

## Professor Boris Sket (1936–2023): the SpeleoBiologist and much more

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Professor Boris Sket (Fig. 1) passed away on May 7, 2023, in Ljubljana at age 86. Many of us will remember him as a great naturalist, with a broad interest in zoology, botany, evolution, ecology, biogeography, and his main passion: subterranean fauna. Ashes to ashes; however, his research legacy remains. It is our honor to look back on his life and work to say goodbye.

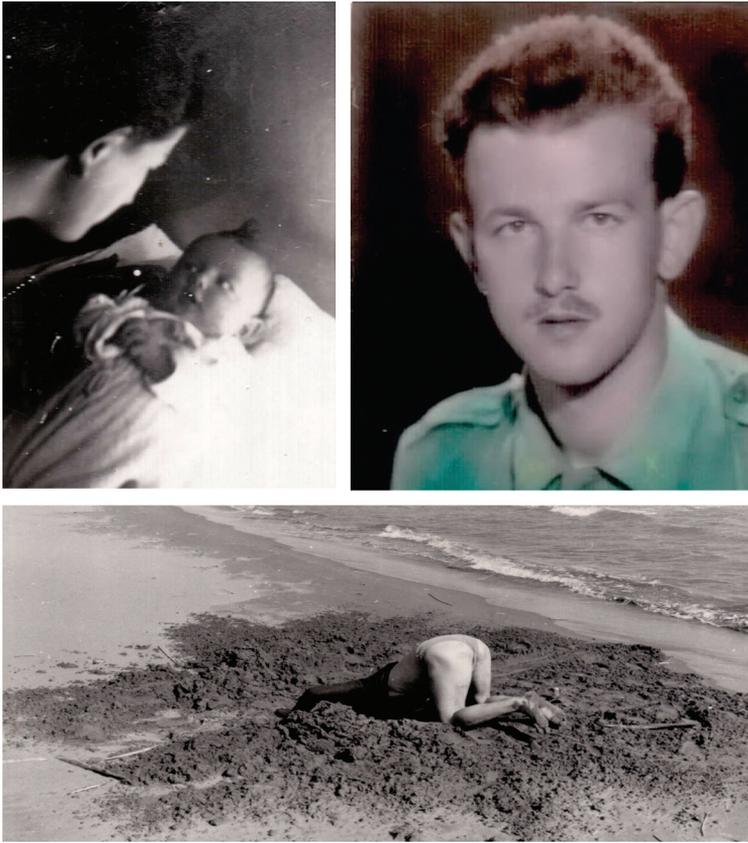
To truly grasp and appreciate his nearly seven decades of research, we must journey back to the aftermath of the Second World War, when the map of Europe was redrawn. The Kingdom of Yugoslavia underwent a formal transformation into the Socialist Federative Republic of Yugoslavia led by communist party. Although the Yugoslavian communist regime cannot compare to much harsher communist rulers in countries of Eastern Europe, the nation faced economic challenges, less porous borders, and greater difficulty in communicating with the outside world compared to today. Nonetheless, Yugoslavia encompassed almost the entire Dinaric Karst, nowadays well known as a global hotspot of subterranean biodiversity. Exploration of caves was at that time already established and much of this exploration was led by biologists (Sket 2008a); however, large parts of the territory were unexplored at that time and much of the fauna was unknown.



**Figure 1.** Boris Sket, 1936–2023 (Photo: Boris Sket archive).

Young Boris became acquainted with subterranean fauna early, amidst the turmoil of war, when Ljubljana was occupied and surrounded by barbed wires. During that period, he frequented the National Museum in Ljubljana (today Slovenian Museum of Natural History), where his attention was captured by two preserved specimens of subterranean crustaceans of the genera *Niphargus* and *Troglocaris*. Immediately following the war, he embarked on cycling expeditions with his grandfather to smaller caves in the vicinity of Ljubljana, where he was fascinated by whitish animals, most likely *Niphargus*. His early education was marked by frequent relocations between Ljubljana and Belgrade. Boris' professional journey into the exploration of subterranean life truly began with his enrollment at the University of Ljubljana, and his subsequent role as a teaching assistant to Professor Janez Matjašič (Box 1, Fig. 2).

The fieldwork activities at that time were far more time-consuming and relied heavily on improvisation compared with modern practices. Transportation options were limited, and commonly relied on trains and bicycles. The caving equipment was less sophisticated and under the development: the clothing resembled that of mountaineers, carbide flames preceded the powerful LED lamps of today, ladders ruled before ropes, homemade masks, pipes and air pumps were utilized before the advent of scuba diving gear. Nets, sieves, and filters were crafted at home with the assistance of his technical assistant, the malacologist and close friend France Velkovrh. One of Boris's most notable



**Figure 2.** Timeline of Boris Sket. Upper left: just arrived in 1936. Upper right: serving army near Valjevo, Serbia. Bottom: sampling interstitial near Ulcinj, Montenegro. (Photo: Boris Sket archive).

inventions was the so called “Sket bottle” (Chevaldonné et al. 2008; Sket 2018), a cleverly designed plastic bottle used for animal suction during snorkeling or diving. This period of field work importantly contributed to the accumulation of empirical evidence that the subterranean environment extends beyond caves, encompassing both the fissure systems of consolidated cracked carbonate rock and unconsolidated riverine sediments.

The Yugoslav regime was supporting nature exploration, although there was no imperative for publishing results. Much of Boris’ research results from that period was documented in what is now termed “grey literature”. Some of his findings were disseminated at international conferences and subsequently published in conference proceedings. Reports of his studies were submitted in multiple copies to funding authorities in Slovene language. Despite the absence of pressure to publish internationally, Boris’ research opus is impressive, both in terms of breadth and depth. His attitude toward life and work can be summarized in three words: passion, curiosity, and persistence. He was a biologist *par excellence*, a researcher of numerous interests, ranging from pure nature observation through the lens of a camera to taxonomy, ecology, evolution, and

**Box 1.** The academic career of Boris Sket.**Education:**

1961: PhD thesis entitled “Specialization of our freshwater isopods”; University program in Ljubljana (at that time named as Prirodoslovno-matematična fakulteta)

**Employment:**

1959–1969: Teaching assistant of professor Janez Matjašič.  
1969–1974: Assistant professor for the zoology and speleobiology.  
1974–2005: Full professor for the zoology and speleobiology  
2005–2013: Researcher.  
2013–2023: Retired yet active.

**Mentorship:**

10 PhD students  
5 MSc students  
25 Graduate students

**Professional activities at the University:**

1974–2012: Leader of the Research group for invertebrate zoology and speleobiology  
1981–1983: Vice-dean of the Biotechnical Faculty at the University of Ljubljana.  
1983–1985: Dean of the Biotechnical Faculty at the University of Ljubljana.  
1985–1987: Vice-dean of the Biotechnical Faculty at the University of Ljubljana.  
1989–1991: Rector of the University of Ljubljana.

**Other professional activities:**

1976–1980: President of Caving Society of Slovenia.  
1998–2011: Leader of research Program “Zoology and speleobiology” (P1–0184, funded by Slovenian Research Agency).  
2004–2008: President of the International Society for Subterranean Biology.  
2011–2023: A member of Slovenian Academy of Science and Arts  
2009–2023: A member of Bosnian Academy of Science and Arts

**Awards:**

Student’s award of France Prešern.

1965: Award of Boris Kidrič.  
1979: Order of labor, third class (silver wreath).  
1988: Honorary member of Yugoslavian Cave association.  
1991: Order of republic, third class (silver wreath).  
1995: Jesenko Award of Biotechnical Faculty of University of Ljubljana.  
2003: Zois Award for scientific excellence.  
2008: Golden award of Slovenian Caving Association.  
2010: Award for life work of Miroslav Zei of the National Institute of Biology.  
2016: Honorary membership of the International Society of Speleobiology.

**Editorial activities:**

1997–2022: Acta Biologica Slovenica  
2002–2023: Subterranean Biology  
2005–2023: Zootaxa

**Research output:**

Over 350 articles  
Over 570 bibliographic units (source: Slovenian bibliographic database)

conservation. While he was interested in both surface and subterranean life, the majority of his research efforts were dedicated to the latter. Over his long and fruitful life, he witnessed the transformation of the Dinaric Karst: from the pristine natural state during the pioneering years, to expanding urbanization, river channelization, damming and general degradation of the environment.

His contribution to science is impressive. Sometimes, he acted as the leading researcher, sometimes as a provider of data and ideas, and sometimes as a knowledgeable peer with immense field experience. Above all, he was a dedicated teacher who passed on his knowledge to successive generations of biologists of all formats and specializations. Here, we broadly expose his contributions to science, including work of his collaborators and students. We divided his opus into five arbitrary topic sections and a box summarizing his academic career.

## **Taxonomy & natural history**

Many researchers will remember Boris as a taxonomist of broad interests, delving into the taxonomy of species across numerous phyla. According to his own words, his taxonomic expertise was “an unwanted need rather than his primary research interest” on a way to comprehend the subterranean Dinaric fauna. Taxonomic descriptions were the *sine qua non* for the rest of his work. Indeed, many discoveries of Dinaric species can be attributed to his research efforts.

Boris advocated a pragmatic use of the biological species concept, wherein morphological characters served as hints to potential or actual reproductive barriers. He maintained skepticism towards the uncritical usage of the term “cryptic species” asserting that genuine morphological crypticity could not be reliably distinguished from inadequate morphological examination. He was playful and humorous in naming new species: the black olm was named “parkelj”, which is the Slovenian name of a traditional infernal figure accompanying St. Nicholas. Black with a red tongue, it resembles the black and red color combination in the non-troglophobic morph of the olm. His main taxonomical contributions are outlined in five subsections, and the list of taxa he described is available in Table 1.

### **Annelida: Clitellata**

Findings of leeches in Dinaric caves had two important consequences for Boris. First, he became one of the few global authorities in leech taxonomy, who curated several regional and global leech checklists (Sket 1986c; Sket and Trontelj 2008; Minelli et al. 2014), and served as a subject editor at *Zootaxa*. He studied distribution, ecology and taxonomy of glossiphoniid (Sket 1968), piscicolid (Sket 1985b) and several erpobdellid leeches (Sket 1968, 1981c; Sket and Šapkarev 1986; Sket 1989, 1992b), including the peculiar *Croatobranchus mestrovi* from deep caves of Velebit (Sket et al. 2001).

**Table 1.** List of taxa described by Boris Sket. Families and genera are described with G and F, respectively.

Classification	Taxon described	Category
<b>Porifera</b>		
Spongillidae	<i>Eunapius subterraneus</i> Sket & Velikonja, 1984	
<b>Cnidaria</b>		
Hydrozoa:	<b><i>Velkovrbia</i></b> Matjašič & Sket, 1971	<b>G</b>
Bougainvilliidae	<i>Velkovrbia enigmatica</i> Matjašič & Sket, 1971	
<b>Annelida: Clitellata: Rhynchobdellida</b>		
Erpobdellidae	<i>Dina eturpshe</i> Sket, 1989	
	<i>Dina krasensis</i> (Sket, 1968)	
	<i>Dina krilata</i> Sket, 1989	
	<i>Dina lepinja</i> Sket & Šapkar, 1986	
	<i>Dina dinarica</i> Sket, 1969	
	<i>Dina lacustris</i> Sket, 1970	
	<i>Dina montana</i> Sket, 1971	
	<i>Dina ohridana</i> Sket, 1968	
	<i>Dina svilesta</i> Sket, 1989	
	<i>Trocheta dalmatina</i> Sket, 1968	
Glossiphoniidae	<i>Glossiphonia complanata maculosa</i> Sket, 1968	
	<i>Glossiphonia pulchella</i> (Sket, 1968)	
Piscicolidae	<i>Cystobranchus paulowskii</i> Sket, 1968	
	<i>Piscicola hadzii</i> Sket, 1985	
<b>Arthropoda: Malacostraca</b>		
<b>Decapoda</b>		
Atyidae	<b><i>Ficticaris</i></b> Sket & Zakšek in Jugovic, Zakšek, Petković & Sket, 2019	<b>G</b>
	<i>Ficticaris serbica</i> Jugovic & Sket in Jugovic, Zakšek, Petković & Sket, 2019	
	<b><i>Gallocaris</i></b> Sket & Zakšek, 2009	<b>G</b>
	<i>Spelaecaris kapelana</i> Sket & Zakšek, 2009	
	<i>Spelaecaris neglecta</i> Sket & Zakšek, 2009	
	<i>Spelaecaris prasence</i> Sket & Zakšek, 2009	
	<i>Troglocaris anophthalmus legovici</i> Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	<i>Troglocaris anophthalmus ocellata</i> Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	<i>Troglocaris anophthalmus periadriatica</i> Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	<i>Troglocaris anophthalmus sontica</i> Jugovic, Jalžić, Prevorčnik & Sket, 2012	
	<i>Troglocaris bosnica</i> Sket & Zakšek, 2009	
Gecarcinucidae	<i>Sundathelphusa boex</i> Ng & Sket, 1996	
	<i>Sundathelphusa sottoae</i> Ng & Sket, 1996	
	<i>Sundathelphusa urichi</i> Ng & Sket, 1996	
	<i>Sundathelphusa vedeniki</i> Ng & Sket, 1996	
<b>Amphipoda</b>		
Anisogammaridae	<b><i>Fuxiana</i></b> Sket, 2000	<b>G</b>
	<i>Fuxiana yangi</i> Sket, 2000	
	<b><i>Fuxigammarus</i></b> Sket & Fišer, 2009	<b>G</b>
	<i>Fuxigammarus antepinosus</i> Sket & Fišer, 2009	
	<i>Fuxigammarus barbatus</i> Sket & Fišer, 2009	
	<i>Fuxigammarus cornutus</i> Sket & Fišer, 2009	
Bogidiellidae	<i>Bermudagiella bermudiensis</i> (Stock, Sket & Iliffe, 1987)	
	<i>Bogidiella gammariformis</i> Sket, 1985	
	<i>Bogidiella sinica</i> Karaman & Sket, 1990	
Gammaridae	<b><i>Dinarogammarus</i></b> Sket & Hou, 2018	<b>G</b>
	<b><i>Relictogammarus</i></b> Hou & Sket, 2016	<b>G</b>
	<b><i>Iberogammarus</i></b> Sket & Hou, 2018	<b>G</b>
	<i>Gammarus parvioculatus</i> Sidorov, Hou & Sket, 2018	
	<i>Gammarus troglomorpha</i> Sidorov, Hou & Sket, 2018	
	<i>Neogammarus gordankaramani</i> (Özbek & Sket, 2020)	

Classification	Taxon described	Category
Crangonyctidae	<i>Tadzocrangonyx alaicus</i> Sidorov, Hou & Sket, 2018	
Melitidae	<i>Melita mirzajanii</i> Krapp-Schickel & Sket, 2015	
Niphargidae	<b><i>Carinurella</i> Sket, 1971</b>	<b>G</b>
	<i>Carinurella paradoxa</i> (Sket, 1964)	
	<b><i>Chaetoniphargus</i> Karaman G.S. &amp; Sket, 2019</b>	<b>G</b>
	<i>Chaetoniphargus lubuskensis</i> Karaman G.S. & Sket, 2019	
	<b><i>Niphargobates</i> Sket, 1981</b>	<b>G</b>
	<i>Niphargobates orophobata</i> Sket, 1981	
	<i>Niphargobatooides lefkodemonaki</i> (Sket, 1990)	
	<i>Niphargus aberrans</i> Sket, 1972	
	<i>Niphargus brevirostris</i> Sket, 1971	
	<i>Niphargus carniolicus</i> Sket, 1960	
	<i>Niphargus dabarensis</i> Fišer, Trontelj & Sket, 2006	
	<i>Niphargus dohati</i> Sket, 1999	
	<i>Niphargus factor</i> Sket & G. Karaman, 1990	
	<i>Niphargus jadranko</i> Sket & G. Karaman, 1990	
	<i>Niphargus labacensis</i> Sket, 1957	
	<i>Niphargus liburnicus</i> G. Karaman & Sket, 1989	
	<i>Niphargus lourensis</i> Fišer, Trontelj & Sket, 2006	
	<i>Niphargus microcerberus</i> Sket, 1972	
	<i>Niphargus minor</i> Sket, 1957	
	<i>Niphargus multipennatus</i> Sket, 1957	
	<i>Niphargus numerus</i> G. Karaman & Sket, 1990	
	<i>Niphargus pachytelson</i> Sket, 1960	
	<i>Niphargus pectencoronatae</i> Sket & G. Karaman, 1990	
	<i>Niphargus pectinicauda</i> Sket, 1971	
	<i>Niphargus polymorphus</i> Fišer, Trontelj & Sket, 2006	
	<i>Niphargus pretneri</i> Sket, 1959	
	<i>Niphargus pupetta</i> (Sket, 1962)	
	<i>Niphargus rejici</i> Sket, 1958	
	<i>Niphargus rostratus</i> Sket, 1971	
	<i>Niphargus scopicauda</i> Fišer, Coleman, Zagmajster, Zwittnig, Gerecke & Sket, 2010	
	<i>Niphargus stenopus</i> Sket, 1960	
	<i>Niphargus subtypicus</i> Sket, 1960	
	<i>Niphargus transitivus</i> Sket, 1971	
	<i>Niphargus trullipes</i> Sket, 1958	
	<i>Niphargus vinodolensis</i> Fišer, Sket & Stoch, 2006	
Pseudoniphargidae	<i>Pseudoniphargus carpalis</i> Stock, Holsinger, Sket & Iliffe, 1986	
	<i>Pseudoniphargus grandimanus</i> Stock, Holsinger, Sket & Iliffe, 1986	
Seborgiidae	<i>Seborgia kanaka</i> Jaume, Sket & Boxshall, 2009	
	<i>Seborgia sanctensis</i> Jaume, Sket & Boxshall, 2009	
	<i>Seborgia vietnamica</i> Jaume, Sket & Boxshall, 2009	
Ingolfiellidae	<i>Ingolfiella (Tethydiella) longipes</i> Stock, Sket & Iliffe, 1987	
<b>Isopoda</b>		
Anthuridae	<i>Stygocyathura filipinica</i> (Botosaneanu & Sket, 1999)	
Asellidae	<i>Asellus (Asellus) aquaticus carniolicus</i> Sket, 1965	
	<i>Asellus (Asellus) aquaticus cyclobranchialis</i> Sket, 1965	
	<i>Asellus (Asellus) aquaticus irregularis</i> Sket, 1965	
	<i>Asellus (Asellus) aquaticus longicornis</i> Sket, 1965	
	<i>Proasellus anophthalmus bosnicus</i> (Sket, 1965)	
	<i>Proasellus coxalis nanus</i> Sket, 1990	
	<i>Proasellus deminutus</i> (Sket, 1959)	
	<i>Proasellus intermedius intermedius</i> (Sket, 1965)	
	<i>Proasellus orientalis</i> (Sket, 1965)	

Classification	Taxon described	Category
Asellidae	<i>Proasellus parvulus</i> (Sket, 1960)	
	<i>Proasellus slavus histriae</i> (Sket, 1963)	
	<i>Proasellus slavus serbiae</i> (Sket, 1963)	
	<i>Proasellus slavus styriacus</i> (Sket, 1963)	
	<i>Proasellus slavus zeii</i> (Sket, 1963)	
	<i>Proasellus slovenicus</i> (Sket, 1957)	
	<i>Proasellus vulgaris</i> (Sket, 1965)	
	<i>Remasellus</i> Bowman & Sket, 1985	
Atlantasellidae	<b>Atlantasellidae Sket, 1979</b>	<b>F</b>
	<b>Atlantasellus Sket, 1979</b>	<b>G</b>
	<i>Atlantasellus cavernicolus</i> Sket, 1979	
Brasileiriniidae	<b>Brasileiriniidae Prevorčnik, Ferreira &amp; Sket, 2012</b>	<b>F</b>
	<b>Brasileirinho Prevorčnik, Ferreira &amp; Sket, 2012</b>	<b>G</b>
	<i>Brasileirinho cavaticus</i> Prevorčnik, Ferreira & Sket, 2012	
Cirolanidae	<i>Sphaeromides virei mediodalmatina</i> Sket, 1964	
	<i>Sphaeromides virei montenigrina</i> Sket, 1957	
	<i>Turcolana lepturoides</i> Prevorčnik, Konec & Sket, 2016	
Lepidocharontidae	<i>Microcharon luciae</i> Sket, 1990	
Protojaniridae	<i>Anneckella srilankae rectecopulans</i> Sket, 1982	
	<i>Anneckella srilankae srilankae</i> Sket, 1982	
	<i>Enckella lucei major</i> Sket, 1982	
Sphaeromatidae	<b>Bilistra Sket &amp; Bruce, 2004</b>	<b>G</b>
	<i>Bilistra cavernicola</i> Sket & Bruce, 2004	
	<i>Bilistra millari</i> Sket & Bruce, 2004	
	<i>Bilistra mollicopulans</i> Sket & Bruce, 2004	
	<b>Merozoon Sket, 2012</b>	<b>G</b>
	<i>Merozoon vestigatum</i> Sket, 2012	
	<i>Monolistra (Microlistra) bolei</i> (Sket, 1960)	
	<i>Monolistra (Microlistra) bolei bolei</i> (Sket, 1960)	
	<i>Monolistra (Microlistra) bolei brevispinosa</i> Sket, 1982	
	<i>Monolistra (Microlistra) calopyge</i> Sket, 1982	
	<i>Monolistra (Microlistra) fongi</i> Prevorčnik, Verovnik, Zagmajster & Sket, 2010	
	<i>Monolistra (Microlistra) jalzici</i> Prevorčnik, Verovnik, Zagmajster & Sket, 2010	
	<i>Monolistra (Microlistra) pretneri</i> Sket, 1964	
	<i>Monolistra (Microlistra) pretneri pretneri</i> Sket, 1964	
	<i>Monolistra (Microlistra) pretneri spinulosa</i> Sket, 1965	
	<i>Monolistra (Monolistra) coeca intermedia</i> Sket, 1964	
	<i>Monolistra (Monolistra) monstrosa</i> Sket, 1970	
	<i>Monolistra (Monolistrilla) Sket, 1964</i>	
	<i>Monolistra (Monolistrilla) velkourbi</i> Sket, 1960	
	<i>Monolistra (Pseudomonolistra) bosnica</i> Sket, 1970	
	<i>Monolistra (Pseudomonolistra) hercegovinensis atypica</i> Sket, 1965	
	<i>Monolistra (Pseudomonolistra) hercegovinensis brevipes</i> Sket, 1965	
	<i>Monolistra (Pseudomonolistra) radjai</i> Prevorčnik & Sket, 2007	
	<i>Monolistra (Typhlosphaeroma) bericum hadzii</i> Sket, 1959	
	<i>Monolistra (Typhlosphaeroma) matjasici</i> Sket, 1964	
	<i>Monolistra (Typhlosphaeroma) racovitzae conopyge</i> Sket, 1964	
	<i>Monolistra (Typhlosphaeroma) racovitzae karamani</i> Sket, 1959	
	<i>Monolistra (Typhlosphaeroma) racovitzae pseudoberica</i> Sket, 1964	
Stenasellidae	<i>Magniezia studiosorum</i> Sket, 1969	
<b>Chordata</b>		
Amphibia: Proteidae	<i>Proteus anguinus parkelj</i> Sket & Arntzen, 1994	
Teleostei: Nemacheilidae	<i>Triplophysa longibarbata</i> (Chen, Yang, Sket & Aljančić, 1998)	

Second, the intricate leech taxonomy was frustrating. As he stated in his interview with Traudl Krapp in *Amphipoda Newsletters* 40, the unsolved taxonomy of erpobdellid leeches motivated him to integrate molecular methodology into taxonomic expertise. In the mid 1990-ies he initiated Peter Trontelj's study visit to Tübingen, where he acquired training in molecular systematics. Upon return to Ljubljana, Peter established a molecular laboratory within the Boris' research team. Molecular phylogenies offered a new perspective on leech taxonomy. Some lineages, such as Erpobdellidae, emerged as well-supported monophyla (Trontelj et al. 1996). In a similar line, fine scale analyses confirmed species status of morphological forms within the *Glossiphonia complanata* species complex (Verovnik et al. 1999). More commonly, however, molecular phylogenetic structure deviated from traditionally accepted groupings and challenged higher taxa such as Rhynchobdellidae (Trontelj et al. 1999), or unveiled inadequate taxonomy in erpobdellid genera *Dina* and *Trocheta* (Trontelj and Sket 2000).

### Crustacea: Decapoda

The cave shrimps of the genus *Troglocaris* are remarkable and common animals of the subterranean waters of the Dinaric Karst. Boris admired cave shrimps since he was a boy, but his contributions to knowledge about cave shrimps were mostly revisionary (but see Jugovic et al. 2019), confronting morphological and molecular variation of subterranean freshwater atyid shrimps in Europe. The molecular phylogeny of cave shrimps and surface atyids in Europe revealed unexpected phylogenetic relationships within the group, identified potential new species of cave shrimps and highlighted the necessity for taxonomic reassessment of the group (Zakšek et al. 2007). A comprehensive phylogeographic study of the species with holodinaric distribution pattern, i.e., *Troglocaris anophthalmus* species complex, showed that some large-ranged species are genetically deeply structured, possibly comprising several species (Trontelj et al. 2009; Zakšek et al. 2009). Under Boris' mentorship, PhD student Jure Jugovic utilized these phylogenetic insights to demonstrate that much of the morphological variation observed in cave shrimps is sex and age specific, that size alone is not indicative of an individual's age, and that adults represent the taxonomically most distinct stage in *Troglocaris* (Jugovic et al. 2010a). Furthermore, their research underscored that rostrum length, a traditionally important taxonomic character, is influenced by the presence of predatory olms, rendering it unreliable for species diagnosis (Jugovic et al. 2010b).

Using molecular phylogenies and reliable taxonomic characters, Boris and co-authors redefined the subgeneric structure of the genus *Troglocaris* (Sket and Zakšek 2009), described new species of cave shrimps (Sket and Zakšek 2009; Jugovic et al. 2011), as well as disentangled the species structure of the *Troglocaris anophthalmus* species complex (Jugovic et al. 2012).

### Crustacea: Isopoda

Many of Boris' contributions to isopod taxonomy can be considered as footprints of his cave explorations around the globe, including Africa (Sket 1969), Bermuda (Sket

1979a), Sri Lanka (Sket 1982a), Mediterranean region (Sket 1990b), Philippines (Botosaneanu and Sket 1999), New Zealand (Sket and Bruce 2004) and Brazil (Prevorčnik et al. 2012). These expeditions yielded unexpected finds that contributed to global taxonomy of Asellota, Cymothida, Sphaeromatida and Calabozoa, with descriptions of new species, genera and families (e.g. (Sket 1985a).

Nevertheless, Boris' systematic isopod research primarily focused on groups inhabiting the Dinaric Karst and broader Mediterranean Region. He authored the very first revisions of the taxonomy and distribution of surface and subterranean populations of *Asellus aquaticus* (Sket 1963, 1965b, 1994a), an isopod that subsequently became a model for studying cave colonization, morphological differentiation and speciation. Other contributions addressed taxonomic status and occurrence of cirolanids and sphaeromatids in a broader Mediterranean region. Boris's contributions to the knowledge of the relatively few cirolanids of the region were mostly faunistic (Sket 1964a; Delić and Sket 2015), while his taxonomic endeavors focused on partial revisions of generic structures, renaming, and the description of new genera (Prevorčnik et al. 2016; Sket and Baratti 2021).

By contrast, the subterranean sphaeromatids are a common and speciose group, distributed along Dinaric Karst, southern slopes of Alps and Tyrrhenian coast on Apennine Peninsula. Boris laid foundations of taxonomy and biology of subterranean sphaeromatids of the genus *Monolistra* from the Dinaric region, dividing it into subgenera based on sexual size dimorphism, defensive spine structures and degree of reduction of the uropods (Sket 1964b, 1965a, 1982b, 1986e; Prevorčnik and Sket 2007; Prevorčnik et al. 2010).

The marine origin of subterranean sphaeromatids intrigued him deeply. Decades ago, he collected a posterior half of an unknown sphaeromatid in the anchihaline cave Šipun near the town of Cavtat (Croatia). This piece of an animal showed a morphology potentially transitional between a marine ancestor and its alleged descendants from subterranean freshwater (Sket 2012). It has become some sort of holy grail, and several lab members had the mission to complement their holidays at the Adriatic coast with a visit to Šipun Cave. Unfortunately, with no luck yet, so Boris passed away while the riddle still unsolved.

Although terrestrial isopods are common in caves, Boris never looked into their diversity. However, he did provide support for studies conducted by other authors on terrestrial isopods. Nonetheless, he compiled a checklist of this group (Sket 1986d).

## Crustacea: Amphipoda

Amphipods were a particular passion of Boris (Fig. 3). He served in international consortia dedicated to compiling global amphipod checklists (Väinölä et al. 2008; Horton et al. 2023). A minor part of his taxonomic works can be associated with his expeditions, resulting in species descriptions from the families Bogidiellidae from China and Ecuador (Sket 1985c; Karaman and Sket 1990a); Sebidae from SE Asia (Jaume et al. 2009), Melitidae from Iran and Philippines (Sawicki et al. 2005; Krapp-Schickel and Sket 2015) and Pseudoniphargidae from Bermuda (Stock et al. 1987).



**Figure 3.** Left: The parkelj, or Krampus, from Boris' childhood memories, after which he named the black olm, *Proteus anguinus parkelj*. Right: Boris' favourite amphipods, *Niphargus balcanicus* (upper), and *Jugogammarus kusceri* (bottom). (Photo: Boris Sket archive).

More systematic research was devoted to two families, the predominantly subterranean Niphargidae and predominantly epigeal Gammaridae s. lat. The genus *Niphargus* was the one that attracted his attention and some of his earliest papers are reports on Niphargidae (Sket 1956, 1958, 1960). His research of niphargid biology revolved around a few key topics. He described several species, subspecies and genera (Sket 1974, 1981b; Karaman and Sket 1989, 1990b; Sket 1990a; Sket and Karaman 1990; Sket 1999b; Fišer et al. 2006a, 2007a; Sket and Karaman 2018; Karaman and Sket 2019). To contribute towards the complex taxonomy of the family, he trained his PhD student, Cene Fišer. Boris had an excellent overview of the niphargid morphological variation, including changes of morphology during development (Sket 1974; Fišer et al. 2008b). He dearly hoped that the high number of species within genus *Niphargus* could be classified into a few phylogenetically supported subgenera. To this end, he conducted several revisions with in-depth discussions on individual characters (Sket 1971, 1972), followed by a few partial cladistic revisions (Sket and Notenboom 1993; Fišer et al. 2006b, 2010) and pioneering attempts of web-based morphological taxonomy that were ahead of their time (Fišer et al. 2009b, 2009a). The first molecular phylogenies, however, revealed a repeated evolution of multiple convergences, with no reliable characters that could satisfactorily diagnose subgenera (Fišer et al. 2008a; Trontelj et al. 2009).

His interest in Gammaridae s. lat. manifested relatively late and was closely tied to his passion for the fauna of ancient freshwater lakes. His vivid interest for ancient lakes resulted in the descriptions of species from the gammaridean family Anisogammaridae from the Chinese lake Fuxian Hu (Sket 2000; Sket and Fišer 2009). An important breakthrough in gammaridean research was a global phylogenetic analysis of the Gammaridae s. lat., conducted in collaboration with Chinese researches. In this study was shown that gammarids colonized freshwater multiple times and subsequently diversified in it (Hou et al. 2011), yet diversification patterns of different lineages varied between evolutionary stasis and rapid diversifications corresponding to adaptive radiations (Hou et al. 2014). These influential studies fully exposed the extent of the taxonomic complexity of Gammaridae s. lat., which encompass several morphological distinct yet phylogenetically non-justified families and genera (Hou and Sket 2015; Sket and Hou 2018b). The phylogenetic framework prompted several attempts to revise the taxonomic structure of the family (Hou and Sket 2015; Sket and Hou 2018a), as well as discussions on taxonomic status of several species complexes (Mamos et al. 2014; Sidorov et al. 2018; Sket et al. 2019; Hou et al. 2022).

## Other taxa

The Dinaric stygofauna is renowned for its exotics, which include suspension feeders like sponges, subterranean hydroids, clams, tube worms, and notably, the olm, the only European subterranean amphibian. Boris made significant contributions to the taxonomy and overall understanding of all these species.

Boris described the first troglobitic sponge, *Eunapius subterraneanus*, which was later primarily studied by his teaching assistant, Milan Velikonja. Together, they compiled an overview of the distribution and taxonomic status of both obligate and non-obligate subterranean sponges (Sket and Velikonja 1986).

The only Dinaric subterranean hydrozoan was discovered accidentally in preserved samples. This weird animal was initially noticed by Boris' technical assistant, France Velkovrh. When he reported his finding to Boris and their superior, Prof. Janez Matjašič, his report was met with disbelief. Subsequent examinations confirmed the presence of the subterranean species in the Rak Channel of the Planinska jama (Postojna Planina cave system). In recognition of France Velkovrh's contribution, the enigmatic cnidarian was named as *Velkovrhia enigmatica* (Matjašič and Sket 1971).

Although Boris was not the primary describer, his work played a crucial role in the recognition of the unique subterranean clam *Congeria kusceri*. The species was described in 1962 by Professor Jože Bole. At that time, malacologists considered *Congeria* to be an extinct genus, known only from diverse and widespread fossil records. The original description of the species was in Slovene, which led to it being overlooked internationally. The collaboration with Brian Morton resulted in a systematic revision of morphology and extensive review of the biology of this living fossil (Morton et al. 1998). Later on, Boris challenged the validity of its classification within the genus *Congeria*, and proposed it be reclassified under the extant genus *Mytilopsis* (Sket 2011). This proposal, however, received little attention and is not consistent with molecular phylogeny.

Boris made significant contributions to our understanding of the natural history of the olm through several influential papers. Most notably, he described the non-troglo-morphic form discovered in the late 1980s in Bela Krajina, naming it *Proteus anguinus parkelj* (Sket and Arntzen 1994; Arntzen and Sket 1996, 1997). The discovery of the black proteus was a major surprise, and Boris openly admitted that he “envied Andrej Mihevc who actually caught the first specimen.” The description was augmented by allozyme polymorphism data, which was the standard molecular taxonomic tool of that time. Based on distributional evidence, Boris hypothesized that i) the olm was a recent, post-Pleistocene colonizer of caves, ii) which colonized caves in several colonization events, from iii) the ancestral surface populations that were already genetically differentiated, and iv) that subterranean populations convergently evolved a similar morphological phenotype (Sket 1997).

Finally, his curiosity extended beyond the metazoan life: he encouraged the first explorations of the microbial composition of the “cave gold” in Slovenia (Megušar and Sket 1977). Recognizing the importance of biofilm, he kept eyes open to pursue this topic. His patience was paid-off decades later, with two studies. The first follow up of the early explorations of cave gold revealed a completely unknown bacterial flora in the Slovenian cave Pajsarca (Pašić et al. 2010). The second study meticulously explored the physical and biological structure of a sprout-like biofilm from Vjetrenica, uncovering a diverse microbial flora and the complex physical structure of cortex and medulla of these sprouts (Kostanjšek et al. 2013).

## The origin and evolution of subterranean fauna

The question of the origin of subterranean organisms was a recurring theme in Boris' discussions, albeit in various contexts. He viewed evolution as a fundamental aspect of the scientific work in speleobiology. His primary questions regarding most speleobiological phenomena were “how or why did it develop, why did it happen—to be different from the epigeal?”

The origin of subterranean organisms was a topic of lively debate in the 1970s and the 1980s. Researchers recognized the relatedness between subterranean aquatic organisms and both freshwater and marine faunas, suggesting its dual origin. Boris hypothesized that Dinaric subterranean aquatic fauna derived i) directly from marine ancestors, ii) directly from the freshwater ancestors, and iii) from marine ancestors via transitional surface freshwater phase. He inferred the epigeal ancestry of Dinaric subterranean fauna based on his observations of global species distributions. The olm as an amphibian, clearly derived from freshwater species (Sket 1997). Likewise, the origin of subterranean water lice (*Asellus aquaticus*) or *Synurella ambulans* in presence of surface populations was not in question. The cave tube worm (*Marifugia cavatica*) is a marine element, that presumably colonized freshwater through anchialine caves or submerged springs. This hypothesis was consistent with molecular phylogeny indicating that the close relatives of the cave tube worm are *Ficopomatus* living also in the Adriatic Sea. Importantly, *Ficopomatus* species live in a wide range of salinities, from fully marine to

brackish waters (Kupriyanova et al. 2009). An intriguing case presented subterranean sphaeromatid isopods. Sphaeromatidae are predominantly a marine crustacean family. However, Boris noted that the distribution of some species followed the boundaries of paleodrainage basins, leading him to assume that marine species initially colonized surface freshwater, dispersed, and speciated in the surface realm before subsequently colonizing the subterranean realm (Sket 1986b).

Boris argued that subterranean realm was colonized independently on different occasions, refereeing, for example, to morphology and distribution of water lice and olm (Sket 1994a, 1997; Turk et al. 1996). This hypothesis was supported later by molecular phylogenies (Verovnik et al. 2004). He suggested that the varying degrees of morphological similarity between subterranean organisms (in comparison to surface ancestors) resulted from convergent evolution during cave colonization (Sket 1985c, 1997; Turk et al. 1996). Generally, Boris was critical of comparisons between distantly related surface and subterranean species, advocating for model systems comprising closely related species, ideally sister pairs (Simčič and Sket 2019, 2021). To this end, he encouraged research on *Asellus aquaticus*. The efforts of his PhD students and close associates, Simona Prevorčnik, Rudi Verovnik and Peter Trontelj, resulted in Europe-wide phylogeography and extensive morphometrics of water lice providing the evidence that i) Dinaric region acted as a refugium during Pleistocene glaciations, ii) most subterranean populations are genetically completely isolated from adjacent surface populations despite occasional contact, and iii) water lice colonized caves on several occasions relatively recently (Sket 1994a; Verovnik et al. 2003, 2004, 2005). Morphological analyses revealed a rather uniform morphology of surface populations (Prevorčnik et al. 2009), while subterranean populations showed substantial differences from surface ones, including the lack of eyes and pigment. Nevertheless, subterranean populations varied among different caves, suggesting imperfect convergence due to differences among subterranean habitats (Turk et al. 1996; Sket 1997; Prevorčnik et al. 2004).

Boris vividly disagreed with many peers who hypothesized that cave animals no longer evolve. He supported his claims with evidence from various cases, including species living in cave hygropetric environments and *Niphargus* amphipods. Cave hygropetric is a habitat of a permanent weaker or stronger current flowing along the vertical cave rock. Boris became aware of this peculiar subterranean habitat when he noted that some species were regularly found in it (Sket 2004). Despite being unrelated, e.g., beetles and amphipod crustaceans, these species shared characters such as prehensile claws and filter-like mouthparts. This similarity suggests that cave hygropetric is a distinct habitat within the subterranean environment, and some specialized subterranean inhabitants exploit its resources (Sket 2004). A different, yet compatible line of reasoning was used to explain the enormous morphological variation in the amphipod genus *Niphargus*. Boris suggested that *Niphargus* variation in morphology could be associated with ecological differentiation (Sket 1999a). Phylogenetic analyses suggested that much of this variation cannot be attributed to cladogenetic events alone (Fišer et al. 2008a). Many morphologically similar species evolved multiple times (Trontelj et al. 2009). These cases of convergence within entire subterranean clades indicated that the vague term “subterranean environment” comprises replicated subterranean habi-

tats with similar selection pressures, and ongoing evolution within the subterranean realm. The proximal mechanism driving morphological variation could be attributed to heterochrony (Fišer et al. 2008b).

## **Biodiversity patterns and biogeography**

Since his early career, Boris paid attention to data collection and data management. His systematic collection of species distributions in the Western Balkans predated the computer era. The very first records were kept in registers on data-cardboards. These were later digitized in MS Word and MS Excel files. The systematic storage using relational databases began when Maja Zagmajster enrolled in her PhD program, resulting in the development of the SubBioDB database (Zagmajster et al. 2012).

Boris was deeply interested in biogeographical and biodiversity patterns at different scales, asking, for example, where the areas with the highest numbers of troglobionts are, what the general biodiversity patterns are, how much these patterns can be trusted, and which factors shaped them. He advocated that species richness needs to be corrected by the size of a region, and demonstrated that the Dinaric Karst was a global hotspot in subterranean species richness. In studies of biodiversity patterns, he served as both a collaborator and a primary investigator. His biogeographic opus revolved around the distribution of species-rich caves and regions, and biodiversity patterns within the Dinaric Karst.

## **Species-rich caves and species-rich regions**

In 2000, David Culver and Boris Sket published one of the most influential papers in subterranean biology, addressing a straightforward question: how many “species-rich” caves, each counting 20 or more troglobionts are there, and where in the world they are (Culver and Sket 2000). By introducing the arbitrarily defined measure of “richness” or “hotspot,” this paper enabled the scaling of any faunistic list and established a comparative framework for studying species richness in individual caves. It marked a milestone in the exploration of subterranean hotspots and patterns of subterranean biodiversity. Noteworthy, the paper already indicated that most of species-rich caves are located outside the tropics, at mid-latitudes.

Data from Slovenian caves facilitated further pioneering spatial studies led by David Culver. An analysis of Slovenian subterranean species richness showed that the spatial position of hotspots was stable and could be predicted from the position of species-rich caves, that the species composition of the region is far from complete (Culver et al. 2004a) and that the length of cave passages, their altitude and depth may predict terrestrial species richness (Culver et al. 2004b). These regional studies grounded considerations of the first global analysis that eventually resulted in another influential hypothesis of “mid-latitude ridge of high subterranean species richness”, stating that the regions with the highest numbers of species were aligned along mid-latitudes, presumably reflecting the availability of habitat and high productivity on a surface (Culver et al. 2006).

## Dinaric Karst as a global hotspot in subterranean biodiversity

Spatial representations of the collected data on the map of the Western Balkans brought Boris to three main findings.

First, the patterns of subterranean terrestrial and aquatic fauna differ. While terrestrial species richness peaks in the NW and SE, aquatic species richness is highest in the NW (Sket 1994b; Sket et al. 2004a). Detailed analyses decades later corroborated this observation, even after taking into account the spatial extent of analysis and sampling bias (Zagmajster et al. 2008, 2010; Bregović et al. 2019).

Second, Boris recognized that subterranean taxa in the Western Balkans can be classified into five major biogeographic groups (Sket 1994b). Some taxa, such as the olm, cave shrimp and tube worm had holodinaric distribution, spanning from the northwest margins of the Dinaric Karst to the political border between Herzegovina and Montenegro for *Proteus* and *Marifugia*, and even beyond for *Troglocaris*. This distribution was subsequently confirmed in later studies, although recent research acknowledges that these patterns pertain to the genus or species complex level (Sket 1997; Fišer et al. 2007a; Zakšek et al. 2009). Other groups of taxa were found to inhabit smaller areas within the Dinaric Karst, displaying a merodinaric distribution, which encompassed the northwest, southeast, epi-, and paralittoral compartments of the Dinaric Karst. Apart from these, Dinaric Karst inhabit also transdinaric species, which extend their distributional ranges beyond the Dinaric Karst, either in southern Europe or in the southeastern Mediterranean region (Sket 1994b).

Third, Boris hypothesized that distribution patterns are primarily associated with geological history, whereas recent ecological conditions and dispersal play only minor roles. He observed that some species distributions follow paleo-drainages rather than recent ones (Sket 1986b, 2002). He assumed that distributional patterns of the subterranean species were often shaped already on the surface, prior the surface ancestor in multiple colonization events evolved into subterranean descendant (Sket 1994b). By comparing distributional patterns of surface and subterranean relatives, he suggested that distribution of Dinaric subterranean species should be associated with disjunct karstification centers of the Dinaric Karst, the extent of the Pannonian Sea and drying up of the Paratethys, the Messinian Crisis, and Pleistocene glaciations (Sket 1981a, 1988, 1994b). Calibrated molecular phylogenies subsequently provided additional evidence that much of the Dinaric fauna pre-dated the Pleistocene (Trontelj et al. 2007).

On a local scale, Boris acknowledged the significance of ecological dynamics, which emerged as an interplay between interspecific competition and ecological specialization. His analyses of fauna associated with anchialine caves (Sket 1977, 1986a) and thermal water (Sket and Velkovich 1981a) provided indirect evidence that physical and chemical properties of water could deterministically shape species distribution. In many papers he assumed a covariation between the degree of species ecological specialization and species competitive strength, resulting in outcompeting weaker generalists by more specialized species (Sket 1981a, 1986a). He never doubted the role of interspecific relationships and used it as a *post hoc* explanation for distribution of many species (Sket 1986a), as a

mechanism for maintaining allopatric distributions (Sket 1994b) and as a possible driver of the colonization of the subterranean realm (Sket 1981a, 2002). His later research showed that the outcome of the interspecific relationship between surface and subterranean species might be less predictable than previously thought (Fišer et al. 2007b).

## Ecology

The properties of subterranean environment such as darkness, oligotrophy and stable conditions have rendered ecology an inevitable part of subterranean biology. Understanding the diversity of ecological factors within the subterranean realm was probably pivotal for Boris' views on imperfect convergent evolution (previous section), and also shaped his opinion on threats to subterranean ecosystem. Boris examined the interaction between organism and its environment from two aspects.

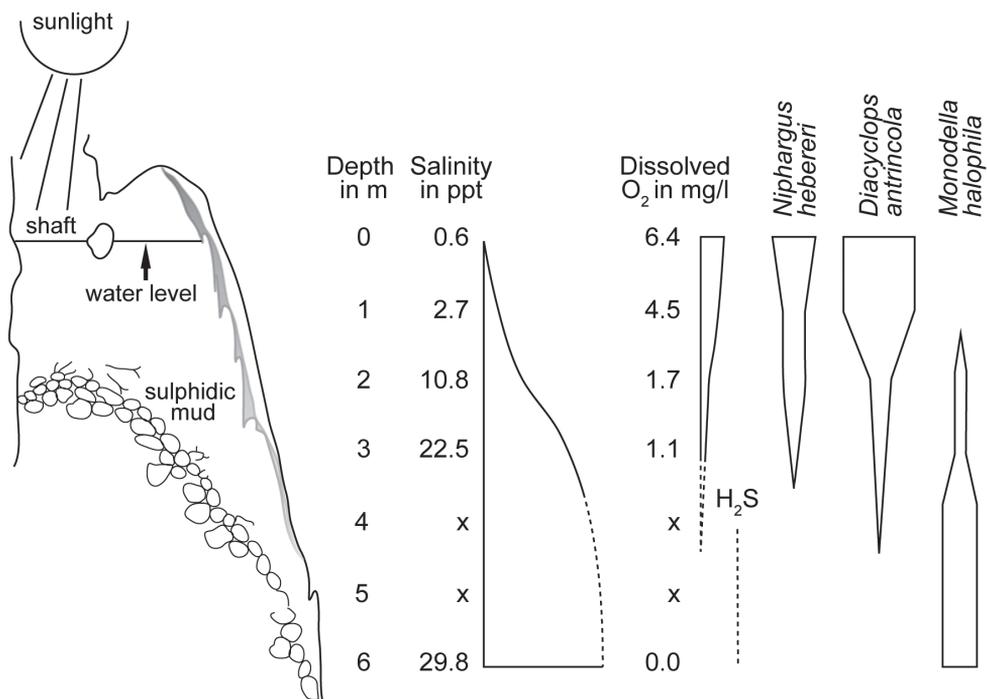
The old question, how to treat species found in a cave, Boris addressed theoretically (Sket 2008b). In his review, he was seeking for the simplest compromise among existing classifications of cave organisms, and proposed criteria for their delimitation based on the ecology of species' life cycles. An essential takeaway from his own observations was the necessity for rigorous testing to determine the ecological status of a species, emphasizing that conclusions should not be based solely on superficial impressions. He highlighted that troglobionts may not necessarily exhibit troglomorphism, and conversely, surface-dwelling animals can lack eyes.

In addition, Boris studied the variation of ecological conditions within the subterranean ecosystems in conjunction with community composition. He significantly advanced our understanding of sinking streams, anchihaline caves, fissure systems, and cave hygropetric. Sinking streams were explored in Postojna-Planina cave system between 1965–76 (Sket 1970, 1979b; Sket and Velkovich 1981b). Sket and collaborators regularly monitored 16 sampling sites along the Pivka River. They measured annual variation in temperature, oxygen, nitrates and bacterial oxygen consumption, as well as community structure. Apart from the updated checklist of the system and vicinity (Sket 1979b), they showed daily and annual temperature fluctuations, gradually declining in dependence of distance from sink and water volume, i.e. the impact from the surface penetrated deeper into cave system at high water level and strong currents. Moreover, they showed that water during its flow through the cave gets oxygenated, whereas nitrogen wastes remain intact (Sket 1970). These studies were a basis for a Slovenian-Brazilian bilateral project 50 years later, with the aim of geographically broadening the study system and evaluating the impact of decades of anthropogenic activities on subterranean biota. Boris was the leader of the Slovenian team, the results still pending the final publication.

As a part of his investigation of the Postojna-Planina cave system, Boris paid focused on water drips. In collaboration with Anton Brancelj and Cvetka Žagar, they showed that these waters harbor unique communities, primarily dominated by copepod crustaceans (Sket 1981b; Sket et al. 2004b). The study allowed the discovery of

a point endemic, *Niphargobates orophobata*, found in a single jet of percolating water. Their findings underscored the exceptional nature of the fauna inhabiting percolated water and significantly contributed to our understanding of epikarst and water-filled fissure systems (Sket 1981b).

Boris conducted pioneering research on the ecology of anchihaline caves globally, focusing on several caves along the Adriatic coast (Sket 1986a, 1996b) (Fig. 4). Water chemistry measurements clearly showed three layers of water: bottom marine, uppermost freshwater and an intermediate, thin layer of halocline with depleted oxygen and rapid transition from poly- to oligohaline conditions. Each of these layers comprised unique ecological habitat, each supporting its own fauna. Using comparative data, Boris elegantly demonstrated that species vertical distribution within the anchihaline water column reflected the interplay between species needs for abiotic environment and interspecific interactions. For example, the amphipod *Niphargus hebereri*, predominantly found in fresh- and only rarely in brackish water, preferred freshwater layer despite its tolerance for mesohaline water; its distribution mostly reflected species' habitat choice. By contrast, the thermosbenacean *Monodella halophila* was found in a presumably predation-free zone within the halocline layer, although it lives in fresh-water. The distribution of this species was indicative of its generalistic nature and weak competitiveness (Sket 1986a, 1996b).



**Figure 4.** Ecological stratification of water column in anchihaline caves. Boris was one the first who studied the vertical stratification of abiotic factors and with it associated community structure. After Sket 1896.

## Conservation biology

Boris advocated that subterranean fauna comprises an important part of global and Slovenian natural heritage. His analyses of Slovenian subterranean fauna revealed that the proportion of subterranean species in Slovenia surpassed that found on a global scale (Sket 1999a, 1999c). An important part of his research was devoted to recognition of threats and processes that could aid in the protection of subterranean natural heritage.

He early realized that cave fauna is threatened by the anthropogenic disturbance originating at the surface. One of his early notifications was that of organic pollution in the subterranean flow of the Pivka River in the Postojna-Planina Cave system. This pollution led to an influx of immigrants from the surface and the subsequent disappearance of specialized subterranean species. Boris presumed that eutrophication weakened surface-subterranean barrier resulting in altered community structure and increased interspecific competition pressure on subterranean species (Sket 1970).

Most of subterranean species are endemic (Bole et al. 1993). This view was further rectified by systematic analyses conducted within the European project PASCALIS (Deharveng et al. 2009). Many species live only in small areas, and subterranean communities are characterized by a high beta diversity (Malard et al. 2009), leading to high global (gamma) diversity. Species with large distribution ranges - i.e., larger than 200 km - are often taxonomic artifacts (Trontelj et al. 2009). Boris argued that endemism, in conjunction with K-strategies, makes subterranean fauna vulnerable (Sket 1999a, 1999c).

To actively contribute to the protection of subterranean fauna, Boris undertook several initiatives. He prepared a series of checklists (Sket 1986f; Sket et al. 1991, 2004a) and conducted assessments of the endangerment status for various species in Slovenia, including leeches (Sket 1992c, 1996a), crustaceans (Sket 1992d; Sket and Brancelj 1992), amphibians (Sket 1992e), and the other species from groundwater (Sket 1992f). Together with David Culver, Boris provided recommendations for the monitoring of caves, advocating for the standardization of sampling effort using fixed time-person units, as well as the use of baiting of terrestrial pitfall traps and aquatic traps, as well as the potential utilization of the capture-mark-recapture method, with a caution note that an increase of population size may indicate eutrophication (Culver and Sket 2002). He also developed criteria and provided a list of caves as habitat type "caves not open to the public" of the Annex II of the Habitat's Directive, that are part of Natura 2000 network in Slovenia.

Several efforts were made to safeguard species-rich caves (Sket 1992a) and/or regions (Michel et al. 2009). Boris had ambitious plans that aimed to establish a network of species-rich regions along the Dinaric Karst, ultimately seeking UNESCO protection. Unfortunately, these efforts were in vain. Boris firmly believed that protecting Slovenian rich-natural heritage is our moral imperative. The message he frequently reiterated was "There is no reason to be proud of our natural heritage, as long the Pivka River draining through the global subterranean hotspot of Postojna-Planinska Cave system, remains polluted".



**Figure 5.** Field work. (Photo: Boris Sket archive).

## The outreach

Boris stood out as one of the most prominent and influential zoologists in Slovenia. As a professor at the University of Ljubljana, he played a pivotal role in shaping the education of numerous generations of biology students and teachers. While teaching courses such as Invertebrate Zoology and Evolution, he also introduced the subject of “Subterranean Biology” into the biology curriculum. Under his mentorship, ten PhD students, five MSc students, and 25 graduate students successfully completed their studies. Many of these individuals have become respected zoologists in various research fields. Among these, we must mention Milan Velikonja, who studied subterranean sponges, Anton Brancelj, who established the model of epikarst and became one of the world-leading taxonomists for microcrustaceans, Tone Novak, who studied cave fauna outside Dinaric Karst with an emphasis on opilionid taxonomy and physiological adaptations, and the research team SubBioLab.

Beyond his teaching and research endeavors, he also paid attention to broader audience interested in natural sciences. He regularly contributed to the popular science magazine “Proteus,” sharing his insights and knowledge with a wider readership. Furthermore, in the 1970s, he edited a series of identification keys for various groups of animals, making valuable information accessible to enthusiasts and researchers alike. Together with Meta Povž, he co-authored a comprehensive book on Slovenian fishes in 1990. This impressive

volume detailed the Slovenian fish fauna, providing descriptions and insights into the biology of various species. Moreover, Boris was a writer and co-editor of the expansive monograph “Živalstvo Slovenije” (The Fauna of Slovenia). This exhaustive volume presented Slovenian fauna in an accessible and comprehensive manner, covering anatomy, ecology, and diversity, catering to students and naturalists alike. Lastly, he authored a high school textbook on Evolution, further contributing to science education at various levels.

Boris influence extended beyond the biological and naturalist communities. Through his writings in daily newspapers, he persistently advocated for the protection of our natural heritage, with a voice of a man who eyewitnessed the transformation of society and environmental degradation. He was one of the giants, whose shoulders allow us seeing further.

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## Supplementary material I

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