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Cave Size Doesn't Matter but Persistence and Sampling Techniques Do—Rich Cave-Dwelling Fauna Revealed in the Epikarstic Velika Pasica Cave (Slovenia, Europe)

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Abstract

Velika Pasica cave is situated in central Slovenia (Europe); it is 105 m long and 12 m deep, at an elevation of 670 m, and only has a 2–7 m thick roof and four permanent trickles from the epikarst zone. The second troglobiotic beetle, *Anophthalmus hirtus* Sturm, 1853, was described in this cave, twenty years after the first species, *Leptodirus hochenwartii* Schmidt, 1832, was described from Postojnska Jama cave (Slovenia). In the following decades, nine more terrestrial species and subspecies were described from Velika Pasica cave, which belong to the Mollusca, Pseudoscorpiones, Collembola and Coleoptera groups. After 2000, intensive research of the pools and trickles revealed an abundance of aquatic fauna, resulting in the description of four new species of Copepoda and two not yet determined epibiotic protozoans. A complete list of the terrestrial and aquatic fauna in Velika Pasica cave has never been published. To fill this gap, data from the literature and from intensive field work are presented here. To date, 89 terrestrial and 36 aquatic taxa have been recorded from the cave and the adjacent temporary spring and reservoir. Twenty-nine aquatic (including two epibionts) and 18 terrestrial species are strict cave-dwelling organisms. Thus, Velika Pasica cave ranks among the top global subterranean hotspots for species richness.

Keywords: troglobionts; stygobionts; biodiversity; epikarst; habitats; endemics; ecology; subterranean hotspots

1. Introduction

Velika Pasica cave (hereafter Velika Pasica) is registered in the Slovene Cave Cadastre as No. 75. It is located next to the village of Gornji Ig, which is 15 km south of Ljubljana (capital of Slovenia) at an elevation of 670 m in the Krim Massif (Figure 1). The massif is part of the NW Dinaric karstic region. The cave is in intensively dolomitized Jurassic limestone [1,2]. Hydrologically, it is considered a dry cave with no permanent water flow [3].

The most recent studies on the hydrogeological age of Velika Pasica cave revealed that the very first galleries formed more than five million years ago, at an elevation of about 300 m a. s. l. Since that time, tectonic up-lift has raised it to the present-day elevation, which was reached about 1.8 million years ago. At that time and during the Pleistocene period, there was active water flow through the cave, which alternatively filled and eroded older galleries while forming new ones. Active water flow stopped during the late Pleistocene

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about 40,000 years ago when the hydrologically active cave turned into a fossil cave [4]. Along with the geological up-lift, deep valleys (up to 300 m deep) formed as a result of the erosion by two local rivers, the Iška and Borovniščica, and the Krim Massif became a kind of "biological island" separated from nearby areas hydrologically as well as by tectonic fractures, which is reflected in the several subterranean stenoendemic taxa confined to the Krim Massif [3,5].

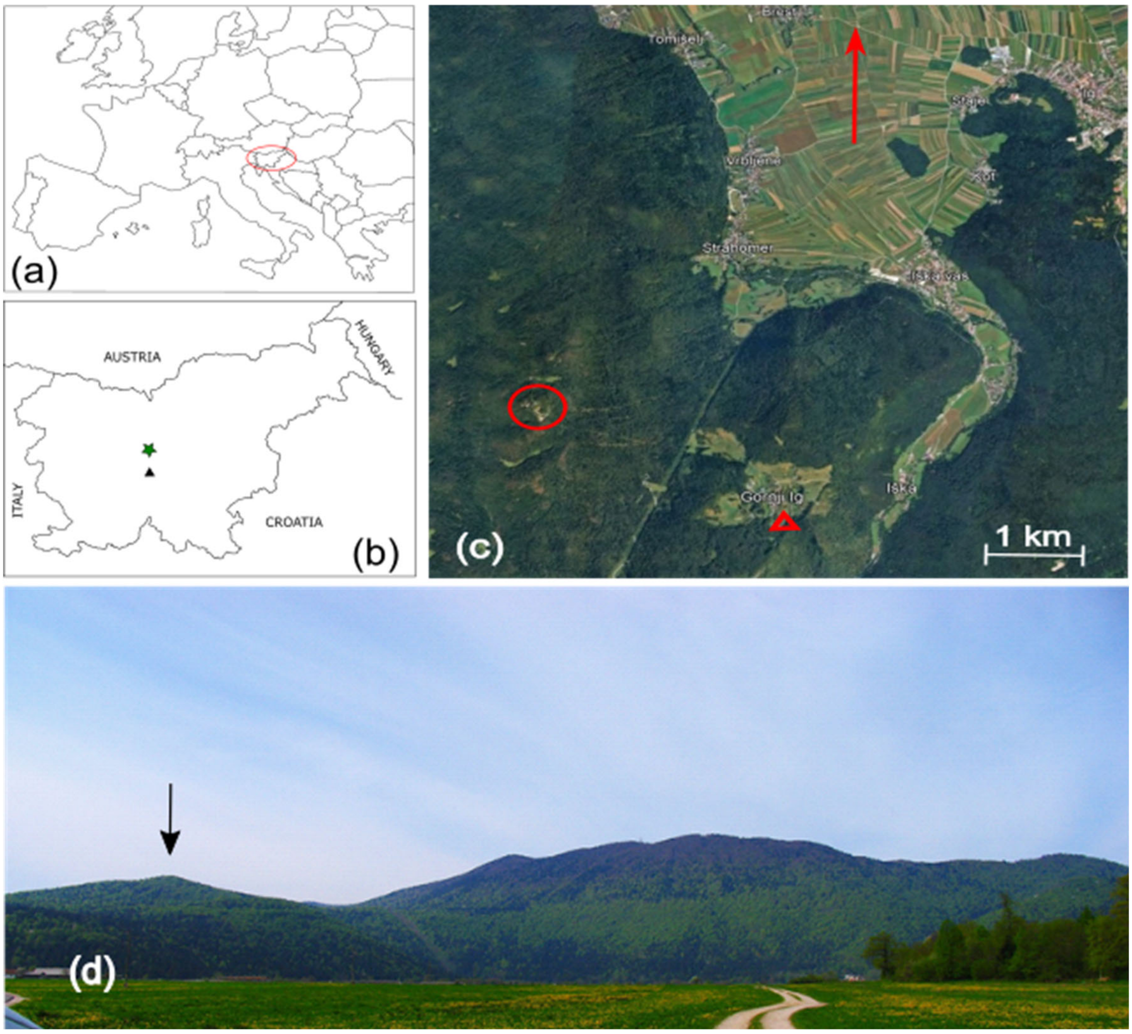

Figure 1. (**a**) Map of Europe showing location of Slovenia (red ellipse). (**b**) Map of Slovenia: pentagram—Ljubljana (capital), triangle—Velika Pasica. (**c**) Detailed position of Velika Pasica: triangle—entrance to the cave; circle—Krim Mt. (1107 m high); arrow—direction toward Ljubljana (capital) (after Google Earth). (**d**) Panoramic view of the Krim Massif; arrow indicates the cave location (photo: A. Brancelj).

In 1831, Luka Čeč, a cave guide, found the first identified troglobiotic beetle in Postojnska Jama cave (known as Adelsberg Grotte at that time). The beetle was described in the next year as *Leptodirus hochenwartii* Schmidt, 1832. In 1847, more specimens of *Leptodirus* were found in the cave. In the same period, more troglobiotic/stygobiotic species were described from Postojnska Jama or nearby caves, namely, amphipods (*Niphargus stygius* (Schiodte, 1847)), isopods (*Titanethes albus* (Koch, 1841)) and decapods (*Troglocaris anophthalmus* (Kollar, 1848)), as well as several terrestrial arachnids, pseudoscorpions and beetles. It was in this period that a new branch of biology, "biospeleology" (or "speleobiology"), started, with its origin in Postojna (named Adelsberg (German) at that time, which later became Postumia (Italian)) [6,7]. The discovery of cave-dwelling species in Postojnska Jama

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cave and other nearby tourist caves triggered a search for new cave-dwelling species, not only in Slovenia but worldwide.

The very first mention of cave-dwelling species was a report by Johann Weikhard von Valvasor in his book *Die Ehre dess Hertzogthums Crain* (*The Glory of the Duchy of Carniola*), which was published in 1689. He discovered it in a spring near "Laibach, Crain" (current-day Ljubljana, Slovenia) and described it as "cave dragon's offspring". At that time, it was not recognized as a strict cave-dwelling species. Later, it was described as *Proteus anguinus* by Laurenti in 1768 [8].

Among the first localities where the search for cave-dwelling animals was focused were already well-known tourist caves within an area known, at that time, as "Crain" (in German) or "Carniola" (in Italian), which is current-day central Slovenia. The tourist caves at that time were Postojnska Jama, Križna Jama, Želnjske Jame, and Jama pod Predjamskim Gradom. Velika Pasica was not a tourist cave but it attracted occasional visitors due its proximity to the capital (Ljubljana), easy access by foot (about three hours walk from the city) and being technically rather simple to enter. The first documented visitor left his signature in the most distant chamber, about 90 m from the entrance. It is signed "I. Virant 1841". Afterwards, many visitors followed him, some of whom are well-known specialists for different taxonomic groups, who added their signatures next to his [3,5].

Most visitors were probably not attracted by the natural beauty of the cave, but by the rush to discover new cave-dwelling species (troglobionts), and then to commercialize them. *Anophthalmus hirtus* Sturm, 1853, is the most sought after. This species appears to only inhabit Velika Pasica (translates to Great Dog's Cave) and some other nearby caves and is thus stenoendemic to the Krim Massif. Before the year 2000, the aquatic fauna in this cave were poorly studied. There were only records of one amphipod species (*Niphargus stygius* (Schiodte, 1847)) and one copepod species (*Speocyclops infernus* Kiefer, 1931). The situation changed later when intensive studies were conducted on percolation water and the adjacent pools that feed it [3,9].

Despite frequent visits of specialists for certain groups of terrestrial animals in the last 180 years, no comprehensive list of the taxa living in the cave has been compiled. The aim of this study is to present an up-to-date list of the terrestrial and aquatic fauna found there. All species have been already recorded in Slovenia, including descriptions of new species from the cave. Exception is *Tegenaria dalmatica* Kulczyński, 1906 which is a new member of cave-dwelling fauna in Slovenia.

2. Site Description

The cave entrance is at an elevation of 670 m (coordinates: 45°55′07.72 N, 14°29′35.19). The cave is horizontal, 105 m long and 12 m deep, with a roof that is 2–7 m thick (Figures 2–4). It is located predominantly in the epikarst zone; thus, we refer to it as an "epikarstic cave". The thickness of the soil cover above the cave does not exceed 15 cm and is interrupted by several stone outcrops. The cave is surrounded by a mixed forest where the dominant species are Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*).

The entrance into the cave is at the bottom of a 10 m deep depression (doline). It is about 1 × 1 m in cross-section, with about 2 m of passageway. The passageway extends into an entrance chamber, with a 20–30° inclination, which levels off after about 10 m of descent. The rest of the cave is a rather simple horizontal gallery, about 4 × 6 m in cross-section, which is separated into three chambers by one narrow passage and one wider passage. The narrow passage lies between the entrance chamber and the inner section, at about 30 m from the entrance, and has dimensions of 0.8 × 1 × 0.5 m (length); it is situated at the level of the gallery floor. The wider passage, with dimensions of about 2 × 2 m, is about 80 m from the entrance. Two narrow 5 m deep pits are filled with fine sediment (clay) at the bottom. The distal-most point of the cave is about two meters from the surface (Figures 2 and 3).

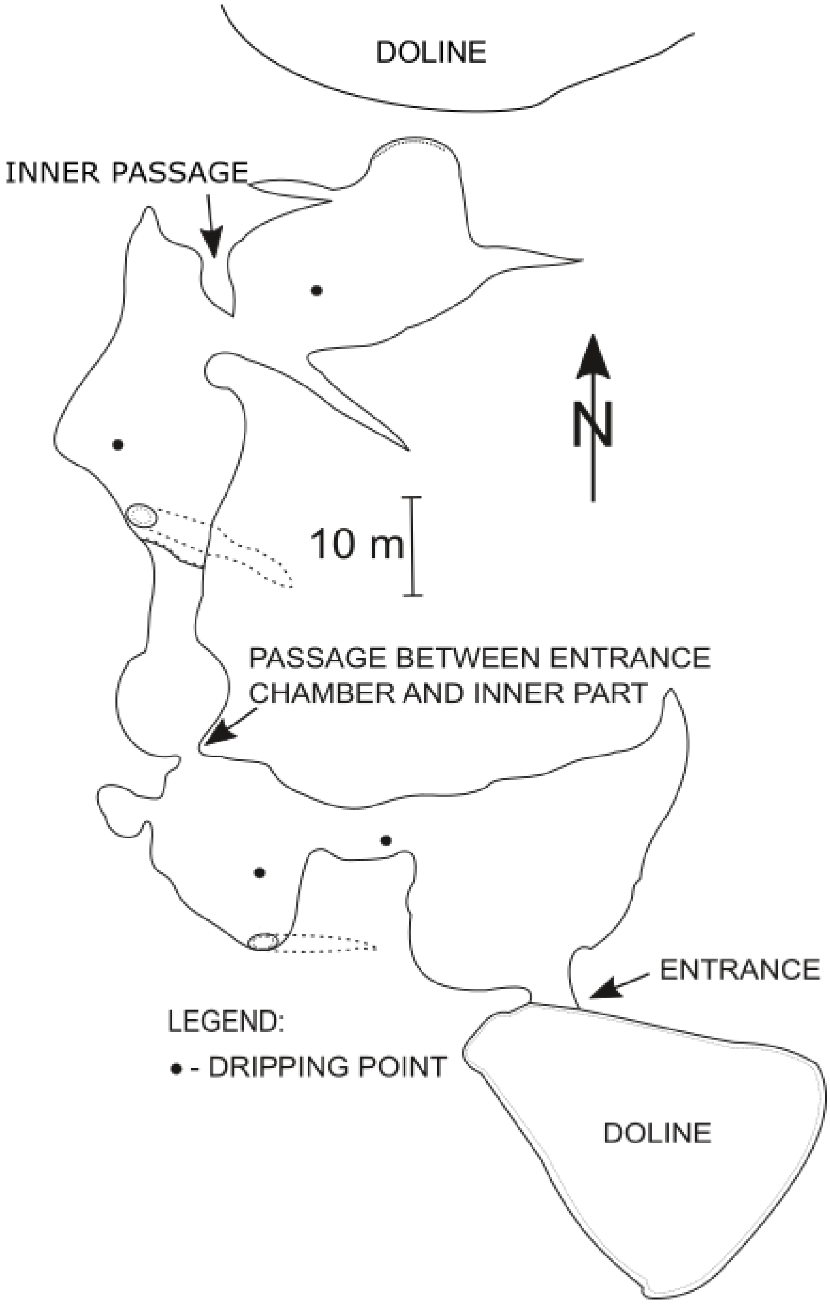

Figure 2. Map of Velika Pasica (Slovenia) (cartography: A. Brancelj and P. Dular).

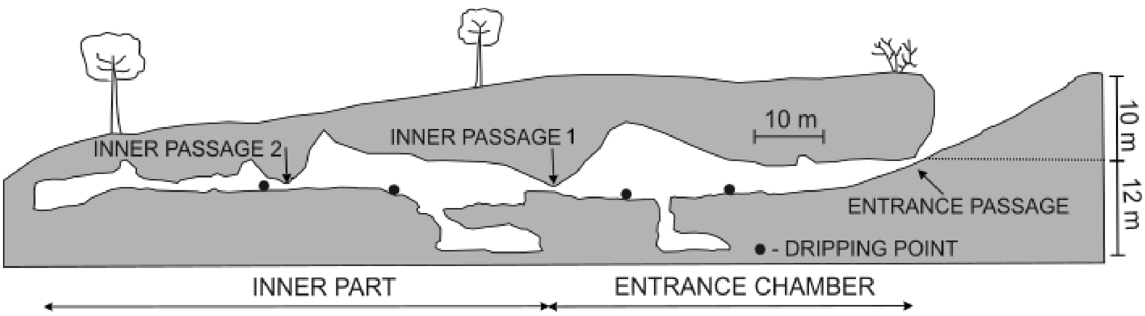

Figure 3. Cross-section of Velika Pasica (Slovenia) (cartography: A. Brancelj and P. Dular).

Figure 4. Details of Velika Pasica (Slovenia) (photos: A. Brancelj (**left**); D. Tome (**right**)).

Due to the small entrance and deep entrance depression (doline), the illuminated zone is limited to a few meters around the entrance. During winter, frozen soil and small ice formations are present a few meters into the cave near the entrance. Since the roof of the entrance room is higher than the level of the entrance, a "balloon" of relatively warm air (>8 °C) is present there all at times. The inner part of the cave is well protected, with another narrow passage preventing cold air from entering the interior parts of the cave. The temperature at the bottom of the entrance chamber (at a height of 1 m) varies between 5 and 10 °C throughout the year, while in the inner parts, it oscillates between 8 and 10 °C. For other morphometric and physical details of the cave, see [3].

Although the cave has no observable stream, there are four permanent drips of percolating water from the epikarst zone, with a discharge of a few drops per minute during the dry season to a few liters per minute during rain or snowmelt periods. During heavy rain or snowmelt, some temporary drips can appear. Drip-water fills several small puddles on the bottom of the gallery, which have a volume of a few milliliters to about ten liters of water each. Their base is covered by mud or sinter. Only few of these puddles are permanent.

Most of the percolating water from the ceiling directly infiltrates through cracks on the floor into a nearby roofed concrete reservoir with a volume of 400 m^3, which was built in 1918 and was used by local people as a water supply in the past. It was closed after 2000. The reservoir is filled with a small but permanent seepage spring. After heavy rain or snowmelt, some of the water also appears in a nearby temporary spring, which lasts only few hours or, in rare cases, days. It is located about 20 m from the reservoir and about 5 m higher. The maximal discharge of the spring (up to several tenths of a liter per second) indicates that majority of water originates from direct infiltration into the soil and the underlying geology, which is then directed as a shallow subsurface flow into the spring. The spring and reservoir are located about 150 m north and 25–30 m below the end-point of the cave on the slope of a hill [3]. The average annual precipitation is about 1400 mm, and ranged between 1064 and 2054 mm in the period of 2000–2015 [10].

3. Materials and Methods

Data and descriptions of new terrestrial species from Velika Pasica were collected from the literature (i.e., *locus typicus*) and the records of the National History Museum collection in Ljubljana.

Some non-systematic observations of larger species of trogloxenes (Opiliones, Orthoptera, Lepidoptera, and Chiroptera) present on the cave walls in the entrance chamber were made. The first observations were recorded in the winter of 2000 and several times between 2006 and 2014.

In 2017 and 2018, terrestrial fauna were collected during a survey that used pitfall traps with rotten meat as a bait. The traps were set on the floor of the cave for up to one week in monthly intervals. After inspection, the animals were released.

An intensive survey of parietal and bottom-dwelling fauna was performed in April 2019. April was selected since this is the period when hibernating species (troglophiles and trogloxenes) are still within the cave, mostly near the entrance. Over a period of two days, a three-member team made a step-by-step inventory of the 105 m long gallery from the inner part of the cave towards the entrance. Animals on the walls up to two meters in height and on the floor of the gallery were recorded. Specimens that could not be identified on-site were collected in vials and preserved in 70% alcohol. In parallel, most of the animals were photographed alive on-site.

Samples of leaf litter and soil, collected not far from the entrance, were taken out of the cave to extract the arthropods using a Berlese funnel.

Aquatic fauna were collected from small pools filled with percolating water using a pipette (samples of a few milliliters) and from larger pools using a suction pump (up to 5 L of water was collected) on several occasions between 2000 and 2014. In addition, the adjacent temporary spring and concrete reservoir were sampled twice in 2012 using a hand net and drift net.

In the period from 2006 to 2014, continuous sampling of four permanent drips within the cave was performed and data on fauna composition, water discharge, and water and air temperature were collected. Discharge and temperature data were collected using a data logger (Delta-T Device Company, Cambridge, UK) on an hourly basis. Fauna were filtered using specially designed "Brancelj" bottles attached to two outlets of an ombrometer (Figure 5). Samples were collected at approximately one-month intervals. The mesh size in all sampling equipment was 60 μm [3,11,12]. In total, about 150 sampling visits to the cave were made between 2000 and 2014.

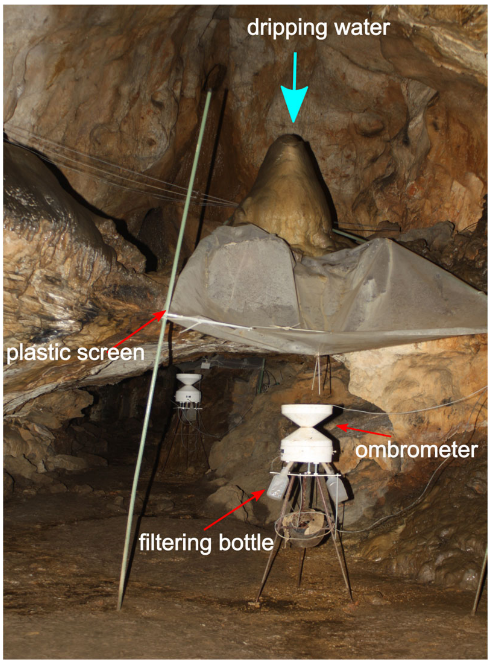

Figure 5. Sampling station used to measure discharge and water temperature and collect aquatic fauna from the epikarst (photo: A. Brancelj).

In the laboratory, the specimens were identified by the authors or sent to specialists (see list in Acknowledgements).

4. Results

4.1. Terrestrial Fauna

Eighty-nine taxa have been recorded so far from the cave. Sixty-one of them were identified to the species level (six of them labeled as cf. and two as gr.), 15 to the genus level and 13 to the family level (incl. "morphotype" categories). In the latter group, several species were tentatively included; therefore, the actual number of species is higher (Table 1, Figure 6).

Table 1. List of terrestrial fauna from Velika Pasica (Slovenia, Europe). Tb—troglobiont; Tf—troglophile; Tx—trogloxene; E—edaphic; *—described as *Zospeum spelaeum schmidti*; #—only paratype; p.o.—personal observations of the authors in the period of 2000–2019, including specialists' determination (see Acknowledgements).

Higher Taxon	Family	Species + Author	Ecological Status	Loc. Typ.	Reference
Gastropoda	Ellobiidae	*Zospeum amoenum* (Frauenfeld, 1856)	Tb	X	[13], p.o.
		Zospeum frauenfeldi (Freyer, 1855)	Tb		p.o.
		Zospeum schmidti (Frauenfeld, 1854) *	Tb	X	[14], p.o.
	Helicidae	*Helicigona (Chilostoma) illyricum* (Stabile, 1864)	Tf/E		p.o.
	Zonitidae	*Aegopis verticillus* (Lamarck, 1822)	Tf/E		p.o.
	Pristilomatidae	*Vitrea diaphana* (Studer, 1820)	Tf/E		p.o.
	Oxychilidae	*Oxychilus glaber* (Ferussac, 1822)	Tf/E		p.o.
	Gastrodontidae	*Aegopinella nitens* (Michaud, 1831)	Tf/E		p.o.
Oligochaeta	Lumbricidae	*Lumbricus terrestris* Linnaeus, 1758	E		p.o.
		Dendrobaena subrubicunda (Eisen, 1878)	Tx/E		p.o.
Isopoda	Ligiidae	*Ligidium germanicum* Verhoeff, 1901	Tx/E		p.o.
	Trachelipodidae	*Porcellium fiumanum* (Verhoeff, 1901)	Tx/E		p.o.
	Trichoniscidae	*Androniscus stygius* (Nemec, 1897)	Tb		p.o.
Diplopoda	Anthogonidae	*Acherosoma largescutatum* Strasser, 1935	Tb	X	[15], p.o.
		Haasia troglodytes (Latzel, 1884)	Tb		p.o.
	Glomeridae	*Trachysphaera costata* (Waga, 1857)	Tf/E		p.o.
	Polydesmidae	*Brachydesmus subterraneus* Heller, 1858	Tb		p.o.
Chilopoda	Lithobiidae	*Lithobius* sp.	Tx/E		p.o.
Ixodida	Ixodidae	*Ixodus vespertilionis* Koch, 1844	epiparasite on mammals		p.o.
		Ixodus cf. *ricinus* (Linnaeus, 1758)	epiparasite on mammals		p.o.
Acarina	Mesostigmata	morphotype A	Tb (?)		p.o.
		morphotype B	Tf/E		p.o.
	Oribatida	about 8 morphotypes	E		p.o.
Pseudoscorpiones	Chthoniidae	*Chthonius raridentatus* Hadži, 1930 #	Tb	X	[16]
		Globochthonius spelaeophilus (Hadži, 1930)	Tb		p.o.

Table 1. *Cont.*

Higher Taxon	Family	Species + Author	Ecological Status	Loc. Typ.	Reference
	Neobisidae	*Neobisium (Blothrus) spelaeum* (Schiödte, 1874)	Tb		p.o.
Opiliones	Phalangiidae	*Amilenus aurantiacus* Simon, 1881	Tf		p.o.
	Sironidae	*Cyphophtalmus* gr. *duricorius* Joseph, 1869	Tf		p.o.
Araneae	Agelenidae	*Tegenaria dalmatica* Kulczyński, 1906	Tf		p.o.
		Tegenaria sylvestris L. Koch, 1872	Tx		p.o.
	Dysderidae	*Harpactea lepida* (C.L. Koch, 1838)	Tf		p.o.
	Linyphiidae	*Troglohyphantes excavates* Fage, 1919	Tf		p.o.
		Troglohyphantes sp.	Tf		p.o.
	Mimetidae	*Ero* sp.	Tx		p.o.
	Nesticidae	*Kryptonesticus eremita* (Simon, 1880)	Tf		p.o.
		Nesticus cellulanus (Clerck, 1757)	Tf		p.o.
	Tetragnathidae	*Meta menardi* (Latreille, 1804)	Tf		p.o.
		Metellina merianae (Scopoli, 1763)	Tf		p.o.
Diplura	Campodeidae	*Campodea* cf. *staphylinus* Westwood, 1842	Tb		p.o.
Pauropoda	?	morphotype A	E		p.o.
Archaeognatha	?	morphotype A	E		p.o.
Collembola	Arrhopalitidae	*Pygmarrhopalites* sp.	E		p.o.
	Entomobryidae	*Lepidocyrtus* cf. *curvicollis* Bourlet, 1839	E		p.o.
		Lepidocyrtus sp.1	E		p.o.
		Pseudosinella sp.	E		p.o.
	Hypogastruridae	*Hypogastrura* cf. *boldorii* Denis, 1931	E		p.o.
	Isotomidae	*Folsomia ksenemani* Stach, 1947	E		p.o.
		Isotoma spelaea Joseph, 1882	Tb	X	[17]
		Parisostoma notabilis (Schäffer, 1896)	E		p.o.
	Neanuridae	*Bilobella* cf. *massoudi* Cassagnau, 1968	Tx/E		p.o.
		Deutonura sp.1 (n.sp.).	E		p.o.
		Friesea mirabilis gr. (Tullberg, 1871)	E		p.o.
	Neelidae	*Megalothorax* sp.	E		p.o.
	Onychiuridae	*Heteraphorura steineri* Arbea, 2014	E		p.o.
		Onychiuroides cf. *anelli* Denis, 1938	Tb		p.o.
		Protaphorura sp.	E		p.o.
	Sminthuridae	morphotype A	E		p.o.
	Tomoceridae	cf. *Tritomurus* sp.1	Tb		p.o.
Orthoptera	Rhaphidophoridae	*Troglophilus cavicola* (Kollar, 1833)	Tf		p.o.
		Troglophilus neglectus Krauss, 1879	Tf		p.o.
Trichoptera	Limnephilidae	*Limnephilus rhombicus* (Linnaeus, 1758)	Tx		p.o.
		Stenophylax permistus McLachlan, 1895	Tx		p.o.
Lepidoptera	Erebidae	*Scoliopterix libatrix* (Linnaeus, 1758)	Tf		p.o.
	Geometridae	*Triphosa dubitata* (Linnaeus, 1758)	Tf		p.o.

Table 1. *Cont.*

Higher Taxon	Family	Species + Author	Ecological Status	Loc. Typ.	Reference
Diptera	Chironomidae	Chironomidae spp.	Tx		p.o.
	Culicidae	*Culex* sp.	Tx		p.o.
	Limoniidae	*Limonia nubeculosa* Meigen, 1804	Tf		p.o.
	Mycetophilidae	Mycetophilidae sp.	Tx		p.o.
		Exechia spp.	Tx		p.o.
		Rymosia sp.	Tx		p.o.
	Phoridae	*Triphleba aptina* (Schiner, 1853)	Tb		p.o.
	Sciaridae	Sciaridae spp.	Tx		p.o.
	Trichoceridae	Trichoceridae spp.	Tx		p.o.
Coleoptera	Carabidae	*Anophthalmus hirtus* Sturm, 1853	Tb	X	[5,18], p.o.
		Anophthalmus schmidti motschulskyi Schmidt, 1860	Tb	X	[5,19]
		Typhlotrechus bilimekii hacqueti Sturm, 1853	Tf	X	[5,18]
	Curculionidae	Entiminae: Peritilini	Tx/E		p.o.
		Troglorhynchus anophthalmus Schmidt, 1854	E		[5], p.o.
	Leiodidae	*Aphaobius milleri* (F. J. Schmidt, 1855)	Tf	X	[5,20]
		Batyschia montana Schiödte, 1848	Tf		[5]
	Salpingidae	*Vincenzellus ruficollis* (Panzer, 1794)	E		p.o.
	Staphylinidae	*Bythoxenus subterraneus* Motschulsky 1858	Tb	X	[5,21]
		Othius punctulatus (Goeze, 1777)	Tx		p.o.
		Aleocharinae	Tx		p.o.
		Scydmaeninae: Scydmoraphes?	E		p.o.
Chiroptera	Rhinolophidae	*Rhinolophus ferrumequinum* (Schreber, 1774)	Tx		p.o.
		Rhinolophus hipposideros (Bechstein, 1800)	Tx		p.o.
	Vespertilionidae	*Myotis emarginatus* (Geoffroy Saint-Hilaire, 1806)	Tx		p.o.
Rodentia	Gliridae	*Glis glis* (Linnaeus, 1766)	Tx		p.o.

The list of terrestrial inhabitants spans from Gastropoda to Mammalia and includes 21 categories labeled as "higher taxon". The most common are representatives of Arthropoda, extending from terrestrial Isopoda to Coleoptera (48 families), followed by Gastropoda (six families), Mammalia (three families) and Oligochaeta (one family).

The representatives of terrestrial fauna belong to four ecological categories: edaphic species, trogloxenes, troglophiles and troglobionts [22–24]. Some species/groups were difficult to assign to an exact or only one ecological category. Twenty-four of them were determined to be edaphic (mostly Collembola), 24 are trogloxenes (with an edaphic preference), 27 are troglophiles (with an edaphic preference) and 18 are troglobionts. The troglobionts exhibit typical troglomorphic characteristics and have never been found outside of caves [25]. Two terrestrial species (Ixodida = ticks) are epiparasites, which were transported into the cave by trogloxene mammals hibernating there and could also be considered trogloxenes.

Nine species were described for the first time from this cave; therefore, it was designated as their *locus typicus* (Table 1). For one species (*Chthonius raridentatus* Hadži, 1930), the cave was designated a paratype location; the holotype was described from a nearby cave.

4.2. Aquatic Fauna

Thirty-six taxa have been recorded in the hydrologically inactive cave, adjacent temporary spring and concrete reservoir. Twenty-seven taxa were determined to the species level, five to the genus level and four to higher taxa (Table 2, Figure 7).

Figure 6. Troglobionts from Velika Pasica (Slovenia): (**a**) *Zospeum* sp.; (**b**) *Androniscus stygius*; (**c**) *Acherosoma largescutatum*; (**d**) *Brachydesmus subterraneus*; (**e**) *Globochthonius spelaeophilus*; (**f**) *Neobisium (Blothrus) spelaeum*; (**g**) *Tritomurus* sp.; (**h**) *Anophthalmus hirtus* (photos: (**b**,**d**,**h**) A. Brancelj; (**a**) T. Delić; (**c**,**e**–**g**) B. Lips).

The list of aquatic inhabitants spans from Protozoa to Crustacea (Isopoda) and includes 12 higher taxa. The most common are representatives of Crustacea (seven families), followed by Protozoa, Rotifera and Oligochaeta (two families each). Three higher taxa (Turbellaria, Gastropoda and Polychaeta) are represented by one family each, while the Nematoda representatives include several undetermined morphotypes with an unknown taxonomic position and number of families.

Table 2. List of aquatic fauna from Velika Pasica and the nearby reservoir and temporary spring (Slovenia, Europe) (modified from Brancelj [3]). Sb—stygobiont; Sf—stygophile; E—edaphic; E?—could also be edaphic; X?—probably new species/locus typicus; *—species collected only in the cave; #—collected from the epikarst during filtration period; p.o.—personal observations of the authors in the period of 2000–2019, including specialists' determination (see Acknowledgements).

Higher Taxon	Family	Species + Author	Ecological Status; Comment	Loc. Typ.	Reference
Protozoa: Cilliata	unknown	one species; undetermined	Sb; epibiont on *Maraenobiotus slovenicus*; drift from spring	X?	[3], p.o.
Protozoa: Suctoria	unknown	#one species; undetermined *	Sb; epibiont on *Morariopsis dumonti*; cave	X?	[3], p.o.
Turbellaria: Rhabdocoela	unknown	#one species; undetermined *	Sb/E?; cave	X?	[3], p.o.
Nematoda	unknown	#several morpho-species/undetermined	Sb/E?; cave		[3], p.o.
Rotifera	Adinetidae	#*Adineta gracilis* Jansen, 1893 *	Sb/E?; cave		[3], p.o.
	Habrotrichidae	#*Habrotrocha* sp.	Sb/E?; cave		[3], p.o.
Gastropoda	Hydrobiidae	*Frauenfeldia kusceri* (A. Wagner, 1914)	Sb; cave & reservoir		[3], p.o.
		Hauffenia michleri (Kuscer, 1932)	Sb; cave & reservoir		[3], p.o.
Polychaeta	Aelosomatidae	#*Aelosoma* sp. *	Sb/E?; cave		[3], p.o.
Oligochaeta	Enchytraeidae	#*Enchytraeus* gr. *Buchholzi* *	Sb/E?; cave		[3], p.o.
		#*Fridericia* sp. A *	Sb/E?; cave		[3], p.o.
		#*Fridericia* sp. B *	Sb/E?; cave		[3], p.o.
	Haplotaxidae	#*Haplotaxis gordioides* (Hartman, 1821) *	E; cave		[3], p.o.
Ostracoda	Candonidae	#*Pseudocandona albicans* (Brady, 1864)	Sb; cave & drift from spring		[3], p.o.
Copepoda: Cyclopoida	Cyclopidae	*Acanthocyclops venustus* (Norman & Scott, 1906)	Sf; reservoir & drift from spring		[3], p.o.
		Diacyclops clandestinus Kiefer, 1933	Sb; drift from spring		[3], p.o.
		Diacyclops languidoides (Lilljeborg, 1901)	Sb; drift from spring		[3], p.o.
		Graeteriella unisetigera (Graeter, 1908) *	Sb; drift from spring		[3], p.o.
		Paracyclops fimbriatus (Fischer, 1853)	Sf; reservoir		[3], p.o.
		#*Speocyclops infernus* (Kiefer, 1930)	Sb; cave & drift from spring		[3], p.o.
Copepoda: Harpacticoida	Canthocamptidae	*Bryocamptus balcanicus* (Kiefer, 1933) *	Sb; in the puddles in 2000		[3], p.o.
		#*Bryocamptus pyrenaicus* (Chappuis, 1923)	Sb; cave &, drift from spring		[3], p.o.
		Bryocamptus pygmaeus (G.O. Sars, 1862)	Sf; drift from spring		[3], p.o.
		#*Bryocamptus typhlops* (Mrazek, 1893) *	Sb; cave		[3], p.o.
		Elaphoidella cvetkae Petkovski, 1983 *	Sb; one specimen in a puddle in 2000		[3], p.o.
		#*Elaphoidella millennii* Brancelj, 2009	Sb; cave & drift from spring	X	[3,26], p.o.
		#*Elaphoidella tarmani* Brancelj, 2009 *	Sb; cave	X	[3,26], p.o.
		Epactophanes richardi Mrazek, 1893	Sf; reservoir		[3], p.o.
		Maraenobiotus slovenicus Brancelj & Karanovic, 2015	Sb; drift from spring	X	[3,27], p.o.
		#*Moraria poppei* (Mrazek, 1893)	Sb; cave & drift from spring		[3], p.o.
		#*Moraria varica* (Graeter, 1910) *	Sf; cave & drift from spring		[3], p.o.
		#*Morariopsis dumonti* Brancelj, 2000 *	Sb; cave	X	[3,28], p.o.
	Parastenocarididae	#*Parastenocaris nolli alpina* Kiefer, 1969 *	Sb; cave		[3], p.o.
	Phyllognathopoidae	*Phyllognathopus vigueri* (Maupas, 1892)	Sf/E; drift from spring		[3], p.o.
Amphipoda	Niphargidae	*Niphargus stygius* (Schiodte, 1847)	Sb; cave & the reservoir & drift from spring		[3], p.o.
Isopoda	Sphaeromatidae	*Monolistra caeca* Gerstaeker, 1856	Sb; reservoir		[3], p.o.

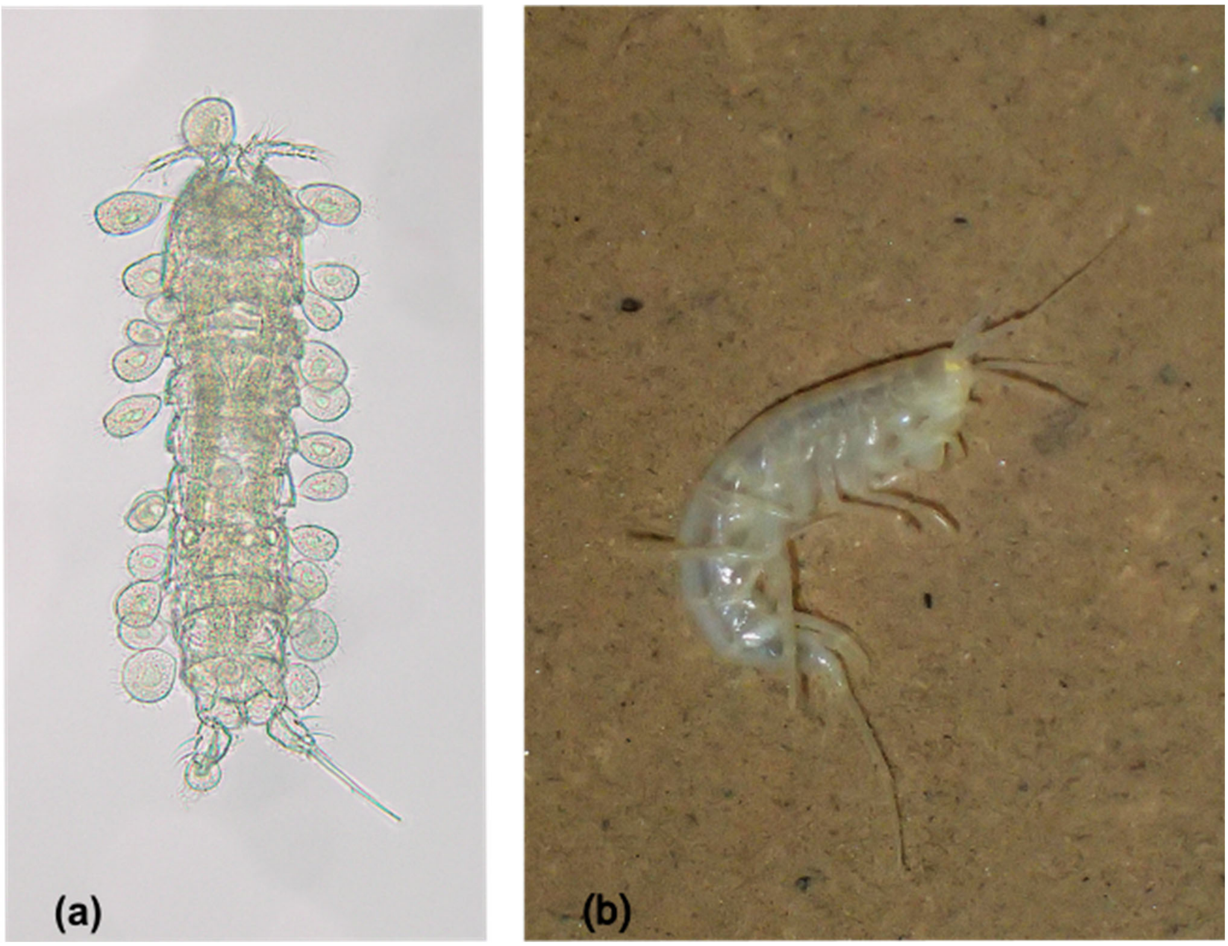

Figure 7. Stygobionts from Velika Pasica (Slovenia): (**a**) *Morariopsis dumonti* from the epikarst heavily infested with Suctoria epibionts; (**b**) *Niphargus stygius* in a muddy pool (photos: A. Brancelj).

The representatives of aquatic fauna in the cave, spring and reservoir belong to three ecological categories: edaphic species, stygophiles and stygobionts [22,23]. One of them is edaphic and five are stygophile/edaphic (?) species. Twenty-nine species including two epibionts on Copepoda are stygobionts, with most of them (22) having drifted from the tiny fractures from the epikarst. Four species (*Frauenfeldia kusceri*, *Hauffenia michleri*, *Niphargus stygius* and *Monolistra caeca*), due to their body size, are limited to the pools and reservoir.

Four aquatic species were described for the first time from this cave; therefore, it was designated as their *locus typicus* (Table 2). Three of them are only known from the cave; the fourth one was found also in the gravel bed of the Iška river, about 300 m below the cave. There are three more undetermined and undescribed species (two protozoans and one turbellarian) for which the cave could be their *locus typicus*.

4.3. Biodiversity

In total, 125 taxa have been recorded from the cave, which belong to different ecological groups. Some of them are strict epigean or edaphic species that entered the cave by accident; they were followed by two other groups that show an increasing affinity to the subterranean environment. The most specialized groups are stygobionts and troglobionts, which are represented by 47 taxa (29 stygobionts and 18 troglobionts). To date, 14 new species have been described from the cave (four stygobionts and ten troglobionts) and three more stygobionts awaiting identification (Tables 1 and 2).

At the family level, 125 species/taxa are included in 75 families. Most families only include one or two species/taxa. Among the aquatic fauna families, Canthocamptidae includes 12 species and Cyclopidae has six species. Among the terrestrial fauna families, Entomobrydae, Isotomidae, Onychiuridae, Neanuridae (members of Collembola) and Carabidae and Staphylinidae (members of Coleoptera) include three species each (Tables 1 and 2).

5. Discussion

5.1. General Comments

A complete list of terrestrial and aquatic fauna is only available for 19 caves from around the world [29,30]. The lack of more complete lists is primarily due to many of the caves being visited by specialists only once or only for a certain group. For these reasons, it is easier to find extensive lists of all troglobionts and stygobionts for a certain region or country [31–34].

Complete lists for single caves (or cave systems) are available for Europe and North America. The most intensively explored caves in Europe (designated as "subterranean biodiversity hot spots") are the Postojna-Planina Cave System (PPCS), Križna Jama, Logarček and the Šica-Krka Cave System, which are all in Slovenia. Other intensively explored caves include Vjetrenica in Bosnia and Herzegovina, Pestera de la Movile in Romania and the Mammoth Cave System in the USA [7,35–37]. The lists of cave-dwelling species for the PPCS, Križna Jama and Vjetrenica were slightly amended recently. The PPCS is now recorded as hosting 116 species (71 sytgobionts and 45 troglobionts), Križna Jama hosts 60 species (32 stygobionts and 28 troglobionts) and Vjetrenica hosts 93 species (48 stygobionts and 45 troglobionts) [7,35,36]. The Lukina Jama-Trojama Cave System in Velebit Mt. (Croatia) was discovered in 1992 and was recently added to the list of intensively studied caves. It harbors 45 species (16 stygobionts and 25 troglobionts) [38]. Cave-dwelling species are also present in the deepest cave in the world, the Krubera-Voronja Cave System (Caucasus; 2191 m deep), which harbors 16 species (2 stygobionts, 6 troglobionts) [39]. Velika Pasica harbors 47 species (29 stygobionts and 18 troglobionts), positioning it in seventh place based on the cumulative number of troglobiont and stygobiont species [29]. The most recent paper on subterranean hotspots set the criteria at as a minimum of 20 troglobiotic or stygobiotic species per cave and they must be separate ecological groups [30]. Based on these criteria, Velika Pasica only fulfills the hotspot requirements for aquatic fauna but not terrestrial fauna (though it is close).

It is worth noting that Velika Pasica is in the same 45° ridge of European hotspot caves and just below the maximum extent of Pleistocene glaciers [30]. The cave is in a zone with high primary production and mixed coniferous and deciduous forests as the dominant vegetation. It is also located in a region with a high cave density within the Dinaric part of Slovenia. In addition, within a radius of about 30 km, there are other caves with high biodiversity, including hotspot caves: the PPCS, Križna Jama and Logarček. This explains the high biodiversity recorded in Velika Pasica. In the past, the systems were interconnected but later became separated due to geological activities. Up-lift of the Krim Massif resulted in five stenoendemic species, while the rest of them are distributed elsewhere in Slovenia and Europe. Stenoendemic species could be considered "young" species (<1.8 million years old), while common species are older subterranean inhabitants.

All the above 19 listed caves, except for Pestera Movile and Velika Pasica, are complex ecosystems that have all the general cave zones. In the terrestrial part, there are the entrance, transition and inner-cave zones while in the aquatic part, there are epikarst, vadose, amphibious and phreatic zones. Each of those zones harbor many different habitats, some of which are very specific (e.g., Pestera Movile has a hypoxic atmosphere dominated by sulfuric compounds) [40–45]. The caves are long and have a roof covering that is several tens of meters thick, which supports water storage and its lowest parts reach the phreatic zone. The Mammoth Cave System is 686 km long, the PPCS is 34 km, Križna Jama is 8.3 km, Vjetrenica is 7.3 km and Logarček is 2.2 km. Lukina Jama-Trojama, which is 3.7 km long and 1431 m deep, is a system of vertical shafts with a sump at the bottom. Compared with these cave systems, the Šica-Krka Cave System (0.8 km long) and Pestera Movile (0.3 km long) are rather short. Most of the listed caves, except for the Lukina Jama-Trojama Cave System, have well-developed horizontal galleries that are organized on several levels, which are connected through short shafts. The Pestera Movile Cave has no entrance zone as it was opened artificially [42].

At only 0.1 km long, Velika Pasica has no active water flow and a thin roof and is therefore "disadvantaged" compared with large-size caves where terrestrial and aquatic zones are well developed. In the terrestrial part of Velika Pasica, all three zones exist, although at a small scale, and are comparable with other caves, while the aquatic part is truncated. The roof above the cave is only up to seven meters thick, which reduces its water storage capacity, though it does receive about 1400 mm of precipitation (rain and snow combined) annually [10]. During prolonged dry periods, drips from the ceiling cease or are significantly reduced. There are only four permanent drips and a reduced vadose zone, represented by a few permanent and/or temporary pools with a muddy or solid bottom, while permanent running water or a phreatic zone is completely absent. However, the limited amount of water supports an abundance of aquatic fauna in the cave. Most of them are epikarst stygobiotic species that permanently live in tiny fractures, voids and micropools between the surface and cave roof or they are edaphic fauna. The capillarity in the fractured dolomitized rocks retains enough water during dry periods to keep the habitat wet enough to support epikarst fauna. As a result of the tiny available space, the body size of the inhabitants rarely exceeds 0.5 mm. During increased water discharge, some of the animals are accidentally washed into small permanent or temporary pools on the gallery floor where, after some time, they die due to predation by larger species or due to the pools drying out [9]. They are representatives of "sink populations" that are unable to survive in other habitats [46].

Unlike the tiny epikarst inhabitants, *Niphargus stygius*, the only larger representative in the upper vadose zone (body size 15 mm+), can survive dry periods in wet mud. Over several observations, small pits excavated by animals were observed in the wet mud before the pools dried out, which persisted for up to two months (Brancelj, pers. observ.). During prolonged dry periods, surface layers can form deep cracks but the mud stays permanently wet. When the pools were filled again by drip water, specimens re-appeared in a few hours/days and were very active.

5.2. Distribution of Species Within the Cave

The species distribution followed a classical pattern for terrestrial fauna: torgloxenes/troglophiles near the entrance and transition zones and troglobionts in the inner zone, similar to the patterns observed elsewhere [22–24,47]. Most representatives of the terrestrial fauna were abundant in the entrance chamber, while the number of species and their abundance declined with distance from the entrance chamber. This distribution is correlated with the available energy (particulate organic matter (POM) and dissolved organic matter (DOM) contents) from microbial production [43]. Trogloxenes and troglophiles were rare after the narrow passage between entrance chamber and the inner part of the cave as POM is almost absent in these areas. Most of non-flying representatives of both groups belong to superficial subterranean habitat (SSH) communities, which are randomly distributed around entrances and shallow (i.e., epikarstic = root zone) parts of the cave [24]. Members of two trogloxene taxa (a dead adult of Trichoptera and larvae of Chironomidae) were only found on two occasions in the inner part of the cave, about 80 m from the entrance, along with a skeleton of *Rhinolophus hipposideros*.

Troglobionts were present throughout whole cave length, but most species were in the dark part of the entrance chamber. In the inner part, only *Haasia troglodytes*, *Triphleba aptina*, *Bythoxenus subterraneus* and *Anophthalmus hirtus* were present. One specimen of *Zospeum* sp. was observed only once on a wet stalagmite in the inner part of the cave. The rest of the troglobionts were only present in the entrance chamber, where more organic material (including prey) is available. The same troglobiont distribution pattern was observed in many other caves in Slovenia and elsewhere in Europe [24].

The aquatic species mostly originated from the dripping water from the epikarst and are completely dependent on microbial production. Long-term filtration of epikarst water reveals no presence of POM (>60 µm in size) [3]. Four permanent drips constantly provide a low abundance of epikarst fauna to adjacent pools. In a period 2006–2014 about 1300 specimens were collected from permanent drips. After heavy rain or snowmelt, specimens are present in small pools (few milliliters to centiliters in volume) all around the cave, which persist until the pools dry out.

Long-term observations between 2006 and 2014 revealed that four drips located 80 m apart each support a unique fauna composition. Some copepod species were present in all four drips, while others were only present in one or two. Similar observations were obtained for the other epikarst inhabitants (Protozoa, Rotifera, Oligochaeta and Ostracoda) [3]. The site-specific fauna compositions are a reflection of the ecological parameters within the epikarst, mainly void size, local water storage capacity, discharge volume and pattern, and connection with soil. Fauna from an intermittent spring, located about 150 m from the end point of the cave, indicates that there is an inaccessible vadose zone as some of the species listed in Table 2 were never recorded in the cave. However, the presence of some species from the cave drifting away from the intermittent spring indicates a direct connection between both habitats (e.g., the cave and temporary spring). All species, except for *Acanthocyclops venustus*, *Paracylops fimbriatus*, *Bryocamptus pygmaeus* and *Phyllognathopus vigueri* that were collected during spring sampling, are stygobionts.

Two larger species (>5 mm), *Niphargus stygius* and *Monolistra caeca*, were found in the reservoir. Both are common in springs, pools and streams in vadose zones in lowland caves. Their location in a hydrologically isolated area near the top of a hill at elevation of 670 m could be explained by the intensive geological activity in the area, where the Krim Massif (and the cave) was uplifted by at least 300 m in the last five million years [4]. Their populations were probably formed at lower altitudes and were afterwards uplifted and became geographically and hydrologically isolated. The presence of *Niphargus* in intermittent pools within the cave suggests not only passive downward transport of animals (as drift), but also active local migration from the reservoir and an unknown section of shallow subsurface flow upwards through small cracks. This is likely the reason why a viable *Niphargus* population exists in two intermittent pools in the cave.

5.3. Trophic Dynamics

5.3.1. Terrestrial Fauna

Food webs in some caves can be complex [48]. However, in Velika Pasica, the food web is rather simple. The majority of terrestrial fauna in the cave are bacteriophages or detritivores. They feed on decaying organic material rich in bacteria (Gastropoda, Oligochaeta, Isopoda, Diplopoda, Collembola, Acarina and Orthoptera). The top predators are represented by trogloxene Lithobiidae (*Lithobius* sp.), troglobiotic Pseudoscorpiones (*Chthonius raridentatus*, *Globochthonius spelaeophilus*, *Neobisium* (*Blothrus*) *spelaeum*), troglophile/trogloxene Araneae (with *Meta menardi* and *Metellina merianae* as the most common) and troglobiotic/troglophile/trogloxene Coleoptera (excluding Curculionidae) (Table 1). Most of predators are only present in the entrance chamber. However, some Colepotera (i.e., *Anophthalmus hirtus*) are non-selective predators that directly contact their prey like Lithobiidae, Pseudoscorpiones. They are opportunistic scavengers, too. In contrast, the Aranea representatives collect their food passively using webs and are likely dependent on trogloxene Diptera entering the cave in autumn. The two Ixodida representatives are epiparasites on Mammalia and are not directly involved in the food web within the cave.

5.3.2. Aquatic Fauna

Most of the representatives of aquatic fauna originated from the epikarst zone and are detritivores or bacteriophages. The only top predator is the omnivorous *Niphargus stygius* (Amphipoda) (Table 2). It is opportunistic predator and scavenger that feed by filtering sediment rich in biofilms (Brancelj, pers. observ.). Two epibionts on Copepoda (Ciliata and Suctoria) are (probably) not directly involved in the food web within the cave.

5.4. Interseasonal and Winter-Time Movements of Some Species

Some non-systematic observations of larger species of trogloxenes (Opiliones, Orthoptera, Lepidoptera and Chiroptera) present on the cave walls were made. The first observations were recorded in the winter period of 2000 and afterwards during intensive studies on hydrological discharge and aquatic fauna composition between May 2006 and August 2014 (in the entrance chamber only) [3].

A few Opiliones specimens were observed in the entrance chamber during the first visit to the cave in the winter of 2000, and they were absent after 2006.

Orthoptera specimens were rather common in the entrance chamber during the winters of 2000–2010 (about 200 specimens), but their population decreased afterwards (less than 100 individuals) and were almost absent in 2014. During the winter, they changed their position between consecutive observations. They were distributed individually or in small groups (up to five individuals). Adults and juveniles were present. During warmer periods, they were absent from the cave.

The two representatives of Lepidoptera (*Scoliopterix libatrix* and *Triphosa dubitata*) exhibited slightly different behavior. Specimens of both species were only present in the entrance chamber. *Scoliopterix libatrix* was rather rare in winter (about 10 specimens). They remained permanently in the same location, as confirmed by the presence of rather large drops of condensed water on their wings. In contrast, the *Triphosa dubitata* population, which occupied similar locations, was larger (about 30 specimens). The specimens probably changed their location from time to time as drops of condensed water were observed on the wings of some specimens but not others. They were distributed individually or in groups of up to three individuals. At the end of the winter, several of them were dead and covered with mold. Both species were absent in the cave during warmer periods.

A small population of bats (*Rhinolophus hipposideros* (up to ten specimens) and *R. ferrumequinum* (two specimens)) were regularly observed in the entrance chamber during winter and from time to time, they changed their locations. They were absent during the warm season. The third species, *Myotis emarginatus*, was recorded only once in the entrance chamber during winter.

The European dormouse (*Glis glis*; polh in Slovenian) was never directly observed in the cave, but several trails were observed in the entrance chamber. However, there are several small holes (from 10 × 10 cm to 20 × 10 cm) in the vicinity of the cave (called "polšna" (dormouse holes) in Slovenian). In the past, locals put traps at the mouth of the holes in October to catch them. These animals are active from late April/May to late October, feeding on buds, leaves, nuts and other seeds, but they then hibernate during winter.

Seasonal differences in terrestrial trogloxene and troglophile fauna compositions regarding invertebrates and vertebrates were observed in temperate [49] and tropical zones [50]. One of the best well-known and well-studied trogloxenes with seasonal and daily dynamics are bats. In temperate zones, they hibernate during winter, but some species use the caves for mating and raising their young [51,52].

5.5. Stenoendemic Species vs. Common Species

5.5.1. Terrestrial Fauna

Ten terrestrial species were described from Velika Pasica, but only one, *Anophtalmus hirtus*, is strictly stenoendemic to the Krim Massif. Two other species, *Acherosoma largescutatum* and *Isotoma spelaea*, could also be stenoendemic to the Krim Massif, but there is lack of data from nearby regions to confirm this. Two species, *Anophthalmus schmidti motschulskyi* and *Typhlotrechus bilimeki hacqueti*, are known from several caves in the Krim Massif and the nearby Mt. Mokrc (just across the Iška river). Another five species described from the cave have been recorded elsewhere in Slovenia and are considered endemic to Slovenia. The remaining six troglobiotic species found in the cave are also present in a few caves in Bosnia and Herzegovina. A similar distribution of stenoendemics vs. common species was observed during an extensive study of terrestrial fauna in 54 caves in Slovenia between 1977 and 2001 [24].

Three (or five) stenoendemic species likely evolved during the uplift of the Krim Massif within the last five (or 1.8) million years, while the remaining troglobites with wider distributions are descended from older fauna.

5.5.2. Aquatic Fauna

In the epikarst above the cave, each drip has a small local watershed (in the range of 100–200 m^2) where water drains vertically and lateral connections are rather limited [12,53]. This supports the hypothesis of "biological islands" within the epikarst where speciation occurs [12]. An example is the genus *Morariopsis* (Copepoda). There are three known species: *M. scotenophila* (Kiefer, 1930), which is found in several locations in western Slovenia; *M. dumonti* Brancelj, 2000, which is stenoendemic to the Krim Massif; and *M. kieferi* Petkovski, 1959, which has been found in several locations in Herzegovina [28]. The size of the *Morariopsis dumonti* population is intermediate between those of the other two species. The evolution of stenoendemic species probably resulted due to a combination of confined watersheds in the epikarst coupled with the uplift of the Krim Massif within the last five million years, which further contributed to hydrological isolation. The ancestors of either *M. scotenophila* or *M. kieferi* became "trapped" within the uplifting Krim Massif, where further speciation took place. The same could have occurred with the three other aquatic stenoendemic species: *Elaphoidella millennii*, *E. tarmani* and *Maraenobiotus slovenicus*. Apart from the stenoendemic species, there are several common species that occur in different habitats in Slovenia and across Europe that show no morphological differences compared with other populations. However, detailed genetic analyses are required to reveal the potential presence of cryptic species and lineages.

6. Conclusions

Velika Pasica has five terrestrial and aquatic stenoendemic species due to the geological activity in the area in the last five million years when uplift processes formed the Krim Massif and isolated it from the surrounding areas. The detailed knowledge on terrestrial and aquatic fauna biodiversity derives from about 180 years of speleobiological research.

Before 2000, most of the research was focused on terrestrial fauna with very little data published. After 2000, intensive study of aquatic fauna started, which revealed an abundance of fauna in the epikarst zone. Additional information on terrestrial fauna was collected during the intensive study in 2019, although no new species for science were recorded.

Although Velika Pasica is rather small and shallow, with truncated habitats, its biodiversity is comparable with the long horizontal caves located between 35–45° N (the Mammoth Cave System; the PPCS, Križna Jama, Vjetrenica) and is not affected by glaciation. Apart from geological activity resulting in five stenoendemic species in the cave (~10% of the strict cave-dwelling species), there are three additional important environmental parameters that support the cave's high biodiversity: (a) the proximity to other hotspot caves and the high local/regional density of caves and fractures, which enable some limited horizontal communication of cave-dwelling organisms within the region; (b) it is in a zone with high primary production, supported by photosynthesis (forests) and chemosynthesis (chemoautotrophic organisms); and (c) its geological structure (dolomitized Jurassic limestone) has a higher water storage capacity compared with pure limestone and can support aquatic fauna in its thin roof due in combination with its high annual precipitation.

Similar techniques and methods for studying terrestrial and larger aquatic fauna are used globally. Most studies employ pitfall traps with different types of baits, Berlese funnels and individual picking of terrestrial fauna specimens. Traps with certain types of bait, coarse nets (with mesh size > 1 mm) or individual picking are used for aquatic fauna. In most studies, fine nets with mesh size < 0.1 mm are rarely used. The result is an almost complete exclusion of important cave-dwelling fauna (Ostracoda and Copepoda), including those from the epikarst zone, which contribute significantly to aquatic biodiversity.

Once more sampling of aquatic microfauna is conducted elsewhere, Velika Pasica will lose its position among the top ten hotspot caves based on terrestrial and aquatic fauna diversity and abundance. Due to intensive studies in the past, the discovery of new cave-dwelling species is not expected unless biochemical analyses can provide new information.

In conclusion, the length of a cave is not important—it is the persistence, interest, and sample collection of specialists that allows us to obtain a detailed list of cave-dwellers and understanding of the cave's environmental parameters which support them.

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Glossary

Chemoautotrophs	A group of lower organisms (bacteria and archaea) that produce organic materials for growth and life processes through oxidation of inorganic compounds such as hydrogen sulfide or iron and magnesium compounds. They do not require solar energy for energy production.
Edaphic organisms	Terrestrial or aquatic organisms that normally live in soil but also occasionally live in leaf litter or mosses. Terrestrial edaphic organisms can survive in wet environments, while aquatic ones need some liquid water.
Epikarst	The uppermost zone of a karst, usually up to 10 m thick.
Epikarstic cave	A horizontal cave in the epikarst zone with only a thin roof a few meters in thickness.
Pleistocene	The geological period between 2.6 million and 11,700 years ago when extensive glaciation covered large parts of the northern hemisphere.
Stenoendemic species	Species restricted to small areas or even a single location (e.g., cave or spring).
Stygobiont (stygobite)	An obligatory aquatic subterranean inhabitant that feeds and reproduces underground.
Stygophile	An organism that can survive for part of its life in either subterranean or light-protected environments and can also reproduce there. They are common in sinking rivers or springs.
Troglobiont (troglobite)	An obligatory terrestrial subterranean inhabitant that feeds and reproduces underground.
Troglophile	An organism that can spent part of its life in caves and also reproduce there. Common in the entrances of caves. During warm periods, some of them feed outside during the night.
Trogloxene	An organism that can spent part of its life in caves, usually as a hibernation period in temperate zones. When they are active, they feed exclusively outside of caves.

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