

Article

The Subterranean Species of the Vjetrenica Cave System in Bosnia and Herzegovina

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Abstract: The Western Balkan's Vjetrenica Cave in southern Bosnia and Herzegovina is renowned for high richness of subterranean species. However, the data on its fauna have been published only in monographs printed in a small number of copies, making them hardly accessible to the wider scientific community. To overcome this issue, we compiled the data from published monographs with the data from our own recent field surveys. Further, as they are connected via water channels or small crevices in bedrock, we defined the Vjetrenica Cave System as a system comprising Vjetrenica and Bjelušica Caves and Lukavac Spring. Altogether, 93 troglobiotic, i.e., obligate subterranean aquatic (48) and terrestrial (45), taxa were reported for the system, verifying the Vjetrenica Cave System as the second richest locality in subterranean biodiversity in the world. The global uniqueness of the system is also reflected in the fact that as many as 40 troglobiotic species were described from the system. Finally, we reviewed the factors endangering this unique subterranean community and questioned whether it will withstand human-induced changes and pressures due to infrastructural development in southern Bosnia and Herzegovina.



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1. Introduction

The Western Balkan's Dinaric Karst is one of the global hotspots of subterranean biodiversity [1,2]. The long history of research in subterranean habitats [3] resulted in recognition of two geographically distant hotspots of species richness. The northwestern one, situated in southwestern Slovenia and northwestern Croatia, and the southeastern one, geographically settled at the territories bordering Bosnia and Herzegovina, Croatia and Montenegro [4–7]. Besides being exceptionally rich in subterranean taxa, each of the two bears its own unmistakable “crown gem” cave. While the updated subterranean species list of the northwestern gem, the Postojna-Planina Cave System (PPCS), was published fairly recently in the first special issue of *Subterranean Hotspots* [8], similar presentation of the southeastern gem, the Vjetrenica Cave, was already published 13 years ago [9]. The paper, however, did not include the species list. In addition to the paper, two extensive monographs have been published on Vjetrenica, both including data on its fauna but also paleontological and cultural heritage [10–12]. Yet, due to a limited number of copies and an outdated overview of fauna, there was a need to assemble and present the updated species list for the cave itself and the accompanying system.

In this contribution, we present the updated list of obligate subterranean taxa of the Vjetrenica Cave System, which includes not only Vjetrenica Cave but also Bjelušica Cave and Lukavac Spring; both are confirmed to be connected to Vjetrenica via water channels or crevices in bedrock. We mark the species that have been found in recent studies, and comment on dubious findings. We conclude with emphasizing the threats and conservation issues of the subterranean communities in southern Bosnia and Herzegovina.

History of Biological Studies of Vjetrenica Cave

The first document mentioning an undefined cave characterized by strong winds, similar to those occurring in Vjetrenica, was written 2000 years ago [13]. Pliny the Elder's (Plinius Senior) script mentions it in a way that it leaves us little doubt about the described cave being Vjetrenica. Archaeological artefacts demonstrate that the entrance parts of the cave were used by the poljes' settlers already in the Neolithic (7000–3000 BC) [12], while prehistoric animals, including leopards and hyenas, push its usage even further into past [14–16]. Up to 19th century, Vjetrenica was only occasionally mentioned in naturalists' manuscripts regarding Popovo Polje or the cave itself [13,17,18]. This largely changed with the annexation of modern Bosnia and Herzegovina territories, including Popovo Polje and Vjetrenica, by the Austro-Hungarian Empire (1878) [19–22]. Only a few decades before that, the first subterranean animal, *Leptodirus hochenwartii* Schmidt, 1832, from the Postojna Cave was described, and speleobiology—the biology of subterranean habitats—was born [23]. Southward extension of the empire suddenly enabled naturalists and admirers of subterranean caves to sample specialized fauna in Vjetrenica and other caves in Popovo Polje [24].

Thanks to its early recognition and proximity of the railway, Vjetrenica gained a lot of research interest in the early stages of speleobiology. By the end of the 19th and beginning of 20th century, some of the most eminent European scientists studied its fauna, transforming it into one of the most intensively sampled caves in the world [25–29]. Although preceded in sampling by K.W. Verhoeff [9], the earliest efforts to summarize its subterranean richness were made by Czech archeologist, geographer, paleontologist, and biologist Karel Absolon. Absolon [24] recognized Vjetrenica and the wider area of Popovo Polje as a hotspot of subterranean life and described some of Vjetrenica's outstanding life forms. The pace of discovery continued between the two World Wars [30–34], resulting in the cave's first species inventory by Wolf in 1937 [35]. As in other localities listed in his catalogues, Wolf did not pay attention to the "cave-adaptiveness" or ecology of animals occurring in Vjetrenica, fusing surface and subterranean taxa. Stanko Karaman [32,33,36,37] described a dozen specialized aquatic species from Vjetrenica and other caves in the vicinity, additionally emphasizing the uniqueness of area's aquatic fauna. Decades of sampling and numerous field excursions to Vjetrenica inspired Slovenian speleobiologist Boris Sket [11] to publish the first thorough overview, providing a special emphasis on troglobionts and stygobionts. In his comprehensive overview, he reported 40 stygobionts and 35 troglobionts, clearly placing Vjetrenica among the top ranked subterranean biodiversity hotspots [11,38]. Despite the exceptional results, the cave's inventory list did not stop at 75 species. Ozimec and Lučić [9] updated it and reported 101 troglobiotic species, however, without providing an actual list. The last in a series of inventories including specialists (stygobionts and troglobionts) and non-specialists (troglophiles and troglonexes) was published by Ozimec and nearly 30 collaborators [12]. Their count comprised 41 troglobionts and 55 stygobionts for a total of 96 cave-dwelling species.

During a century and a half of systematic research in the area, Vjetrenica Cave received the majority of sampling efforts [9,11,12,39]. Herein, we chose a slightly different approach. In addition to carefully evaluating and updating Vjetrenica's subterranean fauna, we compiled an inventory list by combining it with the two nearby localities, the Lukavac Spring and the Bjelušica Cave (Figures 1 and 2). The main reason for their inclusion is their historical omission from similar inventories despite the fact they naturally contribute to the Vjetrenica Cave System [11]. In 2015, a simultaneous diving expedition into Lukavac and Donja Vjetrenica (lower part of the Vjetrenica Cave) resulted in confirmation of the connectedness of the two—divers from each side met under water (G. Balasz, personal

communication). The other cave, Bjelušica, opens on a slope above the Vjetrenica Cave. It contains a small stream that disappears in the gravel floor. According to the spatial position of Bjelušica's main channel, and reappearance of the water flow in Vjetrenica's channel "Vilino gumno", we conclude that the two caves are connected (Figure 2).

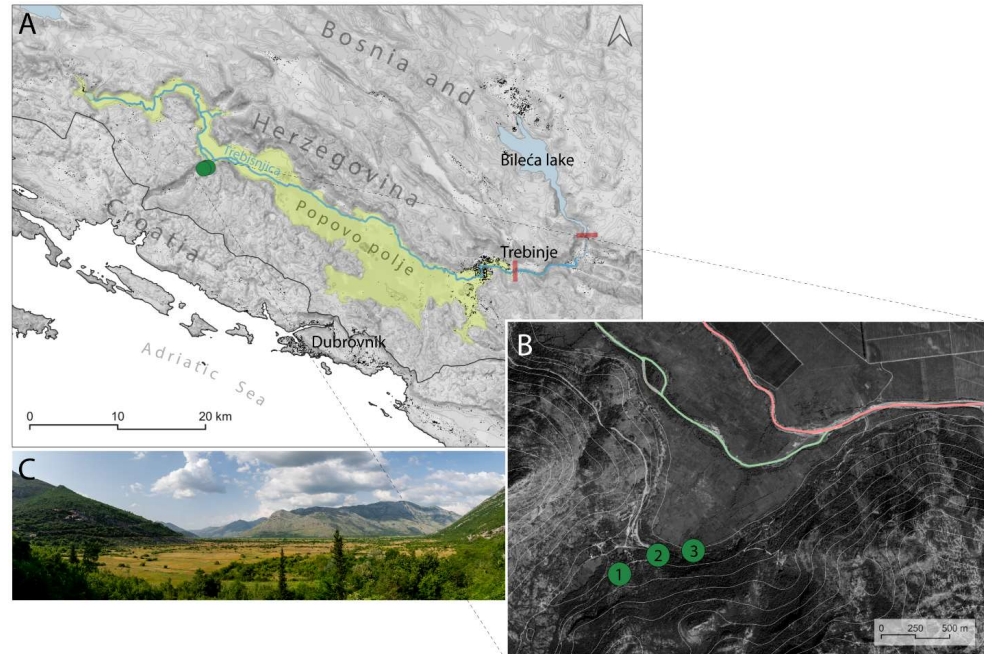


Figure 1. General position of the Vjetrenica Cave System in relation to the major landscape elements, defining the functioning of the Trebišnjica River and Popovo Polje (A). The hydropower plants Trebinje I and Trebinje II formed Bileća and Trebinje Lakes, respectively (dams marked by red lines). Downwards from the city of Trebinje, Trebišnjica is channelized on its way across Popovo Polje (presented in light green). Surface entrances to the Vjetrenica Cave System, marked in the satellite image (B), are situated in the northwestern part of the Popovo Polje; numbers refer to 1—Bjelušica Cave, 2—Vjetrenica Cave and 3—Lukavac Spring. The same image shows the natural (green) and artificial (red) course of the Trebišnjica River. View of the Popovo Polje from the Vjetrenica Cave's entrance (C) (Photo by T. Deliċ).

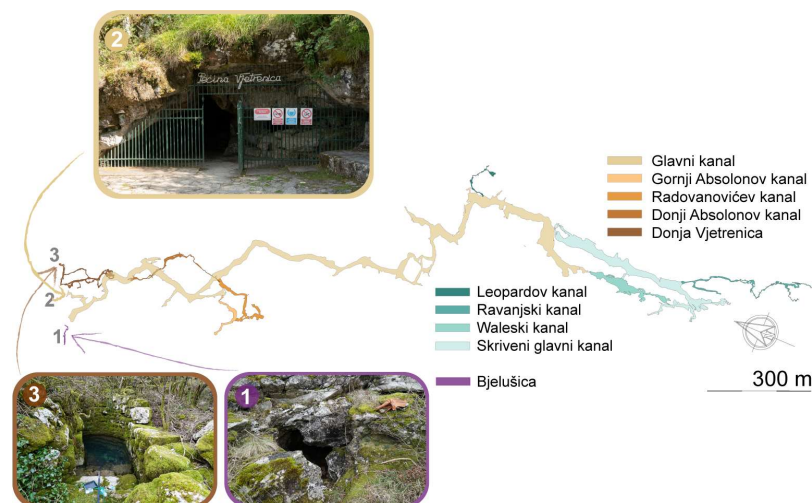


Figure 2. Three entrances to the Vjetrenica Cave System: 1—Bjelušica cave, 2—Vjetrenica cave, and 3—Lukavac spring (numbered as in Figure 1) and their relative positions on a simplified plan of the System (adapted from [12]). The main parts of the system are color coded on the right side. (Photo by E. Premate and T. Deliċ).

2. Geographical Setting and Description of the Vjetrenica Cave System

2.1. Geographic Setting

Due to its importance for the public recognition of the Dinaric Karst and the research fields of speleobiology, hydrology, and karstology [11,12,40–43], the Vjetrenica Cave System must be set into a wider context, which includes Popovo Polje and the sinking river feeding it, the Trebišnjica River. The Trebišnjica River drains from the boundary of the Black Sea and the Adriatic Sea drainages, first appearing at the surface below the ridge of Lebršnik (1985 m a.s.l.) and the area of Čemerno as the Mušnica River and its tributaries. Surface waters disappear in a series of ponors in the southwestern part of Gatačko Polje (930–950 m a.s.l.), reappear again in Cerničko (810 m a.s.l.) and Fatničko Polje (460–500 m a.s.l.), and finally occur as the Trebišnjica River in the resurgences beneath the town of Bileća. The two largest resurgences are Nikšička Vrela (325 m a.s.l.) and the now-submerged Dejanova Pečina (Dejan's Cave at 327 m a.s.l.) [44]. Before the alteration of its natural course, Trebišnjica flowed through Bilečko Polje and the city of Trebinje, across one of the largest karst poljes in the Dinaric Karst, Popovo Polje, on its way to the sinkhole Ponikva in Hutovo [45] (Figure 1). With 96.5 km of surface flow, Trebišnjica was the largest sinking river in Europe. In summers, it sank downstream from the city of Trebinje, making approximately 60 km of its flow seasonal [44]. Subterranean waters disappearing in Popovo Polje re-appear through resurgences in the Neretva River valley and a series of springs in the background of the city of Dubrovnik, the best known being the Ombla Spring (−15 m b.s.l.) [44,46].

The infrastructural works in the second half of the 20th century modified Trebišnjica's natural flow through several stages. The first stage included damming of Bilečko Polje, including the major springs of Trebišnjica, by changing it into a 20 km long artificial lake. Waters from the reservoir, which are accumulated behind a 120 m high dam, are used for the hydropower plant Trebinje I at Grančarevo (constructed between 1968–1975) [47,48]. With more than 1280 km³ of water, Bilečko Jezero (Bileća Lake) is one of the largest lakes in the Dinaric Karst. Another dam, 35 m high and accumulating waters for the hydropower plant Trebinje II, was built in 1981. Along with it, a 60 km channel in the lower portions of the Popovo Polje was built to dispatch waters to the hydropower plant Čapljina. As a side effect, the channel prevented the polje's natural flooding and enabled its agricultural exploitation [44]. Consequently, interventions have had a large impact on the surface and subterranean watercourses in the area [44,49,50], decimating the local fauna and pushing some of the narrowly endemic species to the very edge of existence [51–53].

The largest portion of the Trebišnjica runs through the 65 km long Popovo Polje, one of the largest karstic fields in the Dinaric Karst. Due to its proximity to the Adriatic Sea (only 15 km airline distance), Popovo Polje is characterized by dry winters and mild, wet summers. The mean annual air temperature is around 11.4 °C, while the mean annual precipitation is approximately 1680 mm [12,54]. Both the polje and the major geomorphological elements, including locally more than 3 km thick Mesozoic limestones, are orientated NW–SE, in the so-called Dinaric direction. Based on its surface morphology, Popovo Polje is divided in two parts: the upper and lower Trebinjska Šuma and Popovo Polje, respectively. Trebinjska Šuma (šuma meaning woods) is a highly karstified area, dipping in the southeast–northwest (275–250 m a.s.l.) direction and extending from the city of Trebinje to Poljica [12,55]. Differently from the upper part of the polje, the lower part is covered in alluvial sediments, thickening towards its northwest end and reaching up to 25 m at the lowest part of the polje (220 m a.s.l.) [56]. Before the channelization, more than 500 ponors and estavelas were present in the polje, with the most impressive one being large caves (Plitica, Baba u Strujićima, Provalija, Doljašnica, Crnulja, Žira, and Ponikva) in the polje's lower part [44].

2.2. The Vjetrenica Cave System

For a cave whose entrance is characterized by winds reaching up to 89 km/h (Roman Ozimec, personal data), there is no wonder it bears a name meaning “a windy place” in

local languages [9,10,12,23]. Similar to the polje, the Vjetrenica Cave System developed in the Mesozoic limestones, predominantly during the Cretaceous age, stretching in the NW–SE direction, and is situated in the outskirts of the Zavala Village in Popovo Polje, Bosnia and Herzegovina (42.8458, 17.9838) [55]. The whole system comprises three parts: the Vjetrenica and Bjelušica Caves and the Lukavac Spring (Figures 1 and 2).

Bjelušica (42.84538, 17.97794) is a rather simple, 80 m long cave linked to Vjetrenica by a water drip, reappearing in its “Vilino gumno” channel. Bjelušica opens on a slope westwards to Vjetrenica. Lukavac Spring (42.84646, 17.98456) lies northwards of Vjetrenica, 20 m lower than the cave’s entrance, at the level of the polje (Figures 1 and 2). Although it has been long-hypothesized to be connected to Donja Vjetrenica, this was undoubtedly confirmed only recently by cave diving (G. Balasz, personal communication). Hydrologically, Lukavac Spring presents one of the outflows from the system [57].

The main part of the system, Vjetrenica Cave, is a relatively large and complex cave [12] (Figure 2), with the main channels reaching up to a couple of tens of meters in cross-section. The last topological surveys extended its length to 7324 m, with a vertical extent of 159 m [12]. Three quarters of Vjetrenica’s length, the lowest point reaching 43 m in depth, are below the cave’s entrance. Although the extant entrance is facing into Popovo Polje at the downstream end of the cave, 1500 m into the cave, there is a drainage divide [12], with the water past it presumably flowing towards the Adriatic Sea and the Neretva valley [44]. Due to the inclination of the layers and the overall topography of the cave, it comprises numerous syphons, occasional lakes, and streams of different sizes. Three levels can be recognized in the cave [12]. The most easily reachable and the most explored is the middle level, comprising predominantly horizontal passages—Glavni kanal, Radovanovićev kanal, Gornji Absolonov kanal, Leopardov kanal, Waleski kanal, Skriveni glavni kanal, and Ravanjski kanal (Figure 2). The lowest level of Vjetrenica consists of hydrologically active or even submerged passages, including Donja Vjetrenica, Donji Absolonov kanal, and Radovanovićev kanal. The potential third level, the uppermost, which is rich in domes and chimneys, extends along the whole cave and offers potential for future speleological surveys.

3. Compiling the List of Taxa

The herein presented list derives from the recently published monograph on Vjetrenica [12], additional records from the SubBio Lab (University of Ljubljana, Slovenia), and Jozef Grego. The existing list was critically evaluated, and species with dubious or not sufficiently known sampling origin were removed from the list. To provide support for the relevancy of the listed taxa, we supplemented the list with information on the year when the animal was last collected considering the period of the last 23 years. This information was retrieved from the database *SubBioDB*, which is managed by SubBio Lab (University of Ljubljana), as well as R. Ozimec’s and J. Grego’s field notes. In addition to the overview of the species, we provide the data on the species conservation statuses at national and international levels (Table 1).

Table 1. The list of troglotrophic taxa recorded in the Vjetrenica Cave System in Bosnia and Herzegovina. Ecological classification is marked with A—aquatic and T—terrestrial. Presence of the species in a specific part of the system, i.e., V—Vjetrenica Cave, B—Bjelušica Cave, and L—Lukavac Spring, is marked with “✓”. The asterisk denotes if the cave/spring is a type locality for the respective species. The last two columns mark species conservation status: IUCN—categories according to IUCN Red List of Threatened Species; BIH—categories according to Red List of Threatened Species of Bosnia and Herzegovina. Categories refer to EN—endangered, VU—vulnerable, NT—near threatened, LC—least concern, and DD—data deficient. Data on species and the last collection year (labelled “Year” in the table) were retrieved from SubBio Lab’s database, *SubBioDB* (2023), Ozimec et al. (2021), and J. Grego (Personal communication).

Higher Group	Family	Species	A/T	Cave/Spring			Year	Red List	
				V	B	L		IUCN	BIH
Rhabdocoella	Scutariellidae	<i>Scutariella stammeri</i> Matjašič, 1958	A	✓*			/		
		<i>Stygodyticola hadzii</i> Matjašič, 1958	A	✓*			/		
		<i>Subtelsonia perianalis</i> Matjašič, 1958	A	✓			/		
		<i>Troglocaridicola spelaocaridis</i> Matjašič, 1958	A	✓			/		
		<i>Troglocaridicola capreolaria herzegovinensis</i> Matjašič, 1970	A	✓			/		
Tricladida	Geoplanidae	<i>Rhynchodemus</i> sp.	T		✓		2021		
Trematoda	Stenakridae	<i>Caudotestis protei</i> (Prudhoe, 1945) Yamaguti, 1958	A	✓*			/		
Nemertea	Prostomatidae	<i>Prostoma hercegovinense</i> Tarman, 1961	A	✓*			/		
Polychaeta	Serpulidae	<i>Marifugia cavatica</i> Absolon & Hrabe, 1930	A	✓		✓	2021		
Hirudinea	Erpobdellidae	<i>Dina absoloni</i> Johansson, 1913	A		✓*		2021		
Gastropoda	Cyclophoridae	<i>Pholeoteris euthrix</i> Sturany, 1904	T	✓	✓		2016		LC
		<i>Zospeum troglolbalcanicum</i> Absolon, 1916	T	✓			2016		
	Ellobiidae	<i>Emmericia ventricosa</i> Brusina, 1870	A			✓	/		VU
		<i>Kerkia briani</i> Rysiewska & Osikowski, 2020	A	✓		✓	2020		
	Moitessieriidae	<i>Narentiana vjetrenicae</i> Radoman, 1973	A	✓*		✓*	/		EN
		<i>Pseudammicola troglobia</i> Bole, 1961	A	✓	✓	✓	/		
		<i>Lanzaia vjetrenicae</i> Kuščer, 1933	A	✓*		✓	/		VU
		<i>Paladilhops absoloni</i> (Wagner, 1914)	A	✓		✓	/		LC
		<i>Iglicopsis butoti</i> Falniowski & Hofman, 2021	A	✓			2010		
	Orientalinidae	<i>Radomaniola montana</i> (Radoman, 1973)	A	✓		✓	/		
		Pristilomatidae	<i>Vitrea spelaea</i> (Wagner, 1914)	T	✓			2016	
	<i>Gyalina candida</i> (Wagner, 1909)		A	✓	✓		/		
	Spelaeoconchidae	<i>Spelaeoconcha paganettii polymorpha</i> Wagner, 1914	T	✓	✓*		2016		LC
		Ferussaciidae	<i>Cecilioides spelaea</i> Wagner, 1914	T	✓				
	Agardhiellidae		<i>Agardhiella biarmata</i> (O.Boettger, 1880)	T	✓				
Zonitidae		<i>Aegopis spelaesus</i> Wagner, 1914	T	✓	✓*		2016		NT
	Bivalvia	Dreissenidae	<i>Congerina kusceri</i> Bole, 1962	A	✓		✓	/	VU
Diplopoda			Glomeridellidae	<i>Typhloglomeris coeca</i> Verhoeff, 1898	T	✓	✓	✓	2014
	Julidae	<i>Typhloiulus edentulus</i> Attems, 1951		T	✓*			/	

Table 1. Cont.

Higher Group	Family	Species	A/T	Cave/Spring			Year	Red List	
				V	B	L		IUCN	BIH
Chilopoda	Polydesmidae	<i>Brachydesmus stygiovagus</i> Verhoeff, 1899	T	✓	✓		2021		
	Trichopolydesmidae	<i>Verhoeffodesmus</i> sp.	T	✓			2021		
	Lithobiidae	<i>Lithobius matulici</i> Verhoeff, 1899	T	✓		✓	2021		
		<i>Lithobius sketi</i> Matic & Darabantu, 1968	T	✓*			2021		
		<i>Eupolybothrus leostygis</i> (Verhoeff, 1899)	T		✓		/		
Palpigradi	Eukoeneriidae	<i>Eukoeneria remyi</i> Conde, 1974	T	✓*			2014		
Acari	Labidostommatidae	<i>Labidostomma longipes</i> Willmann, 1940	T	✓	✓		2020		
Opiliones	Sironidae	<i>Cyphophthalmus</i> sp.	T	✓	✓		2021		
Pseudoscorpiones	Travuniidae	<i>Travunia vjetrenicae</i> Hadži, 1933	T	✓*			2021		
	Chtonidae	<i>Chthonius occultus</i> Beier, 1939	T		✓		2013		EN
		<i>Neobisium vjetrenicae</i> Hadži, 1932	T	✓*			/		EN
		<i>Roncus anophthalmus</i> (Ellingsen, 2013)	T	✓			/		
Araneae	Dysderidae	<i>Stalagtia hercegovinensis</i> (Nosek, 1905)	T	✓*	✓		2020		
		<i>Stalitella noseki</i> Absolon & Kratochvil, 1933	T	✓*			/		
		<i>Troglohyphantes salax</i> (Kulczynski, 1914)	T	✓	✓		/		
Copepoda	Linyphiidae	<i>Kryptonesticus fagei</i> (Kratochvil, 1933)	T		✓		/		
	Nesticidae	<i>Acanthocyclops troglophilus</i> (Kiefer, 1932)	A	✓*			/		
	Cyclopidae	<i>Diacyclops charon</i> (Kiefer, 1931)	A	✓			/		
		<i>Diacyclops karamani</i> (Kiefer, 1932)	A	✓*			/		
		<i>Diacyclops tantalus</i> (Kiefer, 1937)	A	✓*			/		
		<i>Eucyclops inarmatus</i> Kiefer, 1932	A	✓*	✓		/		
		<i>Troglodiptomus sketi</i> Petkovski, 1978	A	✓			/		
Ostracoda	Diaptomidae	<i>Pseudocypridopsis hartmanni</i> Petkovski et al., 2009	A	✓*			/		
	Cyprididae	<i>Pseudocypridopsis sywulai</i> Petkovski et al., 2009	A	✓			/		
		<i>Sphaeromicola stammeri</i> Klie, 1930	A	✓			/		
Amphipoda	Entocytheridae	<i>Hadzia fragilis</i> Karaman S., 1932	A	✓*			2021		DD
	Hadziidae	<i>Niphargus hercegovinensis</i> Karaman S., 1950	A	✓			2000		DD
		<i>Niphargus kolombatovici</i> Karaman S., 1950	A	✓			2003		DD
	Niphargidae	<i>Niphargus factor</i> Karaman G. & Sket, 1990	A	✓*			2005		
		<i>Niphargus boskovici</i> Karaman S., 1952	A	✓*	✓		2021		DD
		<i>Niphargus trullipes</i> Sket, 1958	A	✓*			2021		DD
		<i>Niphargus vjetrenicensis</i> Karaman S., 1932	A	✓*		✓	2021		DD
		<i>Niphargus balcanicus</i> (Absolon, 1927)	A	✓*		✓	2021		DD

Table 1. Cont.

Higher Group	Family	Species	A/T	Cave/Spring			Year	Red List			
				V	B	L		IUCN	BIH		
Isopoda	Typhlogammaridae	<i>Niphargus coijici</i> Karaman S., 1950	A	✓			/		DD		
		<i>Niphargus zavalanus</i> Karaman S., 1950	A			✓*	/		DD		
		<i>Typhlogammarus mrazeki</i> (Schäferna, 1907)	A	✓			2021				
		<i>Proasellus hercegovinensis</i> (Karaman S., 1933)	A	✓*	✓	✓	2021				
		<i>Proasellus anophtalmus</i> (Karaman S., 1934)	A	✓	✓		/				
	Decapoda	Microparasellidae	<i>Microcharon</i> sp.	A	✓			/			
			Sphaeromatidae	<i>Monolistra hercegoviniensis</i> Absolon, 1916	A	✓*			2021		
				Trichoniscidae	<i>Alpioniscus heroldii</i> (Verhoeff, 1931)	T	✓		✓	2021	
			<i>Cyphonethes herzegowinensis</i> (Verhoeff, 1900)		T	✓	✓		2021		
			Atyidae		<i>Spelaeocaris pretneri</i> Matjašič, 1956	A	✓			2003	
<i>Spelaeocaris hercegovinensis</i> (Babić, 1922)	A	✓*			✓	2021					
Mysida	<i>Troglocaris anophthalma periadriatica</i> Jugovic et al., 2012	A		✓*		✓	2021				
	Collembola	Entomobryidae	<i>Troglomysis vjetrenicensis</i> Stammer, 1933	A	✓*		✓	2000			
<i>Verhoeffiella verdemontana</i> Lukić & Deharveng, 2018			T	✓		✓	2014				
<i>Verhoeffiella longicornis</i> (Absolon, 1900)			T	✓			2021				
Diplura Thysanura Coleoptera	Campodeidae	<i>Plusiocampa remyi</i> Condé, 1947	T	✓*			2021				
		Nicoletiidae	<i>Coletinia</i> sp.	T	✓			/			
	Carabidae		<i>Neotrechus dalmatinus dalmatinus</i> (Miller L., 1861)	T	✓	✓	✓	2021			
			<i>Scotoplanetes arenstorffianus</i> Absolon, 1913	T	✓*			2021		EN	
			<i>Adriaphaenops pretneri</i> Scheibel, 1935	T	✓*			/		EN	
	Leiodidae		<i>Neotrechus suturalis otiosus</i> (Obenberger, 1917)	T	✓	✓		/			
			<i>Speluncarius anophthalmus</i> (Reitter, 1886)	T		✓		/			
			<i>Speonesiotes schweitzeri</i> Jeannel, 1941	T	✓	✓*		2014			
			<i>Speonesiotes narentinus latitarsis</i> (Apfelbeck, 1919)	T	✓	✓		/			
		Staphylinidae	<i>Graciliella apfelbecki apfelbecki</i> (Müller J., 1910)	T	✓*			2021			
<i>Hadesia vasiceki</i> Müller J., 1911	T		✓*			2021					
<i>Nauticiella stygivaga</i> Moravec & Mlejnek, 2002	T		✓*			2021					
<i>Anthroherpon primitivum</i> (Absolon, 1913)	T		✓			/					
<i>Troglamaurops ganglbaueri</i> (Winkler, 1925)	T		✓			2021					
<i>Nonveilleria</i> sp.	T		✓			/					
Urodela	Proteidae		<i>Proteus anguinus</i> Laurenti, 1768	A	✓		✓	2021	VU	EN	
				85	26	22					

4. The Overview of Troglotrophic Species in the Vjetrenica Cave System

4.1. General Overview

Altogether, 93 different subterranean species have been recorded and are considered as present in the Vjetrenica Cave System: 48 aquatic and 45 terrestrial (Table 1). Overall, 40 species have been scientifically described from the system: 35 from Vjetrenica, 4 from Bjelušica, and 2 from Lukavac (Table 1). Field surveys executed from the onset of the 21st century confirmed 50% of taxa previously reported from the system (Table 1).

Among a plethora of species, dozens of subterranean taxa inhabiting the system have been recognized as threatened. According to the IUCN Red List of Threatened Species (VIR), there are ten threatened taxa (Table 1): two endangered (EN), four vulnerable (VU), three of least concern (LC), and one near threatened (NT). According to the Red List of Bosnia and Herzegovina (VIR), there are fourteen threatened taxa: five endangered (EN) and nine data deficient (DD) (Table 1).

4.2. Comments to Selected Aquatic Taxonomic Groups

One of the most distinguishing characteristics of the Dinaric subterranean fauna is the presence of aquatic sessile and filtering species, deriving from marine or historically rich lacustrine fauna [58,59]. Three of these peculiar species were reported from the Vjetrenica Cave; the only subterranean tubeworm in the world, *Marifugia cavatica*; the only cave cnidarian, *Velkoverhia enigmatica*; and one of only a handful of subterranean clams, *Congerina kusceri* (Table 1; Figure 3C). *Marifugia cavatica* can be observed in the waters of the lower Vjetrenica's channels [60]. The presence of the other two species is highly questionable and needs additional confirmation. Even though *V. enigmatica* was reported from a cave in Croatia, it has been recently confirmed only in two caves from 500 km distant Ljubljana River catchment in Slovenia [61]. Moreover, there are some indices that the data on *Velkoverhia* in Vjetrenica might be a result of an experimental error (Sket, personal communication). The second questionable species is *Congerina kusceri*, whose shell was presumably collected in an unknown part of Vjetrenica Cave [12]. Recent and intensive diving explorations in the lower parts of the cave did not result in finding live individuals (B. Jalžić and G. Balazs, personal communication). However, as it occurs in other caves in Popovo Polje, with the closest confirmed locality being the 1.7 km away Baba u Čvaljini Cave, its presence in the system cannot be completely ruled out.

The Vjetrenica Cave System harbors one of the most remarkable examples of single-genus diversity. There are as many as nine different species of the subterranean amphipod genus *Niphargus* [11,62] present in the system. To our knowledge, this exceptional richness is the highest number of subterranean congeners occurring in a single locality in the world, followed only by the community of six *Niphargus* species in the Postojna-Planina Cave System in Slovenia [8]. The co-occurring species largely differ in both general morphology and body size (ranging from the 3 mm large *N. factor* to the spiny and more than 30 mm long *N. balcanicus* (Figure 3A)). The species exploit a wide variety of habitats, including water drips, interstitial waters, and phreatic channels [62]. These characteristics have been related to the evolutionary effects of diminishing competition among closely related species [62,63]. In addition, more amphipod species were found in Vjetrenica, including *Hadzia fragilis* [32] and the largest and the bulkiest among all Dinaric amphipods, the monotypic *Typhlogammarus mrazeki* [64] (Figure 4C).

High species richness of "shrimp-like" crustaceans (Figure 3B) belonging to two different orders can be found within the system. Three species belong to the decapod family Atyiidae [65], which exhibited multiple transitions into the circum-Mediterranean subterranean habitats [66]. The fourth species is a monotypic Mysidae species found only in Vjetrenica's phreatic waters, *Troglomysis vjetrenicensis* [67].

The largest and the most outstanding animal of the subterranean habitats in the Dinaric Karst is the olm *Proteus anguinus* [68] (Figure 3D). Even though once commonly distributed in caves of Popovo Polje, it seems that its population largely disappeared from caves that had been cut off from the Trebišnjica River following to its channelization [51]. In

Vjetrenica Cave, the olm can be found in its lower parts in partly or completely submerged channels. Recently, olm populations from southern Dinarides, including those bound to the Trebišnjica River catchment, were recognized as a separate species-level lineage [69]. Considering the changes of the water regime in Popovo Polje, the olm's southern populations seem to be even more vulnerable than previously thought and highly threatened.



Figure 3. Diverse stygobionts reported from the Vjetrenica cave system: (A) the spiny amphipod *Niphargus balcanicus*, (B) cave shrimp *Spelaeocaris* sp., (C) the subterranean tubeworm *Marifugia cavatica*, along with the cave mussel *Congeria kusceri*, and (D) the olm *Proteus anguinus* (Photo: Teo Delić).



Figure 4. The cave hygropetric, specialized subterranean microhabitat was first described from Vjetrenica Cave [70]. Some of the specialized animals inhabiting it include (A) the semi-aquatic cave beetle *Hadesia vasickei*; (B) the predatory cave leech *Dina absoloni*; (C) the bulkiest of all Dinaric subterranean amphipods, *Typhlogammarus mrazeki*; and (D) a highly troglomorphic and predatory Trechini beetle, *Scotoplanetes arenstorffianus* (Photo: Teo Delić).

4.3. Comments on Selected Terrestrial Taxonomic Groups

The most notable characteristics of Vjetrenica's terrestrial fauna is the existence of the species living in the special cave habitat, the so-called hygropetric [70]. The cave hygropetric is a specialized type of subterranean habitat, first recognized and described from Vjetrenica's depths. It refers to water flowing over the cave walls, forming a thin laminar flow or, sometimes, strong turbulent currents [70,71]. Organic matter dissolved in the water flowing down the vertical walls enables formation of microbial communities [72], which are scraped off the walls and used as nutrients by various groups of arthropods. Species or communities bound to this peculiar habitat are known only from the "hygropetricolous arc" spanning throughout the Dinaric Karst and Italian Prealps [71–74] and geographically distant Caucasus [75,76].

Probably the most known of all the hygropetricolous animals is the elusive beetle genus *Hadesia*, first to be recognized for its peculiar ecology and a semi-aquatic lifestyle [77,78]. Vjetrenica's *Hadesia vasiceki* (Figure 4A) bears some of the characteristics common to all terrestrial taxa inhabiting hygropetricolous habitats, including long claws, densely pubescent body, and mouthparts modified for scraping and grazing on organic matter [79]. The other hygropetricolous beetle in Vjetrenica, *Nauticiella stygiovaga*, is rarely encountered. Following its description in 2002 [80] and despite many attempts, only two specimens were found in the cave's deeper sections in 2021 [81]. This semi-aquatic habitat is also exploited by the largest of Vjetrenica's amphipods, *Typhlogammarus mrazeki* [82] (Figure 4C), and the cave leech, *Dina absoloni* [83] (Figure 4B). Both species are known to climb the vertical walls and confront the hygropetric's waters in search of prey. In addition to the animals occurring in the water flow itself, a couple of them are known to occur at the edges of the hygropetric, presumably exploiting similar nutrient resources or preying on smaller invertebrates feeding on it. These include the millipede *Typhloiulus edentulus*, for which modified grazing mouthparts were also reported [84], and one of the most troglomorphic representatives of subterranean Trechini beetles in Europe, the predatory *Scotoplanetes arenstorffianus* [85,86] (Figure 4D).

Another remarkable characteristic of terrestrial fauna in the Vjetrenica Cave System is the high diversity of arachnids (Table 1), including mites (Acari), spiders (Araneae), harvestmen (Opiliones), palpigrades (Palpigradi), and pseudoscorpions (Pseudoscorpiones) [12]. The most recognizable among them are surely the large Dysderidae spiders, *Stalagtia hercegovinensis* (Figure 5A) and *Stalitella noseki*, which do not produce webs but freely walk and prey within the cave [87,88]. The predatory *Travunia vjetrenicae* (Figure 5B) is a member of a small opilionid family, Travuniidae, encompassing less than a dozen species worldwide. Despite its small size but due to its robust and spiny pedipalps, *Travunia* is considered a fierce predator of smaller invertebrates [89]. Some of the arachnids, including palpigrades, are rarely encountered due to its small size. Only a couple of millimeters long, *Eukoenenia remyi* [90] is, despite being a terrestrial animal, often found gliding on the calcite crusts on the surface of water pools (own observation).

Another species-rich group is the myriapods, including both diplopods and chilopods. Diplopods inhabit a wide variety of habitats, from the ones in transition to surface habitats to the already-mentioned cave hygropetric. Differences in their natural histories are well reflected onto morphologies, which range from the relatively short and round *Typhloglomeris coeca* (Figure 5C) to the elongated *Typhloiulus edentulus* [12,84]. The predatory chilopods are represented by three subterranean species, relatively small *Lithobius matulici*, and a large and highly troglomorphic *Lithobius sketi* [91,92] (Figure 5D).

High variability in size and ecology can also be noted in gastropods, whose representatives range in size from only two and a half millimeters to a centimeter and a half [12]. All of them except *Spelaeoconcha paganettii* (Figure 6A) are endemic to either Popovo Polje or the southeastern Dinaric Karst [12].

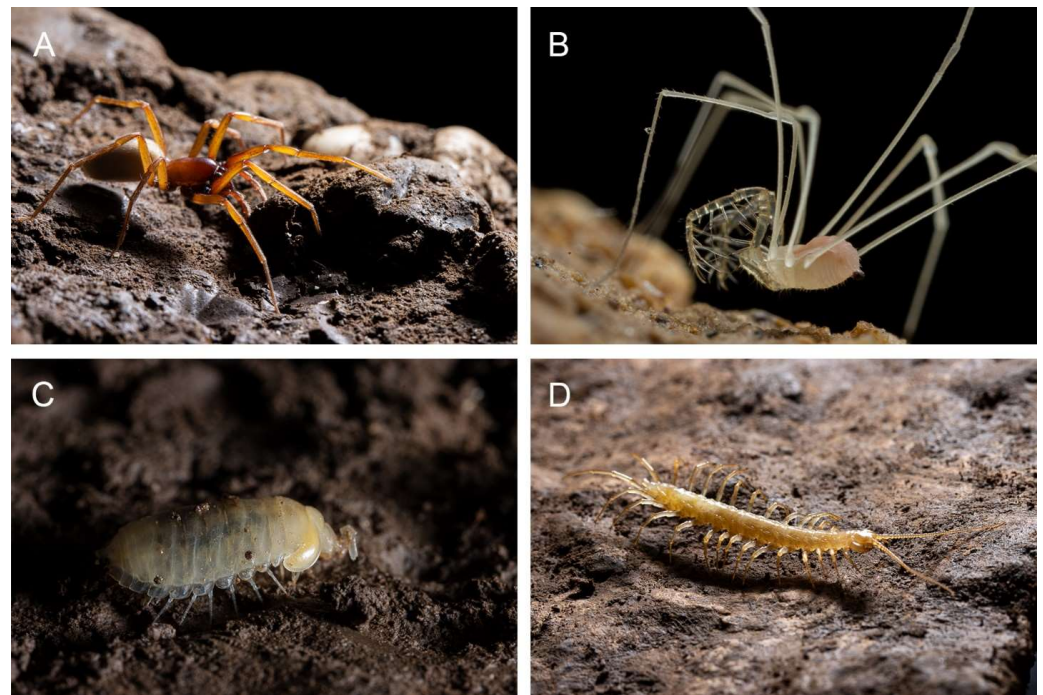


Figure 5. The examples of the striking terrestrial arthropod diversity in the Vjetrenica Cave System: (A) large and predatory spider *Stalagtia hercegovinensis*; (B) tiny opilionid *Travunia vjetrenicae*; (C) one of few subterranean representatives of Glomeridellidae family, *Typhloglomeris coeca*; and (D) the large and troglomorphic *Lithobius sketi*, named after late speleobiologist Boris Sket (1936–2023) (Photo: Teo Delić).

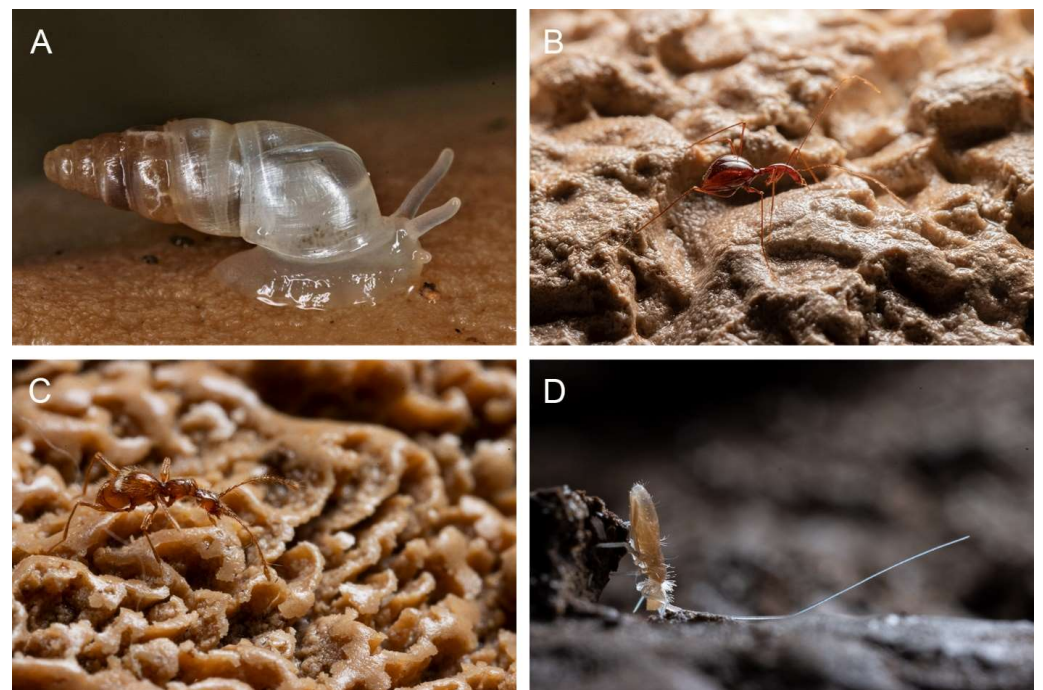


Figure 6. Additional diversity is brought into the system by (A) a rich molluscan community, including both aquatic and terrestrial species, such as *Speleaoconcha paganettii*, and (B) rich subterranean beetles fauna, including one of the largest leiodid beetles, *Graciliella apfelbecki*, (C) the tiny and elusive *Troglamaurops ganglbaueri*, and (D) the poorly studied collembolans, depicted by *Verhoeffiella longicornis* (Photo: Roman Ozimec and Teo Delić).

Besides hygropetric beetles, all three families with numerous subterranean representatives in the Balkans were recorded in Vjetrenica. The family Leiodidae is, besides *Hadesia* and *Nauticiella*, represented by *Graciliella apfelbecki* (Figure 6B), one of the largest (8 mm) and extremely troglomorphic leiodid species [93]. In addition to *Scotoplanetes*, the family Carabidae is represented by two congeners, *Neotrechus dalmatinus dalmatinus* and *Neotrechus suturalis otiosus* [12], and another presumably ecologically specialized species, *Adriaphaenops pretneri* [94]. Finally, the third family commonly distributed in the Balkan's subterranean habitats, Staphylinidae, is known by a yet undescribed species of *Nonveilleria* [12] and *Troglamaurops ganglbaueri* (SubBioDB) (Figure 6C).

5. Comments on Some of the Non-Troglbiotic Species Adding to the Conservation Importance of the Vjetrenica Cave System

Even though this paper is oriented towards presenting the list of obligate subterranean species, we need to bring forward some non-troglbiotic species that occur in the Vjetrenica Cave System. Three fish species found in subterranean waters of Vjetrenica Cave and are listed among endangered species. Two species, *Delminichthys ghetaldii* (Steindachner, 1882) and *Squalius svallize* Heckel & Kner, 1858, are declared as vulnerable under the IUCN criteria, while the third species, *Phoxinus lumaireul* (Schinz, 1840) is considered of least concern [95]. In addition, *Delminichthys ghetaldii* is considered endangered by the Red List of Bosnia and Herzegovina. Preceding the regulation of Trebišnjica (Figure 1), all three species were abundant in Popovo Polje. Moreover, the local inhabitants were exploiting them as a food source [13]. However, these customs gradually changed by the end of 1960s due to anthropogenic activities and the downfall of the limited habitats of fish species [96].

As for bats, five occasionally occurring species were recorded; all are listed as of least concern on the IUCN Red List. Additionally, are three Vespertilionidae species, namely *Myotis emarginatus* (E. Geoffroy Saint-Hilaire, 1806), *M. nattereri* (Kuhl, 1817), and *Plecotus* cf. *kolombatovici*, and two Rhinolophidae species, namely *Rhinolophus ferrumequinum* (Schreber, 1774) and *R. hipposideros* (Bechstein, 1800) [12,97,98]. In addition, three of these species have a higher threat status according to the Red List of Bosnia and Herzegovina; *M. emarginatus* and *R. ferrumequinum* are listed as vulnerable, while *R. hipposideros* is considered as endangered. Generally, the low number of bat species is presumably related to prevalent winds or limited size, which make Vjetrenica and Bjelušica, respectively, less suitable for hibernation or the establishment of nursery colonies.

6. Discussion

6.1. General Overview and Significance of the New Species List

Differently from most of the existing overviews of Vjetrenica's fauna, which focus only on the specialized fauna of the cave itself [9–13], we chose to broaden our scope by inclusion of the two nearby localities: Bjelušica Cave and Lukavac Spring. Their inclusion resulted in the listing of additional troglbiotic taxa and, finally, a higher number of troglbiotic species in the whole system than in the cave alone (Table 1). Due to morphological differences and the connectedness of the system's localities, not all of the listed species are found in all of them. Vjetrenica remains the richest locality with 85 troglbiotic species, followed by Bjelušica with 26 and, finally, Lukavac with 22 species.

Despite the long tradition of speleological surveying and high numbers of troglbiotic species, we are far from the final point of knowledge on both the Vjetrenica Cave System and its specialized fauna. Further increases in numbers of troglbiotic taxa may be expected by systematic sampling of overlooked microhabitats or taxa in addition to the usage of novel sampling and analytical techniques. Epikarst, which often includes its own specialized communities [99,100] and was never subjected to a thorough research in Vjetrenica, presents one of such habitats. Similarly, collembolans probably present the most illustrative example of overlooked taxa. Only two species of *Verhoeffiella* are listed for the whole system [12] (Figure 6D), although more species belonging to different genera and even families are known from it (Lukić M., personal communication). Finally, numbers might further increase

by identification of morphologically cryptic species, which are repeatedly identified among specialized subterranean taxa, including Dinaric collembolans [101–103].

6.2. Monitoring of the Subterranean Communities

The proximity of the railway and infrastructural development along with the fascination about its size and accessibility changed Vjetrenica into a show cave more than half a century ago. E. Pretner questioned the rationality of this move already before its opening in 1960s. He proposed not to set the tourist needs ahead of the conservation of the cave and its peculiar fauna [39]. Tourism paved the way to educate visitors about the functioning and meaning of karst and karstic phenomena. At the same time, the arrangement of pathways and the growing number of visitors, as stressed already by Pretner, present a constant threat to fragile subterranean habitats [104]. Although relatively late, the monitoring scheme in Vjetrenica started in 2016, with an idea to detect changes in the physical and hydrological status of the cave and its microclimate, habitat conditions, the quantity of fauna, as well as modifications in its taxonomic composition. Both can serve as an alarm system for predicting potentially detrimental changes [105,106]. Along with the monitoring of fauna, special interest has been directed towards monitoring of the so-called lampenflora [107], the autotrophic communities developing near artificial light in caves. Algae, bryophytes, mosses, or plants otherwise absent from internal parts of the caves can alter the composition of subterranean communities by providing easily accessible nutrients to some of the species. Additional upgrades of monitoring practices will be assessed by the constant and long-term monitoring of physical parameters such as air and water temperature and the pH of the water and ground or air composition. Implementation of diverse and complementary monitoring practices is of crucial importance, as Vjetrenica and the whole area of Popovo Polje, due to its proximity to Dubrovnik (Figure 1), receive a growing number of tourists. In recent years, the number of tourists rose to more than 17,000 visitors in 2022, while the only exception was around 6000 visitors in 2020, which was heavily affected by the coronavirus pandemic [108]. Compared to the pre-Balkan war years, the number of visitors more than doubled after the cave's reopening. Such an increase presents additional pressure on subterranean ecosystems, calls for additional conservationist attention, and enhances the need for precise and thorough monitoring schemes.

6.3. Past, Present, and Future Threats and Conservation

Due to its geographical setting and connectedness to the Trebišnjica River, tourism does not present the largest issue for the Vjetrenica Cave System. This can be recognized in the progressing industrialization and engineering coupled with a growing need for agricultural land, which triggered construction of a series of dams over the course of the Trebišnjica, with its channelization and the transformation of the lower parts of the polje into agricultural land [44,109,110]. Before its damming and channelization, 155 sinkholes and estaveles existed in the polje [44]. Following the changes, Trebišnjica's hydrological networks, both surface and subterranean, were largely changed [43–47]. Excluding all of its natural meanders and overflowing areas caused the decimation of locally rich and endemic surface and subterranean fauna [51,52,69,111–113]. Despite its uniqueness on the world scale, destruction of Popovo Polje and Vjetrenica were only seldom documented by a couple series of publications, nature conservation actions, and scientific appeals for their conservation [43,46–51].

The effect of these anthropogenic alterations were never properly studied in Vjetrenica or in Popovo Polje. However, some hallmarks, like meters-thick layers of dry tubes of *M. cavatica* in Ponor Crnulja [114], testify to the irreversible changes. Iconic species such as *C. kusceri* and *M. cavatica* seem to have disappeared from some of most known localities in the Popovo Polje. Some papers report the catastrophic aftermath of these changes, resulting in extirpation of more than 99% of local populations [51]. In addition to changes of the water regimes, the land use also changed dramatically. Before channelization, the lower parts of the polje were flooded on average 240 (204–303) days per year [44].

Following channelization, approximately two-thirds of Popovo Polje was changed into agricultural land [109,110], coupling the changes in quantity of water with the potential changes in its quality. Although none of the available studies were executed on Vjetrenica's or Trebišnjica's subterranean fauna, increased concentrations of salt or nitrates were shown to have detrimental effects on subterranean communities [115–117].

As if not all of this was enough, the whole area of Popovo Polje suffered additional obstruction due to disintegration of Yugoslavia in the Balkan Wars during the 1990s [118,119]. The surroundings of the entrances to the Vjetrenica Cave System (Vjetrenica, Bjelušica, and Lukavac Spring) were literally changed into minefields. The wider area was demined in numerous actions following the war; still, some parts of the area may remain inapproachable—like the ridges above Vjetrenica's entrance.

Although the whole system, along with the Trebišnjica River, remains largely affected by the anthropogenic influence, not everything is being lost. Both Bosnia and Herzegovina and the Republic of Srpska proposed Vjetrenica as a future Natura 2000 site, and some of the species were listed on the IUCN's list of endangered and vulnerable species [95]. To further promote the uniqueness of the system and the accompanying Trebišnjica Basin, a Biospeleological Museum was founded in 2016 in close proximity to the system's entrances [120]. Finally, the attempts for conservation of these sites were crowned by an official application for the inclusion of Vjetrenica and the surrounding landscapes under the UNESCO's world heritage conservation scheme [121]. This might be a proper place to question how the possible inclusion of the Vjetrenica System onto UNESCO's list might help against the growing pressures, represented by the ambitious economic-developmental plans of Gornji Horizonti, which are already transforming landscapes in the Trebišnjica Basin. The Gornji Horizonti comprise an infrastructural plan for building additional series of dams and channels meant to feed a set of hydropower plants by draining waters from different, interconnected poljes or even drainages [44,45,122–125]. Despite the deluge of "green deals", "sustainability", and similar terms on the continental level [126] and the known effect of damming rivers on biodiversity [127,128], for now, it seems that nature and its conservation, along with the human wellbeing, are put aside.

6.4. Concluding Remarks

Only successful conservation attempts will enable further usage of Vjetrenica as a show cave, a touristic development of the area, and a scientific work, both in Vjetrenica and other parts of the system. For us, the scientific perspective is of a vital importance. Herein, we will list only two topics connected to evolutionary patterns and the mechanisms underlying them, wherein Vjetrenica's role cannot be overlooked. Vjetrenica's subterranean amphipod assemblage presents the richest subterranean amphipod community in the world. It comprises nine *Niphargus* congeners, largely differing in morphology and spatial use, and additional representatives of other amphipod families [11,62,63]. At least the *Niphargus* community was shown to originate through the mechanisms of adaptive radiation [129]. However, and despite the soundness of the topic, only the first steps towards understanding the mechanisms of community assembling have been made. In addition to this, Vjetrenica is renowned by its semi-aquatic hygropetricolous environment [70] and its peculiar inhabitants. The mechanisms and processes underlying the assembling of the hygropetricolous communities remain even less studied than those underlying the assembling of the niphargid communities.

Fieldworks expeditions after 2000 resulted in the repeated collection of approximately 50 percent of all the species recorded from the system. These are mostly larger taxa (Table 1), which are taxonomic groups that at least some of the authors, or their collaborators, are studying. Data on 50 percent of listed species, including hydrobiid snails or specialized trematodes, remain only literature-based and clearly demonstrate the lack of taxonomists in the scientific field. For most of the species, their presence in the system remains to be confirmed. Therefore, we found no better way to demonstrate how needy we are of both

systematic sampling and thorough recording of the species occurring in the Vjetrenica Cave System.

The whole system, along with the Popovo Polje and the Trebišnjica River, present a unique combination of natural history and cultural heritage coupled with tourism and business opportunities. Long-term sustainability of the whole area is largely dependable on a wide variety of factors, including local inhabitants, scientists, farmers, decision makers and governmental agencies, employees in the tourism and energetic sectors, etc. With so many variable groups of interest, this is the right place to ask if we can cope with the burden and whether we, as a community, will be successful in attempts to preserve the second richest subterranean locality in the world?

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