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Subterranean Fauna of the Lukina Jama–Trojama Cave System in Croatia: The Deepest Cave in the Dinaric Karst

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Abstract: The Dinaric Karst is a global hotspot for subterranean diversity, with two distinct peaks of species richness in the northwest and southeast, and an area of a lower species richness in the central part. In this article, we present a species list and describe the ecological conditions of the Lukina jama–Trojama cave system, located in the central part of the Dinaric Karst. This cave system is the deepest and one of the most logistically challenging cave systems sampled so far in the Dinaric Karst. Repeated sampling resulted in a list of 45 species, including 25 troglobionts, 3 troglophiles, 16 stygobionts, and 1 stygophile. Most of the recorded species are endemic to the Velebit Mountain, while three species are endemic to the Lukina jama–Trojama cave system. Within the system, species richness peaks in the deepest third of the cave, most likely reflecting the harsh ecological conditions in the upper parts, including ice, cold winds, and occasional waterfalls. Milder and more stable deeper parts of the cave contain a rich subterranean species community, part of which is associated with two very distinct aquatic habitats, the cave hygropetric and the phreatic zone. The newly recognized hotspot of subterranean biodiversity in the central Dinaric Karst, which has emerged between the two known centers of biodiversity, further highlights the species richness in large cave systems, but also challenges the diversity patterns in the Dinaric Karst overall.

Keywords: Velebit Mt.; biospeleology; biodiversity; checklist; cave hygropetric; obligate cave species; troglobionts; stygobionts

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1. Introduction

Sampling subterranean fauna and describing the subterranean communities are challenging tasks. The majority of subterranean species live in habitats inaccessible to humans, such as permanently flooded zones or systems of narrow fissures, and voids in fractured rock [1]. Hence, species inventories remain incomplete even for the most well-known and best-explored cave systems. Restricted access to the subterranean environment, the so-called Racovitzan impediment [2], but see [3–5], remains the main obstacle in biospeleological research.

Caves are the easiest access points where humans can enter soluble rocky massifs and explore subterranean diversity. Compiling species lists demands coordinated actions of repeated collecting visits and taxonomic expertise. This is particularly challenging in large systems, especially those that traverse entire massifs and include deep vertical pits that require both technical expertise and psycho-physical preparedness. Large cave systems often contain high levels of habitat heterogeneity, which is an important predictor of species richness [6,7]. These systems can harbor a variety of terrestrial and aquatic habitats, including fissure systems, cave hygropetric or a permanently flooded phreatic zone. Moreover, deep cave systems experience strong depth-dependent environmental gradients in temperature, moisture, and food availability. Such gradients could, in theory, allow for species to spatially segregate at different altitudes [8–10]. Species inventories from such systems are particularly rare (see [8,11]); however, they remain the prime hotspot candidates, especially when located in a species-rich region.

The Dinaric Karst is a 650 km long limestone mountainous massif, that rises in the Western Balkans along the Eastern Adriatic coast. The entire region is recognized as one of the global hotspots of subterranean biodiversity [12–15]. Species richness along the Dinaric Karst is not evenly distributed and peaks in the northwest and southeast [4,5,16–18]. Four caves from Slovenia and Bosnia and Herzegovina are included in the list of subterranean biodiversity hotspots [19], while the area between the two centers, predominantly situated in Croatia, seems to be less species-rich [6,18,20].

Extensive sampling of Croatian caves over the last three decades, conducted mainly by researchers from the Croatian Biospeleological Society, has led to the recognition of several species-rich regions, e.g., the Ogulin–Plaški plateau dominated by subterranean aquatic species [18,21], and the Biokovo and Velebit Mountains, containing exceptionally rich terrestrial subterranean fauna [21]. However, the species inventories of these regions remain unpublished or are scattered across taxonomic papers, books, reports, or the so-called grey literature. For this reason, none of the caves in the central part of the Dinaric Karst have been listed as subterranean biodiversity hotspot, i.e., a cave inhabited by at least 25 aquatic and terrestrial obligate subterranean species [19].

Herein, we fill this gap by providing a species checklist for one of the deepest cave systems in the world, the Lukina jama–Trojama cave system (−1431 m), situated in the northern part of the Velebit Mt. In the years following its discovery, this cave system was the focus of both speleological and biospeleological research, resulting in numerous publications. However, while the speleological achievements were published in a comprehensive overview, e.g., [22], the biological data remained unpublished or scattered in narrowly focused scientific papers. In this paper, we compile both published and unpublished data, provide a comprehensive checklist of the fauna of the Lukina jama-Trojama cave system, and discuss its ecological and biogeographical significance.

2. Study Area

2.1. Northern Velebit

The Northern Velebit is the northernmost part of the 145 km long Velebit Mountain range, which stands out as the largest massif in the Dinaric Karst [23]. The uplifted karst plateau of the northern Velebit is mainly limestone and is composed of Jurassic carbonate rocks and massive calcareous breccias emerging from the Upper Paleogene to the Lower Neogene age [24]. The highest peaks of the plateau are 1600–1700 m a.s.l., while elevations of the karst poljes in the hinterland range from 400 to 500 m a.s.l. (Figure 1). The Lika and Gacka rivers flow across these karst poljes, and sink beneath the eastern Velebit foothills, resurging as coastal or even submarine springs along the Adriatic coast. Annual precipitation in the northern Velebit massif reaches up to 3000 mm [25], with a rapid water transfer through the limestone bedrock. The mean annual temperature on the plateau ranges from 3 to 8 °C, depending on geomorphological setting or elevation [25,26]. The distinctive surface relief with picturesque landscapes and the great diversity of karst features, including large collapsed dolines and extremely deep caves, together with the high biodiversity, were the reasons for the designation of the Northern Velebit National Park in 1999 [23].

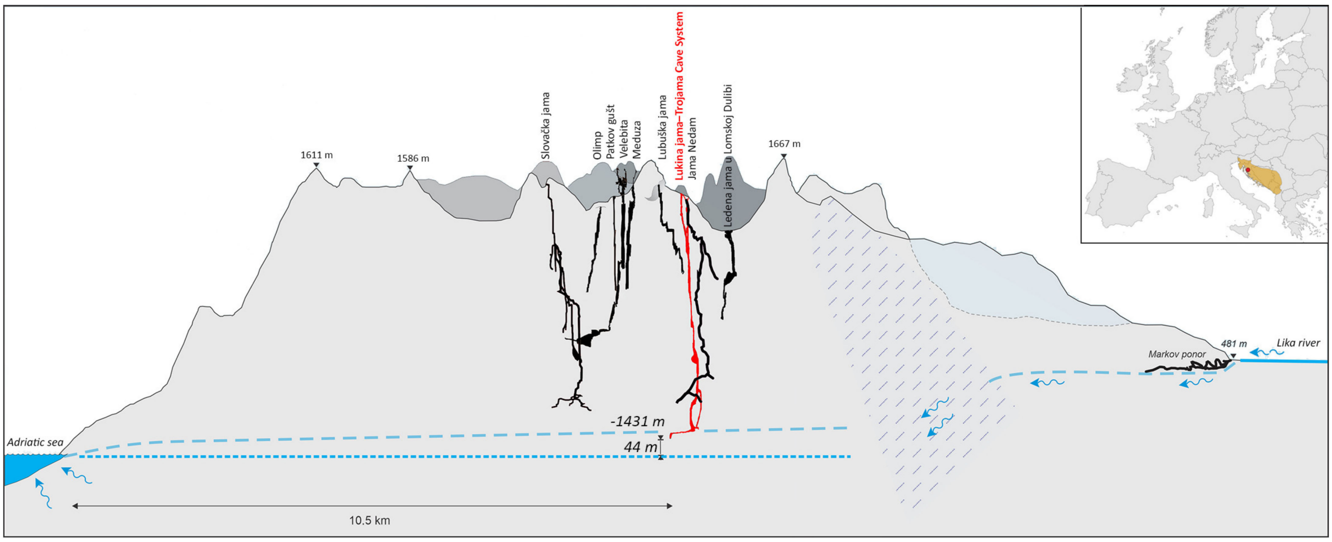

Figure 1. Cross-section of the northern Velebit, with sections of the deep caves and one of the sinkholes of the Lika river. The position of Lukina jama–Trojama cave system and its cross-section is emphasized in red; the area of the Dinaric Karst is marked in orange in the inset map. Modified from the original after Darko Bakšić. Used with permission.

More than 350 caves have been explored in the northern Velebit [27], but the caves for which the area is famous are its deep caves. Four caves exceed the depth of −1000 m and five others exceed the depth of −500 m (Figure 1). The vertical parts of the caves are predominantly of vadose origin, related to karstification processes of unbedded breccia [27], while only the deepest parts of the deepest caves might be of phreatic or epiphreatic origin. Large chambers (50–100 m in diameter) found in several caves at approximately 500 m a.s.l. [27] remain of uncertain origin and were, presumably, largely modified by collapse processes [26]. These chambers have a variety of terrestrial and aquatic habitats, and are important sampling sites for subterranean fauna. Among the deep caves of Velebit, the Lukina jama–Trojama cave system (−1431 m) stands out as the deepest cave in the whole Dinaric Karst.

2.2. The Lukina Jama, Trojama Cave System

The Lukina jama–Trojama cave system is located in the Hajdučki kukovi strict nature reserve in the Northern Velebit National Park. It was discovered in 1992 and explored in the following two years to a depth of −1392 m. At the time of its initial exploration, it was the 10th deepest cave in the world, and exploration of the sump at the bottom was one of the deepest dives in caves for a long time. It has been the subject of biospeleological, geological, hydrogeological, meteorological, and physical studies [22,26,28–33]. It is important from a historical point of view, as its discovery marked the initiation of intense speleological explorations of Velebit Mt., which resulted in the discovery of numerous impressive caves in the following decades.

The cave system is currently −1431 m deep and 3741 m long, and has two entrances (Figure 2): Trojama and Lukina jama, which open at 1475 and 1440 m a.s.l., respectively. The two cave channels join at about −550 m and form an extremely vertical cave morphology with a continuing sequence of shafts and very few chambers and ledges. The largest chamber, with a diameter of about 80 m, is located at −980 m (Figure 3). At the bottom, at a depth of about −1370 m, there is a small chamber with a lake and a sump (100 m a.s.l.). The phreatic channel was explored 120 m in length and a total depth of 60 m [34].

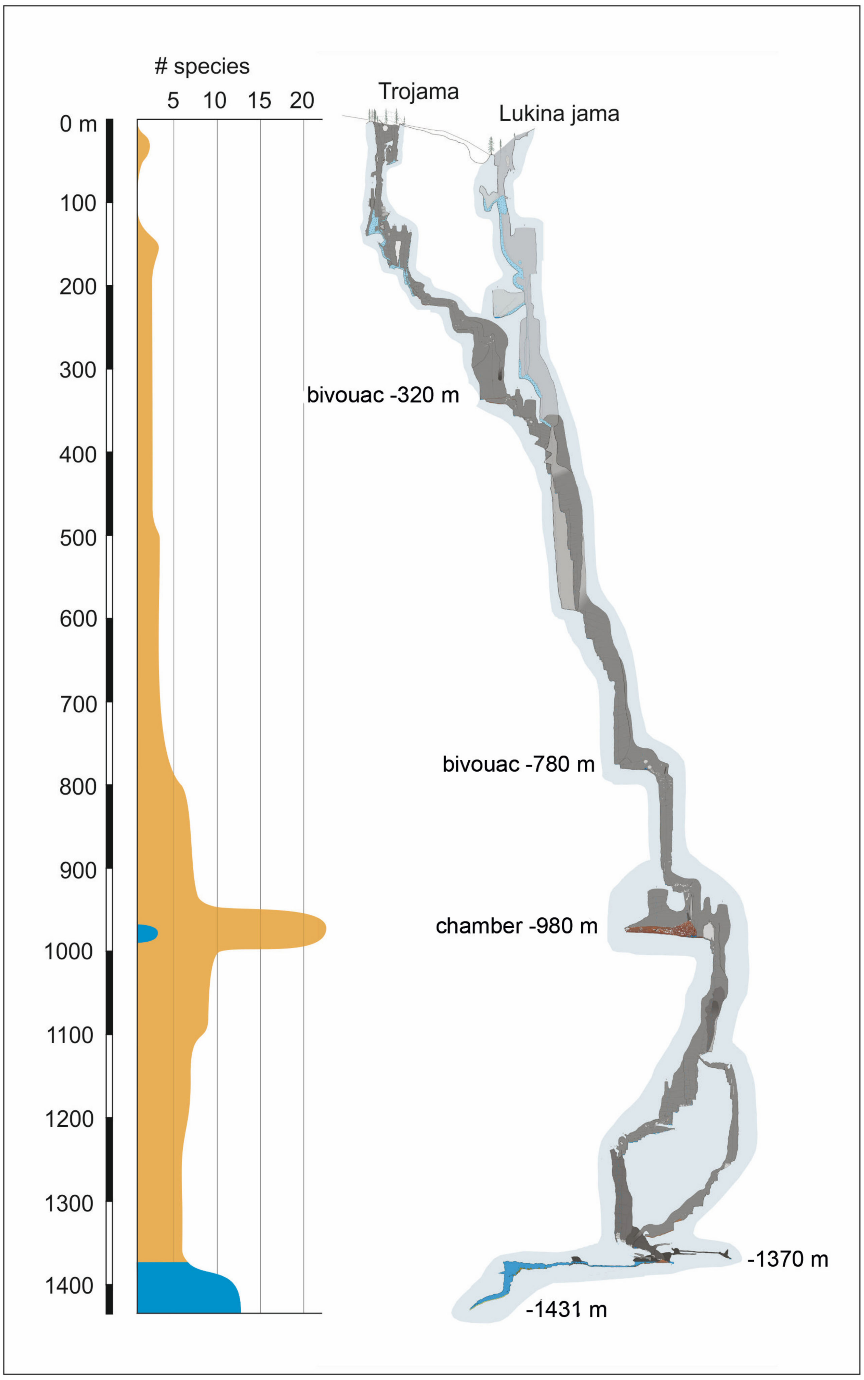

Figure 2. Cross-section of the Lukina jama–Trojama cave system with a histogram of vertical species richness distribution (orange, terrestrial species; blue, aquatic species). Cave map modified from the original after Darko Bakšić. Used with permission.

Studies of water dynamics and air circulation in the system suggest that they significantly alter the temperature profile of the system [26]. Two entrances and their morphology are open to a strong inflow of cold air in winter and a much weaker outflow in summer, resulting in the accumulation of ice in the upper parts of the cave. Intense air circulation ceases at a depth of 500 m. The snow, ice and ice crust accumulated in the passages reach a depth of 320 m in the Lukina jama branch, and 200 m in the Trojama branch (Figure 2). The cave system has a bimodal thermal gradient. From the top to a depth of 200 m, temperature gradually decreases from 4 °C to 0 °C in the summer, and from that point downward, rises again at the rate 0.39 °C/100 m, eventually reaching 5 °C at the bottom of the cave.

Figure 3. The large chamber at −980 m with bivouacs for researchers, the species-richest part of the system. Photo by Vedran Jalžić. Used with permission.

The upper parts of the system are fed mainly by percolating water, resulting in the first vadose streams just at −980 m and −1200 m. Therefore, the water regime of the system is mainly influenced by surface precipitation and snowmelt. During the rainstorms, some drip water areas turn into waterfalls, with a discharge of several tens to several hundreds of liters per second, especially in the lower parts of the cave [26]. The phreatic water in the siphon lake is under the influence of the vadose stream within the cave and broader watershed inflows [26]. Water tracing experiments in the northern Velebit revealed extremely complex groundwater drainage patterns [35]. The occasional inflow of groundwater from the broader area causes major floods in the bottom chamber and the channel above it. This was confirmed by year long water level monitoring, where the water rose rapidly by more than 100 m on one occasion, and by more than 20 m on another four occasions [26]. The water temperature of the vadose stream in the chamber at −980 m is constant and is around 3.1 °C, while in the siphon, it is between 4.5 and 7.5 °C [26]. Although drip water is present in many places throughout the cave, a permanent thin water film flowing over the walls, also known as the cave hygropetric [36], is present in the chamber at −980 m and near the syphone lake. Although these remain the only sites where it is reachable, it is possible that the cave hygropetric is also present in the upper parts, but remains inaccessible to researchers.

3. Materials and Methods

The biospeleological data presented in this paper have been accumulated over the course of three decades during caving expeditions in the Lukina Jama–Trojama cave system. In the 1990s, fauna was collected by a few cavers and biologists while they were exploring and mapping new channels. In more recent expeditions (2010, 2011, and 2013), dedicated teams of biospeleologists had each spent several days in the cave, collecting and surveying the subterranean biodiversity. Most of the data presented here were gathered during these expeditions.

Cave fauna was collected by hand using forceps in all the explored habitats. Baits were placed on the shaft walls near the ropes and in the horizontal parts of the channel. Baited pitfall traps were placed with an aqueous solution of sodium chloride as fixative. Adhesive tapes were used to collect the flying dipteran *Troglocladius hajdi*. Aquatic fauna was collected by hand using the plankton net, both in the vadose stream and phreatic water at the bottom. The fauna in the siphon lake was collected with traps for aquatic fauna and a Sket's bottle [37] during cave diving.

The collected material was identified to the lowest possible taxonomic level, and classified into the following categories: stygo-/troglobionts, stygo-/troglophiles, and stygo-/trogloxenes (Table 1). The categories were defined, following the definition of Sket [38], with a slight modification (we use the prefixes "stygo" instead of "aquatic troglo" and stygo-/troglophiles instead of eustygo-/eutroglophiles). Subtroglophiles and trogloxenes were scarce and not listed in the checklist.

Collection abbreviations: CBSS coll.—Croatian Biospeleological Society collection, Zagreb, Croatia; RO coll.—Roman Ozimec collection, Zagreb, Croatia; RS coll.—Rajko Slapnik collection, Slovenia; NHM coll.—Croatian Natural History Museum collection, Zagreb, Croatia; SubBio Lab coll.—SubBio Lab collection, Department for Biology, Biotechnical Faculty, University of Ljubljana, Slovenia.

4. Results

4.1. Checklist of the Lukina Jama–Trojama Cave System

The Lukina jama–Trojama cave system is both the best-studied and the most species-rich cave in the northern Velebit. The species list comprises 25 troglobionts, 16 stygobionts, 3 troglophiles, and 1 stygophile, listed in Table 1.

Table 1. Cave fauna of the Lukina jama–Trojama cave system. Ecology abbreviations: Sb–stygobiont; Sp–stygophile; Tb–troglobiont; Tp–troglophile. Species described from the Lukina jama–Trojama are marked with #. Undescribed species and genera are marked with *.

Taxonomic Group	Taxon	Ecology	Depth (m)	Distribution	Source
Porifera: Spongillidae	*Eunapius subterraneus* Sket and Velikonja, 1984 [39]	Sb	>1370	NW Dinarides	[32]
Gastropoda: Hydrobiidae	*Hauffenia* sp.	Sb	>1370	Velebit Mt.	[22]
Gastropoda: Hydrobiidae	*Lanzaia* sp.	Sb	>1370	Velebit Mt.	[22]
Gastropoda: Hydrobiidae	*Sadleriana* sp.	Sb	>1370	Velebit Mt.	RS coll.
Gastropoda: Acroloxidae	*Acroloxus* sp.	Sb?	>1370	NA	RS coll.
Gastropoda: Carychiidae	*Zospeum isselianum* Pollonera, 1887 [40]	Tb	800–1370	NW Dinarides	RS coll.
Gastropoda: Carychiidae	*Zospeum tholussum* Weigand, 2013 [31] #	Tb	980	northern Velebit	[31]
Gastropoda: Carychiidae	*Zospeum subobesum* Bole, 1974 [41]	Tb	800–1370	Dinarides	[22]
Gastropoda: Carychiidae	*Zospeum robustum* Inäbnit, Jochum & Neubert, 2019 [42]	Tb	800–1370	NW Dinarides	[42]
Bivalvia: Dreissenidae	*Congeria jalzici* Morton and Bilandžija, 2013 [43]	Sb	>1370	NW Dinarides	[43]
Polychaeta: Serpulidae	*Marifugia cavatica* Absolon and Hrabe, 1930 [44]	Sb	>1370	Dinarides	[22]
Clitellata: Erpobdellidae	*Croatobranchus mestrovi* Kerovec, Kučinić and Jalžić, 1999 [30] #	Sb	1370	northern Velebit	[30]
Clitellata: Erpobdellidae	*Dina.* sp. *	Sb	980	northern Velebit	SubBio Lab coll.
Clitellata: Haplotaxidae	*Haplotaxis* cf. *H. gordioides* (Hartmann, in Oken 1819) [45]	Sp	980	Holarctic	CBSS coll.
Palpigradi: Eukoeneniidae	*Eukoenenia* sp. *	Tb	980	northern Velebit	RO coll.
Acari: Rhagidiidae	*Rhagidia* sp. *	Tb	980	northern Velebit	[32]
Acari: Labidostommatidae	*Nicoletiella* sp. *	Tb	980	northern Velebit	[32]
Araneae: Dysderidae	cf. *Stalita* sp. *	Tb	980	Velebit Mt.	CBSS coll.

Table 1. *Cont.*

Taxonomic Group	Taxon	Ecology	Depth (m)	Distribution	Source
Pseudoscorpiones: Neobisiidae	*Neobisium* sp. *	Tb	980	northern Velebit	[32]
Opiliones: Nemastomatidae	*Hadzinia* sp. *	Tb	980	northern Velebit	RO coll.
Opiliones: Sironidae	*Cyphophthalmus* sp. *	Tb	980	northern Velebit	RO coll.
Isopoda: Trichoniscidae	*Androniscus* sp.	Tp	30	NA	CBSS coll.
Isopoda: Trichoniscidae	*Alpioniscus velebiticus* Bedek and Taiti, 2019 [46]	Tb	980–1370	Velebit	[46]
Isopoda: Trichoniscidae	Gen. * sp. *	Tb	800–980	Velebit	CBSS coll.
Isopoda: Asellidae	*Proasellus* cf. *P. slovenicus* (Sket, 1957) [47]	Sb	>1370	NW Dinarides	SubBio Lab coll.
Amphipoda: Niphargidae	*Niphargus arbiter* Karaman, 1984 [48]	Sb	>1370	Velebit Mt. and Lika	[32]
Amphipoda: Niphargidae	*Niphargus brevirostris* Sket, 1971 [49]	Sb	>1370	Velebit Mt. and Lika	[32]
Amphipoda: Niphargidae	*Niphargus croaticus* Jurinac, 1887 [50]	Sb	>1370	NW Dinarides	[22]
Amphipoda: Niphargidae	*Niphargus* sp. *	Sb	>1370	Lukina jama–Trojama	CBSS coll. & SubBio Lab coll.
Amphipoda: Niphargidae	*Chaetoniphargus lubuskensis* Karaman G.S. and Sket, 2019 [51]	Sb	980	northern Velebit	[51]
Decapoda: Atyidae	*Troglocaris* cf. *T. kapelana* Sket and Zakšek, 2009 [52]	Sb	>1370	Velebit Mt. and Lika	SubBio Lab coll.
Diplopoda: Polydesmidae	*Brachydesmus* sp.	Tp	30	NA	[32]
Diplopoda: Anthogonidae	*Haasia stenopodium* (Strasser, 1966) [53]	Tb	500–1370	NW Dinarides	[22]
Chilopoda: Geophilidae	*Geophilus hadesi* Stoev, Akkari, Komerički, Edgecombe and Bonato 2015 [32]	Tb	980–1100	Velebit Mt.	[32]
Collembola: Onychiuridae	Gen. sp. *	Tb	980–1370	northern Velebit	CBSS coll.
Collembola: Oncopoduridae	*Oncopodura* sp. *	Tb	980	Velebit Mt.	CBSS coll.
Collembola: Isotomidae	*Parisotoma* sp. *	Tb	980	northern Velebit	CBSS coll.
Collembola: Isotomidae	Gen. * sp. *	Tb	980	Lukina jama–Trojama	[32]
Collembola: Sminthuridae	*Disparrhopalites* sp. *	Tb	980	Velebit Mt.	[32]
Diplura: Campodeidae	*Plusiocampa* sp.	Tb	1370	northern Velebit	CBSS coll.
Coleoptera: Cholevidae	*Astagobius angustatus* (Schmidt, 1852) [54]	Tb	150–800	NW Dinarides	[22]
Coleoptera: Cholevidae	*Spelaeodromus pluto* (Reitter, 1881) [55]	Tb	150–800	Velebit Mt. and Lika	[32]
Coleoptera: Cholevidae	*Velebitodromus smidai* Casale, Giachino and Jalžić 2004 [56]	Tb	860–1200	northern Velebit	[56]
Diptera: Chironomidae	*Troglocladius hajdi* Andersen, Baranov and Hagenlund, 2016 [33] #	Tb	800–980	Lukina jama–Trojama	[33]
Diptera: Mycetophilidae	*Speolepta leptogaster* (Winnertz, 1863) [57]	Tp	980	Europe	CBSS coll.

4.2. The Fauna

The Lukina jama–Trojama is inhabited by a large number of endemic and evolutionary unique species (Figures 4–7), of which the ecological, phylogenetical and biogeographical significances are discussed below.

Scattered individuals of sponges were found in the middle part of the sump at the bottom of Lukina jama–Trojama. Using a molecular genetics approach, the sponges were identified as *Eunapius subterraneus* (Figure 6A). This stygobiotic species is distributed in the subterranean waters of the Dobra and Mrežnica rivers in the nearby Ogulin–Plaški valley and the adjacent regions [58]. The population in the underground parts of the Lika River basin, including Lukina jama–Trojama and Markov ponor, is the only one in the Adriatic Sea basin (all others are in the Black Sea basin). This species is known to occur in large aggregations and has a diverse habitus, ranging from small round to large flattened [58]. The sponges of Lukina jama–Trojama are up to 2 cm in diameter, spherical in shape, and have an irregular, wrinkled surface.

Figure 4. Troglobionts of the Lukina jama–Trojama cave system: (**A**) snail *Zospeum tholussum*; (**B**) Dysderidae spider; (**C**) harvestmen *Hadzinia* sp.; (**D**) mite *Rhagidia* sp.; (**E**) millipede *Haasia stenopodium*; and (**F**) centipede *Geophilus hadesi*. Photo by (**A**,**C**,**E**,**F**) Jana Bedek; (**B**) Branko Jalžić, and (**D**) Martina Pavlek.

Gastropods are the species-richest taxonomic group in this system. The empty shells of four stygobiotic species assigned to the genera *Hauffenia*, *Lanzaia*, *Sadleriana*, and *Acroloxus* were found in the sediment of the phreatic zone. In addition, four troglobiotic species of the family Carychiidae were recorded from −800 m to the bottom of the system: *Zospeum* *tholussum* (Figure 4A), which is also described in the system, *Z. isselianum*, *Z. subobesum*, and *Z. robustum*.

The cave-dwelling bivalve genus *Congeria* is a Miocene relict and endemic to the Dinaric Karst. It is one of the few cave-adapted bivalves found in the world [43,59]. Molecular phylogenetic analysis showed that the specimens found in the bottom sump belong to *C. jalzici* (Figure 6B), a species known from the sinkholes in the Lika River basin and a single submerged cave (spring) in Slovenia [43]. However, the morphological characteristics of the population from the Lukina jama–Trojama are surprising and unique. Their shell is thin and rounded in the ventral part, while all the other *Congeria* populations, regardless of species, have a much more robust and ventrally flattened shell. The particular morphology of the specimens is probably influenced by the specific environmental conditions in the sump. The absence of a turbulent water flow has possibly led to the development of a fragile, rounded shell.

Figure 5. Troglobionts of the Lukina jama–Trojama cave system: (**A**) springtail *Disparrhopalites* sp.; (**B**) springtail *Parisotoma* sp.; (**C**) beetle *Astagobius angustatus*; and (**D**) dipteran *Troglocladius hajdi*. Photo by (**A**) Marko Lukić; (**B**,**D**) Jana Bedek; and (**C**) Tin Rožman.

The cave tubeworm, *Marifuria cavatica*, is the only polychaete of the family Serpulidae adapted to freshwater caves (Figure 6C). *Marifugia* is a Pliocene relict and is widely distributed in the underground waters of the Dinaric Karst [60]; however, on the Velebit mountain, it is known only from two deep caves: Lukina jama–Trojama and Nedam. In certain areas, it forms massive colonies known as *Marifugia* deposits or Marifugia-tufa, which are classified as a special type of subterranean habitat, because it creates a substrate for many other species [61]. The population in Lukina jama–Trojama is not very large, but interesting because animals build their tubes perpendicular to the walls (Figure 6C). So, here they stick out into the water, unlike in most other places, where they are firmly attached to the walls with the entire length of the tube. This is another indication that the water flow in the sump is calm and steady.

Figure 6. Stygobionts of the Lukina jama–Trojama cave system: (**A**) sponge *Eunapius subterraneus*; (**B**) bivalve *Congeria jalzici*; (**C**) tubeworm *Marifugia cavatica*; (**D**) isopod *Proasellus* cf. *P. slovenicus*; (**E**) amphipod *Niphargus croaticus*; and (**F**) decapod *Troglocaris* cf. *T. kapelana*. Photo by (**A**) Vedran Jalžić; (**B**) Helena Bilandžija; (**C**,**F**) Jana Bedek; and (**D**,**E**) Tvrtko Dražina and Ana Komerički.

Two stygobiotic species of leeches belong to the family Erpobdellidae. *Croatobranchus mestrovi* was described from the Lukina jama–Trojama cave system (Figure 7D) [30] and is only known from four other deep caves of northern Velebit: Velebita cave system, Slovačka jama, Olimp, and Nedam. It is a peculiar species, easily recognizable by branchiae-like lateral processes, which made this leech a symbol of deep caves in northern Velebit. It has been found in the cave hygropetric or in drip pools with a water flow, with temperatures ranging from 4 to 6 °C [62]. They often move actively along the cave walls in a weak water flow, with their anterior part facing the water flow. The second species found in this system, based on preliminary data, is a new, yet undescribed species of the genus *Dina*.

Although spiders are a very species-rich group in the Dinaric caves, only one species is recorded for the system. The single specimen collected is actually a remnant of a dead spider, found in a chamber at −980 m. It belongs to the Dysderidae family, all of which are active hunters, meaning that they do not spin webs. This new, undescribed species is eyeless, and found in several other deep caves on Velebit Mt (Figure 4B).

Pseudoscorpions are highly diversified in the caves of Dinaric Karst; however, only one troglobiotic species of the genus *Neobisium* is recorded for the system. The species is also known from numerous caves on the high mountain plateau of the northern Velebit. It is probably a new, yet undescribed species morphologically similar to *N. svetovidi*. Recent molecular analyses from many caves of the Velebit Mt. revealed large intraspecific distances for this species [63].

Figure 7. Evolutionary and ecologically unique cave hygropetric specialists of the Lukina jama–Trojama cave system: (**A**) beetle *Velebitodromus smidai*; (**B**) amphipod *Chaetoniphargus lubuskensis*; (**C**) an undescribed isotomid springtail; (**D**) leech *Croatobranchus mestrovi*; (**E**) isopod *Alpioniscus velebiticus*; and (**F**) an undescribed trichoniscid isopod. Photo by (**A**) Branko Jalžić; (**B**) Ana Komerički and Tvrtko Dražina; and (**C**–**F**) Jana Bedek.

Harvestmen are represented by two new and undescribed species, attributed to the genera *Cyphophthalmus* and *Hadzinia* (Figure 4C). Both species are troglobiotic and troglomorphic. *Hadzinia* was also recorded in the caves on the northern slopes of the Velebit Mt.

Four isopod species from the families Trichoniscidae and Asellidae were recorded for the system. In the uppermost part of the cave, only females of the genus *Androniscus* were found, which probably belong to the species *A. roseus*, already recorded on the northern Velebit [64]. Two species endemic to the Velebit Mt., *Alpioniscus velebiticus* and a yet undescribed trichoniscid, were found in or near the cave hygropetric. *Alpioniscus velebiticus* (Figure 7E) is known across the Velebit Mt. mostly from the caves situated at higher altitudes [46]. The undescribed trichoniscid (Figure 7F) is known only from two caves in the northern Velebit, where it is associated to the cave hygropetric, and one cave in the southern Velebit, where it was recorded in the cave ponds. The preliminary identification of the aquatic *Proasellus*, suggests that it might belong to the species *P. slovenicus* (Figure 6D), which could extend the range of the species more than 100 km to the south.

Amphipods are represented by five species of the family Niphargidae. Two species, *Niphargus arbiter* and *N. croaticus* (Figure 6E), are large-bodied species, found in the lake at the bottom of the cave, and are distributed over a broader region [65–67]. Two other species, *N. brevirostris* and *Niphargus* sp., are smaller and more narrowly distributed. The former is a stouter species known from a broader region of Lika [49], while the latter is slender, presumably living in the flowing water, and may represent a new, yet undescribed species. The fifth species of the family has been described as *Chaetoniphargus lubuskensis* (Figure 7B) [51]; however, molecular phylogeny unambiguously places it within the genus *Niphargus* [68]. It was found in the cave hygropetric and in a small water pond in the chamber at −980 m. Its mouthparts imply it likely feeds on biofilm in percolating water or in the cave hygropetric, similarly to the genus *Niphargobates* [36].

Decapod crustaceans are represented by a single stygobiotic species, morphologically close to *Troglocaris kapelana*, found in the phreatic zone of the system (Figure 6F). This species has a wider distribution, including the areas of Velika Kapela Mt. [52] and the Lika region (unpublished data).

Millipedes are represented by two species. The most common is *Haasia stenopodium* (Figure 4E), found from −500 m to the bottom of the system. This genus, which encompasses only troglobiotic species, is endemic to NW Dinarides, with *H. stenopodium* having the largest range, from Nanos Mountain in western Slovenia, to the southeastern Velebit [69]. Juvenile specimens of the genus *Brachydesmus* were collected in the entrance part of Trojama, at a depth of −30 m.

The single centipede species recorded for the system is *Geophilus hadesi* (Figure 4F). This is only the second known troglobiotic species of the genus that is common in endogean habitats. It was collected in the chamber at −980 m, and also observed at −1100 m, but out of reach for collection. The species exhibits high troglomorphism and is known only from three deep caves on Velebit Mt. [32].

Five troglobiotic springtails, all new and yet undescribed species, are known from the system. Two species from the family Isotomidae are one of the few troglobiotic species of the family in the world. The first one is a new genus found in the cave hygropetric (Figure 7C). It has very thin and extremely elongated claws used for walking on the wet walls, a character shared with other hygropetricolous springtails, e.g., [70–73]. The second species belongs to the genus *Parisotoma* and is the first troglobiotic species of the genus that has a worldwide distribution (Figure 5B). All springtail species from the system exhibit a number of morphological traits typical for troglobiotic springtails (Figure 5A,B) [74]. Surprisingly, the species of the family Entomobryidae, otherwise species rich in the caves of the Dinaric Karst, were not found in the system.

The beetle fauna of the system, when set into a regional framework, is relatively poor. No subterranean representative of the tribe Trechini, which is otherwise very species-rich and -abundant in the Dinaric Karst, has ever been found in the system or any other cave in the vicinity. The other species-rich family, Leiodidae, is represented by three species. Two of them, *Astagobius angustatus* (Figure 5C) and *Spelaeodromus pluto*, are distributed in the northern part of the Dinaric Karst [75,76]. Both species are known exclusively from the caves located on high karstic plateaus, characterized by near-zero temperatures and often rich in ice formations [77]. The third species, the hygropetricolous *Velebitodromus smidai* (Figure 7A), is known only from a few caves in the vicinity of the system [56]. It was found in the deeper parts of the system, in places with a permanently existing cave hygropetric. Based on the present knowledge and the regional species pool [6,75], other troglobiotic species are expected within the system.

Two dipteran species were recorded at the depths between −800 and −980 m. The first is a chironomid *Troglocladius hajdi* (Figure 5D), endemic to the cave, and probably the only troglobiont in the world capable of flying [33]. Two specimens were collected by hand, while all other specimens were found trapped on the adhesive tapes placed on the walls of the −980 m chamber. Large and well-developed wings and halteres, as well as specimens that were found in the middle of the adhesive tape, suggest that the species is able to at least hover, if not actively fly. All specimens collected were females, indicating a possibility of parthenogenesis, a lifestyle not uncommon for chironomids living in extreme environments [78]. Little is known about its life cycle as no larvae were found, but shallow vadose streams with fine sediment in the chamber at −980 m that were not well sampled, are promising habitat for future sampling. The second dipteran species is a troglophile *Speolepta leptogaster*, which is widely distributed in Europe [79]. The obligate subterranean larvae spin silk nets on the cave walls, while short-lived adults are occasionally found in surface habitats [80]. Only larvae were collected in Lukina jama–Trojama, all within the chamber, at −980 m.

5. Threats and Conservation

The Lukina jama–Trojama cave system is located in a remote and difficult to access strict nature reserve Hajdučki and Rožanski kukovi, within the Northern Velebit National Park. Therefore, the entire surface area of the cave system and adjacent deep caves is well-protected from human impact. Thus, the habitats on the surface, below the surface and terrestrial deep cave habitats are in pristine condition. On the other hand, the phreatic zone, inhabited by a unique stygobiotic community, is threatened by the changes in the hydrological regime, caused by infrastructural and hydropower development. The most imminent threat is the construction of a dam for hydroaccumulation Kosinj, expected to be finished by 2028, which would build upon the existing Senj hydropower plant and the remaining hydropower potential of Lika river [81]. Velebit's underground aquifer is hydrologically connected to the Lika river, which sinks at its foothills. The hydrological regime of the Lika river has already been severely altered with construction of the first Kruščica reservoir for the same power plant. The extent of damage to the phreatic community of the Lukina jama–Trojama cave system is difficult to foresee, but it is likely that any further intervention in the hydrological regime of the Lika river could have lasting negative effects on this phreatic community, due to the change in the water regime, and lower nutrient input [82].

6. Discussion

The data presented in this paper reveal several peculiar features of the subterranean community of the Lukina jama–Trojama cave system: (i) a high proportion of endemic and obligate cave species; (ii) a distinct vertical distributional pattern and; and (iii) a high number of evolutionary and ecologically unique species associated with the cave hygropetric and the phreatic zone. Below, we discuss each of the three features and try to interpret them in light of the cave's morphology, ecology, and geographic position.

The fauna of the Lukina jama–Trojama cave system is characterized by both a high number of obligate cave species (41) and a high number of endemic species (Table 1). A relatively low share of troglophiles and trogloxenes can be partially attributed to sampling bias and harsh conditions in the upper parts of the cave (discussed below). Slightly less than half of the species are found within the broader region, namely 11 (27%) species in the broader Velebit–Lika region and 8 (20%) in the NW Dinaric Karst. Almost half of the recorded species (19 species, 46%) are endemic to the northern Velebit, and 3 of them have been reported so far only from this cave system, namely the amphipod *Niphargus* sp., dipteran *Troglocladius hajdi* [33], and an undescribed springtail genus. Nevertheless, we cannot rule out that these single-site endemics also live in other, insufficiently sampled caves of the northern Velebit. In accordance with the published data, stygobionts of the Lukina jama–Trojama cave system have larger ranges than troglobionts [12,16,43,58], largely corresponding with the hydrological connections of the deep groundwater aquifer beneath the Velebit Mt. and the Lika river [35].

The sampling revealed an easily discernible vertical distribution pattern of species richness. From the entrance to a depth of 800 m, we found a total of only five species (11%). The vast majority of the fauna (89%) was found in the deepest parts of the cave (Figure 2). As many as 26 species (58 %) were found in the zone between 800 and 1200 m, mostly in the large chamber at −980 m. Below −1200 m, 7 terrestrial and 14 aquatic species (47%) were found, the latter exclusively in the phreatic zone. Preliminary observations from nearby deep caves (Slovačka jama and Velebita cave system) indicate a similar depth-dependent increase in the species richness, although these caves harbor more species in the upper parts (unpublished data). These distributional patterns roughly resemble the vertical distribution of the species richness in deep caves in Slovenia, with more species found in the lower portions of the vertical caves [8]. This seems to be in contrast with the more than 2 km deep Caucasian Krubera Cave, where the highest number of species was found in the uppermost parts of the system (−70 m) [11], at least according to the currently available data for this large cave system.

The vertical distribution of the species richness in the Lukina jama–Trojama cave system could partially be attributed to the cave's morphology and its ecological characteristics. The upper parts are predominantly vertical, offering limited sampling possibilities. Considerable effort was made to search for fauna in these upper parts, especially in the areas in close vicinity of bivouacs, at the depths of 320 and 780 m, and by carefully examining the vertical walls during ascending. Despite these efforts, sampling success was negligible. It seems reasonable to assume that the low species richness reflects the ecological conditions in this part of the cave. The upper zone of the cave is ecologically harsh due to the confounding effects of the cold, wind, ice, and occasional waterfalls. The low mean annual temperature of the northern Velebit Mt. and high precipitation result in the accumulation of ice [83], the volume of which depends largely on the morphology of the cave entrances. The air circulation model proposed for the Lukina jama–Trojama cave system [26] explains how the temperature of the air and percolating water in the cave remains lower than the temperature of the karst massif itself. Up to a depth of approximately −200 m, the air temperature remains at about 0 °C, while a strong air circulation extends down to the depth of −500 m [28]. Moreover, heavy rainfall results in massive waterfalls with high discharge rates. The combination of low temperatures, ice accumulation and vertical water discharge makes the upper part of the system inhospitable for most of the subterranean species, and likely filters out the non-obligatory cave species. In contrast, environmental conditions stabilize in the large chamber at −980 m. Due to milder environmental conditions, but also a greater number of microhabitats comprising clay-like sediments, cave hygropetric, and vadose streams, the species richness increases in this zone. Finally, the chamber at −980 m has served as a main campsite, with several bivouacs for researchers, and was explored more thoroughly than other parts of the cave. In the deepest part of the cave, there is a strong species turnover from terrestrial to aquatic. The epiphreatic zone is mostly free of terrestrial species, possibly due to the devastating effects of periodic flooding, when the water level can rapidly rise over 100 m [26].

The third outstanding feature of the Lukina jama–Trojama cave system refers to a high number of evolutionary and ecologically unique taxa living in the two largely differing aquatic habitats, the cave hygropetric and the phreatic zone [84]. A combination of the geographic position and morphology of the cave is ideal for the development of a hygropetric habitat, characterized by rich microbial communities in the waters permanently flowing down the cave walls. The microbial communities are a sufficiently rich food source [85], and several species in this system have adapted to exploit them. Hygropetricolous species represent a case study of evolutionary convergence, as all of them share strongly modified mouthparts, used for the filtering or scraping of microbial communities, and claws [86,87], needed for standing and walking in a strong water current. The most remarkable cave hygropetric specialists in the Lukina jama–Trojama cave system are the leiodid beetle, *Velebitodromus smidai*, the amphipod, *Chaetoniphargus lubuskensis,* and the yet undescribed springtail genus. Additionally, several species are presumably bound to the cave hygropetric or habitats in its close proximity, e.g., the specialized cave leech, *Croatobranchus mestrovi*, the isopods, *Alpioniscus velebiticus*, and an undescribed trichoniscid, and several collembola species. In the northern Velebit, hygropetricolous species were usually found at depths greater than −500 m, indicating that this habitat develops only in the deep vadose caves, although this is not a general rule for hygropetricolous species [36]. In the deepest parts of the cave, permanently submerged channels of the phreatic zone are accessible only by cave diving. This habitat houses a unique subterranean community comprised of three filter-feeding species: (i) the cave clam, *Congeria jalzici*; (ii) the cave sponge, *Eunapius subterraneus;* and (iii) the cave serpulid, *Marifugia cavatica*. All three species represent the only (*M. cavatica*), or one of only a few subterranean lineages (*C. jalzici* and *E. subterraneus*) of the taxa otherwise rich in surface, marine, or freshwater representatives [40,88,89]. Moreover, filter-feeding animals are extremely rare among stygobionts, and Lukina jama–Trojama is one of only four caves in the world (unpublished data), all four located in the Dinaric Karst, where three filter-feeding cave-dwellers are known to coexist.

Despite the fact that the fauna of Lukina jama–Trojama is relatively well sampled compared to similar systems in the area, the list of species should not be considered complete, due to several reasons. The most obvious reason is the difficult access to the system, which allows for sampling only during logistically demanding speleological expeditions. Furthermore, the abundance of species in oligotrophic habitats is low [90] and the chances of finding a particular species are disproportionately low. An illustrative example is the results of the expedition in 2010. Although different taxa were found, all were collected in extremely low numbers, including the otherwise abundant Collembola. Five different Collembola species, represented by a total of only 29 specimens, were collected by hand in 32 working man-hours in the large chamber at −980 m, while not a single specimen was collected in baited traps. Some caveats in species inventory can also be attributed to taxonomy. Microcrustaceans such as copepods and ostracods were sampled, but not taxonomically studied. There are numerous undescribed (two new genera and 15 new species) or unidentified taxa awaiting further taxonomic evaluation, a process that may happen, if ever, with a substantial delay [91]. Nevertheless, additional species have been discovered for the system with each new expedition, and we can expect the species list to continue to grow. At the very least, there is a high probability that the species collected in neighboring deep caves, including a spider *Stalita pretneri* Deeleman-Reinhold, 1971 [92,93] a pseudoscorpion *Neobisium stygium* Beier, 1931 [63,94], and two hygropetricoulus species (a springtail *Tritomurus* sp. (unpublished data) and a beetle *Croatodirus casalei* Giachino and Jalžić, 2004 [56]), will eventually also be found in Lukina jama–Trojama.

This study did not confirm our hypothesis that species segregate at different altitudinal bands. Instead, most species were found in the deeper parts of the system. This might be attributed to the specific morphology of the cave and its ecological characteristics, and remains to be further tested in other deep cave systems. However, a great number of obligate cave species confirmed that the large cave systems, at least in the Dinaric Karst, indeed represent hotspot candidates. The results also reflect how advances in caving techniques and speleological research greatly increase our ability to sample much more complex and deeper subterranean habitats.

The comprehensive inventory of the species richness of the Lukina jama–Trojama cave system indicates that a seemingly lower species richness in the central part of the Dinaric Karst (see [6,16]) may be an artifact resulting from a limited access to caves in the mountainous area at higher altitudes and historical interest of biospeleologists the already-recognized cave biodiversity centers, such as the Vjetrenica cave [5] in the southeast and the Postojna–Planina cave system in the northwest [4]. The caves of central Dinaric mountain ridges, which might be as species-rich as the caves in the northwestern and southeastern parts of the Dinaric Karst, provide exciting possibilities and prospects for future discoveries.

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