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Terrestrial isopods (Oniscidea) in Slovak caves: species diversity and distribution along regional and geographical gradients

Suchozemské rovnakonôžky (Oniscidea) v jaskyniach na Slovensku: druhová pestrosť a distribúcia v environmentálnom a geografickom gradiente

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Abstract: The area of Slovakia is rich in karst regions and caves, located in the mountainous relief of the western parts of the Carpathian Mountains – the northernmost distributional limit of the obligate cave terrestrial fauna in Europe. Terrestrial isopod fauna in Slovakia comprises 48 species, a third of which lives exclusively in synanthropic habitats. Caves represent prominent undisturbed refugia preserving relict fauna. Despite the long history of Slovak biospeleology, the knowledge about cave terrestrial isopods is scarce. We used the opportunity to prepare a comprehensive study of isopods in Slovak cave environment. We collected and analyzed the complete bibliography, which begins in the 1930s, although the first collections of isopods in our caves are dated to 1913. We used our own field data and the material of isopods from private collections of cave biologists in Czechia and Slovakia including collections from the estates of two deceased zoologists, J. Gulička and V. Ducháč. We gathered 434 samples collected in 111 caves of various types and elevations (from 210 to 1548 m a.s.l.) and one mine gallery, dated from 1948 to present. 5658specimens of 25 taxa at species level from 10 families were recognized. Another 3 species are documented by published data. Despite these relatively high numbers, the occurrence of isopods in deeper zones of Slovak caves is rare. Only 4 taxa from the present list are considered closely connected to deeper zones in caves and other subterranean habitats: *Mesoniscus graniger, Androniscus* cf. *dentiger, Trichoniscus* cf. *pygmaeus*, and one undetermined blind species of the family Trichoniscidae. Results indicate sparse populations of cave colonizers, except for *Mesoniscus graniger*. Two surface species, *Cylisticus convexus* and *Hyloniscus riparius*, occasionally inhabit the deeper zones of some caves. In contrast, cave entrances are inhabited by various isopods and represent important refugia of biodiversity, especially in a monotonous environment. Several species seem to prefer cave entrances, e.g. *Trachelipus difficilis* or *Orthometopon planum*.

Abstrakt: Územie Slovenska je bohaté na kras a jaskyne, najmä v hornatom reliéfe Západných Karpát – najsevernejšej distribučnej hranici pravej jaskynnej suchozemskej fauny v Európe. Fauna rovnakonôžok na Slovensku zahŕňa 48 druhov, z ktorých tretina žije výlučne v synantropných biotopoch. Jaskyne predstavujú prominentné nerušené refúgiá uchovávajúce reliktnú faunu. Napriek dlhej histórii slovenskej biospeleológie boli poznatky o jaskynných suchozemských rovnakonôžkach dosiaľ útržkovité. Zhromaždili sme a analyzovali kompletnú bibliografiu, ktorá sa začína v 30. rokoch 20. storočia, hoci prvé zbery rovnakonôžok v slovenských jaskyniach sú datované už od roku 1913. Spracovali sme tiež vlastné terénne údaje a zbery rovnakonôžok zo súkromných zbierok jaskynných biológov v Čechách a na Slovensku, vrátane dvoch pozostalostí už zosnulých zoológov, J. Guličku a V. Ducháča. Zhromaždili sme 434 vzoriek zozbieraných v 111 jaskyniach rôznych typov a 1 banskej štôlni, situovaných v rôznych nadmorských výškach (od 210 do 1548 m n.m.), datovaných od roku 1948 do súčasnosti. 5658 analyzovaných jedincov patrí do 25 taxónov na druhovej úrovni a reprezentujú 10 čeľadí. Ďalšie 3 druhy dokladajú literárne údaje. Napriek týmto relatívne vysokým počtom je výskyt rovnakonôžok v hlbších jaskynných zónach zriedkavý. Iba 4 taxóny zo zisteného spektra môžeme označiť ako úzko viazané na podmienky hlbších zón v jaskyniach a iných podzemných biotopoch: *Mesoniscus graniger*, *Androniscus* cf. *dentiger*, *Trichoniscus* cf. *pygmaeus* a bližšie neurčený slepý druh z čeľade Trichoniscidae. Výsledky naznačujú riedke populácie jaskynných kolonizátorov, s výnimkou *Mesoniscus graniger*, aj preto je tu druhová determinácia niektorých taxónov neistá (ojedinelé nálezy samičiek alebo nedospelých jedincov bez diagnostických znakov). Dva bežné povrchové druhy, *Cylisticus convexus* a *Hyloniscus riparius*, tiež príležitostne obývajú hlbšie zóny niektorých jaskýň. Naproti tomu jaskynné vchody obýva pestré spektrum druhov, najmä v monotónnom prostredí. Niektoré druhy, napr. *Trachelipus difficilis* alebo *Orthometopon planum,* zrejme uprednostňujú jaskynné vchody pred iným prostredím.

INTRODUCTION

Terrestrial isopods are an exception from crustaceans with their successful land colonising. Their ecological importance lies in their role of organic matter decomposers and the calcium carbonate concentration in their cuticle (Hornung 2011). In caves, they are frequently the only, or the most important macro-decomposers of poor food sources, such as bat guano, decaying wood or leaf litter and nutrients in sedimetns carried in by streams or along the gravitational gradient. Moreover, they are important prey for predators in caves, like spiders or amphibians (Vignoli et al. 2006; Řezáč et al. 2008; Kováč et al. 2014). The body surface and droppings of isopods are an important substrate for microorganisms in caves (Nováková et al. 2005). Forty-eight species of terrestrial isopods are estimated to live in Slovakia (Flasarová 1998; Rendoš et al. 2016; Mock & Tuf 2017). Only the blind and depigmented isopod species *Mesoniscus graniger* is considered strictly subterranean (Košel 2007, 2012).

OVERVIEW OF HISTORICAL DATA

The history of research on terrestrial invertebrates in caves in Slovakia is relatively rich and long (Košel 2007b, 2009, 2012). When Frivaldszky (1865) published an original description of *Mesoniscus graniger* from the Baradla locality, a cave in present-day on the territory of Hungary (at the past the Kingdom of Hungary, covering much of Central Europe), it was not yet known that this type locality is a large underground system, connected with the Domica Cave in Slovakia, created in a famous cross-border karst area called the Slovak-Aggtelek Karst (or the Aggtelek-Slovak Karst). The collections coming directly from the territory of today's Slovakia were still missing. Samplings of the females of *M. graniger* from Jasovská Cave and Silická ľadnica (Silická Ice Cave) from the same region as the Baradla-Domica, were carried out by K. Absolon in 1913 but published much more later by Strouhal (1939). When the Domica Cave, which is the Slovak part of the whole Domica-Baradla Cave System, was discovered in 1926, detailed research on it also yielded the findings of *M. graniger*, which were gradually reported by several authors (Staněk 1932a, b; Kettner 1936; Balthazar & Frankenberger 1937; Frankenberger 1939, 1940). After that, Frankenberger (1959) published a complete list of terrestrial isopods in Czechoslovakia, mentioning *M. graniger* not only from caves, but also from under rocks deep in soil at other localities in the Slovak Karst, the Tatra Mts. and the Vihorlatské vrchy Mts. These distribution data were used in a taxonomical review of the genus *Mesoniscus* by Gruner & Tabacaru (1963); from Slovakia, these authors reflected only the published findings of *M. graniger* in the soil outside the caves. The old find of an individual of the species *Armadillidium vulgare* in the collection of František Miller from the Domica Cave from 1948 was recently recognized by Dolejš & Tuf (2018). Gulička (1975) published a paper on the Slovak cave fauna, mentioning *M. graniger* in caves from the orographic units Slovak Karst, Slovak Paradise, Muráň Plateau, and furthermore from the Stanišovská Cave and from deep soil layers near the Duča Cave. Košel (1975) added another record of this species from the Brázda Chasm in the Slovak Karst. The list of *M. graniger* localities obtained new records from the Medvedia Cave in Slovak Paradise (Košel 1976), Podbanište Cave in the Revúcka vrchovina Highlands (Gaál 1978) and other caves from this orographic unit (Pomichal 1982). Another contribution to the occurrence of *M. graniger* was made by a survey of caves in the Slovak Paradise (Košel 1984). Gulička (1985) published paper on cave fauna, where we can find the first coherent data of terrestrial isopods in Slovak caves. It consisted of terrestrial isopod research on four sites in the Slovak Karst and the Muránska planina Plateau, incorporating 38 sinkholes, chasms, and caves with their surroundings. Unfortunately, samples collected directly from caves and from cave vicinities were not distinguished in this paper, and the author used cave names to identify the localities where the sampling was carried out and the habitat characteristics, such as cave indoor, cave entrance or broad surroundings, are mixed up. Among other taxa, the list of terrestrial isopod species counted 22 species with brief ecological descriptions of them. Košel (1994) characterized cave fauna in the most important karst area in the country, Slovak Karst. His mentions of some localities with *M. graniger* are based on the published and own observations. Subsequent surveys enriched the knowledge of terrestrial isopods in the caves of the Revúcka vrchovina Highlands (Gaál et al. 2000) and the Kremnické vrchy Mts. (Gaál 2000). Slovak biospeleologists are constantly active and regularly contributing to the knowledge of subterranean fauna. More than 7000 caves are known in Slovakia (Bella et al. 2018), and the knowledge of diversity of terrestrial isopods in caves is gradually being revealed. At the turn of the millennium, surveys in the Cerová vrchovina Highlands revealed the occurrence of *M. graniger* in the Ľadová trhlina Cave, Nyáryho cave, and in deep scree on the slope of the Steblová skala Hill. This was also first finding of *M. graniger* in a non-karstic cave in Slovakia (Mlejnek 1999, 2000, 2002). Mlejnek & Ducháč (2001) published an extensive list of more than 80 karstic and non-karstic cave localities where *Mesoniscus graniger* had been found in Slovakia and they extended the list in 2003. Mock et al. (2002) published a study on the terrestrial fauna of the Važecká Cave, mentioning the isopods *Hyloniscus riparius* and *M. graniger*, followed by Mock et al. (2003) where *Protracheoniscus politus* was recorded from the Bystrianska Cave, and the same species was recorded in the Harmanecká Cave (Kováč et al. 2003). *Armadillidium versicolor* from the short caves in Čierna hora Mts. (Mock et al. 2004b) and *M. graniger* with *C. convexus* from the Jasovská Cave (Lukáň et al. 2004) were recorded the following year. Six caves near the village of Veľký Folkmár were surveyed, and *A. versicolor* and *Trachelipus difficilis* (as *T.* cf. *pseudoratzeburgii*) were found in 4 of them (Mock et al. 2004b, 2005). Other surveys shed light on the species composition of terrestrial isopods living in the Plavecká and Driny Caves inhabited by *C. convexus* (Kováč et al. 2005a) and the caves Domica, Čertova diera and Ardovská, consisting of *M. graniger, Porcellium conspersum* and *Trichoniscus* cf. *pygmaeus* (Kováč et al. 2005b). The next data on terrestrial isopods in Slovak caves came from the Dobšinská Ice Cave, with a record of *P. politus* (Kováč et al.

2006), Ponická Cave with *Androniscus* sp. (initially considered a *Haplophthalmus* representative) (Papáč 2006) and *M. graniger, P. conspersum, Lepidoniscus minutus* and *Ligidium hyponorum* from the Majkova Cave (Papáč et al. 2006). A repeated survey carried out in 2007 in the Leontína Cave in the Slovak Karst revealed interesting findings of a blind juvenile isopod belonging to the family Trichoniscidae, and also *C. convexus* (Košel et al. 2007). In the same year, Balciar (2007) mentioned terrestrial isopods from the Šlosiarova Cave and Mock & Papáč (2007) presented the first survey of the cavernicolous species of terrestrial isopods of Slovakia. More information was later added by examination of the Podbanište Cave by Papáč (2008), with a record of *M. graniger*; crevice basalt caves in the Cerová vrchovina Highlands by Papáč et al. (2009) mentioning *M. graniger* and *O. planum*; and the Pod Jankovcom Cave 2 created in sandstone (Višňovská & Barlog 2009) with one terrestrial isopod belonging to the genus *Hyloniscus*. Research in the Čierna hora Mts. summarised data from caves, counting 6 species of terrestrial isopods (Mock et al. 2009). A thorough study on the distribution and ecology of *M. graniger* and other subterranean fauna of the Western Carpathians was synthetized by Košel (2012), describing *M. graniger* as a cavernicolous ubiquist, inhabiting caves, screes and deeper soil strata. Further research enriched the knowledge of terrestrial isopods collected in caves by adding *T. dificillis* and *P. politus* from the Malužinská Cave (Papáč et al. 2015) and *P. politus* from the Zápoľná Cave (Višňovská et al. 2017). A comparison of cave and subsurface isopod assemblages was carried out by Rendoš et al. (2016), listing *A. versicolor, L. minutus, M. graniger, P. politus* and *Trichoniscus carpaticus* from the study of Mock et al. (2009) as species present in caves. This comparison revealed, that only *M. graniger* inhabits subsurface screes and caves in this area continuously, but complex of screes, caves and soil, and mutual ecotones of these, is unique for biodiversity forming. *M. graniger* was also mentioned in the study of Papáč et al. (2019) from the Moldavská Cave in the Košice Basin, together with *C. convexus*. An overview of the findings of invertebrates, including isopods in the Dobšinská Ice Cave and underground localities with this cave genetically linked, was published by Papáč et al. (2020). All published findings of terrestrial isopods from caves in Slovakia are listed in detail in the results of this study.

AIMS AND HYPOTHESES

The unprecedentedly extensive material of isopods collected in the caves of Slovakia by generations of biospelogists has enabled us to seek answers to some questions:

1. What is the species richness of permanent isopod cave dwellers in Slovakia?
2. Are caves an exclusive habitat for specialised fauna, or are they colonized only by opportunistic species from the surface (assuming almost all isopods are predisposed to life in a humid, shaded environment)?
3. How does the assemblage change along the main environmental gradient from cave outdoor to indoor?
4. What are the characteristics of the distribution of cave or cave-preferring species in the studied area?

The aims of the study were:

- to summarize published and unpublished data and provide a list of terrestrial isopods collected from cave environments in Slovakia;
- to outline a regional distributional pattern of terrestrial isopods closely associated with the cave environment;
- to analyse the preference of microhabitats allocated along the main environmental gradient (surface – cave interior) by terrestrial isopods.

MATERIAL AND METHODS

We have examined both unpublished and published material of terrestrial isopods sampled in Slovak caves. The whole examined inventory consists of previous collections of the authors of this study and colleagues mentioned below, sampled in 111 caves and 1 ore mine in Slovakia (Table 1). All items of terrestrial isopods from the caves of Slovakia in the private collection estate of Václav Ducháč (Hradec Králové, Czech Republic) were previously acquired during field research by one of the authors (R. Mlejnek) and were no longer scientifically processed and published during V. Ducháč's life. Ján Gulička's private collection estate (Bratislava, Slovakia) apparently consists of fruits of field works of several zoologists (as J. Gulička, V. Košel. M. Krumpál, A. Krištín, S. Kalúz) and some cavers (Krumpál, pers. com.), but the authority of the collections has not been preserved. In addition to the items that were localized and are processed in this work, we found other 21 not localizated items with isopods in the Gulička estate, which contain 91 individuals and 15 species of terrestrial isopods. The material was not previously determined on the species level. Only numerical codes were labelled and the tubes with isopods were concentrated in a jam bottle marked as "Isopoda zo slovenských jaskýň" (Isopods from the caves of Slovakia). We assume that the collector of this could have been Ján Brtek, a prominent Slovak expert on crustaceans (except terrestrial isopods) and Gulička could have reached that material through Marie Flasarová, an excellent Czech expert on Oniscidea, who respected J. Gulička's eminent interest in cave invertebrates, with whom J. Brtek and J. Gulička cooperated professionally. Unfortunately, none of the three experts mentioned live and we have not found a description of the numerical codes. We excluded this small part of J. Gulička's collection from further analysis. Perhaps an interesting additional fact is that it does not contain any surprising findings that would significantly complement the issues we are addressing here. The vast majority of individuals (97%) of this small part of the J. Gulička's collection represent species common in surface habitats, so the isopods probably came from the cave entrances to caves or their immediate surroundings. All examined collections were dated from 1948 to 2019 and represent a diverse unit of samples collected directly from caves, cave entrances, and their proximities; samples obtained by using baited or unbaited traps; and by individual sampling from cave walls and ceilings, rotting wood, cave floors or by sieving and extraction methods. Since the description of some samples was very scarce and information was missing, we tried to supplement the information concerning these samples based on knowledge about the ecological attributes of the given species, our own experience, and personal communication with collectors.

To assess the spatial distribution of individual species, we divided the cave depth gradient into four groups based on the distance from the entrance and microclimatic conditions. Caves for this analysis were thought of as simple tunnels with one entrance, continually proceeding into the mass, and with greater distance from the entrance, there is less light, fewer food resources, lower temperatures, lower predator pressure and more stable climatic conditions. To graphically display results for the inside-outside gradient, we used bar plots with exponential trendlines and a simple sketch of the cave model with 4 cave zones (Figure 1). Zone A can be described as the cave entrance and its surroundings, usually of stony character, with the microclimate possibly affected by the cave. Zone B is the inside of the cave entrance with shaded cave walls and a rapid decrease of food resources. It does not rain here directly, and sunlight is slightly filtered in this zone. Zone C lies behind the border of minimal sunlight. Matter exchange with the surface is still present through plant roots or groundwater. In the deepest zone D, the climate is stable, food resources are poor, and adaptations to life in complete darkness are fully utilized. This zonation was used only if possible, since zone D is not present in shallow and short caves. The collector amended information about position in the cave, from which the sample was taken. If possible, these data were used for spatial distribution of the species.

Four sampling methods we used for collecting of isopods extraction of organic substrate (natural or brought to the cave as bait by researchers; EX), individual sampling (IS), baited and unbaited pitfall trapping with various design, fixative solution (PT), and sifting of leaf litter and humus in the cave entrance

(SF). Terrestrial isopods were collected in all cave zones A, B, C and D using pitfall trapping and individual sampling. Sifting and extraction methods are not utilised for the environment in cave zones C and D; therefore, no terrestrial isopods were collected by such methods.

The determination or revision of a previous data was carried out according to Frankenberger (1959), Gruner (1966), Radu (1983, 1985) and Tabacaru & Giurginca (2014). Systematics and nomenclature follow the World catalog of terrestrial isopods completed by Schmalfuss (2003). Elevation of the cave entrance and length of the caves were taken from the official list of Slovak caves (Bella et al. 2018). We also came up with the ecological classification of species based on the reasons for the classification of subterranean organisms given by Sket (2008). The revised material is deposited in collections of Pavol Jozef Šafárik University in Košice.

Numerical evaluations provided in the Table 2 are following: Dominance was calculated according to formula: Dom (%) = n/N*100, n = number of individuals of given species, N = total number of all individuals from the revised material (5658 individuals). Constancy: Con (%) = I/L*100, I = number of caves in which the species was recorded, L = all localities under study (112 in total). Shannon's diversity index (Table 2) was calculated by the formula Shannon's diversity index = $-\sum(P_i*\ln P_i)$, where P_i is the fraction of the entire population made up of species *i* (proportion of a species is relative to a total number of species present, not encountered) (Heip et al. 1998).

Three groups of species were set to some form of graphical representation of results. The first group (ENTR, see Figure 2), inhabiting cave entrances, collectively named chasmatophilous and sometimes referred to as parietal fauna (Gulička 1975). The second group of species (TGPH), visiting deeper cave areas and spending a higher amount of time in them but not reproducing in them, are called troglophiles. The third group (TROG) referred to as cavernicolous or closely connected with the cave environment in the region. Decimal logarithms of species individual counts were used to provide more transparent insight in some cases.

RESULTS

Systematic survey of terrestrial isopods in Slovak caves

The collection date is followed by the acronym of the collector's or collection name:

AM = Andrej Mock, AP = Andrea Parimuchová, JG = coll. Ján Gulička, ĽH = Ľubomír Hraško, ĽK = Ľubomír Kováč, MR = Michal Rendoš, RM = Roman Mlejnek, TJ = Tomáš Jászay, VK = Vladimír Košel, VP = Vladimír Papáč, followed by the number of collected individuals (M – males, F – females, J – juveniles.).

Class Malacostraca Latreille, 1802
Order Isopoda Latreille, 1817
Suborder Oniscidea Latreille, 1802

Family: Ligiidae Leach, 1814

1. *Ligidium germanicum* Verhoeff, 1901

Material examined: Eastern Tatra Mts.: Nový Mt. Cave 2, 14.ix.2011–28.vi.2012, PĽ, AM (1F); **Slovak Paradise**: Duča, 11.vi.1976, JG (3M, 7F).

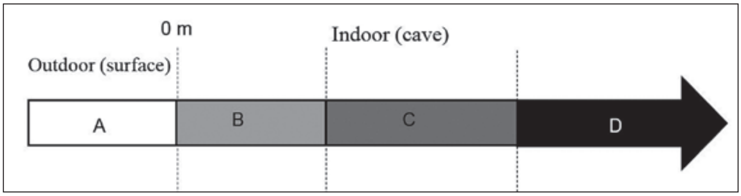


Figure 1: Simplified model used for zonation of outside-inside gradient in caves. For characteristics of each zone, see Material and Methods.
Obrázok 1: Zjednodušený model zonácie jaskyne na gradiente z vonkajšieho prostredia do vnútra. Charakteristiku zón pozri v kapitole Material and Methods.

*Table 1: List of caves where the examined material was collected. Caves marked with * are not listed in the official list of Slovak caves (Bella et al. 2018), or the identity of cave is not clear. The sum of isopod-positive caves is in parentheses after each orographic unit.*
Tabuľka 1: Zoznam jaskýň, v ktorých bol získaný revidovaný materiál. Jaskyne označené * chýbajú v oficiálnom zozname jaskýň Slovenska (Bella et al. 2018), alebo ich identita nie je jasná. Počet jaskýň s nálezmi rovnakonôžok je v zátvorke za každým názvom orografického celku.

Orographic unit	Cave	Entrance altitude (m a.s.l)	Length of cave (m)
Bachureň Mts. (1)	Zlá diera	786	450
Cerová vrchovina Highlands (2)	Nad skalným oknom	570	4
	Nyáryho	570	25
Eastern Tatra Mts. (1)	Nový Mt. Cave 2	1548	154
Horehronské podolie Basin (3)	Bystrianska	566	3531
	Márnikova	770	487
	Mýtska	640	100
Hornád River Basin (6)	Hlboká priepasť	602	43
	Na Dreveníku Ice Cave	557	215
	Pod lipou	565	40
	Pleky	527	400
	Šikmá	522	38
	Veľká	603	38
Juhoslovenská Basin (3)	Dolná mašianska	210	24
	Horná mašianska	218	93
	Šlosiarova	212	58
Košice Basin (2)	Jasovská	257	3924
	Okno (in Jasovská Cave)	260	?
	Pod hradným vrchom	325	25
Kozie chrbty Mts. (2)	Važecká	784	530
	Západná	755	1848
Kremnické vrchy Mts. (1)	Kremnická suchá diera	1193	60
Levočské vrchy Mts. (2)	Pod Jankovcom Cave 2	1060	100
	Pod Spišskou	1022	746
Malé Karpaty Mts. (3)	Driny	434	680
	Plavecká	222	936
	Riečna	301	43
Muráň Plateau (10)	Dolná jaskyňa v Tepličnom	660	8
	Horná jaskyňa v Tepličnom	663	10
	Kostolík	479	404
	Ladzianskeho	845	1212
	Pekárova	812	100
	Rysie hniezdo	770	200
	Šingliarka	1080	20
	Studňa	514	26
	Veľká lúka (sinkhole)	975	35
	Vlčia diera	442	34
Nizke Tatry Mts. (7)	Demänovská Ice Cave	840	650
	Lomená	954	29
	Malužinská	781	328
	Nad Patočinami 3	753	13
	Pustá	943	?
	Strieborná	850	159
	Tunelová	837	211

Orographic unit	Cave	Entrance altitude (m a.s.l)	Length of cave (m)
Pieniny Mts. (1)	Aksamitka	756	335
Považský Inovec Mts. (2)	Beckovská	350	293
	Modrovská	420	581
Revúcka vrchovina Highlands (10)	Burda	380	334
	Chvalovská	263	110
	Praslen	333	133
	Veľká drienčanská	246	50
	Frontová	338	60
	Pivnica	280	19
	Podbanište	352	1570
	Špaňopoľská	310	10
	V Drieňovej	442	27
	Drienocká	312	45
Slovak Karst (29)	Ardovská	314	1510
	Besná diera	551	54
	Čertova diera (Domica-Baradla Cave System)	767	1000
	Diviačia Chasm	590	468
	Domica	339	1315
	Drienovská	245	1588
	Erňa	410	96
	Gemerskoteplická	242	637
	Gombasecká	249	1938
	Hrušovská	295	1139
	Hucínska	280	51
	Jubilejná	484	49
	Leontína	245	231
	Líščia diera (Domica-Baradla Cave System)	373	100
	Mál	380	170
	Milada	420	1309
	Miškov potok	245	59
	Na Kečovských lúkach	345	1010
	Nová brzotínska	270	800
	Orechová Chasm	484	49
	Silická Ice Cave	495	1100
	Snežná diera	888	95
	Snežná jama	589	18
	Stará brzotínska	258	128
	Stará Domica	353	?
	Veľká mutónska	589	18
	Zbojnícka	534	48
Slovak Paradise (5)	Dobšinská Ice Cave	969	1491
	Duča	995	136
	*Glac (sinkhole)	983	-
	Na Košiarnom briežku	?	10
	Psie diery	942	2670
Starohorské vrchy Mts. (2)	Matúšova	375	46
	Rozimova	400	30
Štiavnické vrchy Mts. (1)	Krasová prvá	738	150
Strážovské vrchy Mts. (1)	Jánošíkova	405	11

Orographic unit	Cave	Entrance altitude (m a.s.l)	Length of cave (m)
Veľká Fatra Mts. (4)	Harmanecká	821	3216
	Horná Túfna	975	85
	Pod Prašivou	900	40
	V Čerťazi	630	10
	*V Čiernom Kameni (chasm)	>1400	?
Veporské vrchy Mts. (2)	Čertova	650	297
	Hrončianska	690	100
Vihorlatské vrchy Mts. (1)	Brekovská	260	200
Volovské vrchy Mts. (4)	Feliciani (mining gallery)	409	570
	Homološova diera	776	91
	Kolónia 2	807	25
	Šarkania diera	690	177
Western Tatra Mts. (3)	Brestovská	851	86
	Dúpnica	765	258
	V doline Dobrošovo	?	15
Zvolen Basin (4)	Feďova	515	23
	Medená	530	106
	Oravecká vyvieračka	460	23
	Ponická	515	840
Range	111 caves, 1 mine	210 – 1548	4 – 3924

Published data: Slovak Karst: Brzotínska, Gombasecká, Hučiaca and Kunova Teplica, Kečovská, Krásnohorská, Marciho, Matilda, Milada, Silická Ice Cave, Šingliarova, Zbojnícka v Sokolej skale (Gulička 1985); **Slovak Paradise**: Duča (Papáč et al. 2020).

2. *Ligidium hypnorum* (Cuvier, 1792)

Material examined: Nízke Tatry Mts.: Pustá 24.vi.–9.ix.2015 (1F); Slovak Karst: Silická Ice Cave, 18.v.2006, AM (1F, 6J); **Slovak Paradise**: Dobšinská Ice Cave, 23.v.1958, JG (9M, 22F, 2J), Duča 5.vii.1949 and 11.vii.1971, JG (3M, 28F, 3J); **Zvolen Basin**: Ponická, 8.xi.2007, AM (1M, 1J).

Published data: Čierna hora Mts.: Puklinová v Pečipalke (Mock et al. 2009); **Muráň Plateau**: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Studňa, Veľká lúka Sinkhole, Veľká Stožka and Kľak Chasm, Zlatnica (Gulička 1985); **Slovak Karst**: Majkova (Papáč et al. 2006); Slovak Paradise: Dobšinská Ice Cave (Papáč et al. 2020).

Family: Mesoniscidae Verhoeff, 1908

3. *Mesoniscus graniger* (Frivaldszky, 1865)

Material examined: Bachureň Mts.: Zlá diera, 23.iii.2008, AM (1F); **Cerová vrchovina Highlands**: Nyáryho, 20.v.1998, RM (2M, 3F), 9.v.2000, RM (2F); **Horehronské podolie Basin**: Márnikova, 9.v.2008, VP (1M, 2F), Mýtska, 30.i.1999, RM (1F), 19.iii.–13.v.2000, RM (2M, 6F), 13.v.–24.ix.2000, RM (2M, 4F); **Hornád River Basin**: Hlboká priepasť and Veľká jaskyňa caves, 17.vii.–14.iv.2000, RM ((2M, 9F), 17.vii.2000, RM (6F), Na Dreveníku Ice Cave, 2000, RM (1F), Pleky, 16.iv.2000, RM (1M), 16.vii.2000, RM (2F), 16.vii.–14.xi.2000, RM (2M, 3F), 11.v.2012, AM (3M, 1F, 2J), 11.v.–27.ix.2012, AM, ĽK (6M, 7F, 2J), Pod lipou, 19.vii.2000, RM (2F), 19.vii.–14.x.2000, RM (9M, 30F), Šikmá, 14.x.2000–14.iv.2001, RM (2F); **Juhoslovenská Basin**: Dolná mašianska, 14.iii.–18.x.1998, RM (8M, 7F), Horná mašianska, 18.i.–14.iii.1998, RM (1M, 21F), 28.i.–21.iv.2001, RM (1M, 7F); **Košice Basin**: Jasovská (featuring Okno Cave), 23.ix.1949, JG (1F), 2.vii.2015, VP (1M, 1F), 15.i.–25.11.2003, AM (1F), 25.xi.2003, AM (2M, 1F), 2.vii.2015, AM (1M, 1F), Pod hradným vrchom, 1.iv.2000, RM (3F), 1.iv.–30.vii.2000, RM (1M, 8F); **Kozie chrbty Mts.**: Važecká, 15.v.2001, PĽ (6M, 1F), 17.v.–13.ix.2001, AM (1M, 1J), 13.ix.2001, PĽ, AM (2M, 2F), 29.x.2002, AM (3F), 29.x.2002–18.ii.2003, AM (25M, 3F), RM (67M, 2F), 23.vi.2015, PĽ, VP (4F); **Kremnické vrchy Mts.**: Kremnická suchá diera, 22.viii.1998, RM (2F, 1J); **Levočské vrchy Mts.**: Pod Jankovcom Cave 2, 5.xi.2010, AM (1F), Pod Spišskou, 6.vii.2012, AM (1M), 6.vii.–11.x.2012, AM (2F); **Muráň Plateau**: Dolná jaskyňa v Tepličnom and Horná jaskyňa v Tepličnom, 12.ix.1999, RM (2M, 1F), Ladzianskeho, 18.iv.–8.ix.1998, RM (5M, 1F), Rysie hniezdo, 15.x.2007, VP (3F), Veľká lúka Sinkhole, 20.vi.1974, JG (5M, 9F), 30.vi.1976, JG (6F), Vlčia diera, 27.iii.1999, RM (1F), 27.iii.–12.ix.1999, RM (2M, 7F); **Nízke Tatry Mts.**: Demänovská Ice Cave, 14.ix.2001, RM (1F), Lomená, 10.viii.–10.x.2001, RM (1M, 1F), Malužinská, 27.v.–26.viii.2000, RM (2M, 1F), 26.viii.–16.x.2000, RM (1F), Nad Patočinami 3, 26.vii.–13.x.2001, RM (1F), Strieborná, 26.viii.2000, RM (2M, 4F), Tunelová, 8.vii.2001, RM (1M, 4F), 22.vii.2009, RM (3F); **Pieniny Mts.**: Aksamitka, 15.ix.2011, AM (1F, 2J); **Revúcka vrchovina Highlands**: Burda, 23.ii.–28.iv.1998, RM (3M, 8F), 30.viii.206, VP, Drienocká, 21.ii.–24.xi.1998, RM (5F), Frontová, 22.ii.–26.xi.1998, RM (1M, 1F), Pivnica, 20.iii.–1.viii.2000, RM (1M, 1F), Podbanište, 6.iv.–24.vii.1998, RM (1M, 3F), Praslen, 29.v.2006, VP (1J), 31.xii.2006, VP (2F), Špaňopoľská, 9.iv.–24.vii.1998, RM (4M, 2F), 24.vii.–25.ix.1998, RM (7M, 8F), V Drieňovej, 16.iv.2000, RM (1F); **Slovak Karst**: Ardovská, 10.iv.1970, JG (3M, 7J), 17.vi.1971, JG (104M, 194F, 231J), 3.xi.1972, JG (2M, 3F, 1J), 26.vi.1973, JG (8M, 58F, 6J), 11.viii.1973, JG (9M, 26F, 2J), 21.viii.1973, JG (49M, 221F, 42J), 24.viii.1973, JG (1M, 2F, 4J), 17.vi.1974, JG (5M, 27F, 23J), 27.xi.1974, JG (23M, 53F, 48J), 2.vii.1975, JG (80M, 121F, 290J), 2.ix.1975, JG (76M, 93F, 142J), 1.vii.1976, JG (181M, 219F, 675J), 21.x.2000, RM (2F), 8.xi.2002, PĽ (2F), 5.x.2004, ĽK, AM (5M, 20F, 3J), 14.iv.–6.ix.2010, AM (56M, 125F, 8J), Besná diera, 22.vii.–29.ix.1998, RM (15M, 3F), Čertova diera (Domica-Baradla Cave System), 24.iv.2002, AM (1F), 1.x.2015, AP (1M, 19F), Domica, no date (1970s), JG (2F), 2.vi.1971, JG (1M, 2F), 3.x.2001, AM (1F, 6J), 3.10.2001–24.1.2002, AM (86M, 233F, 13J), 24.4.2002–4.4.2003, AM (19M, 80F, 20J), 23.iv.2003, AM (6F, 2J), 19.v.–2.x.2005, PĽ, AM (113M, 168F, 1J), 3.v.2007–5.v.2008, AM (1M, 37F, 5J), Drienovská, 15.x.2008, AM (1M), 4.iv.2007, VP (1M, 2F), 19.iii.2009, AM (1M, 1F), 19.iii.–20.x.2009, AM (1F), 7.ix.2010, AM (1M), Gemerskoteplická, 27.vii.2003, VP (1J), Hrušovská, 3.v.2007, AM (1M), 3.v.–23.x.2007, AM (3F, 11J), Hucínska, 20.iii.–21.x.2000, RM (2M, 12F), Jubilejná, 7.v.2000, RM (1M, 9F), Leontína, 5.vi.2008, VP (3F), Líščia diera (Domica-Baradla Cave System), 20.iii.–21.x.2000, RM (11M, 8F, 3J), Mál, 10.v.1998–13.iii.1999, RM (1M, 4F), Milada, 15.iv.–18.ix.2010, ĽK (1F), Miškov potok, 13.vii.1998, RM (2F, 1J), Orechová Chasm, 7.vi.2000, RM (5F), 7.vi.–31.vii.2000, RM (6F), Snežná jama, 2.8.2001, RM (3F), Stará brzotínska, 20.vii.1998, RM (1F), 12.iv.–6.ix.2010, AM (1M), Stará Domica, 9.iii.1973, JG (9M, 58F, 5J), 26.vi.1973, JG (4F, 1J), Veľká mutónska, 20.iii.–21.x.2000, RM (2M, 6F), Zbojnícka (Plešivec Plateau), 2.vii.1976, JG (1M); **Slovak Paradise**: Dobšinská Ice Cave, 11.vi.1955, JG (2M, 1F, 5J), Duča, 11.vii.–11.x.2012, ĽK, AM (1F), Glac Sinkhole, 4.9.1975, JG (1M, 3F, 7J); **Starohorské vrchy Mts.**: Matúšova, 3.v.1998, RM (1F), 21.vi.–10.x.1998, RM (8M, 2F), Rozimova, 21.vi.–19.vii.1998, RM (10M, 6F, 1J); **Štiavnické vrchy Mts.**: Krasová prvá, 18.iii.2000, RM (1F); **Veľká Fatra Mts.**: Horná Túfna, 26.vii.2000, RM (1M, 3F), 26.vii.–10.x.2000, RM (2M, 3F), Pod Prašivou Cave, 15.vii.–14.x.2001, RM (4M, 4F),V Čerťaži, 15.vii.2001, RM (1M), 18.vii.-10.x.2001, RM (3M, 7F), V Čiernom Kameni (chasm), 14.vii.–13.viii.2001, RM (1M, 1F); **Veporské vrchy Mts.**: Čertova, 13.i.–9.iii.1998, RM (1M, 5F), 9.iii.–13.xii.1998, RM (1F), Hrončianska, 5.2.–26.2.1998, RM (3M), 26.ii.–4.v.1998 (6M, 6F); **Volovské vrchy Mts.**: Feliciani (Mining gallery), 14.xii.2012, MR (2J), Šarkania diera 22.ix.1999–13.ii.2000, RM (1F), 26.viii.2000, RM (1F); **Western Tatra Mts.**: Brestovská, 13.ix.2006, AM (1F), Dúpnica, 23.vii.2001, RM (2M, 1F), 23.vii.–13.x.2001, RM (1M, 5F), V doline Dobrošovo Cave, 24.vii.2001, RM (1F); **Zvolen Basin**: Feďova, 10.ix.2015, AM (2F), Ponická, 2013, ĽH (1F).

Published data: Cerová vrchovina Highlands: Nyáryho (MLEJNEK 1999, 2000, 2001), Ľadová trhlina, Nyáryho (MLEJNEK & DUCHÁČ 2001, 2003), Stĺpová, Šurický úkryt (PAPÁČ et al. 2009); **Čierna hora Mts.**: Malá kvapľová, Netopieria, Priepasťová (MLEJNEK & DUCHÁČ 2001, 2003), Malá kvapľová, Veľká ružínska (MOCK et al. 2009); **Horehronské podolie Basin**: Mýtňanská (MLEJNEK & DUCHÁČ 2001, 2003); **Hornád River Basin**: Hlboká priepasť, Ľadová, Na Dreveníku Ice Cave, Netopieria, Pod Lipou, Psia, Šikmá, Veľká (MLEJNEK & DUCHÁČ 2001, 2003); **Juhoslovenská Basin**: Horná mašianska (GAÁL 1987), Horná mašianska, Dolná mašianska (MLEJNEK & DUCHÁČ 2001, 2003); **Košice Basin**: Jasovská (STROUHAL 1939; KOŠEL 1994; LUKÁŇ et al. 2004), Jasovská, Pod hradným vrchom (MLEJNEK & DUCHÁČ 2001, 2003), Moldavská (PAPÁČ et al. 2019); **Kozie chrbty Mts.**: Važecká (MLEJNEK & DUCHÁČ 2001, 2003; MOCK et al. 2002, 2004a); **Kremnické vrchy Mts.**: Pod Skalkou (GAÁL et al. 2000), Jánošíkove diery, Kremnická suchá diera (MLEJNEK & DUCHÁČ 2001, 2003); **Muráň Plateau**: Veľká lúka Sinkhole (GULIČKA 1978), Bobačka, Brestová, Dlhý vrch, Studňa, Šindliarka, Veľká lúka Sinkhole, Zlatnica (GULIČKA 1985), Bobačka, Jazerná, Kostolík, Ladzianskeho, Vlčia diera (MLEJNEK & DUCHÁČ 2001, 2003), Bobačka (KOVÁČ et al. 2002b); **Nízke Tatry Mts.**: Stanišovská (GULIČKA 1975), spring near Veľká Stanišovská Cave (GULIČKA 1978), Brtkovičná Valley, Demänovská Ice Cave, Lomená, Malá stanišovská, Malužinská, Nad Patočinami 3, Portálová, Strieborná, Studňa, Tunelová (MLEJNEK & DUCHÁČ 2001, 2003), Demänovská Ice Cave (Kováč et al. 2002a), Demänovská Ice Cave, Portálová, Strieborná, Tunelová (BELLA et al. 2014); **Revúcka vrchovina Highlands**: Podbanište (GAÁL 1978), Dúbravica, Podbanište (POMICHAL 1982), Drienocká, Dúbravica, Frontová, Puklina, Špaňopoľská, Veľká drienčanská (GAÁL 2000), Burda, Drienocká, Dúbravica, Frontová, Pivnica, Podbanište, Puklina, Špaňopoľská, V Drieňovej, Veľká drienčanská (MLEJNEK & DUCHÁČ 2001, 2003), Podbanište (PAPÁČ 2008); **Slovak Karst**: Domica (STANĚK 1932a, b, as white *Asellus* sp.; ŠTORKÁN in KETTNER 1936; BALTHAZAR & FRANKENBERGER 1937; FRANKENBERGER 1939, 1940, 1959, as *M. alpicola graniger*, GIURGINCA et al. 2012; PAPÁČ et al. 2014; GAÁL & GRUBER 2015, SMRŽ et al. 2015; GAÁL 2017), Silická Ice Cave (STROUHAL 1939), Brázda Chasm (KOŠEL 1975), Silická Ice Cave (GULIČKA 1978), Ardovská, Bezodná Ice Cave, Bobková, Brázda Chasm, Brzotínska, Čertova diera (Domica-Baradla Cave System), Gombasecká, Havrania skala Chasm, Kečovská, Kostrová, Krásnohorská, Kvapľová, Majkova, Malá and Veľká Žomboj Chasms, Marciho, Maštaľná, Matilda, Milada, Silická Ice Cave, Stará Domica, Šingliarova, Veľká Bikfa Chasm, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (GULIČKA 1985), Ardovská, Čertova diera, Domica, Drienovská, Hrušovská, Silická Ice Cave (KOŠEL 1994), Ardovská, Besná diera, Blatná, Brázda Chasm, Čertova diera, Domica, Drienovská, Fialová, Gombasecká, Hrušovská, Hucínska, Jubilejná Chasm, Komária, Líščia diera, Majkova, Mál, Miškov potok, Múriková, Nad Vidovským závozom Chasm, Orechová Chasm, Pod Veterníkom, Ponorná Chasm, Priepasť nad Vidovským závozom Sinkhole, Silická, Silická Ice Cave, Snežná diera, Stará brzotínska, Stará Domica, Tepličné Chasm, Veľká mutónska, Závozná Chasm I., Závozná Chasm II., Zbojnícka (Plešivec Plateau) (MLEJNEK & DUCHÁČ 2001, 2003), Ardovská, Domica (ELHOTTOVÁ ET AL. 2003, 2004; KOVÁČ et al. 2005b; KRIŠTŮFEK et al. 2005; NOVÁKOVÁ et al. 2005; ŠUSTR et al. 2005, 2009; GIURGINCA et al. 2015), Čertova diera (Kováč et al. 2005b), Majkova (PAPÁČ et al. 2006), Snežná diera (PAPÁČ et al. 2007), Leontína, Stará brzotínska (KOVÁČ et al. 2010), Drienovská (RATKOVSKÝ et al. 2019); **Slovak Paradise**: Duča (GULIČKA 1975), Duča (GULIČKA 1978), Medvedia (KOŠEL 1976), Čertova, Medvedia, Psie diery, Suchá vyvieračka (KOŠEL 1984), Medvedia (MLEJNEK & DUCHÁČ 2001, 2003), Stratenská Cave System (PAPÁČ et al. 2020); **Starohorské vrchy Mts.**: Matúšova, Rozimova (MLEJNEK & DUCHÁČ 2001, 2003); **Štiavnické vrchy Mts.**: Krasová jaskyňa prvá (MLEJNEK & DUCHÁČ 2001, 2003); **Western Tatra Mts.**: Brestovská, Dúpnica (KOVÁČ et al. 2008), Brestovská (BELLA et al. 2017); **Veľká Fatra Mts.**: Čierny kameň, Dolná Túfna, Horná Túfna, Pod Prašivou, V Čerťaži (MLEJNEK &

Ducháč 2001, 2003); **Veporské vrchy Mts.**: Čertova, Hrončianska (Mlejnek & Ducháč 2001, 2003); **Volovské vrchy Mts.**: Homološova diera (Košel 2009, 2012), Šarkania diera (Mlejnek & Ducháč 2001, 2003; Košel 2007a).

Family: Trichoniscidae Sars, 1899

4. ***Androniscus*** cf. ***dentiger*** Verhoeff, 1908

Material examined Zvolen Basin: Ponická, 26.i.2006, VP (1J).

Published data: Zvolen Basin: Ponická (Papáč 2006, as *Haplophthalmus* sp.), Mock & Papáč (2007), Kováč et al. (2014).

5. ***Haplophthalmus mengii*** **(Zaddach, 1844)**

Material examined: Eastern Tatra Mts.: Nový Mt. Cave 2, 14.ix.2011–28.vi.2012, PĽ, AM (1J). **Malé Karpaty Mts.**: Plavecká, 30.iv.2005, ĽK, AM (2M, 2F); **Slovak Karst**: Gombasecká, 1.x.2009, AM (12F, 3J).

Published data: Slovak Karst: Domica (Papáč et al. 2014).

6. ***Hyloniscus mariae*** **Verhoeff, 1908**

Material examined: Slovak Paradise: Dobšinská Ice Cave, 23.5.1958, JG (6F); **Strážovské vrchy Mts.**: Jánošíkova, 26.iv.–19.ix.2012, AM (1M).

Published data: Muráň Plateau: Bobačka, Brestová, Mokrá Poľana, Studňa, Veľká lúka Sinkhole, Veľká Stožka and Kľak Chasm, Zlatnica (Gulička 1985); **Slovak Paradise**: Dobšinská Ice Cave (Papáč et al. 2020).

7. ***Hyloniscus riparius*** **(Koch, 1838)**

Material examined: Horehronské podolie Basin: Bystrianska, 18.v.1981, JG (1M); **Juhoslovenská Basin**: Šlosiarova, 8.vi.2007, VP (1F); **Kozie chrbty Mts.**: Važecká, 17.v.2001, AM (1M), 23.vi.2001, AM (1M, 1F), 13.ix.2001, AM (1M, 7F); **Malé Karpaty Mts.**: Driny, 13.ix.2005, AM (2F), Plavecká, 14.ix.2005, AM (2M, 2F, 2J); **Muráň Plateau**: Kostolík, 8.viii.2006, VP (5F); **Pieniny Mts.**: Aksamitka, 15.ix.2011, AM (1F); **Považský Inovec Mts.**: Beckovská, 15.ix.–22.vi.2013, AM (1M, 1F), Modrovská, 25.iv.–16.ix.2012, AM (25M, 22F, 5J); **Revúcka vrchovina Highlands**: Burda, 30.v.2006, AM (1F); **Slovak Karst**: Ardovská, 13.vi.1997, ĽK (2F, 2J), 22.v.1999, TJ (1M, 5F), 1.vii.1999, TJ (5M, 1F), Domica, 22.iv.2004, AM (1F), Leontína, 7.x.2006, VP (1M), 5.vi.2008, VP (1F), Líščia diera (Domica), 13.iii.2013, AM (2M, 3F), Milada, 6.x.2010, AM (1M, 2F), Nová brzotínska, 12.v.1998, AM (1F, 1J), Silická Ice Cave, 19.v.1999, TJ (5M, 10F, 28J), Stará Domica, 3.x.2001, AM (1F, 1J), Veľká mutónska, 20.iii.–21.x.2000, RM (2F); **Veľká Fatra Mts.**: V Čerťaži, 18.vii.–10.x.2001, RM (1F); **Vihorlatské vrchy Mts.**: Brekovská, 26.i.2012, AM (2M, 4F); **Zvolen Basin**: Feďova, 3.iv.2015, AM (1F), Medená, 3.iv.2015 (1M), Oravecká vyvieračka, 25.vi.–10.ix.2015, AM, 10.ix.2015, AM (1M, 19F, 6J), Ponická, 25.6.2015, AM (1F).

Published data: Kozie Chrbty Mts.: Važecká (Mock et al. 2002, 2004a); **Malé Karpaty Mts.**: Plavecká (Kováč et al. 2014); **Levočské vrchy Mts.**: Pod Jankovcom Cave 2 (Višňovská & Barlog 2009); **Muráň Plateau**: Bobačka, Dlhý vrch, Zlatnica; **Slovak Karst**: Brzotínska, Hučiaca and Kunova Teplica, Kečovská, Krásnohorská, Marciho, Matilda, Milada, Zbojnícka v Sokolej skale (Gulička 1985), Domica (Papáč et al. 2014).

8. ***Hyloniscus transsilvanicus*** **Verhoeff, 1908**

Material examined: Malé Karpaty Mts.: Riečna, 23.v.1958, JG (2F, 1J).

No published data.

9. ***Trichoniscus carpaticus*** **Tabacaru, 1974**

Material examined: Levočské vrchy Mts.: Pod Jankovcom Cave 2, 1.iv.2011, AM (1M, 2F); **Slovak Paradise**: Duča, 11.vi.1971, JG (1F).

Published data: Čierna hora Mts.: Krížová, Malá kvapľová, Puklinová v Pečipalke, Veľká ružínska (Mock et al. 2009, as *Trichoniscus* sp., see Rendoš et al. 2016); **Slovak Paradise**: Duča (Papáč et al. 2020).

Note: Other individuals of the genus *Trichoniscus*, which were not determined to the species level, are reported by Gulička (1985) from the entrance parts of the caves of the Muráň Plateau: Bobačka, Brestová and Zlatnica, and the Slovak Karst: Brzotínska, Gombasecká, Matilda, Zbojnícka v Sokolej skale and the surroundings of the karst springs Hučiaca vyvieračka and Kunova Teplica.

10. *Trichoniscus* cf. *pygmaeus* Sars, 1898

Material examined: Slovak Karst: Domica, 29.iv.1997, ĽK (1F).

Published data: Slovak Karst: Domica (KOVÁČ et al. 2005b, PAPÁČ et al. 2014).

11. Trichoniscidae gen. sp.

Material examined: Slovak Karst: Leontína, 7.x.2006, VP (1F).

Published data: Slovak Karst: Leontína (KOŠEL et al. 2007; MOCK & PAPÁČ 2007, KOVÁČ et al. 2010, 2014).

Note: blind, depigmented unidentified member of the family.

Family: Philosciidae Kinahan, 1857

12. *Lepidoniscus minutus* (Koch, 1838)

Material examined: Slovak Karst: Čertova diera (Domica-Baradla Cave System), 1.vii.1999 TJ (1M), 22.x.1999, AM (1M, 4F), 3.iv.2002, AM (1M, 1J), 21.iv.2004, AM (1J), Líščia diera (Domica-Baradla Cave System), 2.iii.2001, AM (1F, 5J), 3.iv.2003, AM (3J), 13.ii.2012, AM (2M, 2F, 2J), Zbojnícka (Plešivec Plateau), 2.vii.1976, JG (1F); **Slovak Paradise**: Dobšinská Ice Cave, 23.v.1958 (1F, 1J).

Published data: Čierna hora Mts.: Hadia, Komín nad Previsovou, Krížová a Previsová, Puklinová v Pečipalke, Zákrutová (MOCK et al. 2009; RENDOŠ et al. 2016); **Slovak Karst**: Bezodná Ice Cave, Bobková, Brzotínska, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Kostrová, Krásnohorská, Majkova, Matilda, Milada, Silická Ice Cave, Šingliarova, Zbojnícka v Sokolej skale (GULIČKA 1985), Majkova (PAPÁČ et al. 2006); **Slovak Paradise**: Dobšinská Ice Cave (PAPÁČ et al. 2020).

Family: Platyarthridae Verhoeff, 1949

13. *Platyarthrus hoffmannseggii* Brandt, 1833

Material examined: Slovak Paradise: Dobšinská Ice Cave, 23.v.1958, JG (9J).

Published data: Slovak Karst: Kečovská (GULIČKA 1985); **Dobšinská Ice Cave** (PAPÁČ et al. 2020).

Family: Oniscidae, Latreille, 1802

14. *Oniscus asellus* Linnaeus, 1785

No material examined.

Published data: Muráň Plateau: Zlatnica; **Slovak Karst**: Bobková, Čertova diera (Domica-Baradla Cave System), Gombasecká, Hučiaca and Kunova Teplica springs surrounding, Kečovská, Kostrová, Krásnohorská, Stará Domica (GULIČKA 1985), Domica (PAPÁČ et al. 2014).

Family: Trachelipodidae Strouhal, 1953

15. *Porcellium collicola* (Verhoeff, 1907)

Material examined: Slovak Karst: Ardovská, 1.vii.1976, JG (3J), 13.vi.1997, ĽK (7F, 2J), 22.v.1999, TJ (1F), 1.vii.1999, TJ (1M, 1F, 1J), Čertova diera (Domica-Baradla Cave System), 11.v.1999, AM (3F, 1J), 1.vii.1999, AM (1M, 6F, 3J), 22.x.1999, AM (1M, 18F, 2J), 3.iv.2002, AM (24M, 18F, 11J), 21.iv.2004, AM (2M, 5F, 1J), Domica, 29.iv.1997, ĽK (1J), Erňa, 21.ii.2014, AM (1F), 31.iii.2014, AM (1F), Líščia diera (Domica-Baradla Cave System), 1.vii.1999, TJ (2M, 5F, 2J), 8.iii.2001, PĽ (7M, 7F, 6J), 3,iv.2003, AM (20M, 37F, 10J), 13.iii.2012 (1M), Milada, 8.ix.2012, AM (1F), Na Kečovských lúkach, 16.iv.–8.ix.2010, AM (3F), Silická Ice Cave, 1.vi.1971, JG (1F), 17.v.1999, TJ (4F), 18.v.2006, AM (1F).

Published data: Slovak Karst: Ardovská, Bobková, Brázda Chasm, Brzotínska, Červená, Gombasecká, Hučiaca and Kunova Teplica, Kostrová, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Majkova, Malá and Veľká Žomboj Chasms, Marciho, Maštaľná, Matilda, Milada, Ortováň, Silická Ice Cave, Šingliarova, Veľká Bikfa Chasm, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (GULIČKA 1985), Domica (PAPÁČ et al. 2014).

16. *Porcellium conspersum* (C. Koch, 1841)

No material examined.

Published data: Čierna hora Mts.: Puklinová v Pečipalke (MOCK et al. 2009); **Muráň Plateau**: Bobačka, Brestová, Zlatnica; **Slovak Karst**: Bobková, Brzotínska, Kostrová, Marciho (GULIČKA 1985); Domica (KOVÁČ et al. 2005b; PAPÁČ et al. 2014), Majkova (PAPÁČ et al. 2006).

17. *Trachelipus difficilis* (Radu, 1950)

Examined material: Muráň Plateau: Ladzianskeho (1F); **Slovak Paradise**: Dobšinská Ice Cave, 5.vii.1947, JG (1M), July 1948, JG (2M, 2F), Na Košiarnom briežku, 26.i.2008, VK (1F), Psie diery, 10.ix.2019, AM (1F); **Strážovské vrchy Mts.**: Jánošíkova, 19.ix.2012, AM (1F); **Zvolen Basin**: Medená, 3.iv.2015 (1J).

Published data: Čierna hora Mts.: Nová galéria, Klenbová (Mock et al. 2005 – as *T.* cf. *pseudoratzeburgi*; Mock et al. 2009); **Nízke Tatry Mts.**: Malužinská (Papáč et al. 2015); **Slovak Karst**: Bobková, Kostrová, Majkova, Marciho, Zbojnícka v Sokolej skale (Gulička 1985 – as *T. pseudoratzeburgi*), **Slovak Paradise**: Dobšinská Ice Cave, Psie diery (Papáč et al. 2020). Quite a rare but characteristic representative of parietal fauna dwelling the cave entrances in Slovakia (Mock & Papáč 2007; Kováč et al. 2014).

18. *Trachelipus nodulosus* (Koch, 1838)

Material examined: Hornád River Basin: Na Dreveníku Ice Cave, 11.v.2012, AM (1M, 2J).

Published data: Slovak Karst: Ardovská, Bezodná Ice Cave, Bobková, Brázda Chasm, Brzotínska, Čertova diera (Domica-Baradla Cave System), Červená, Gombasecká, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Kostrová, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Malá and Veľká Žomboj Chasms, Marciho, Maštaľná, Matilda, Milada, Ortováň, Šingliarova, Veľká Bikfa Chasm, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (Gulička 1985), Domica (Papáč et al. 2014).

19. *Trachelipus rathkii* (Brandt, 1833)

Material examined: Slovak Karst: Milada, 8.x.2010, AM (1F), Silická Ice Cave, 1.vi.1971, JG (1M, 1F), Na Kečovských lúkach, 16.iv.–9.ix.2010, AM (4F).

Published data: Muráň Plateau: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Studňa, Šindliarka, Veľká lúka Sinkhole, Veľká Stožka and Kľak Chasm, Zlatnica; **Slovak Karst**: Ardovská, Bezodná Ice Cave, Bobková, Brázda Chasm, Brzotínska, Čertova diera (Domica-Baradla Cave System), Červená, Gombasecká, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Kostrová, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Majkova, Malá and Veľká Žomboj Chasms, Marciho, Maštaľná, Matilda, Milada, Ortováň, Silická Ice Cave, Snežná diera, Stará Domica, Šingliarova, Veľká Bikfa Chasm, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (Gulička 1985), Snežná diera (Papáč et al. 2007), Domica (Papáč et al. 2014).

20. *Trachelipus ratzeburgii* (Brandt, 1833)

Material examined: **Slovak Karst**: Silická Ice Cave, 24.ix.1949, JG (1M, 3F), 23.x.–19.xii.2013, AM (1F); **Strážovské vrchy Mts.**: Jánošíkova, 19.ix.2012, AM (1M).

Published data: Čierna Hora Mts.: Klenbová, Nová Galéria (Mock et al. 2005), Komín nad Previsovou (Mock et al. 2009); Muráň Plateau: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Studňa, Šindliarka, Veľká lúka Sinkhole, Veľká Stožka and Kľak Chasm, Zlatnica (Gulička 1985); **Slovak Karst**: Ardovská, Bezodná Ice Cave, Brázda Chasm, Brzotínska, Gombasecká, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Majkova, Malá and Veľká Žomboj Chasms, Marciho, Maštaľná, Matilda, Milada, Snežná diera, Stará Domica, Šingliarova, Veľká Bikfa Chasm, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (Gulička 1985), Snežná diera (Papáč et al. 2007), Domica (Papáč et al. 2014).

Family: Cylisticidae Verhoeff, 1949

21. *Cylisticus convexus* (De Geer, 1778)

Material examined: Hornád River Basin: Na Dreveníku Ice Cave, 11.v.–27.ix.2012, AM (4J); **Košice Basin**: Jasovská, 3.iii.1999, AM (1M, 1F), 3.iii.1999 – 24.xi.2000, AM (1M, 1F, 1J), 11.ix.2015, AM (1F), 2.7.–11.9.2015, ĽK, AM (5M, 5F, 1J), Okno (Jasovská) 25.xi.2000, AM (1M, 1F) (1M, 1F); **Malé Karpaty Mts.**: Plavecká, 30.iv.2005, AM (5F, 1J), 14.ix.2005, AM (1M); **Muráň Plateau**: Pekárova, 15.x.2007, VP (1M); **Pieniny Mts.**, Aksamitka, 15.ix.2011, AM (1M), 15.ix.2011-9.v.2012, AM (1M, 2J); **Revúcka vrchovina Highlands**: Chválovská, 18.iv.2006, VP (1M); Slovak Karst: Domica, 8.vii.1998–11.v.1999, AM (3M, 1F, 1J), 24.i.2002, AM (1F), 2.x.2002, AM (1M), 24.iv.2003, AM (1M), 7.x.2007, AM (1M, 2J), Gombasecká, 18.v.2005, PĽ (1F), Leontína 21.ix.1949, JG (1F), 7.x.2006, VP (1F), Stará Domica, 3.10.2001, AM (1M, 2F), 3.x.2001–24.i.2002, AM (4M, 1F, 1J), 9.x.2003, AM (1M, 1F, 1J); **Veľká Fatra Mts.**: Harmanecká, 24.x.2010, AM (1F); **Vihorlatské vrchy Mts.**: Brekovská, 12.vi.–20.ix.2001, AM (3F).

Published data: Čierna hora Mts.: Humenecká, Kysacká, Puklinová v Pečipalke (MOCK et al. 2009; RENDOŠ et al. 2016); **Košice Basin**: Jasovská (2M, 1F) (LUKÁŇ et al. 2004), Moldavská (PAPÁČ et al. 2019); **Kozie chrbty Mts.**: Važecká (MOCK et al. 2004a); **Malé Karpaty Mts.**: Plavecká (KOVÁČ et al. 2005a, 2014); **Muráň Plateau**: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Studňa, Veľká lúka Sinkhole, Zlatnica (GULIČKA 1985); **Slovak Karst**: Bezodná Ice Cave, Bobková, Brzotínska, Gombasecká, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Kostrová, Krásnohorská, Kvapľová, Majkova, Marciho, Matilda, Milada, Silická Ice Cave, Šingliarova, Zbojnícka v Sokolej skale (GULIČKA 1985), Leontína (KOŠEL et al. 2007), Domica (PAPÁČ et al. 2014). The species is characterized as frequent coloniser of eutrophized cave environment in Slovakia (MOCK & PAPÁČ 2007; KOVÁČ et al. 2014).

Family: Agnaridae Schmidt 2003

22. *Orthometopon planum* (Budde-Lund, 1855)

Material examined: Cerová vrchovina Highlands: Nad skalným oknom, 10.xi.2006, VP (2J), Nyáryho 26.x.2006, VP (2F), 10.xi.2006, VP (1F); **Malé Karpaty Mts.**: Plavecká, 14.ix.2005, AM (1M, 1F); **Považský Inovec Mts.**: Modrovská, 16.ix.2012, AM (1F); **Revúcka vrchovina Highlands**: Praslen, 13.xii.2006, VP (1M), Veľká driénčanská, 18.1.2008, VP (1F); **Slovak Karst**: Ardovská, 1.vii.1999, TJ (1F), 22.v.1999, TJ (1F), 3.x.2002, AM (1F), 21.iv.2004, AM (1M), Čertova diera (Domica-Baradla Cave System), 1.vii.1999, TJ (1J), 21.iv.2004, AM (1M, 1F, 2J), Diviačia Chasm, 21.x.2004, AM (2F), Domica, 22.x.1999, AM (1F), 9.x.2008, AM (1M), Hrušovská, 3.v.2010, AM (3M), Leontína, 7.x.2006, VP (1F), Líščia diera (Domica-Baradla Cave System), 8.iii.2001, AM (1F, 5J), 3.iv.2003, AM (2M, 3F, 16J).

Published data: Cerová vrchovina Highlands: Nad Skalným oknom, Nyáryho, Labyrintová, Stĺpová, Šurický úkryt (PAPÁČ et al. 2009); **Malé Karpaty Mts.:** Jaskyňa nad Kameňolomom (Papáč 2018); **Slovak Karst**: Bobková, Brzotínska, Gombasecká, Kečovská, Kečovské škrapy, Kostrová, Kvapľová, Marciho, Maštaľná, Milada, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (GULIČKA 1985), Domica (PAPÁČ et al. 2014). Marked as frequent on the walls of cave entrances in Slovakia (MOCK & PAPÁČ 2007).

23. *Protracheoniscus politus* (Koch, 1841)

Material examined: Horehronské podolie Basin: Bystrianska, 23.x.2002, AM (1F); **Kozie chrbty Mts.**: Važecká, 24.x.2002, AM (1F), Zápoľná, 22.vi.2015, AM (1F); **Muráň Plateau**: Studňa, 19.ix.1971, JG (2F), 24.viii.1973, JG (1F), 20.vi.1974, JG (1M), 28.ix.1974, JG (1M, 5F), 19.xi.1975, JG (1F), Šingliarka, 20.6.1974, JG (1M, 4F); **Slovak Karst**: Na Kečovských lúkach, 1958, JG (2M, 2F), Stará brzotínska, 1.x.2009–12.iv.2010, ĽK (1M); **Slovak Paradise**: Dobšinská Ice Cave, 23.v.1958, JG (1F, 4J); Veľká Fatra Mts.: Harmanecká 4.v.–12.x.2002, ĽK (1F); **Volovské vrchy Mts.**: Kolónia 2, 2.iii.2011, AM (1J); **Zvolen Basin**: Feďova, 3.iv.2015, AM (2F, 1J), Oravecká vyvieračka, 26.5.-10.9.2015, AM (1M, 1F), 9.iv.2015, VP (4M, 4F, 8J), Ponická, 8.xi.2007, AM (1M, 5F).

Published data: Čierna hora Mts.: Antonova, Bokšov rock, Hadia, Komín nad Previsovou, Kysacká, Malá kvapľová, Puklinová v Pečipalke, Zákrutová (MOCK et al. 2009; RENDOŠ et al. 2016); **Horehronské podolie Basin**: Bystrianska (MOCK et al. 2003); **Kozie chrbty Mts.**: Važecká (MOCK et al. 2004a), Zápoľná (VIŠŇOVSKÁ et al. 2017); **Muráň Plateau**: Bobačka, Brestová, Dlhý vrch, Studňa, Šindliarka, Zlatnica (GULIČKA 1985); **Nízke Tatry Mts.**: Malužinská (PAPÁČ et al. 2015); **Slovak Karst**: Gombasecká, Kvapľová, Majkova, Matilda, Milada, Ortováň, Silická Ice Cave, Zbojnícka v Sokolej skale (GULIČKA 1985); Majkova (PAPÁČ et al. 2006); **Slovak Paradise**: Dobšinská Ice Cave (KOVÁČ et al. 2006; PAPÁČ et al. 2020); **Veľká Fatra Mts.**: Harmanecká (Kováč et al. 2003).

Family: Porcellionidae Brandt, 1831

24. *Porcellio scaber* Latreille, 1804

No material examined.

Published data: Muráň Plateau: Brestová in Hrdzavá Valley, Dlhý vrch, Mokrá poľana, Studňa, Zlatnica; **Slovak Karst**: Ardovská, Bezodná Ice Cave, Brzotínska, Červená, Gombasecká, Kečovská, Krásnohorská, Líščia diera, Majkova, Maštaľná, Ortováň, Zbojnícka v Sokolej skale (Gulička 1985).

25. *Porcellio spinicornis* Say, 1818

Material examined: Košice Basin: Jasovská, 23.ix.1949, JG (1J); **Slovak Karst**: Silická Ice Cave, 24.ix.1949, JG (1J).

Published data: Malé Karpaty Mts.: Zbojnícka (Krištín 1977); **Muráň Plateau**: Bobačka, Brestová; **Slovak Karst**: Ardovská, Bobková, Brzotínska, Červená, Gombasecká, Hučiaca and Kunova Teplica, Kečovská, Kečovské škrapy, Kostrová, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Majkova, Maštaľná, Ortováň, Stará Domica, Zbojnícka v Sokolej skale (Gulička 1985), Domica (Papáč et al. 2014).

Family: Armadillidiidae Brandt, 1833

26. *Armadillidium opacum* (Koch, 1841)

Material examined: Slovak Karst: Na Kečovských lúkach, 16.iv.-9.ix.2010, AM (12F, 2J), Silická Ice Cave, 22.xiii.1973, JG (2J).

No published data.

27. *Armadillidium versicolor* Stein, 1859

Material examined: Hornád River Basin: Na Dreveníku Ice Cave, 16.iv.–9.ix.2010, AM (1M), 27.ix.2012, AM (2F), 11.v.–27.ix.2012, ĽK, AM (4M, 1F, 2J), Pleky, 27.ix.2012, AM (2F); **Košice Basin:** Jasovská, 23.ix.1949, JG (1F); **Slovak Karst**: Ardovská, 10.ix.1970, JG (1M, 2J), Domica, 5.x.2004, AM (3M, 6F), Silická Ice Cave, 24.ix.1949, AM (1M, 2F), 1.vi.1971, JG (3M, 1J), 22.viii.1973, JG (1M), Snežná diera, 21.xi.2005, AM (1M).

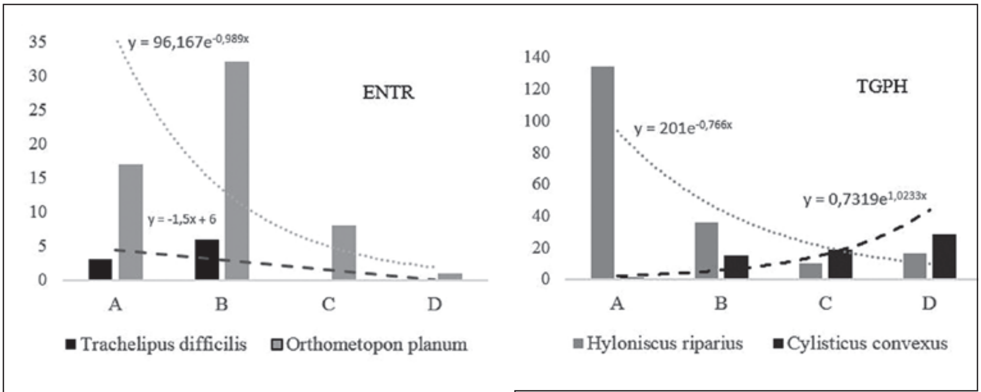
Published data: Čierna hora Mts.: Predná veľká (Mock et al. 2004b), Márnica, Predná veľká (Mock et al. 2005), Hadia, Medvedia, Predná veľká, Puklinová v Pečipalke, Zákrutová (Mock et al. 2009); **Muráň Plateau**: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Veľká lúka Sinkhole, Zlatnica; Slovak Karst: Brzotínska, Gombasecká, Havrania skala Chasm, Hučiaca and Kunova Teplica, Kečovská, Krásnohorská, Kvapľová, Marciho, Matilda, Milada, Zbojnícka v Sokolej skale (Gulička 1985), Domica (Papáč et al. 2014), Domica (Dolejš & Tuf 2018); **Slovak Paradise**: several caves without giving their names (Košel 1984).

28. *Armadillidium vulgare* (Latreille, 1804)

Material examined: Slovak Karst: Čertova diera (Domica-Baradla Cave System), 22.ix.1949, JG (2M).

Published data: Muráň Plateau: Bobačka, Brestová, Dlhý vrch, Mokrá Poľana, Zlatnica; **Slovak Karst**: Ardovská, Bezodná Ice Cave, Bobková, Brázda Chasm, Brzotínska, Čertova diera (Domica-Baradla Cave System), Červená, Hučiaca and Kunova Teplica, Kečovská, Kečovské škrapy, Kostrová, Krásnohorská, Kvapľová, Líščia diera (Domica-Baradla Cave System), Majkova, Marciho, Maštaľná, Ortováň, Stará Domica, Šingliarova, Zbojnícka v Sokolej skale, Zbojnícka (Plešivec Plateau) (Gulička 1985), Domica (Papáč et al. 2014; Dolejš & Tuf 2018).

Systematic survey of all data consists of 28 taxa in total. We examined 5658 individuals of terrestrial isopods from 25 taxa at the species level in 10 families from 434 data entries (Table 2). One specimen was identified to the family level only. Three species, *Oniscus asellus, Porcellio scaber* and *Porcellium conspersum* were not in the examined material, only previously published data were reviewed. Most of the determined individuals belong to the species *Mesoniscus graniger* (4822 inds.), followed by *Porcellium collicola* (222 inds.) and *Hyloniscus riparius* (197 inds.). *M. graniger* reached maximal values for dominance (85.2%) and constancy (69.6%) of all species. Most individuals of isopods (3289) were obtained in the Ardovská Cave in the Slovak Karst orographic unit. The sample with most individuals was from the same cave: 488 individuals of *M. graniger* were found in a trap in the Ardovská Cave in 1976. Out of the 25 species determined, 4 taxa can be described as cavernicolous or strongly preferring cave environment: *M. graniger, A.* cf. *dentiger, Trichoniscus* cf. *pygmaeus* and another undetermined blind specimen of the family Trichoniscidae.



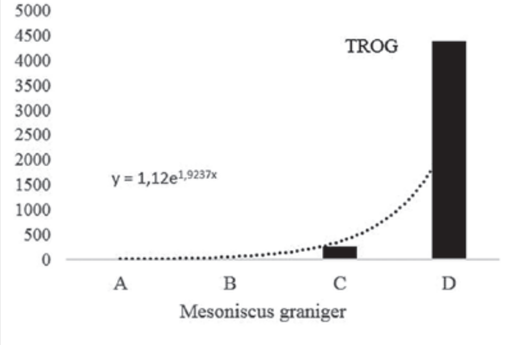


Figure 2: Distribution of three isopod groups along the outside-inside gradient. ENTR – cave entrance dwellers, TGPH – troglophiles, TROG – troglobiont – M. graniger as the only abundant cavernicolous species. A, B, C, D – cave zones, explained in the chapter Material and Methods.
Obrázok 2: Distribúcia troch ekologických skupín rovnakonôžok na gradiente povrch-vnútro jaskyne. ENTR – druhy obývajúce vchodovú časť, TGPH – troglofilné druhy, TROG – troglobiont – *M. graniger*, jediný hojný jaskynný druh. A, B, C, D – zóny v jaskyni, definované v kapitole Material and Methods.

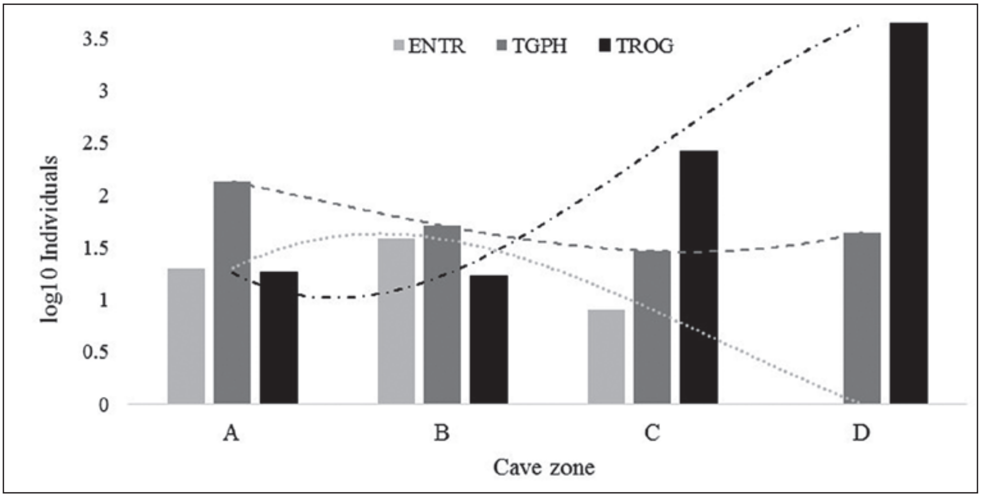


Figure 3: Spatial distribution of selected terrestrial isopod groups based on the depth gradient in the cave.
Obrázok 3: Priestorová distribúcia vybraných skupín rovnakonôžok v hĺbkovom gradiente jaskýň.

Table 2: Summary of species counts, ecological attributes values, and distribution along cave zones. M – males, F – females, juv. – juveniles, n – number of individuals, n_{caves} – number of caves in which the species was recorded, Dom (%) – dominance, Con (%) – constancy. A, B, C, D – cave zones (see Material and Methods and Figure 1).

Tabuľka 2: Prehľad získaných jedincov, ekologické charakteristiky a distribúcia rovnakonôžok pozdĺž zonácie jaskýň. M – samce, F – samice, juv – nedospelé jedince (juvenily), n – počet jedincov, n_{caves} – počet jaskýň, v ktorých bol druh nájdený, Dom (%) – dominancia, Con (%) – konštancia, A, B, C, D – jaskynné zóny (pozri kapitolu Material and Methods a Obrázok 1).

Species	M	F	juv.	n	$n_{(caves)}$	Dom (%)	Con (%)	A	B	C	D
Androniscus cf. *dentiger*			1	1	1	0,02	0,89				1
Armadillidium opacum		12	4	16	2	0,28	1,79	1	8	7	
Armadillidium versicolor	15	14	5	34	7	0,60	6,25	9	18	6	
Armadillidium vulgare	2			2	1	0,04	0,89		2		
Cylisticus convexus	24	26	14	64	12	1,13	10,71	1	15	19	28
Haplophthalmus mengii	2	14	4	20	3	0,35	2,68	15		3	2
Hyloniscus mariae	1	6		7	2	0,12	1,79	5	2		
Hyloniscus riparius	53	99	45	197	25	3,48	22,32	134	36	10	16
Hyloniscus transsilvanicus	0	2	1	3	1	0,05	0,89		3		
Lepidoniscus minutus	5	7	16	28	4	0,49	3,57	10	17		
Ligidium germanicum	3	8		11	2	0,19	1,79	10		1	
Ligidium hypnorum	13	52	12	77	5	1,36	4,46	75	1	1	
Mesoniscus graniger	1117	2134	1571	4822	78	85,22	69,64	18	17	265	4391
Orthometopon planum	10	17	26	53	13	0,94	11,61	17	32	8	1
Platyarthrus hoffmannseggii			9	9	1	0,16	0,89	9			
Porcellio spinicornis			2	2	2	0,04	1,79	2			
Porcellium collicola	59	120	43	222	8	3,92	7,14	86	155	6	1
Protracheoniscus politus	12	32	14	58	13	1,03	11,61	36	18	3	1
Trachelipus nodulosus		1	2	3	1	0,05	0,89		2	1	
Trachelipus difficilis	3	6	1	10	6	0,18	5,36	3	6		
Trachelipus rathkii	1	6		7	3	0,12	2,68	2	4	1	
Trachelipus ratzeburgii	2	4		6	2	0,11	1,79	5	1		
Trichoniscus carpaticus	1	3		4	2	0,07	1,79	4			
Trichoniscus cf. *pygmaeus*		1		1	1	0,02	0,89				1
Trichoniscidae gen. sp.		1		1	1	0,02	0,89				1
TOTAL	1323	2565	1770	5658	112	100	100	442	337	331	4443
Shannon's diversity index	-	-	-	-	-	-	-	2,14	1,9	0,9	0,08

Colonization of caves along the main environmental gradient

An evaluation of the spatial distribution along the depth gradient in caves (Table 2) groups data for 4443 terrestrial isopods, since in some samples it was not possible to obtain information about their position on gradient. The gradient begins with the zone A, representing close surroundings of cave entrances and the zone with the most intense surface-subterranean communication. This zone shows the highest diversity, with 19 sampled species, the second highest abundance of individuals, and the highest value of diversity index (2.14). Some species do not visit deeper parts of the cave than zone A, as we can see in *L. hypnorum* or *L. germanicum*. Two species, *O. planum* and *T. difficilis*, inhabit cave entrances, but they prefer deeper entrance zones with shaded stone walls (Figure 2); this is represented by zone B in our gradient model, and we refer to them as chasmatophilous, or as elements of the parietal fauna. The deeper cave parts B and C shows the decrease of species diversity (with values 1.9 and 0.9, respectively) and we can spot patterns in the terrestrial isopods exploring these zones for better conditions. This can be visible in *P. collicola.* The most abundant zone was the deepest zone D due to dense populations of *M. graniger*. On the other hand, we can see that this zone is also the least diverse in terms of number of species and diversity index value (0.08). Most species sampled in this zone were only in the form of singletons. If more individuals were sampled in this part of the cave, they were usually individuals of one species only. The ability of some species, not considered to favour cave habitats, to actively visit the deeper parts of caves (*H. riparius, C. convexus*) can be confirmed, as these species are the only ones occurring in this zone in higher numbers, aside from *M. graniger* (Figure 2). The highest affinity to aphotic cave zones was observed in *M. graniger,* with 86% of the specimens collected in the deepest aphotic zones of caves (Figure 2, Figure 3).

Sex ratio results show that in most of the sampled species, females of terrestrial isopods represent the largest portion of the assemblages. In total, 68.7% of sampled specimens were recognized as adults and females represent 45.3% of all sampled isopods (males, females and juveniles). Nevertheless, in the vast majority of species, except *A. versicolor*, *C. convexus* and *O. planum,* most of the individuals were females. A similar pattern was observed in every cave zone. The highest percentage of males and females was recorded in zone C. Juveniles were found in all cave zones, although in zone D there were only juveniles of *M. graniger.* Assessment of methodological approaches showed the pitfall trapping as the most useful method for collection of high numbers of individuals, while individual sampling covers the highest number of species. The most suitable method for collecting adults is pitfall trapping, whereas for juveniles it is the extraction method (Table 3). To sample fauna from cave zones A and B, sifting or individual sampling appears to be the most useful in terms of individuals count. To obtain the highest numbers of individuals from deeper cave zones, C and D, pitfall trapping should be used (Table 3). Males, females and juveniles of *H. riparius* were collected by all used methods. Other species collected by all methods were *P. collicola* and *L. hypnorum,* but not every sex of these species was recorded by every method. The optimal methods for collecting cavernicolous terrestrial isopods are individual sampling or pitfall trapping (Table 3).

Most of the species were collected in a small number of caves, but despite that, our examined material covers a solid part of the geographical areas of Slovakia (Table 1, Figure 4). The geographical distribution of the surveyed caves is uneven. South-eastern Slovakia's richness in cave fauna is caused by many karst localities and by historical development of this land, allowing fauna migration from various sources. It appears that species which were recorded in higher counts and in deeper cave parts can be considered as the most common in caves (*C. convexus, H. riparius, O. planum*), but only *M. graniger* is cavernicolous. The occurrence of this species was confirmed in samples from 78 caves; hence, we consider

Table 3: Representation of sexes and immature individuals depending on the collection method used. M – males, F – females, J – juveniles, ∑ – total number of individuals. EX – heat extraction of substrate, IS – individual sampling, PT – pitfall traps, SF – sifting of leaf litter.
Tabuľka 3: Zastúpenie pohlaví a nedospelých jedincov v závislosti od metódy zberu. M – samce, F – samice, J – nedospelé jedince (juvenily), EX – tepelná extrakcia materiálu zo substrátu, IS – individulány zber, PT – zemné pasce, SF – presev listového opadu.

Species / Sampling	EX				IS				PT				SF				∑
	M	F	J	∑	M	F	J	∑	M	F	J	∑	M	F	J	∑	
Androniscus cf. *dentiger*							1	1									1
Armadillidium opacum										12	2	14					14
Armadillidium versicolor			2	2	10	11	1	22	5	3	2	10					34
Armadillidium vulgare					2			2									2
Cylisticus convexus			1	1	13	13	4	30	10	12	7	29					60
Haplophthalmus mengii					2	14	3	19			1	1					20
Hyloniscus mariae						6		6	1			1					7
Hyloniscus riparius	5	14	31	50	8	27	2	37	25	33	1	59	11	12	1	24	170
H. transsilvanicus						2	1	3									3
Lepidoniscus minutus						4	1	5					5	3	15	23	28
Ligidium germanicum					3	7		10		1		1					11
Ligidium hypnorum		1	6	7	9	39	6	54		1		1	1			1	63
Mesoniscus graniger					49	154	40	243	565	1081	96	1742		1		1	1986
Orthometopon planum					7	7	2	16					3	6	24	33	49
Pl. hoffmannseggii							9	9									9
Porcellio spinicornis							2	2									2
Porcellium collicola		4	7	11	1	3		4		3		3	59	110	35	204	222
Protracheoniscus politus					6	9	12	27	3	9		12	1	7	1	9	48
Trachelipus nodulosus										1		1					1
Trachelipus difficilis					2	5		7		1		1			1	1	9
Trachelipus rathkii					1	2		3		3		3					6
Trachelipus ratzeburgii					1	3		4	1	1		2					6
Trichoniscus carpaticus						1		1	1	2		3					4
T. cf. *pygmaeus*										1		1					1
Trichoniscidae gen. sp.						1		1									1
TOTAL	5	19	47	71	114	308	84	506	611	1164	109	1884	80	139	77	296	2757

it to be the most distributed terrestrial isopod living in caves in Slovakia with the north-western distributional limit of this species in Western Carpathians (Figure 5). The other three cavernicolous species, *Androniscus*.cf. *dentiger*, *Trichoniscus* cf. *pygmaeus* and an un-

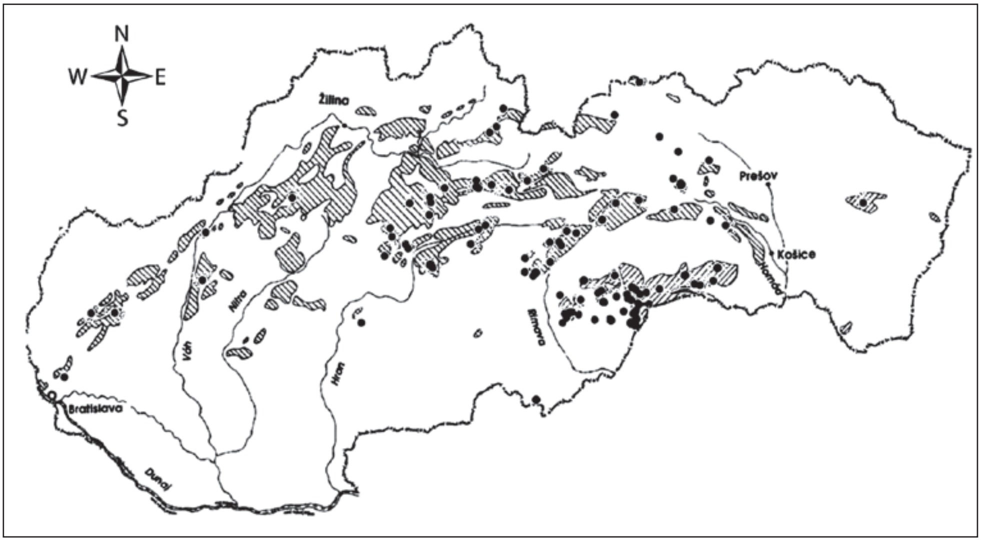


Figure 4: Map of karst areas of Slovakia (after Hochmuth 2008, modified) with location of caves (black dots) where the examined material was collected.
Obrázok 4: Mapa krasových území Slovenska (podľa Hochmutha 2008, upravené) s polohou jaskýň (čierne body), z ktorých pochádzal skúmaný materiál rovnakonôžok.

determined blind species of the Trichoniscidae family were sampled in each case in only one cave (Figure 6) and in one specimen (subadult or adult female). It does not allow a more accurate species determination or a deeper analysis of their geographical distribution or the preference for cave microhabitats and estimation of their abundance. It has not yet been possible to collect more individuals, although two of the localities have been visited repeatedly (Domica, Ponická caves); the third site (Leontína Cave) is inaccessible because its

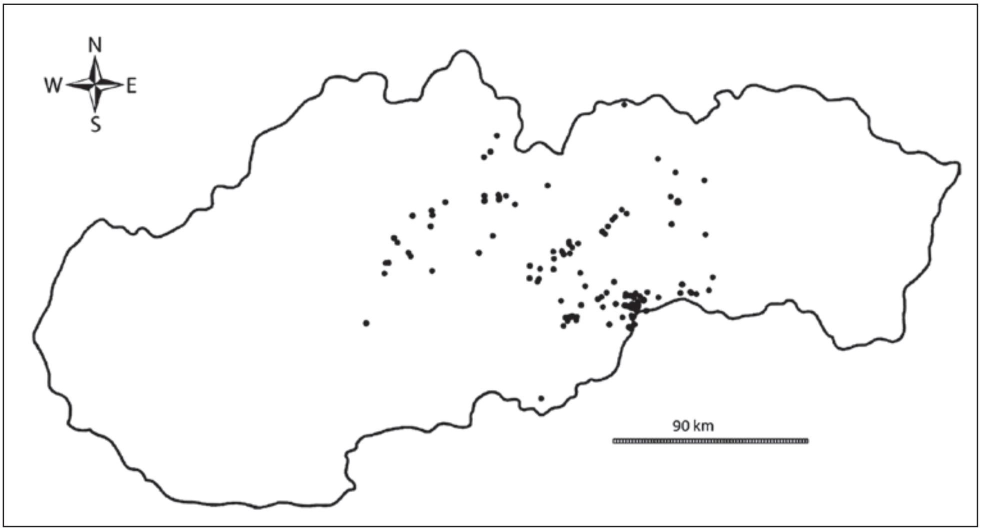


Figure 5: Distribution of Mesoniscus graniger *in caves of Slovakia. Dots are depicting published and new data (78 caves).*
Obrázok 5: Rozšírenie *Mesoniscus graniger* v jaskyniach na Slovensku. Body označujú publikované aj nové údaje (spolu 78 jaskýň).

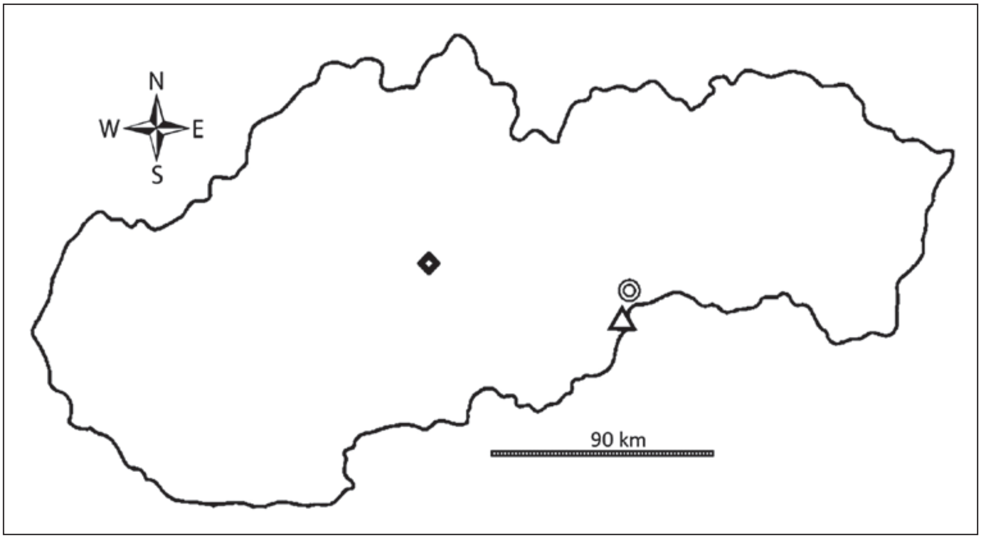


Figure 6: Locations of caves where other species with a close relationship to the cave environment were sampled: Circle – Trichoniscidae gen. sp. (blind), square – Androniscus *cf.* dentiger, *triangle –* Trichoniscus *cf.* pygmaeus.
Obrázok 6: Poloha jaskýň, kde boli zaznamenané rovnakonôžky s tesným vzťahom k podzemnému prostrediu: Krúžok – Trichoniscidae gen. sp. (slepý), štvorec – *Androniscus* cf. *dentiger,* trojuholník – *Trichoniscus* cf. *pygmaeus.*

entrance is in an active quarry and, in addition, it is closed by a pile of stone rubble.

DISCUSSION

Until today, there was only partial knowledge about cave colonisation by terrestrial isopods in the north-western part of Carpathians; they have focused mainly on the distribution of the blind depigmented species, *M. graniger* (Mlejnek & Ducháč 2001, 2003; Košel 2009, 2012), other papers carried faunal inventory of several caves. Preliminary attempts to synthesize existing knowledge about the whole fauna of terrestrial isopods in Slovak caves can be found in 2 published sources (Mock & Papáč 2007; Kováč et al. 2014). Such data were insufficient for comprehensive insight into this topic. Detailed long-term field research focused on terrestrial invertebrates from the shallow underground of forested screes and from caves of the Western Carpathians offers us an integrated picture of how terrestrial isopods have recently been colonizing the underground and an opportunity to analyse and compare different environment types. A comparison of forested scree slope fauna (Rendoš et al. 2016; Rudy et al. 2018) revealed similarities in species composition, when 10 out of 11 species occurring in scree slope underground were also recorded in caves. *C. convexus* was not recorded by Rudy et al. (2018), but numerous occurrences of this species in stony screes were confirmed by Tuf et al. (2008) in the Czech Republic, where it was the dominant terrestrial isopod species. Another similarity is the dominance of *M. graniger* in both habitats. These two habitats are considered closely connected, because scree is often found above the caves (Rendoš et al. 2016). Active migration of terrestrial isopods between these two habitats has not yet been confirmed.

Cave diversity of terrestrial isopods in the Carpathians is generally low. Decrease of species diversity of cavernicolous isopods can be observed from the south-east towards the north and west, which is the distributional limit of some species and we can say that the western part of the Carpathians is absent of cavernicolous species. Caves in the Western Carpathians are not rich in isopod troglobionts compared to the southern parts of the Carpathian massif in Romania (Mock et al. 2007; Christian & Spötl 2010; Tabacaru &

Giurginca 2013; Kocot-Zalewska & Domagała 2020). The caves in our survey have been surveyed for fauna repeatedly. We can state that the Slovak cave environment, especially deeper zones, is rarely colonized by soil-dwelling species. The phenomenon of low terrestrial isopod diversity in caves can be observed worldwide (Culver & Sket 2000; Zagorodnik & Vargovich 2004; Beron et al. 2004; Tuf et al. 2008; Bedek et al. 2011; Tabacaru & Giurginca 2013; Reboleira et al. 2015; Taiti & Montesanto 2018).

One of the terrestrial isopod families favouring moist habitats is the family Trichoniscidae. Out of the 16 known terrestrial isopod families, Trichoniscidae gathers the largest number of subterranean species (Taiti 2004). Predisposition to life in the cave environment is observable in species of this family, reaching small body sizes leading to higher water evaporation, they also favour constantly moist, shaded habitats, and together with the family Mesoniscidae, Trichoniscidae are predisposed for cave colonisation by weak regulation of water balance and non-ideal breathing on soil surface (Frankenberger 1959). Most of the species in our samples belongs to the Trichoniscidae family.

Species in the families Trachelipodidae, Agnaridae and Philosciidae represent epigean terrestrial isopods well adapted to life in forest topsoil with fallen leaves and other organic material to process (Hornung 2011; Vilisics et al. 2011; Alexiou & Sfenthourakis 2013; Tajovský et al. 2018). Most species of these families can be described as trogloxenes, or troglophiles at the utmost.

Species of family Ligiidae, living optionally amphibious life in the proximity of streams (Frankenberger 1959), can move to caves searching for moisture in drier periods or environments. Only *T. difficilis,* a rare Carpathian endemite (Vilisics et al. 2011), is known for its affinity to cave entrances and shaded cave walls. *O. planum* and *P. politus* appear to favour cave entrances, because despite being found in many caves, they were rarely found deeper than zone B.

P. hoffmannseggii from the family Platyarthridae occurred in one cave and only juveniles were recorded. The highest probability of collecting this myrmecophilous species is at cave entrances, which are not directly affected by rain and in ideal conditions can be warmer than the proximal environment, so ants can be found there. In general, *P. hoffmannseggii* is not expected to be found in caves. We can describe this species as a myrmecophilous trogloxene, despite anophtalmia and the absence of pigment.

Member of Cylisticidae family, *C. convexus,* represents one of the most euryvalent species in our list. This cosmopolitan species is well known from a variety of environments. It can be found in synanthropic habitats (Korsós et al. 2002), sinkholes (Giurginca & Ćurčić 2003), shallow subterranean habitats possibly interconnected with caves (Tuf et al. 2008) and caves (Tabacaru & Giurginca 2013). Our data supports the classification of this species as a subtroglophile, and it reached the second highest count of individuals in the deepest cave zone D.

The families Armadillidiidae and Porcellionidae favour the stony calcareous environments of cave entrances and often dwell under rocks (Vilisics & Hornung 2009; Ianc & Ferenți 2014). They are broadly distributed, but our findings of this species were not numerous. *A. versicolor* represents an epigeic species often found aggregated (Frankenberger 1959) near or directly in cave entrances (Gulička 1985).

The best-studied cavernicolous terrestrial isopod of Slovakia is *M. graniger* of the family Mesoniscidae. The Western Carpathians are the north and north-western distributional limits of the species, and our results detail previous data on the distribution of this species (Mlejnek & Ducháč 2001, 2003; Piksa & Farkas 2007; Košel 2009, 2012). The westernmost finding of *M. graniger* in the Western Carpathians is in two volcanic massifs, the Štiavnické vrchy Mts. and the Kremnické vrchy Mts. Being among the main troglobiotic species, not only in Slovakia, it gets a lot of scientific attention. The ecology, morphology, anatomy, distribution, and life cycle of this species has been studied very thoroughly (Gruner & Tabacaru 1963; Gere 1970; Gulička 1985; Šustr et al. 2005, 2009; Košel 2012; Giurginca et al. 2015; Smrž et al. 2015; Giurginca et al. 2016; Derbák et al. 2018; Rendoš et al. 2019). After many different classifications and multiple occasions of endogean occurrence of this species (Mlejnek & Ducháč 2003), we consider it as a troglophilous terrestrial isopod with the best adaptations to the subterranean environment in Slovakia. This species forms numerous populations at localities with higher air temperatures and in caves rich in organic material. Numerous populations of *M. graniger* in deeper cave zones were often concentrated around a source of organic material on which they can feed, such as a guano heap or a place where surface water with nutrients flows into the cave. *M. graniger* represents the most abundant, dominant, and constant species in our results.

The finding of a blind, non-pigmented member of the family Trichoniscidae indicates the presence of another exclusively subterranean species whose taxonomy is still unclear. Finding of one female does not allow us to decide whether the species is not yet described, although it is very likely, due to the remote occurrence of other blind species (Taiti 2004; Tabacaru & Giurginca 2013). For collecting more specimens to realise an integrative taxonomy and description of its distribution and ecology, further field research is needed. Other field study is impossible for the time being, because the Leontína Cave, where this individual was found, is in a private quarry and its entrance is covered with rock rubble. This undetermined blind trichoniscid possesses morphological adaptations to the subterranean environment, and the findings of this species only in the Slovak Karst orographic unit may point to the endemism of this species.

A. dentiger and *T. pygmaeus* could be closely connected to the subterranean environment, as it is described in some regions of Central Europe (Orsavová & Tuf 2018). Taxonomy of the specimens found in Slovak caves is still unclear due to the absence of adult males in the collections. These two mentioned species are broadly distributed in Europe, but in Slovakia they appear to be rare and limited to just a few localities, where they create low abundant populations, and in caves only juveniles or females were collected. Individual counts of this species were very low, and we cannot be sure what caused the paucity of not only males, but individuals in general. The reasons may lie in coincidence, methodological approach, parasitic infections (Moreau & Rigaud 2000) or parthenogenetic reproduction, which is also known from other trichoniscid *T. pusillus* (Vandel 1960). The dominance of females over males in the assemblages of the cave species *M. graniger* was documented in the caves of the Western Carpathians (Hungary, Slovakia) already by Derbák et al. (2018).

Even though Gulička (1985) published the most complex overview on cave isopods in Slovakia by detailed study of the Slovak Karst and Muráň Plateau, his findings are most questionable. Based on his publication, we can not determine the exact location of each sampling, hence it is unclear if a given species was sampled in cave, cave entrance, cave surroundings, or location represents a combination of these. In addition, sampling of three species (*O. asellus, P. scaber, P. spinicornis*) in caves seems unprobable. These species favour a strongly synanthropised environments in Central Europe, which caves are not and these species have not been confirmed at sites by later studies. We assume that findings of these species near a cave environment should be possible only in caves opened to the public, with strongly modified entrances. In the time of material collection for paper of Gulička (1985), only Domica and Gombasecká caves were meeting this requirement. Another example challenging Gulička's data (1985) is the frequent occurrence of the steppe species *Trachelipus nodulosus* documented in cave entrances, many of which are located in forest complexes and the environment is rather humid, shady and cold, atypical for this species. The disappearance of this species on several of these sites may be evidence of changes in the environment in recent decades (overgrown karst pastures, etc.), but this certainly does not apply to all the mentioned sites. Based on these facts, we must question the accuracy of the published list of species by Gulička (1985).

Spatial analysis divided the examined caves into 4 interconnected zones based on the findings of the species at a given distance from the cave entrance. Cave entrances are well diversified parts of the cave ecosystem and the coexistence of higher biodiversity of terrestrial isopod species often occurs here. The reason is the highest availability of food resources, since cave entrances are most linked to the surface, from where decaying organic material from plants and animals comes (Venarsky & Huntsman 2018). The highest numbers of species were sampled in zone A (19 species). We cannot say which species are tied to these spaces permanently, since we can find many of those in soils or in the proximity of cave entrances, the microclimate of which is not affected by the caves.

Species, which showed affinity for the deeper parts of cave entrances (zone B), are *O. planum* and *T. difficilis.* We follow Gulička (1985), who named this group of species chasmatophilous, favouring shady rock crevices and cave entrances, after a similar term used in botany. The first mentioned species can be found under the rocks, in leaf litter or at the cave entrance walls, and sampling this species in the deep part of a cave is quite coincidental. The second above mentioned species was found solely on the shaded cave entrance walls at higher elevations, no deeper than zone B.

In addition to the previously mentioned species inhabiting deeper cave zones, two other epigean species can spend a significant part of the life cycle in caves. *H. riparius* and *C. convexus,* both considerably mobile and vagile (Norden 2008; Hornung et al. 2015), counting numerous records from zones C and D in caves with a higher level of eutrophication, frequently temporarily colonise hypogeic spaces. We have no clear evidence they reproduce there, but at sites with nutritious and lasting food sources it can be expected. It should be noted that *C. convexus* is primarily dweller of various epigean habitats (Frankenberger 1959; Orsavová & Tuf 2018), so the indication given by sample set (Figure 2), that deeper in the cave we can find more individuals of these species than in subsurface zone, is inaccurate consequence of field work: the biospeleologists have focused primarily on the deeper sections of caves during field work.

The most often sampled species, *M. graniger,* inhabited all the zones mentioned by spatial analysis with clear preference of deeper stabile climatic zone of caves (Figure 2) and screes (Rudy et al. 2018). The findings of pregnant fe-

Figure 8: Two terrestrial isopods colonising Slovak caves. Left: cave entrance inhabitant Trachelipus difficilis *(foto: Andrej Mock), right: caverincolous species* Mesoniscus graniger *(Photo: Andrej Mock, Peter Ľuptáčik)*
Obrázok 8: Dva druhy rovnakonôžok charakteristické pre jaskyne na Slovensku. Vľavo *Trachelipus difficilis*, osídľujúci skalné steny vstupných častí jaskýň (foto: Andrej Mock), vpravo: kavernikolný druh *Mesoniscus graniger* (foto: Andrej Mock, Peter Ľuptáčik).

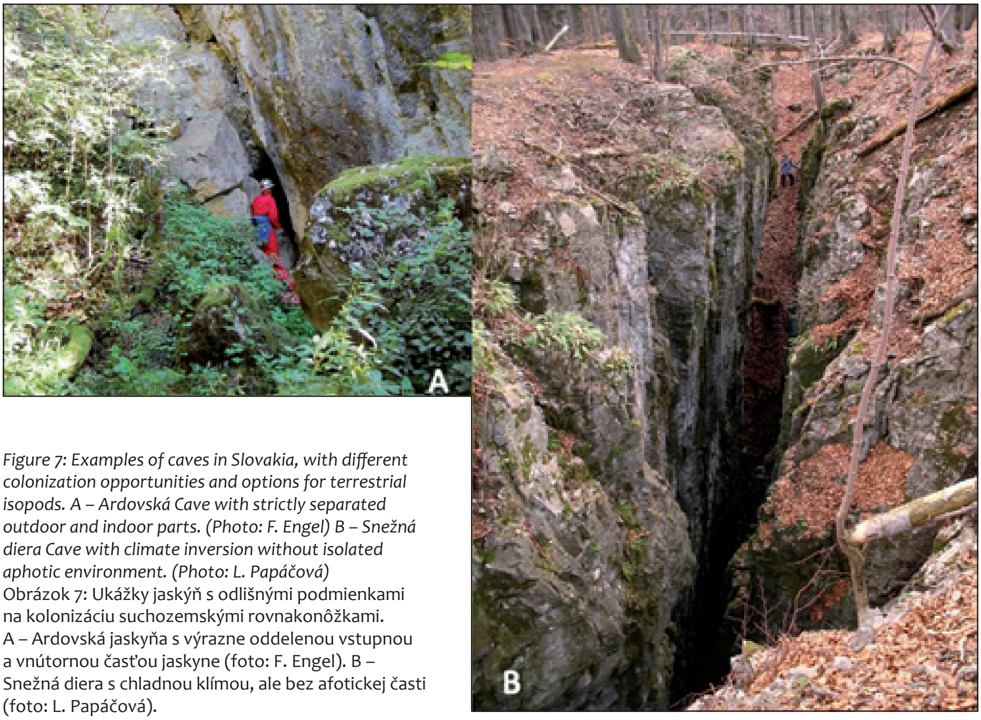


Figure 7: Examples of caves in Slovakia, with different colonization opportunities and options for terrestrial isopods. A – Ardovská Cave with strictly separated outdoor and indoor parts. (Photo: F. Engel) B – Snežná diera Cave with climate inversion without isolated aphotic environment. (Photo: L. Papáčová)
Obrázok 7: Ukážky jaskýň s odlišnými podmienkami na kolonizáciu suchozemskými rovnakonôžkami. A – Ardovská jaskyňa s výrazne oddelenou vstupnou a vnútornou časťou jaskyne (foto: F. Engel). B – Snežná diera s chladnou klímou, ale bez afotickej časti (foto: L. Papáčová).

males and juveniles of this species confirmed reproduction in the cave environment. We counted only 18 ovigerous females (0.83 % of all adult females in the dataset) in the 5 samples, obtained in spring (March) or summer (July). Ovigerous females were individually sampled under stones, pieces of wood and deeper in a cave sediment; none was trapped. We presume that females spend the period of pregnancy deeper in the substrate. The females had a small number of offspring in the marsupium, up to a maximum of 8 mancas, which is slightly more than the 3-5 recorded by Derbák et al. (2018). This species formed numerous populations on cave floors in zone D, but at higher elevations, it was found in less abundant assemblages, inhabiting deeper parts of soil sediments in zone B or C. To sample more individuals from these zones, where the substratum appears to be stony, individual sampling from under rocks is needed.

CONCLUSIONS

A summary of all published and unpublished materials on terrestrial isopods from Slovak caves revealed a considerable amount of scientific potential. It showed that caves can be a suitable environment for some terrestrial isopod species, even if conditions around the cave are not very satisfactory for them. Here we can mention *C. convexus* or *H. riparius.* Numerous occurrences of small individual counts show us that most species move to the deep cave zones sporadically. Among almost half of the known species in Slovakia and omitting only one family of autochthonous terrestrial isopod fauna (Oniscidae), we found faunistically interesting species such as *A. opacum, A.* cf. *dentiger*, *H. mariae, H. transsilvanicus* or *T.* cf. *pygmaeus.* Species fully adapted to deep aphotic cave zones are *M. graniger* and one species of the Trichoniscidae family. The former species is a very well-known and studied, it was in the spotlight of cave fauna research for many years. Findings of the other mentioned species encourage us to broaden our focus on systematic cognition of caves, which may unveil new data.

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