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Postojna-Planina Cave System in Slovenia, a Hotspot of Subterranean Biodiversity and a Cradle of Speleobiology

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Abstract: The Postojna-Planina Cave System (PPCS) in central Slovenia is a globally exceptional site of subterranean biodiversity, comprised of many interconnected caves with cumulative passage length exceeding 34 km. Two rivers sink into the caves of the PPCS, called the Pivka and Rak, and join underground into Unica River, which emerges to the surface. The studies of fauna of PPCS began in the 19th century with the first scientific descriptions of specialized cave animals in the world, making it "the cradle of speleobiology". Currently, the species list of PPCS contains 117 troglobiotic animal species belonging to eight phyla, confirming its status as the richest in the world. Of these, 47 species have been scientifically described from the PPCS, and more than 10 await formal taxonomic descriptions. We expect that further sampling, detailed analyses of less studied taxa, and the use of molecular methods may reveal more species. To keep the cave animals' checklist in PPCS up-to-date, we have supplemented the printed checklist with an online interface. As the revised checklist is a necessary first step for further activities, we discuss the importance of PPCS in terms of future research and conservation.

Keywords: hotspot; speleobiology; subterranean biodiversity; troglobionts; Postojna-Planina Cave System; Slovenia

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1. Introduction

Sampling subterranean fauna is a challenging task, considering that humans have limited access to the subterranean environment. Caves are access points to reach subterranean species that can inhabit very narrow spaces in fractured rock. Inventories of subterranean biodiversity are time consuming and require technically demanding fieldwork and broad taxonomic engagement [1]. The highest conservation priority is usually given to sites with high species richness, so completing species inventories of such hotspots should be highly prioritized [2].

The Dinaric Karst in the Western Balkans in Europe is one of the global hotspots of subterranean biodiversity [3–5]. Species richness within this region is not evenly distributed [6,7]. Many caves are consistently listed among the species richest on a global scale [8]. The species richest among them is Postojna-Planina Cave System (in Slovenian: Postojnsko planinski jamski sistem; hereafter referred to as PPCS) in Slovenia (Figure 1), outstanding not only because of its biological, but also historical, touristic, and conservation importance.

The PPCS is a complex system of many caves connected by dry or flooded channels. The inner parts of the Postojnska jama ("jama" means cave in Slovenian) at the southernmost end of the PPCS were discovered in 1818 and revealed the extraordinary richness and beauty of speleothems (Figure 2). The attractive ornamentation initiated guided tours of the cave and triggered a worldwide beginning of cave tourism. The construction of the first underground railway (Figure 3) and electric lighting in 1872 and 1884, respectively, promoted tourist visits to Postojnska jama. Along with tourism, scientific research developed, which laid the foundation for speleology and karstology as sciences. Biological studies of the subterranean world began with the discovery of Luka Čeč, a cave guide and assistant lamplighter, who found an unusual beetle in Postojnska jama in 1831. He gave the beetle to Count Franz Joseph Hochenwart, the curator of the Provincial Museum of Carniola in Ljubljana, who recognized the value of the find. The specimen was examined by the renowned entomologist Ferdinand Josef Schmidt, who in 1832 produced the scientific description of *Leptodirus hochenwartii* [9]. In this work he declared the animal to be a cave-adapted beetle, which was the first scientific recognition of specialized subterranean animal in the world. News of the discovery spread and in the next years, many eminent naturalists came to study the fauna of Postojnska jama, describing cave species of other animal taxa. The snowball effect triggered by the description of *L. hochenwartii* is considered the starter of speleobiology and PPCS the "cradle of speleobiology" [10].

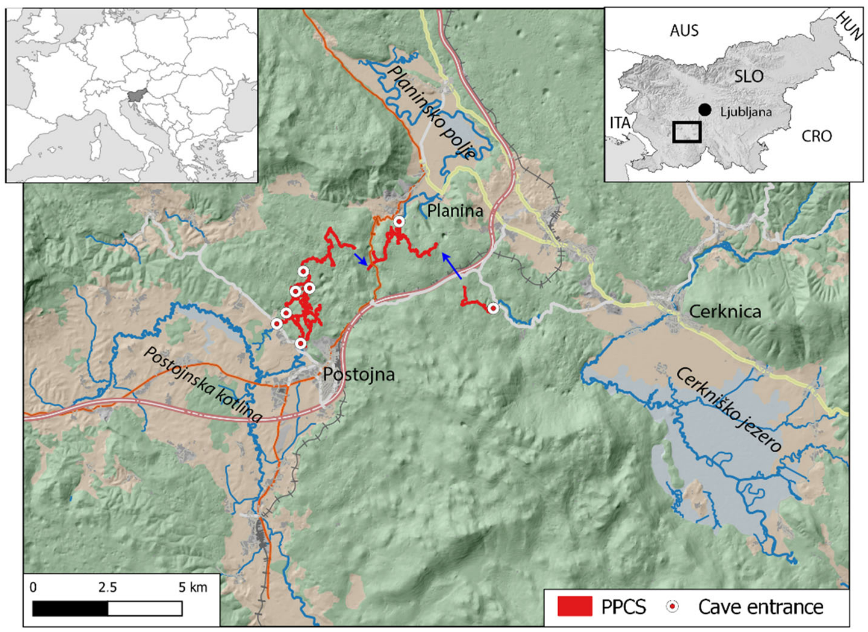

Figure 1. Location of the Postojna-Planina Cave System in central Slovenia. Top left: position of Slovenia within Europe; top right: position of PPCS within Slovenia; middle: red lines depict the planar views of all caves of the system; red dots: entrances to caves; blue arrows: parts of the system connected via subterranean rivers, but not yet passed by man.

The pace of new discoveries by numerous scientists in caves of the PPCS (see detailed review of the beginnings in [10]) produced the first checklists of the PPCS already in the 19th century. An important milestone in cataloguing was made by Benno Wolf, who collected all data on animals in caves of the world, and compiled them in Animalium Cavernarum Catalogus, issued between 1934 and 1938 [11]. However, he listed all taxa from published sources without critically evaluating their taxonomic validity, and did not distinguish the troglobiotic from non-troglobitic species. His list included 134 species for PPCS, of which about 50 could be considered troglobiotic. It was not until 30 years later, that Egon Pretner produced the next list of cave animals for PPCS, taking into account caves excluding Planinska jama in the northern part of the system [12]. Pretner listed 131 species, including about 50 troglobiotic ones. The comprehensive list of aquatic taxa from the entire PPCS, which considered the ecological status of the species, was prepared by Boris Sket in 1979 [13]. Among more than 190 species, he listed 34 aquatic troglobionts. The total number of troglobionts for PPCS, 84, was given in a comparative study of the richest subterranean sites in the world [8], but the actual species list was not included. We fill this gap with this paper, in which we have carefully evaluated and updated the list of troglobionts and discussed its importance within a broad socio-scientific-conservation context.

Figure 2. Postojnska jama is a tourist cave, but there are still many beautifully ornamented passages, where only cavers can enter—as the example of "Pisani rov". Photo: Peter Gedei.

Figure 3. As a unique tourist attraction, Postojnska jama takes tourists to deep parts of the cave with the underground railway. Photo: Slavko Polak.

Description of the PPCS

The PPCS is located in central Slovenia (Figure 1). It is the main cave system in the densely forested and uninhabited karst area between the town of Postojna in Postojnska kotlina, the town of Planina on Planinsko polje, and the town of Cerknica on Cerkniško polje (Figure 1) [14]. In the area above the PPCS, there are 16 large collapsed dolinas interrupting some of these underground passages. The cave system developed in an about 800-m-thick layer of Cretaceous limestones and dolomites, between two NW-SE oriented faults, namely the northern Idrija fault and the southern Predjama fault [15]. The thickness of the bedrock above the cave ranged from 60 to 120 m. The PPCS is typically defined as a system of six caves with large separate entrances with individual cadastre numbers in Slovenian Cadastre of Caves, namely Postojnska jama (No. 747), Otoška jama (No. 779), Pivka jama (No. 472), Črna jama (No. 471), Magdalena jama (No. 820), and Planinska jama (No. 748). Two other caves that should be considered part of the PPCS, connected via impassable flooded channels, are Lekinka (No. 1867) and Tkalca jama (No. 857) [16] (Figure 4), both of which are often excluded from biological observations of the system [12,13]. The entire cave system reaches depths of up to 115 m and includes at least 34 km of channel length (24 km of caves from Postojnska jama to Pivka jama, and approximately 10 km sum of the length of Lekinka, Planinska jama, and Tkalca jama).

The PPCS is located in the Black Sea drainage basin, but at least some species in the PPCS also occur in Adriatic drainage basin, indicating a complex history of drainage connectivity (Delić et al., in rev.). The PPCS contains two subterranean rivers that enter the system in the South (Pivka River) and East (Rak River). The Pivka River sinks in Postojnska jama and is directly accessible in caves up to the syphon in Pivka jama (Figure 4). It receives inflows from Lekinka and deep groundwater from the east. In 2015, parts after the siphon in Pivka jama were dived through and the length of the cave increased by about 3.5 km, leaving a section of about 800 m straight line between Pivka jama and Planinska jama unexplored [17]. The Pivka River reappears in Planinska jama, the last and northernmost cave of the PPCS. In this cave, the river flows within the Pivka channel for about 2 km, until it joins Rak River. Rak River sinks from the surface into the Tkalca jama in the east, whose channels are about 3 km long. Also in the Tkalca jama, one of the siphons of Rak River has stopped divers, leaving about 1 km of straight line distance to Planinska jama unexplored [18] (Figure 4). After the syphon, Rak River reappears in Planinska jama and flows for about 2 km through the Rak channel, and joins Pivka River. The new river, called Unica, is formed about 500 m away from the cave entrance, where it springs to Planinsko polje (Figures 1,4). The channels of the system along the Pivka River are vertically on two levels. The upper ones are older and dry, with many beautiful formations and speleothems (Figure 2), while the younger and lower ones called "Rov podzemne Pivke" (the channels of the subterranean Pivka River), were formed after the deepening of the riverbed.

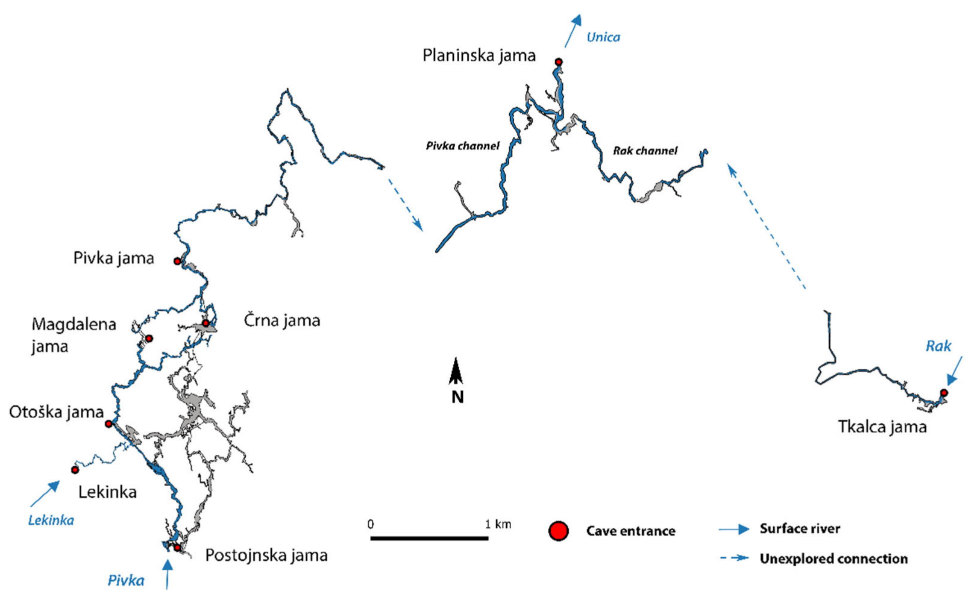

Figure 4. The plan of the Postojna-Planina Cave System, with labelled entrances to individual caves. Subterranean connections, which have not yet been explored by man, are marked with dashed blue arrow lines, while full blue arrow lines and blue names indicate surface rivers entering/leaving the system. We modified the base line outline of the caves, originally provided by the Karst Research Institute in Postojna, Slovenia.

Temperatures within the PPCS vary depending on the location of cave entrances and the distance from rivers sinks into the system. The temperature in the inner, isolated parts of Postojnska jama is about 8.5 °C, while in the parts closer to the entrances it varies mainly between 3 and 13 °C [19]. The temperature of Pivka River varies daily and seasonally, with the amplitude of fluctuations decreasing with distance from its sink [20]. Oxygen concentration in Pivka River varies similarly to surface conditions near the sink to Postojnska jama, while with distance from the sink the water becomes aerated and saturated with oxygen [20].

There are two main sources of organic material for subterranean communities. One is via the sinking rivers, which transport substantial amounts of particulate organic matter and, in the near-surface areas, also abundant plant and animal material that can become food sources. The transport capacity is strongly influenced by precipitation and is enhanced during high water levels [19]. The second source of organic matter is epikarst water, which drips from the ceiling and brings mainly diluted organic matter [21,22]. Another food source, albeit spatially limited, is bat guano and the remains of terrestrial accidentals coming into the PPCS. In general, the amount of organic matter in Pivka River decreases in the direction from Postojnska jama to Planinska jama [21].

2. Compiling the Data

We compiled the data of all troglobionts or troglobiotic populations found in PPCS (sensu Sket [23]). The latter are populations of surface species that form morphologically and ecologically distinct specialized cave populations in PPCS [24]. Non-troglobiotic species found in PPCS and dubious records were omitted from the checklist. The main source of information was published sources as well as material kept in Zoological collection of Department of Biology, Biotechnical Faculty, University of Ljubljana and Notranjska Museum Postojna. The information was collected in SubBioDB, the database on biodiversity of subterranean habitats managed in the SubBioLab at the University of Ljubljana. The data were revised and supplemented with unpublished records, either from reports or from personal communication with taxonomic authorities.

The list contains the species or the lowest taxonomic rank that could be identified. If the subspecies level was determined, we list it. We did not distinguish the level of subgenera. In some cases, taxonomic authorities specifically indicated that some individuals belonged to new species awaiting formal description. These records were added to the checklist as "*Genus* sp. n.".

We marked whether the PPCS presents a type locality for the taxon. Whenever data were available, we added information about the specific cave of the PPCS where the taxon was recorded.

We used the most current taxonomic nomenclature available for specific taxonomic groups. To list only valid species names, we consulted taxonomists or online databases maintained by specialists, namely World Register of Marine Species [25], Millibase [26], A World Catalogue of Centipedes (Chilopoda) [27], Pseudoscorpiones of the World [28], World Spider Catalogue [29], and Checklist of the Collembola [30]. To keep track of species names listed in previous checklists, we have retained the original species name in the list.

Because checklists may be outdated at the time they are published, we developed an online checklist of PPCS species (www.subbio.net/PPCS-checklist (accessed on 8 June 2021) that is fed from the SubBioDB database.

3. The Checklist of Taxa in PPCS

The checklist contains 116 species, of which 71 are aquatic and 45 terrestrial. They belong to eight phyla: 85 species of arthropods (45 crustaceans, 18 hexapods, 13 arachnids, and 9 myriapods), 12 molluscs, 11 annelids, 4 turbellarians, 1 sponge, 1 cnidarian, 1 vertebrate, and 1 protist (Table 1). Three species were found as parasitic on cave shrimp, the protist, and both thamnocephalids (Table 1). Nearly half, 47 species, have been scientifically described from PPCS (Table 1). In addition, two species remain to be identified at species level, while 12 are awaiting taxonomic description. Some of the most notable species are presented in Figure 5.

Not all species were reported from all caves of the PPCS. The highest number was reported from Planinska jama (66 species) and Postojnska jama (64 species). From Črna jama, Pivka jama, Otoška jama Magdalena jama, and Tkalca jama, 35, 26, 11, 7, and 2 species were reported, respectively.

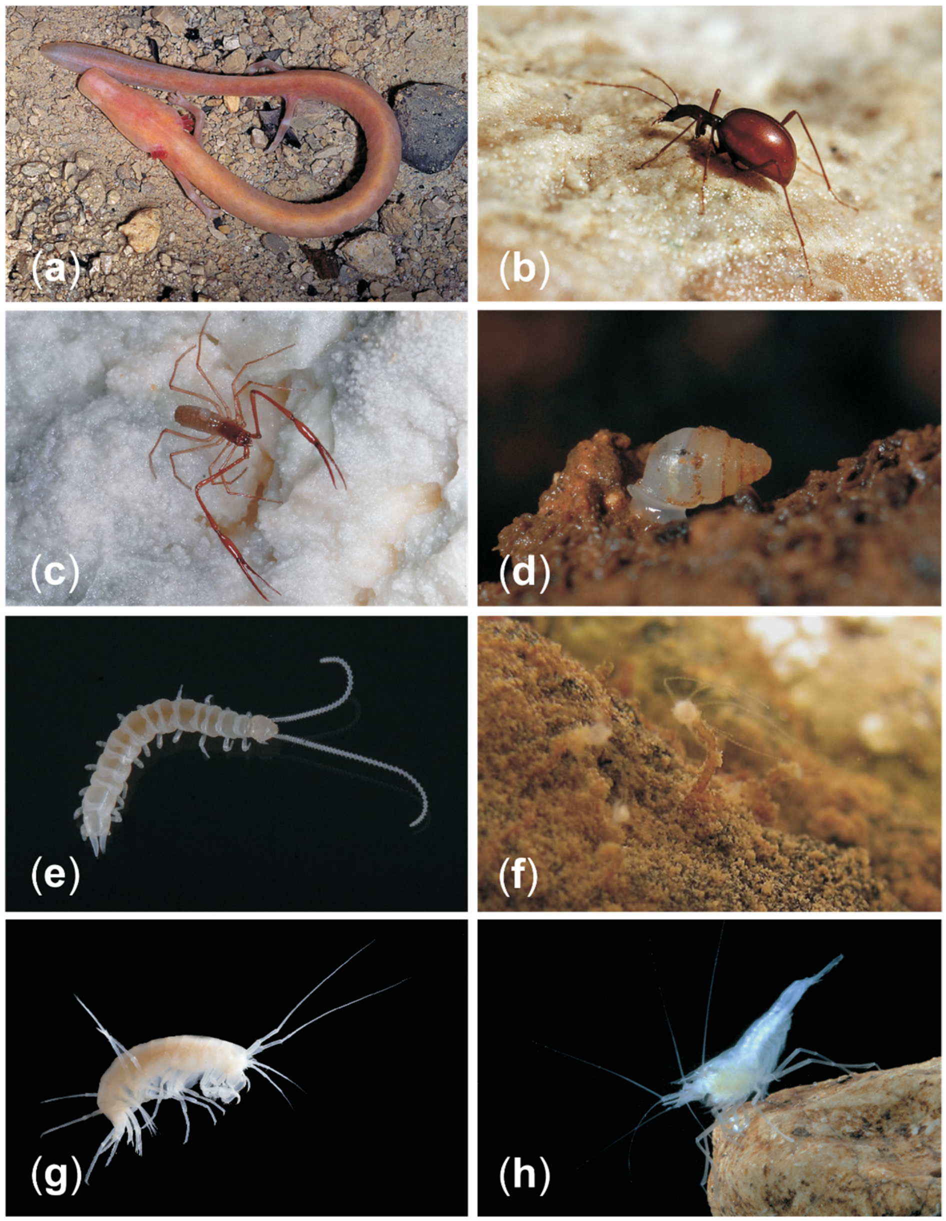

Figure 5. The famous eight: (**a**) proteus or the olm *Proteus anguinus* Laurenti, 1768; (**b**) slenderneck beetle *Leptodirus hochenwartii hochenwartii* Schmidt, 1832; (**c**) giant cave pseudoscorpion *Neobisium spelaeum spelaeum* (Schiødte, 1848); (**d**) Postojna cave herald snail *Zospeum spelaeum spelaeum* (Rossmaessler, 1839); (**e**) symphylan *Scutigerella hauserae* Scheller, 1990; (**f**) cave hydrozoan *Velkovrhia enigmatica* Matjašič & Sket, 1971; (**g**) giant cave amphipod *Niphargus orcinus* Joseph, 1869; (**h**) Planina cave shrimp *Troglocaris planinensis* Birstein, 1948. Photo credits: (a–e)—Slavko Polak, (f)—Rodrigo Lopes Ferreira, (g)—Teo Delić, (h)—Rollin Verlinde.

Table 1. The list of obligate subterranean (troglobiotic) species recorded in the Postojna-Planina Cave System in Slovenia. Species with type locality in PPCS are marked with [1], and troglobiotic populations of surface species are marked with *. The letter in the column A/T marks whether the species is A—aquatic or T—terrestrial. If the species was reported from a specific cave(s) of the system, the X is under the abbreviation: POJ—Postojnska jama, OJ—Otoška jama, MJ—Magdalena jama, ČJ—Črna jama, PIJ—Pivka jama, PLJ—Planinska jama, TKJ—Tkalca jama.

Taxonomic Group	Family	Species [Original Mentioning]	A/T	POJ	OJ	MJ	ČJ	PIJ	PLJ	TKJ	References
Protozoa-Ciliata											
Suctoria	Spelaeophryidae	[1] *Spelaeophrya troglocaridis* Stammer, 1935	A						X		[31]
Porifera											
Demospongia	Spongillidae	* *Ephydatia fluviatilis* (Linne, 1759)	A	X					X		[32,33]
Cnidaria											
Hydrozoa	Bougainvilliidae	[1] *Velkovrhia enigmatica* Matjašič & Sket, 1971	A						X		[13,34,35]
Turbellaria											
Temnocephalida	Scutariellidae	[1] *Bubalocerus pretneri* Matjašič, 1958	A						X		[13,36]
		[1] *Troglocaridicola capreolaria* Matjašič, 1958	A						X		[13,36]
Tricladida	Dendrocoelidae	*Dendrocoelum spelaeum* cf (Kenk, 1924)	A						X		Zoological Collection of Dept. Biology, University of Ljubljana
		[1] *Dendrocoelum tubuliferum* de Beauchamp, 1919	A	X			X				[11–13,37,38]
Mollusca											
Gastropoda	Acroloxidae	*Acroloxus tetensi* (Kuščer, 1932)	A	X					X		[12,13,39,40]
	Ancylidae	* *Ancylus fluviatilis* Mueller, 1774	A	X					X		[13,39]
	Carychiidae	*Zospeum kusceri* Wagner A.J., 1912	T				X	X			[41]
		Zospeum lautum (Frauenfeld, 1854)	T				X				[41]
		[1] *Zospeum spelaeum spelaeum* (Rossmässler, 1839) [*Carychium spleaeum; Z. alpestre rossmäsleri*]	T	X	X		X	X	X		[12,41–43]
	Hydrobiidae	* *Belgrandiella fontinalis* (Schmidt F.J., 1847)	A						X		[13,44]
		Belgrandiella schleschi Kuščer, 1932	A								[13]
		Belgrandiella kusceri (Wagner A.J., 1914)	A						X		[45]
		Hadziella ephippiostoma Kuščer, 1932	A								[13]
		Hauffenia michleri Kuščer, 1932	A						X		[13,45]
		Hauffenia subpiscinalis (Kuščer, 1932) [*Neohoratia subpiscinalis*]	A						X		[12,13,40]
		Iglica luxurians (Kuščer, 1932)	A						X		[12,13,34,45]
Annelida											

Hirudinea	Erpobdellidae	* *Dina krasensis* (Sket, 1968) [*Trocheta bykowskii krasense*]	A					X	X	[13,46]
	Glossiphoniidae	* *Glossiphonia complanata complanata* (Linne, 1758)	A						X	[13,46]
Oligochaeta	Lumbriculidae	*Trichodrilus ptujensis* Hrabe, 1963	A							[13]
		Trichodrilus strandi Hrabe, 1936	A	X				X	X	[13,47]
	Tubificidae	[1] *Epirodrilus slovenicus* Karaman Sp., 1976	A						X	[13,48,49]
		[1] *Potamothrix postojnae* Karaman Sp., 1974	A						X	[49,50]
		[1] *Psammoryctides hadzii* Karaman Sp., 1974	A						X	[49,50]
		[1] *Rhyacodrilus caudosetosus* Karaman Sp., 1983	A						X	[49,51]
		[1] *Rhyacodrilus maculatus* Karaman Sp., 1983	A						X	[49,51]
		[1] *Rhyacodrilus sketi* Karaman Sp., 1974	A						X	[49–51]
		Sketodrilus flabellisetosus (Hrabe, 1966)	A						X	[48,49]
Arthropoda-Arachnida										
Acarina	Eremaeidae	*Oppia cavatica* nomen nudum	T						X	[52]
	Eremaeidae	*Oppia malograjskiella* nomen nudum	T						X	[52]
	Labidostommidae	[1,*] *Labidostomma lyra* Willmann, 1932 [*Nicoletiella denticulata*]	T	X						[11–13,53]
Araneae	Dysderidae	*Mesostalita nocturna* (Roewer, 1931)	T	X						[12,42,54]
		[1] *Stalita taenaria* Schioedte, 1847	T	X	X	X	X		X	[11,12,42,54–60]
	Linyphiidae	[1] *Troglohyphantes excavatus* Fage, 1919 [*Troglohyphantes anellii*]	T	X						[60–62]
Palpigrada	Eukoeneniidae	*Eukoenenia austriaca austriaca* (Hansen, 1926)	T	X						[12,63–66]
Pseudoscorpiones	Chthoniidae	*Chthonius spelaeophilus* Hadži, 1930	T	X						[62]
		[1] *Chthonius cavernarum* Ellingsen, 1909	T	X						[11,12,67,68]
		Troglochthonius doratodactylus Helversen, 1968	T	X						[62]
	Neobisiidae	[1] *Neobisium pusillum* Beier, 1939	T				X			[12,13,69]
		[1] *Neobisium spelaeum spelaeum* (Schioedte, 1848)	T	X	X					[12,13,42,57,68]
		Roncus stussineri (Simon, 1881)	T							[12]
Arthropoda-Myriapoda										
Chilopoda	Lithobiidae	*Lithobius* sp.n.	T							[42]
		[1] *Lithobius stygius* Latzel, 1880	T	X	X				X	[12,42,70,71]

		[1] *Lithobius zveri* (Matić & Stentzer, 1977) [*Monotarsobius zveri*]	T						X	[72]
Diplopoda	Attemsiidae	[1] *Attemsia stygia* (Latzel, 1884) [*Attemsia stygium*]	T	X	X			X		[11–13,73–76]
	Haasiidae	[1] *Haasia troglodyta* (Latzel, 1884) [*Acherosoma troglodytes*, *Haasia troglodytes*]	T	X						[12,73,74]
	Iulidae	*Typhloiulus illirycus* (Verhoeff, 1929)	T	X	X					[11,62,76]
	Polydesmidae	[1,*] *Brachydesmus subterraneus* Heller, 1857	T	X			X	X		[11,12,77]
Symphyla	Scolopendrellidae	[1] *Scolopendreilopsis pretneri* Juberthie-Jupeau, 1963	T	X						[62,78]
	Scutigerellidae	[1] *Scutigerella hauserae* Scheller, 1990	T	X						[62,79]
Arthropoda-Crustacea										
Cladocera	Chydoridae	* *Chydorus sphaericus* (O.F.Mueller, 1776)	A							[80,81]
Copepoda -Calanoida	Diaptomidae	*Troglodiaptomus sketi* Petkovski, 1978 [*Troglodiaptomus sketi postojnae*]	A	X					X	[82]
Copeopoda-Cyclopoida	Cyclopidae	*Acanthocyclops kieferi* (Chappuis, 1925)	A	X					X	[82,83]
		Acanthocyclops venustus venustus (Norman & Scott, 1906) [*Acanthocyclops venustus stammeri*]	A	X					X	[82,84]
		[1] *Diacyclops charon* (Kiefer, 1931) [*Cyclops charon*]	A	X				X	X	[12,13,82,84–86]
		Diacyclops languidoides (Lilljeborg, 1901) [*Diacyclops languidoides goticus*]	A	X						[12,13,82,83]
		Diacyclops slovenicus Petkovski, 1954	A	X					X	[82,84]
		[1] *Metacyclops postojnae* Brancelj, 1987	A	X						[82,84]
		Speocyclops infernus (Kiefer, 1930)	A	X			X	X	X	[13,82–84]
Copepoda-Harpacticoida	Ameiridae	*Nitocrella* n.sp.	A	X						[83]
	Canthocamptidae	*Bryocamptus balcanicus* (Kiefer, 1933)	A	X			X	X	X	[83,87]
		Bryocamptus n.sp.	A					X		[83]
		Bryocamptus pyrenaicus (Chappuis, 1923)	A	X				X	X	[83,84,87]
		Bryocamptus typhlops (Mrazek, 1893)	A	X				X	X	[83,87]
		Bryocamptus zschokkei caucasicus Borutzky, 1960	A	X				X	X	[13,87]
		[1] *Elaphoidella cvetkae* Petkovski, 1983	A	X			X	X	X	[83,84,87,88]

		Elaphoidella elaphoides (Chappuis, 1924)	A					X	X		[87]
		[1] *Elaphoidella franci* Petkovski, 1983	A						X		[84,87,88]
		[1] *Elaphoidella jeanneli* (Chappuis, 1928)	A	X			X		X		[12,13,84,87,89]
		Elaphoidella stammeri Chappuis, 1936	A	X					X		[84,87]
		Maraenobiotus cf. *brucei* (Richard, 1898)	A					X			[83]
		Moraria n.sp.	A				X				[83]
		Morariopsis scotenophila (Kiefer, 1930)	A	X			X				[83,84,87]
		Pilocamptus pilosus (Douwe, 1910) [*Echinocamptus georgevitchi E. pilosus*, *E. unicus*]	A	X			X	X	X		[12,13,84,87]
		Stygepactophanes sp.n.	A				X				[83]
	Parastenocarididae	*Horstkurtcaris nolli alpina* (Kiefer, 1960) [*Parastenocaris nolli*]	A				X	X			[83]
		Parastenocaris sp.n. 1	A				X				[83]
		Parastenocaris sp.n. 2	A	X			X	X			[83]
Ostracoda - Podocopida	Candonidae	[1] *Typhlocypris trigonella* (Klie, 1931) [*Candona trigonella*]	A	X							[11–13,90,91]
		Typhlocypris schmeili nomen nudum	A				X				[11–13,92]
Decapoda	Atyidae	[1] *Troglocaris planinensis* Birstein, 1948 [*Troglocaris anophthalmus*]	A	X			X	X	X	X	[12,18,34,93–95]
Amphipoda	Crangonyctidae	* *Synurella ambulans* Mueller, 1846 [*Synurella jugoslavica*]	A						X		[13,34]
	Niphargidae	*Niphargus dobati* Sket 1999 [*Niphargus aquilex*]	A						X		[96,97]
		Niphargus orcinus Joseph, 1869	A								[13,97]
		[1] *Niphargus orophobata* (Sket, 1981) [*Niphargobates orophobata*]	A						X		[97,98]
		[1] *Niphargus spoeckeri* Schellenberg, 1933	A				X	X	X		[12,13,34,62,97]
		[1] *Niphargus stygius* (Schioedte, 1847)	A	X			X		X		[12,13,34,57,97]
		Niphargus sp. *stygius*-complex (Schioedte, 1847)	A	X			X		X		[12,34,57,97]
		[1] *Niphargus wolfi* Schellenberg, 1933	A	X					X		[12,13,34,97]
Isopoda	Asellidae	* *Asellus aquaticus aquaticus* (Linne, 1761)	A	X			X	X	X		[11–13,99–103]
		[1,*] *Asellus aquaticus cavernicolus* Racovitza, 1925	A	X			X	X	X		[11–13,101,102,104,105]
		Proasellus istrianus (Stammer, 1932)	A					X			[12,13]
	Sphaeromatidae	*Monolistra racovitzai racovitzai* Strouhal, 1928	A	X					X		[106,107]

	Trichoniscidae	*Androniscus stygius* (Nemec, 1897) [*Andronicus cavernarum tschammeri*]	T	X		X	X		X		[12,108–111]
		[1] *Titanethes albus* (Koch C., 1841)	T	X	X	X	X	X	X		[12,13,42,108,110]
Arthropoda-Hexapoda											
Collembola	Arrhopalitidae	[1] *Pygmarrhopalites postumicus* (Stach, 1945) [*Arrhopalites postumicus*]	T	X							[62,112]
	Paronellidae	*Troglopedetes pallidus* Absolon, 1907	T	X	X						[12,42,62]
	Neelidae	*Neelus* n.sp.	T	X							Lukić M., pers. comm. (2021)
	Oncopoduridae	[1] *Oncopodura cavernarum* Stach 1934	T	X							[12,13,62,113]
	Onychiuridae	*Absolonia gigantea* (Absolon, 1901) [*Onychiurus giganteus*]	T				X				[11–13,62,112–114]
		[1] *Onychiuroides postumicus* Bonet, 1931 [*Onychiurus postumicus*]	T				X				[11–13,112–114]
		[1] *Onychiurus boldorii* Denis, 1938	T	X							[12,13,114]
	Tomoceridae	*Tritomurus scutellatus* (Frauenfeld, 1854)	T	X					X		[62,114]
Diplura	Campodeidae	*Plusiocampa nivea* (Joseph, 1882) [*Campodea nivea*, *Plusiocampa erebophila*]	T	X							[12,13,42,115]
Coleoptera	Carabidae	*Anophthalmus amplus sedulus* (Knirsch, 1926) [*Anophthalmus pubens/pubescens*]	T						X		[116]
		Anophthalmus schmidtii schmidtii Sturm, 1844	T	X			X		X		[12,117]
		[1] *Anophthalmus severi confusus* (J. Müller, 1935) [*Anophthalmus hirtus confusus*]	T			X	X				[12,116]
	Leiodidae	*Aphaobius milleri* Schmidt, 1855	T				X				[12,118]
		Bathyscimorphus sagarum Bognolo, 2002	T						X		[118]
		[1] *Bathyscimorphus byssinus byssinus* (Schiödte, 1848)	T	X	X		X				[12,42,118,119]
		[1] *Bathysciotes khevenhuelleri khevenhuelleri* (L. Miller, 1852)	T	X	X	X			X		[12,42]
		[1] *Leptodirus hochenwartii hochenwartii* Schmidt, 1832	T	X	X	X	X		X		[9,12,42,56,119]
	Staphylinidae	[1] *Machaerites ravasinii* (J. Müller, 1922)	T	X					X		[12,120–123]
Vertebrata											[11–13,18,124]
Amphibia-Urodela	Proteidae	*Proteus anguinus* Laurenti, 1768	A	X		X	X	X	X	X	

4. Importance of Updated Checklist

4.1. General Comments

The revised checklist revealed the presence of at least 116 troglobiotic species in PPCS, increasing the number by nearly 40 species since the last publication [8]. Not all species were reported from all caves of the PPCS. Due to the connectivity between the different parts of the system, the current differences in the number of species mainly reflect the differences in sampling, but also their positions in relation to the river sinks and surface influences. Although PPCS has the longest history of biological exploration, and the highest troglobiotic species richness in the world, new species are still expected. This is no surprise considering that PPCS is located in the heart of a region that has been consistently recognized as a global hotspot of subterranean biodiversity, where sampling is still not complete [125]. This supports the view that further studies in the system should be encouraged as they may reveal additional species for a variety of reasons: sampling of new microhabitats or more thorough sampling of less studied cave channels, use of new sampling techniques, study of currently less studied taxa [126], identification changes due to continued taxonomic activity, or introduction of molecular methods to identify cryptic species and their co-occurrence [127–129].

4.2. PPCS as a Model System for Key Biological Questions

PPCS retains its appeal for biological research, with organisms that have the potential to answer key questions in speleobiology [130]. One research direction could address cave colonization in the context of adaptation and speciation processes from surface ancestor to subterranean descendant [131]. In the PPCS, there are at least four species with extant surface ancestral populations, which provide an exceptional model system for studying these ecological and evolutionary processes during the transition from surface to subterranean environments [131–133].

The next potential of PPCS is to study the dynamics of community structure and interspecific interactions [97,134], including distances to the entrances and/or the surface. Since the main parts of PPCS are organized along the Pivka River, this gives the opportunity to observe gradual changes in surface influences downstream. An open question is how surface and subterranean species exchange and interact along this gradient, and whether the aquatic community follows this gradient. Although it has been shown that the dynamics of the relationship between surface and subterranean taxa changes from the sink of Pivka River to the deeper parts of the cave [20], their interactions are still poorly understood. Sket [20] suggested that the degree of eutrophication affects the interactions between subterranean species and accidentals and that eutrophication may favor the competitive strength of surface invaders, a hypothesis indirectly supported in other studies [135,136].

The third attractive direction is ecosystem-level oriented research on nutrient cycling, energy budget, and its top-down effects on interspecific interactions and community structure. Early studies suggest a complex pattern of organic input, likely due to the multiple windows through which PPCS communicates with the surface [21,22]. Such additional inputs in the system can affect the gradual changes of organic matter downstream. Even though more complicated, these inputs may present replicas of starting points of organic matter input and possibilities for repeated studies of changes downstream from the sources, which present an attractive venue for research.

4.3. Challenges in Cave Management and Conservation

PPCS is the system with one of the longest tourist uses in the world. Management of the PPCS must balance protection of high species richness with potential tourism pressure and other surface threats. Sustainable management is a serious challenge in show caves with such high visitor numbers as the PPCS, where Postojnska jama alone receives up to 500,000 visitors per year. Direct consequences are microclimatic changes, and also the introduction of artificial light, which promotes the growth of the so-called “lampenflora” as well as airborne bacteria of anthropogenic origin [137] with unknown effects on biotas. The negative impact of tourist use on the spatial arrangement of animals has been demonstrated, as they move to more remote dark/less disturbed passages [12,42].

A greater and less controlled threat to the PPCS comes from the surface, through agriculture and overuse of fertilizers and pesticides, and pollution from industry [138]. The Pivka River transports pollutants deep into the cave system, which is especially critical during high flow that tends to homogenize chemical and bacterial parameters throughout the river system [139]. Their impact on troglobiotic fauna is not studied and monitored, not even for the most charismatic species, the olm (*Proteus anguinus*).

In order to detect any changes in the PPCS, regular monitoring of abiotic parameters and its inhabitants should be carried out. Chemical and physical parameters of percolating water and allogenic enrichment have been monitored for decades by experts from the Institute for Karst Research in Postojna [140]. Permanent monitoring of cave air temperature, humidity, wind flow, and CO_2 to determine human impact on the natural cave environment started in 2007. So far, only terrestrial fauna in the tourist part of Postojnska jama has been monitored since 2009. Monitoring should be extended to the entire PPCS and include aquatic fauna as well. This is especially important, considering that both *L. hochenwartii* and the olm are listed in the European Habitat's directive as species of special conservation concern, whose habitat must be protected and whose populations must be adequately monitored [141]. New methods, such as the use of DNA barcoding system for species identification [142], or protocols for metabarcoding [143] and e-DNA technologies [144,145], offer new opportunities for monitoring.

4.4. PPCS Outreach and Public Awareness

Public opinion can strengthen the long-term protection of a cave or, more generally, of subterranean habitats and their biotas. For the vast majority, tourist caves such as Postojnska jama are the only unique opportunity to personally experience the underground world. Such visits, associated with emotion, are an exceptional, albeit somewhat controversial, opportunity to engage visitors and inform them about the fragility and importance of subterranean habitats and their inhabitants, as well as about conservation issues. By restricting tourist use to a limited part of the PPCS, the rest of the system can be safeguarded from such visits, while benefitting from the personal experience gained by the visitors. This is an important prerequisite to affect their attitude toward conservation and positive view on the protection of the whole PPCS and subterranean biodiversity in general.

The fact that the PPCS is a global hotspot of subterranean biodiversity is an important opportunity to promote and present the uniqueness of subterranean environments. Steps in this direction have been made by establishing a vivarium near the entrance of Postojnska jama, an internal aquarium with olms inside the cave and two permanent exhibitions: the interactive exhibition Expo at Postojnska jama and a special speleobiological exhibition Karst Museum at Notranjska Museum Postojna.

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