoscorpions

Holsinger J., 1994. *Amphipoda.* In: Juberthie C. & Decu V. (Eds). - *Encyclopaedia Biopspeologica, Tome I.* Moulins-Bucarest: Société de Biospéologie: 147-163.

Hüppop K., 2000 - *How do cave animals cope with the food scarcity in caves?* In: Wilkens H, Culver D. & Humphreys W.F. (Eds). - *Subterranean Ecosystems.* Amsterdam: Elsevier: 159-188.

Jeannel R., 1930 - *Monographie des Trechinae. Morphologie Comparée et Distribution Géographique d'un Groupe de Coléoptères.* Livraison 4, Abeille, **34**: 59–122.

Jordana R., Baquero E., Reboleira S. & Sendra A., 2012 - *Reviews of the genera* Schaefferia *Absolon, 1900,* Deuteraphorura *Absolon, 1901,* Plutomurus *Yosii, 1956 and the* Anurida *Laboulbène, 1865 species group without eyes, with the description of four new species of cave springtails (Collembola) from Krubera-Voronya cave, Arabika Massif, Abkhazia.* Terrestrial Arthropod Reviews, **5**: 35–85. http://dx.doi.org/10.1163/187498312X622430

Klimchouk A. B., 1990 - *Karst circulation systems of the Arabika massif.* In: *Peschery (Caves)*, Perm: Perm University: 6-16 (in Russian).

Klimchouk A. B., Samokhin G.V. & Kasian, Y., 2009 - *The deepest cave in the world in the Arabika massif (Western Caucasus) and its hydrogeological and paleogeographic significance.* In: White W.B. (Ed)., *Proceedings of the International Congress on Speleology.* Kerrville (USA): 898-898.

Kryzhanovskij O.L., Belousov I.A., Kabak I.I., Kataev B.M., Makarov K.V. & Shilenkov V.G., 1995 - *A Checklist of the ground-beetles of Russia & adjacent lands (Insecta, Coleoptera, Carabidae).* Pensoft Series Faunistica #3. Pensoft Publishers, Sofia-Moscow, 271 p.

Ljovuschkin S. I., 1972 - *Biospeologica sovietica. XLIX. The first troglobite representative of Trechinae (Coleoptera, Carabidae) in Ciscaucasia.* International Journal of Speleology, **4**: 357-364.

Lukić M., Houssin C. & Deharveng L., 2010 - *A new relictual and highly troglomorphic species of Tomoceridae (Collembola) from a deep Croatian cave.* ZooKeys, **69**: 1–16.

Matile L., 1994 - *Diptera.* In: Juberthie C. & Decu V. (Eds)., *Encyclopaedia Biopspeologica, Tome I.* Moulins-Bucarest: Société de Biospéologie: 341-357.

Plachter H., 1983 – *Cave-dwelling flies in Central Europe: adaptation to environment, especially low temperatures (Diptera, Nematocera: Trichoceridae and Sciaridae).* Oecologia, **58**: 367-372. http://dx.doi.org/10.1007/BF00385237

Prendinia L., Franckeb O. & Vignoli V., 2010 - *Troglomorphism, trichobothriotaxy and typhlochactid phylogeny (Scorpiones, Chactoidea): more evidence that troglobitism is not an evolutionary dead-end.* Cladistics, **26**: 117–142. http://dx.doi.org/10.1111/j.1096-0031.2009.00277.x

Racovitza E.G., 1907 - *Essai sur les problèmes biospéologiques.* Archives de Zoologie Expérimentale et Générale, 4 série, 6, Biospéologica, **1**: 371-488.

Sánchez-Dehesa J. M. & Zaragoza J.A., 2010 - *Sima Krubera-Voronya, Cáucaso occidental, nueva cita del pseudoescorpión troglobio* Neobisium (Blothrus) birsteini *Lapschoff, 1940 (Arachnida: Pseudoscorpiones: Neobisiidae).* Monografías Bioespeleológicas, **5**: 22-25.

Schiner J.R., 1854 - *Fauna der Adelsberger, Lueger und Magdalener-Grotte.* Verhandlungen der Zoologisch-Botanischen Gesellschaft in Wien, **3**: 1-40.

Schneider K. & Culver D.C., 2004 - *Estimating subterranean species richeness using intensive sampling and rarefaction curves in a high density cave region in West Virginia.* Journal of Caves and Karst Studies, **66**: 39-45.

Sket B. & Zakšek V., 2009 - *European cave shrimp species (Decapoda: Caridea: Atyidae), redefined after a phylogenetic study; redefinition of some taxa, a new genus and four new* Troglocaris *species.* Zoological Journal of the Linnean Society, **155**: 786–818. http://dx.doi.org/10.1111/j.1096-3642.2008.00473.x

Stoch J.H., 1972 - *The Existence of Interstitial Members of the* Gammarus*-Group (Amphipoda).* Crustaceana, **24(3)**: 339- 341. http://dx.doi.org/10.1163/156854073X00731

Turquin M.J & Bouvet Y., 1977 - *Energy flow and faunistical distribution inside karst; the influence of module of openness.* In: Ford T.D. (Ed)., *Proceedings of the 7th International Congress of Speleology.* Sheffield: International Union of Speleology: 406-407.

Zakšek V., Sket B. & Trontelj P., 2007 - *Phylogeny of the cave shrimp* Troglocaris*: Evidence of a young connection between Balkans and Caucasus.* Molecular Phylogenetics and Evolution, **42**: 223–235. http://dx.doi.org/10.1016/j.ympev.2006.07.009

Zagmajster M., Culver D.C. & Sket B., 2008 - *Species richness patterns of obligate subterranean beetles (Insecta: Coleoptera) in a global biodiversity hotspot - effect of scale and sampling intensity.* Diversity and Distributions, **14**: 95–105. http://dx.doi.org/10.1111/j.1472-4642.2007.00423.x

Zamotajlov A.S., Orlov V.N., Nabozhenko M.V., Okhrimenko N.V., Khatschikov E.A., Shapovalov M.I. & Shokhin I.V., 2010 - *Analysis of the Ways of Formation of the entomofaunistic Complexes in the Northwest Caucasus Based on the Material on Coleopterous Insects (Coleoptera).* Entomologicheskoe Obozrenie, **89**: 178–218.