



The nature of biodiversity in hypogean waters and how it is endangered

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Abstract. The specialised aquatic hypogean, i.e. stygobiotic, fauna has been recognised in some regions moderately rich. Slovenia, the broader Dinaric region, and Europe are particularly rich with about 7–8% of all Metazoa and about 40% of Crustacea species being stygobionts. The hypogean biotic diversity is in general predominantly a crustacean diversity. The high number of stygobiont Crustacea–Malacostraca species can be explained by the near absence of Insecta as well as by their high endemism and sometimes additional specialisation, i.e. the spatial and ecological partition of the environment by the species. Although one cave system may exceptionally shelter up to 40 stygobiont species, they are distributed there into separate associations. Among more than 2000 described stygobiont Malacostraca species, which include close to 950 Amphipoda, the species numbers within some genera are very high (e.g. *Niphargus* with 275 spp.). With 10 orders represented the higher taxonomic diversity of stygobiont Malacostraca matches that of fresh waters or the sea. Comparison of some faunas shows that the limiting factors for biodiversity might be the lower ecological diversity of habitats and restricted food resources underground, both brought about to a high degree by the darkness and absence of plants. Being K-strategists, stygobionts are endangered by any sudden changes in their environment. In the case of an increased food input by modest organic pollution, they can be outcompeted by energetically demanding but competitively stronger recent immigrants from surface.

Key words: biodiversity, endangerment, hypogean waters, stygobios

Introduction

Following a long period of looking upon cave fauna as poor and the hypogean habitats as simple (or non-diverse), unfavourable and restraining (Vandel 1965: p. 325), papers are accumulating nowadays falsifying these designations. Among distinguished advocates of the new paradigm are Danielopol and Rouch (1991) also Rouch and Danielopol (1997), and Stoch (1995) with his very studious analysis supporting a new 'adaptive zone model' that explains the hypogean diversity.

Being a student of an area particularly rich in hypogean fauna, the Dinaric karst with surrounding alluvial areas, I can only appreciate this change (Sket 1991, 1996) and support it with additional data. However, I feel that the conclusions are biased and overemphasised by an inappropriate, somehow reduced, subject of comparison (e.g. surface Crustacea *versus* hypogean Crustacea; Stoch 1995). I will try to show the

high diversity in a less emphasised manner by comparing it with the whole surface faunas which are indeed much more complex in composition.

Methods

For basic comparisons of complete faunas, published faunistic lists were mostly used (Illies 1978; Botosaneanu 1986; Peck 1998) irrespective of some of them being out-dated. Although a number of new stygobiont species were described after the second edition of 'Limnofauna Europaea' (Illies 1978), this was mainly due to non-European countries.

From species list (subspecies excluded) in Illies (1978), all the mentioned taxa specifically from outside Europe (columns X, 24, 25, Y) were not taken into account; parasites, epizoans, water-surface dwellers and inhabitants of wet soil were bypassed as much as possible. To avoid bigger mistakes, all species with the ecological designation '1' (hypogean waters) or '1, 2' (hypogean waters and springs) were taken as stygobionts, to compensate for a part of those stygobionts that have been found by accident only in springs ('2'). All combinations of '1' with other designations were taken as pertaining to stygophiles or stygoxenes. Original data were not corrected or supplemented although we know that a number of insects occur sporadically in cave waters and approximately 15 fish species are regular visitors there.

In order to discuss Crustacea–Malacostraca as a model group, data from Botosaneanu (1986) (excluding the few non-stygobionts in that lists), were supplemented with data from more than 270 taxonomic papers (not listed in the references). In all regions and in all higher taxa new discoveries are a routine (comp. Stoch 1995). In larger groups (Bathynellacea, Isopoda, Amphipoda, Decapoda) the numbers of species known today appear to be 10–35% higher than in 1985 and the percentage of newly named genera is the same. Yet, the picture of the European limnofauna has been changed by this increase only to a minor degree. The newly obtained numbers cannot be absolutely complete but neither can they be far out. The data for Amphipoda are now accessible as a supplement to 'Stygofauna Mundi' (Botosaneanu 1986) in the Internet site '<http://www.odu.edu/~jrh100f/amphipod>'. Equally prepared data for other groups are in the author's files.

Some data were updated for the hypogean aquatic fauna of Slovenia, while its surface fauna was newly summarised consulting some faunistic lists; some groups had to be estimated taking into account the few investigated subgroups and their share in the European fauna. The list of higher Malacostraca taxa (order, family) was taken from Bowman and Abele (1982) but parts of the system are largely unsettled, like on the family level in Amphipoda (comp. Barnard and Barnard 1983) or on the ordinal level in Isopoda (comp. Brusca and Wilson 1991).

It is understood that all these numbers are very inexact and of a transitory value. Although criteria distinguishing stygobionts are inexact, the real nature of many

species virtually unknown and numbers of taxa continuously changing, most higher numbers and percentage values in tables were not rounded off. To avoid comparing the incomparable, only numbers from the same source (and of the same age) were compared. Data from 'Limnofauna Europaea' were used for comparison of the richness of epigeal and hypogean faunas in Europe; data from 'Stygofauna Mundi' (Botosaneanu 1986) were used for comparisons between stygofaunas of different regions in the world; the updated list of stygobiotic Malacostraca was used to check the degree of (in)completeness of any temporary data set as well as to check the taxonomic (i.e. phylogenetic) levels of diversity. This is the source of the apparent and annoying differences between numeric data in different parts of this paper. Please note that 'Slovenia' in the sense of 1.7a in 'Stygofauna Mundi' is not the whole Republic's territory as understood in some other parts of the paper.

Data and discussion

How high is the diversity of the European stygobiotic fauna?

According to 'Limnofauna Europaea' (Illies 1978), the European aquatic fauna (Table 1) comprises over 12 500 metazoan species, approximately 50% of them being Insecta (either as larvae or also as adults). There are only two stygobiont Dytiscidae (Coleoptera) in Europe and there are only few stygobiont insects in the world (Botosaneanu 1986). The number of troglophile or troglone insect species tolerant to hypogean habitats seems not to be negligible but is largely unknown. There is only one stygobiont amphibian species and approximately 15 troglone fishes; some of them, mostly from the genera *Phoxinellus* and *Leuciscus*, and the monotypic *Aulopyge*, are orderly seasonal immigrants. Approximately 17% of 'lower' invertebrate (i.e. excluding Insecta) species are stygobionts but the percentage does vary through subgroups; it is highest in Crustacea (over 40%) where it varies again between zero, in primitive Branchiopoda (i.e. with the exclusion of Cladocera), and 100% in Bathynellacea.

Stygobionts are much less evenly distributed throughout Europe than the non-stygobionts. Their concentration seems to be higher in the extensively karstified peri-Mediterranean region and the highest in the Dinaric region (Sket et al. 1991; Sket, in press: Table II). In Copepoda Cyclopoida, one of the most omnipresent groups, the species number relation between stygobionts and non-stygobionts could be 50:50 (according to the 'Limnofauna' corrected by a factor from Stoch 1995) in the Dinaric region. Unfortunately, there are very few lists of surface fauna for this region, therefore comparisons are difficult.

According to more recent data in 'Stygofauna Mundi' (Botosaneanu 1986), the number of stygobiont taxa (species and subspecies) in 153 400 km² of the Dinaric region was 396 while in 20 000 km² of Slovenia, largely overlapping with the former,

Table 1. Relations of aquatic fauna to hypogean habitats. For Europe, strictly according to Illies (1978); amphibian and brackish water species included, parasitic, Caspian and extra-European excluded (details in Methods). For Slovenia, different sources; all totals include some estimated values.

Free living aquatic fauna	Europe				Slovenia			
	All aquatic species	Stygo-xenes & stygo-philas	Stygo-bions	Stygo-bions in % of all species	All aquatic species	Stygo-xen. & stygo-phil.	Stygo-bions	Stygo-bions in % of all species
Porifera	14	1	0	0	4	1	1	25
Cnidaria	15	0	1	7	4	1	1	25
Turbellaria	418	17	66	16	15	5	5	33
Nemertini	7	0	1	14	1	0	0	0
Rotatoria	1330	8	0	0	*300	x	0	0
Gastrotricha	151	0	0	0	x	x	0	0
Nematoda	602	28	76	13	*100	x	?8	x
Nematomorpha	78	0	0	0				
Bryozoa + Kamptozoa	20	1	0	0	7	1	0	0
Tardigrada	36	4	2	5	x	x	x	x
DIVERSIA	2671	59	146	5	430	8	15	x
Gastropoda	549	3	106	19	91	8	46	50
Bivalvia	45	0	1	2	21	2	1	5
MOLLUSCA	594	3	107	18	112	10	47	42
ANNELIDA	228	10	27	12	78	22	10	13
CHELICERATA: Acarina	961	20	138	14	x	x	x	x
Copepoda: Calanoida	74	0	2	3	10	0	1	10
Copepoda: Cyclopoida	114	13	60	53	48	15	19	39
Copepoda: Harpacticoida	245	20	171	70	44	15	18	41
Anostr. + Notostr. + Conchostraca	49	0	0	0	3	0	0	0
Cladocera	143	7	1	1	50	10	2	4
Ostracoda	391	13	68	17	47	5	8	17
Bathynellacea	41	0	41	100	2	0	2	100
Decapoda	16	0	5	31	8	1	3	37
Isopoda	168	7	105	62	40	2	32	88
Amphipoda	297	33	140	47	52	5	40	77
Thermosb. + Mysid. + Cumacea	38	0	9	24	?1	0	?1	x
CRUSTACEA	1576	93	602	38	305	53	126	41
Ephemeroptera	204	0	0	0	> 74	> 2	0	0
Plecoptera	341	0	0	0	97	> 3	0	0
Odonata	114	0	0	0	74	0	0	0
Heteroptera	65	0	0	0	20	0	0	0
Coleoptera	938	0	2	0.2	190	5	0	0
Trichoptera	817	0	0	0	201	> 3	0	0
Diptera	3824	0	0	0	*1000	> 20	0	0
Other Insecta	16	0	0	0	x	x	0	0

Table 1. Continued.

	Europe				Slovenia			
	All aquatic species	Stygo-xenes & stygo-philites	Stygo-bionts	Stygo-bionts in % of all species	All aquatic species	Stygo-xen. & stygo-phil.	Stygo-bionts	Stygo-bionts in % of all species
'Lower' INVERTEBRATA	6030	185	1020	16.9	925	93	198	21.0
INSECTA	6324	0	2	0.03	1660	35	0	0.0
VERTEBRATA	215	0	1	0.50	115	3	1	0.8
Total	12569	185	1023	8.1%	2 700	131	199	7.3%

* Estimated.

it was approximately 170. In some other regions of a size comparable with the Dinaric region (= West-Balkan Province), the number of stygobiont species is nearly or more than half lower; these are the East-Balkan, the Pyrenean-Aquitainian, and the Rhodano-Lotharingian Provinces. Comparable to Europe is Japan, while all other areas stay far behind (Sket, in press). Thus, the European stygobiotic fauna richness is high in the global stygobiotic fauna but nevertheless low in comparison with its own surface aquatic fauna.

Taking into account these considerations, the regional, or global, hypogean fauna can only be regarded as comparatively poor – i.e. poorer than its epigean counterparts. If in any context a hypogean fauna or its part is mentioned as comparatively rich, a comparison between local hypogean faunas, or between taxonomic parts of the entire hypogean fauna, is meant.

What restrains the richness of the hypogean fauna?

Thus, numbers of stygobiont species may exceed our formerly modest expectations but even in the richest regions they are not exceedingly high. Even in particularly rich Slovenia (Sket et al. 1991; Sket 1996a), the ultimate number of stygobiont crustacean species will probably reach 150 and equal the number of surface crustacean species while the number of surface bound aquatic insect species is definitely tenfold of that (Table 1). The number of stygobiont species in Slovenia hardly reaches 7.5% of the total registered aquatic fauna, close to the average in Europe. Beside being a part of the speleobiologically rich Dinaric karst, Slovenia also extends through a number of other ecological/biogeographical regions (Matvejev 1961; Wraber 1969), raising the diversity of the surface fauna. We may speculate that the percentage of stygobionts would rise significantly, but not dramatically, if we limit the list to the Dinaric part of the country which is ca. 35% of its area.

In view of the fact that hypogean habitats (interstitial, crevices, caves) are virtually omnipresent the geographical limitation can hardly be regarded as an important limiting factor. Three other reasons for this comparative poverty of hypogean fauna

may be considered: (1) the limited accessibility of habitats, (2) the relative homogeneity (i.e. the small number of different habitats and potential niches) of the environment, (3) its energetic poverty and inhospitability. All these are direct or indirect results of the hypogean habitats being a relatively closed space (comp. Sket 1996b: Figure 1). Since these formerly widely accepted statements (Vandel 1964) have been nowadays repeatedly challenged, the listed statements have to be explained and substantiated.

(1) Accessibility of all hypogean spaces is limited, for aquatic animals in particular. They can penetrate cave waters only through ponors (sinks) or springs/resurgences and interstitial waters through a sieve of unconsolidated sediment. Only in some special cases rock crevices may also be used, a more common access for terrestrial biotas. The extent of the contact zones and therefore of the possible ecotonal regions between epigean and hypogean habitats is much smaller than between different epigean habitats. Mainly only those organisms are able to find the way underground whose normal habitats are in close connection to such 'entrances'.

(2) Although the hypogean realm is definitely ecologically diverse (Danielopol and Rouch 1991; discussion in Stoch 1995), its diversity simply cannot approach the diversity of the epigean environment. While habitats are difficult to define consistently and therefore impossible to count, this difference may be evidenced indirectly by using three important characters as illustration. (a) While most characters of the hypogean habitats can be found in different combinations also in some epigean habitats, the whole hypogean realm lacks any green plants and thus all those numerous habitats or feeding and housing niches dependent on them. (b) Temperature fluctuations underground are null or very low around the value of the local yearly mean temperature; this is between 5 and 12 °C in the inhabited regions of Slovenian hypogean waters, up to 28 °C if we add the scarce thermal waters (Sket and Velkovrh 1981). The temperature regime (i.e. mostly the pattern, in this case the absence of fluctuations) is nearly equal throughout and the temperature value is the same through large areas. In surface habitats, temperatures fluctuate daily and yearly with different amplitudes and with different averages, allowing a number of different combinations with other ecological characters. This might be one of the reasons why the interstitial fauna is much less influenced by elevation than the benthic fauna (Ward and Voelz 1998). (c) The situation is similar in the illumination regime: only one regime – permanent darkness – underground, a number of possibilities in epigean habitats.

(3) The low food resources and their low diversity is a direct consequence of the absence of green plants. It mainly means the absence at least of fresh plant tissues and their easily degradable ingredients, as well as the gradual reduction of resources towards deeper underground zones. The importance of this character can be proven by aggregation even of well adapted and metabolically modest (Vandel 1964) cave animals at points of richer allochthonous food inputs (Sket 1977). Although some other insect species, like the trichopteran *Wormaldia occipitalis* Pictet (as *W. 'subterranea'*

Radovanović 1932; Botosaneanu 1986), are able to build stable populations in relatively rich cave systems, only a few coleopteran groups succeeded to specialise to troglomorphs (i.e. to gain the special morphological traits usually appertaining to cave specialists) and stygobionts. The extreme scarcity of insect stygobionts is very characteristic and may be a consequence of their high energetic requirements enhanced by the energetically demanding metamorphosis, or an ultrastructural inability to adapt to lower energy demands.

Both the energetic poverty and the low habitat diversity reduce the number of candidates for immigration able to build populations underground, within the already restricted pool of organisms that find access to this environment.

The results of a combination of all these factors – they are difficult to separate – can be shown by some local faunas and floras in Slovenia which represent more than one community each (Table 2; Sket 1996a: Table 2). Numbers of represented higher taxa (approximately the order) and species was compared in four ecological systems. The richest is the modestly polluted epigeal karst river, inhabited also by photoautotrophs. The biotic diversity is lower even in the richest hypogean system of Slovenia, the Postojna–Planina Cave System (Sket 1970, 1979; Brancelj 1987), including a sinking stream; some insect ‘populations’ might be only maintained by steady recolonisation. The few insect larvae cannot reach the later stages in the mainly percolated waters of Križna jama (Sket 1986b).

The column ‘thermal waters’ (Table 2) presents all the investigated and populated hypothermal (15–28 °C) waters in Slovenia; only 1–3 species may be found separately in each locality. The impoverishment of the biotic diversity and a growing share in stygobionts, with impoverished food resources, declining ecological diversity, and accessibility, from more than 300 to approximately 15, or even 3, species, is evident. This is in agreement with the relations between faunas of the benthic and interstitial habitats along rivers (Ward and Voelz 1998).

What supports the otherwise restricted diversity of the stygobiotic fauna?

Contrary to entire faunas, the diversity may appear high if we consider only a defined taxonomic group. Such a diversity in hypogean habitats (Stoch 1995) may even surpass the diversity outside. While ranks of such taxa in terrestrial animals may hardly be higher than the family (e.g. Pseudoscorpiones: Neobisiidae, Coleoptera: Bathysciinae and Trechinae), this may happen in the aquatic groups of Crustacea, Gastropoda, and Turbellaria. Since Crustacea–Malacostraca in Europe or Slovenia comprise around 35% of all stygobiont species (and even 80% in North America), this group will be used as a model group for some comparisons.

The reasons that enabled the crustaceans to attain at least a comparatively high number of species in this limited space, poor in resources, may be searched for in (1) the lack of competitors, (2) speciation and resulting space partition, (3) ecological partition, and (4) favourable temperatures.

Table 2. Biotic diversity in different aquatic habitats in Slovenia. Columns show the number of identified species. The sums for river Krka are given separately for the heterotrophic and autotrophic component of the communities. Groups with a pronounced adversity to hypogean habitats are framed. Different sources, mostly own data.

River Krka	Postojna-Planina cave system		Cave Križna jama	Hypothermal waters of Slovenia
(A clean to moderately polluted surface river)	(Percolating waters and moderately polluted to clean sinking river)		(Percolating waters and periodical jets)	(Water from depths & elevated temperature)
35		Cyanobacteria		
101		Algae		
11		Musci		
11		Cormophyta		
?	3	Porifera		
3	6	Turbellaria	3	
x	2	Cnidaria		
x	x	Nematoda	x	
x		Nematomorpha	1	
17	19	Gastropoda	7	7
6	3	Bivalvia		
1		Nemertini		
9	26	Oligochaeta	8	
7	5	Hirudinea		
15	5	Cladocera		
x	5	Ostracoda	1	
20	46	Copepoda	7	
		Bathynellacea		1
2	2	Decapoda		
1	3	Isopoda	2	4
5	8	Amphipoda	4	4
x	3	Acarina	1	
46	25	Insecta (ex Chiron.)	(2)	
x	35	Chironomidae		
35	2	Pisces		
x	1	Amphibia		
21/>167 + 4/157	19/199	Number of groups/species	11/37	4/16
0 = 0%	40 = 20%	stylobionts	24 = 65%	16 = 100%
Interstitial f. excluded	Some spp. only by recolonisation			Only 1–3 spp. in one system

(1) The absence of insects leaves many habitats and potential niches empty; they may be used in a similar manner particularly by some crustacean species. Already Bowman (1981) noticed that Flabellifera (Crustacea) occur in fresh waters mainly in caves, in thermal waters, and as fish parasites. He tried to explain the very restricted occurrence of flabelliferan crustaceans by the competition or predation by numerous insect species. One can only adopt, adapt, and extend his conjectures to Crustacea, or at least Malacostraca, in general. Although insects cannot extinguish the surface freshwater crustacean fauna, they can efficiently restrict it.

One should add here that the richness of Crustacea in the nearly insect-free marine environment speaks in favour of this thesis, while the successful invasion of crustaceans (although of only one particular group) into the insect-rich edaphic terrestrial environment could speak against it. The idea would be nevertheless worth proving by detailed statistical and probably even experimental methods.

(2) High hypogean species numbers in some groups are locally compensated by their smaller distribution areas and their mutual space partition. For example, while most of the surface Cyclopoid species are distributed over a number of Illies' (1978) biogeographic regions and a number of them cross Europe's borders, none of the stygobionts does so, 80% are limited to one region only and many have only been found in a single locality (Table 3). Or, of 199 taxa of Slovenian stygobiont animal species, at least 120, or 60%, seem to be more or less strictly endemic (comp. Bole et al. 1993).

Table 3. Extent of distribution ranges in European stygobiont and non-stygobiont Copepoda Cyclopoida; regions according to Illies (1978), their areas mostly 150 000–350 000 km²; as 'stygobionts' are regarded species with designation '1' only.

	Stygobionts	Non-stygobionts
In 1 region	50 ^a	6
In 2–5 regions	10	6
Six or more regions	2	27
Also outside Europe	0	18

^a Numerous with only one locality.

(3) Even in poorer areas stygobionts appear to be ecologically further specialised (Danielopol and Rouch 1991). The specialisation to particular habitats or niches can be particularly strong because of a presumably high competition for poor resources in the faunistically more saturated Dinaric hypogean habitats. Such an ecological partition of habitats is still regarded as the only possibility for the coexistence of a number of species (Chesson 1991); it is understood that the expression of such a specialisation might be dependent on the presence of competitors. Some extreme limitations in occurrence of species can only be explained by, and can illustrate, their high ecological specialisation.

(a) If the related sphaeromatid (Isopoda: Flabellifera) species *Monolistra caeca* Dormitzer and *M. racovitzai* Stammer inhabit the same cave stream, they are readily separated. In a brook in the cave Stubica, *M. r. conopyge* Sket is limited to pools with a loamy bottom and slow current while *M. c. caeca* inhabits only gravely rapids (Sket 1964). In a different stream ecology and/or historical circumstances one species may have prevented the spreading of the other. Cave waters in Dobropolje are inhabited by *M. c. caeca* while springs along the river Krka only yield *M. r. karamani* Sket. Since these waters are connected underground (Novak 1992), only a high degree of competition could have prevented mixing of the two species. Unfortunately, the contact zone of both species is not accessible to investigations.

(b) A species may be known from one extremely limited locality only. For example, five jets of percolating water were sampled in the cave Planinska Jama throughout a year (C. Filipič, MS), but *Niphargobates orophobata* Sket (Crustacea: Amphipoda) was found only in one of them; its only relative, *N. lefkodemonaki* Sket, was found in a similar habitat in Krete Island, 1300 km away (Sket 1981, 1990). Such a rarity, fictitious or real, can only be caused by extreme habitat specialisation and/or competition. However, in this case possible competitors were evidently not involved.

(c) The cave system of Vjetrenica in Hercegovina with the caves Vjetrenica and Bjelušnica, and the spring Lukavac, is inhabited by 40 stygobiont species (if Nematoda and Oligochaeta are not considered), 19 of them being Malacostraca (Pretner 1963; Sket 1980, unpublished data). However, only in two sites within the system could the real alpha diversity be considered high, with 12 and 13 species together in ca. 10 m of the stream; in most localities only a few of them (Table 4) can coexist. The situation is similar with stygobionts in the rich Postojna–Planina Cave System, where non-stygobiont species are also an important part of their environment.

(4) Temperatures in the inhabited Dinaric hypogean waters are biologically favourable, 5–15 °C, without fluctuations, thus never even approaching the usual sub-zero winter values of this climatic belt. In surface habitats, lower winter temperatures may occasionally occur even in the tropics, e.g. below 20° N in Africa (Gerasimov et al. 1964). So, although non-fluctuating temperatures diminish possibilities for habitat diversity, they augment survival possibilities for a certain category of species.

The historical background of the highest stygobiotic diversity

The history of the land formed from the Dinaro-Hellenic and Alpine chains, since their emergence from the sea in the Oligocene has been very turbulent (comp. Melik 1958; Prelogović et al. 1975; Roegl and Steininger 1983; Dercourt et al. 1985; Sket 1997a). Until the Pliocene, the land alternated repeatedly its insular isolation with connections to the mainland in the east or west. Since the Pliocene, strong orogenic movements changed the climates and the hydrography affecting rivers as well as the sea coasts and lake systems. They also initiated karstification which caused further hydrographic changes and gave birth to the karstic hypogean habitats. In the late

Table 4. Aquatic fauna in the system of the cave Vjetrenica, Zavala, Hercegovina (according to Pretner 1963 and own data). List of species and their cooccurrence in two richest localities within the cave: A – beginning of the Absolon Channel; B – brook behind the breakdown.

Turbellaria:	*e	<i>Scutariella stammeri</i> Matjašič		
Temnocephalida	*e	<i>Stygodyticola hadzii</i> Matjašič		
	*e	<i>Troglocaridicola capreolaria</i> Matjašič		
Cnidaria	*s	<i>Velkovrhia enigmatica</i> Matjašič & Sket		
Nemertina	*	<i>Prostoma hercegovinense</i> Tarman		
Aschelminthes	?	Nematoda		
Gastropoda		<i>Belgrandiella</i> (cf.) sp.		+
	*	<i>Iglica absoloni</i> (A.J. Wagner)		+
	*	<i>Lanzaia vjetrenicae</i> Kuščer		+
		<i>Lithabittella chilodia</i> (Westerlund)		
	*	<i>Orientalina troglobia</i> (Bole)		+
	*	Orientalinidae g. sp. n.		+
Bivalvia	*s	<i>Congeria kusceri</i> Bole (shells)		
Annelida	*s	<i>Marifugia cavatica</i> Absolon & Hrabe		+
	?	Oligochaeta		+
	*	<i>Dina absoloni</i> Johansson		
Arachnida	?	Acarina		
Copepoda:		<i>Acanthocyclops venustus</i> (Norm. & Scott)		
Cyclopoida	*	<i>Diacyclops karamani</i> (Kiefer)		
	*	<i>Diacyclops</i> cf. <i>tantalus</i> (Kiefer)		
	*	<i>Diacyclops charon</i> Kiefer		
	*	<i>Eucyclops inarmatus</i> Kiefer		+
	*	? <i>Cyclops troglophilus</i>		
Ostracoda	?	<i>Cryptocandona</i> sp. (shells)		
		<i>Cypria</i> sp.		+
		<i>Cypridopsis clathrata</i> Klie		+
		<i>Cypridopsis vidua</i> (O.F. Mueller) (shells)		+
	*e	<i>Sphaeromicola stammeri</i> Klie		
Decapoda	*	<i>Troglocaris</i> cf. <i>anophthalmus</i> (Kollar)		+
	*	<i>Troglocaris hercegovinensis</i> (Babić)		+
Mysidacea	*	<i>Troglomysis vjetrenicensis</i> Stammer		
Amphipoda	*	<i>Hadzia fragilis</i> S. Karaman		+
	*	<i>Niphargus boskovici</i> S. Karaman		
	*	<i>Niphargus factor</i> G. Karaman & Sket		+
	*	<i>Niphargus</i> sp.		+
	*	<i>Niphargus trullipes</i> Sket		
	*	<i>Niphargus vjetrenicensis</i> S. Karaman		+
	*	<i>Niphargus balcanicus</i> (Absolon)		
	*	<i>Niphargus zavalanus</i> S. Karaman		
	*	<i>Niphargus kolombatovici</i> S. Karaman		+
	*#	<i>Typhlogammarus mrazeki</i> Schaeferna		+
Isopoda	*#	<i>Illyrionethes heroldii</i> Verhoeff		+
	*#	<i>Titanethes hercegovinensis</i> Verhoeff		
	*	<i>Microcharon</i> sp.		+
	*	<i>Monolistra hercegoviniensis</i> Absolon		+
	*	<i>Proasellus</i> cf. <i>hercegoviniensis</i> (S. Karaman)		
	*	<i>Proasellus hussoni curvifrons</i> (Remy)		+
	*	<i>Proasellus</i> sp.		

Table 4. Continued.

Insecta: Diptera		Chironomidae (larvae)		
Insecta: Coleoptera	*#	<i>Hadesia vasiceki</i> J. Mueller		
Amphibia	*	<i>Proteus anguinus</i> Laurenti		
* Stygobiont			Locality:	A B
# Amphibian			Local number of stygobionts:	13 12
e Epizoic				
s Sessile				

Pliocene, the subtropical climates gradually cooled and passed into an intermittent series of glacials (including the Alpine glacier in the direct proximity of the Dinaric karst) and warm interglacial periods, while maintaining only modest climatic changes in all hypogean habitats. The result of the Pleistocene were reiterated southward and northward shifts of entire faunas that left behind thermophile and psychrophilic relics in isolation and exposed to speciation. Climatic changes also eradicated the surface parts of some populations which resulted in a faster specialisation of their cave immigrated parts. The initial, less extensive, karstification was particularly effective in isolating hypogean biota while the progressive karstification isolated surface populations in the fragmented rests of surface river systems.

The recent result of such a history is a comparatively vast karst territory with good isolation possibilities, phytogeographically–ecologically extremely diverse in the surface (comp. Matvejev 1961). Even within the small (20 000 km²) Slovenia, the Alpine, sub-Mediterranean, and sub-Pannonian influences can be felt, along with their mixtures (Wraber 1969). Such a vivid history must have also caused a rich speciation in species which invaded the territory either from the sea or from the mainland (Sket 1970, 1986a, 1997a). This can explain the unproportionately rich fauna inhabiting this territory (which used to be the main part of the former Yugoslavia; Sket et al. 1991). Comparatively diverse (if compared with other regional underworlds) also is the hypogean environment which enabled thermophile biota to also stay ingredients of the local fauna.

An important component of the fauna-forming processes was the continuation of speciation processes that already started on the surface (Sket 1986a), and continued after the immigration underground (Sket 1997a). The isopod species *Asellus aquaticus* (L.), with a number of its hydrographically isolated and differently specialised cave populations, is a particularly evident example of such a continuing epigeal and hypogean speciation (Sket 1994; Turk-Prevorčnik and Blejec 1998) including a polytopic and polychronous immigration underground. The regularity of such phenomena can be confirmed also by the distribution patterns of some *Monolistra* spp. and *Proteus* (Sket 1997a) as well as by the well studied *Gammarus minus* Say in North America (Culver et al. 1995). The result may be either a number of subspecies and subsequently species, or an unexpectedly high heterozygosity in a cave population (Sket 1997a).

The number of more or less regular non-specialised immigrants into Slovenian hypogean waters (Table 1) is approximately 65% of the stygobionts; if we immediately cancel the evidently non-exapted insects, the number of potential candidates for specialisation is in this moment still 45% that of the stygobionts. However, only few of them have proven their exaptation (i.e. 'preadaptation') either by their regular presence or even by some signs of progressive troglomorphy.

Regular inhabitants of hypogean parts of sinking rivers are e.g. *Spirosperma velutinus* (Grube) (Oligochaeta) and some Cyclopoida (Sket and Bole 1982). Some subpopulations of others exhibit morphological changes, at least partial depigmentation. *Ephydatia fluviatilis* (Linne) (Porifera), *Ancylus fluviatilis* Mueller, *Belgrandiella* sp. (both Gastropoda), *Trocheta bykowskii* Gedroyć (Hirudinea), *Asellus aquaticus* L. (Isopoda), *Synurella ambulans* (F. Mueller) (Amphipoda) are such in the Postojna–Planina Cave system, *Gammarus fossarum* Koch (Amphipoda) only in the hypogean Reka–Timavo (S. Karaman 1931; Sket 1986a).

The behaviour of recent immigrants also confirms the importance of active invasions underground; it has been repeatedly mentioned in the past (e.g. Sket 1969, p. 228; Howarth 1981) but an ecologically and physiologically unsound prejudice about the possibility of a colonisation under constraint prevailed in the speleobiological community, at least until Rouch and Danielopol's (1987) profound study of this problem which offered an active immigration as the only possible explanation of the hypogean fauna formation.

Taxonomic levels of stygobiotic diversity (Malacostraca and the Dinaric area as models)

Hypogean waters in the Dinaric region – to some extent in Slovenia also – have some exceptional stygobionts such as representatives of freshwater Porifera (Spongillidae: *Eunapius subterraneus* Sket and Velikonja), Cnidaria (Bougainvilliidae: *Velkovrhia enigmatica* Matjašič and Sket), Bivalvia (Dreissenidae: *Congeria kusceri* Bole), tubicolous Polychaeta (Serpulidae: *Marifugia cavatica* Absolon and Hrabe), and also Amphibia (Proteidae: *Proteus anguinus* Laurenti) (Sket 1986a). The burden of its faunistic diversity is nevertheless on a low taxonomic level, mainly within the genera *Niphargus* (Amphipoda; with ca. 70 stygobiont species) and *Monolistra* (Isopoda). The world stygobiont fauna is also dominated by some rich amphipod and isopod genera: the European *Niphargus* with 275, North American *Stygobromus* with 180, Mediterranean–European *Proasellus* with 125, world-wide *Bogidiella* with 80 species, etc.

Using approximately the same taxonomic criteria, the number of malacostracan orders, families, genera, and stygobiont species contained in them, in the wider Dinaric region, is of the same magnitude as in continental North America north of Mexico, which comprises 5–6 orders, over 15 families, and around 30 genera. Even small Slovenia is not remarkably lower in higher taxa (Table 5). The number of stygobiont

Table 5. (A) Diversity of the aquatic fauna of Malacostraca, numbers of taxa represented. Mostly updated August 1998; data for the USA by Peck (1998) (with small corrections); system by Bowman and Abele (1982). (B) A more detailed overview for the world fauna; ecologically endemic (or nearly so) groups are emphasised.

	Orders	Families	Genera	Species + subspecies
Stygobionts in:				
Slovenia	5	14	19	59 + 20
Dinaric reg. (incl. Slovenia)	6	21	33	130 + 57
USA	5	16	36	330
Pericaribbean and Mexican zone with Bermuda	6	34	86	270
World stygobiont fauna	10	73 (changing)	455 (rapidly growing)	2130 (rapidly growing)
World fresh waters (stygobionts included)	10	67	x	x
World seas	11	300	x	x
The whole fauna	15	360 (incl. 35 terrestrial)		
(B)				
World stygobites, fam/gen/spp updated August 1998		Leptostraca 1/1/1, Bathynellacea 2/70/210, Anaspidacea 2/7/11, Mictacea 1/1/1, Thermosbaenacea 4/7/34, Spelaeogriphacea 1/3/3, Mysidacea 4/11/28, Amphipoda 23/210/995, Isopoda 19/97/680, Decapoda 16/49/160		
World fresh waters (freshwater stygobionts included), families		Bathynellacea 2, Anaspidacea 4, Thermosbaenacea 4, Spelaeogriphacea 1, Mysidacea 2, Amphipoda 19, Isopoda 14, Tanaidacea 1, Cumacea 1, Decapoda 19		
World seas (anchihaline stygobionts included), families		Leptostraca 1, Stomatopoda 12, Mictacea 1, Mysidacea 6, Amphipoda 96, Isopoda 66, Tanaidacea 18, Cumacea 8, Euphausiacea 2, Amphionidacea 1, Decapoda 90		
World fauna fam/gen/spp (number of included terrestrial taxa in brackets) (Bowman and Abele 1982)		Leptostraca 1/4/10, Stomatopoda 11/68/350, Bathynellacea 2/23/100, Anaspidacea 4/10/15, Thermosbaenacea 1/4/9, Spelaeogriphacea 1/1/1, Mysidacea 6/120/780, Amphipoda 97/840/6000(-180), Isopoda 99 (-35)/700/4000(-1000), Tanaidacea 18/100/500, Cumacea 8/102/800, Euphausiacea 2/11/85, Amphionidacea 1/1/1, Decapoda 104/1200/10 000(-100)		
World fauna species according to Minelli 1993; Mictacea added		Leptostraca 20, Syncarida (= Anaspidacea + Bathynellacea) 145, Amphipoda 8600, Isopoda 10 000, Tanaidacea 800, Cumacea 1000; Mictacea 2/2/3		

malacostracan species known from Slovenia is more than 24% of the most recent number from the USA (comp. Peck 1998) whose main territory without Alaska or islands is nearly 400 times larger; however, the interstitial fauna has been heavily under explored and the hypogean 'Entomostraca' (comp. Reid 1992) is heavily neglected in the USA. One must note that the Dinaric area is within the belt of concentrated biodiversity hot spots for the surface fauna (Gaston and David 1994).

The picture changes if we compare the wider Caribbean region (Pericaribbean and Mexican zone, Botosaneanu 1986, plus Bermuda) which gains in the number of genera and families on account of the particularly diverse faunas in anchihaline habitats (Sket 1996b, 1997b) with an increased possibility for immigration from the rich sea. However, even this difference might be to some degree artificially magnified. The morphological diversity within the family Hadziidae (comp. Stock 1977) hardly surpasses much that of the genus *Niphargus* (comp. Sket, in press, Figure 2); yet some attempts to divide the latter into more genera or subgenera (e.g. Karaman and Ruffo 1986) failed because of the pronounced mosaic manner of its species diversity and a high rate of possible homoplasy. A subdivision of the genus *Niphargus* and a formally excusable promotion of subgenera within *Monolistra* to a generic rank would raise remarkably the number of genera in the Dinaric region as well as in Slovenia. In general, genera and even families are continuously being established and cancelled again. This is particularly the case in Amphipoda but also in less rich groups as in Decapoda (Wicksten 1996).

Of the recognised (Bowman and Abele 1982) 15 orders of Crustacea, 10–11 are represented in either the sea, continental waters, or stygobiont faunas. It is important to note that approximately the same number of higher taxa (order or family category) is represented by stygobiont as by freshwater species; three orders are even limited to hypogean waters, and one is shared only by the deep sea. Half of the 'partly hypogean' orders are also represented in the Dinaric region. Worth mentioning again is the fact, that neither the marine nor the hypogean fauna has any remarkable number of insects.

The comparison of the diversity at the species level is very difficult. The near absence of subspecies in the rich American genus *Stygobromus* (comp. Holsinger 1978) and their high number in its European counterpart *Niphargus* (comp. Karaman 1993) may have been caused either by (1) neglect of the racial polymorphism in *Stygobromus* or by (2) an overvaluation of morphological differences in *Niphargus*, or by (3) an under evaluation of those differences. The Mediterranean–Atlantic genus *Pseudoniphargus* (comp. Notenboom 1988) abounds in nominal species that are morphologically often very similar and allopatric; in fact some of them might be races and subspecies of wider biological species.

Thus, stygobiotic fauna may not reach the species numbers of surface faunas or does it contain representatives of all the highest taxa (classes, phyla). This deficiency is in a sense compensated by the small number of very species-rich genera as well as by the high number of medium rank taxa, families and orders, of Crustacea.

Endangerment of the hypogean aquatic fauna

Like other biota, stygobionts are threatened by the progressing environment degradation (Sket 1972; Malard et al. 1994; Notenboom et al. 1994). The biased and non-self-sufficient composition of hypogean communities, lacking the primary producing

component, makes them, and consequently their members, more vulnerable. Since hypogean waters are poor in food resources, slight organic pollution may even be favourable for their inhabitants, provided the invasion of surface dwellers is not possible. Such a situation was found e.g. in Podpeška Jama, with very high densities of stygobionts in organically polluted parts of the cave stream (Sket 1977). The situation in sinking rivers is different, where such an enrichment may make surface species competitively superior to low-metabolism hypogean specialists which causes a shift in the fauna composition along the stream. Therefore a gradient in the fauna composition (non-stygobionts *versus* stygobionts) along the hypogean part of the stream (Sket 1977) changes with changes in the water's quality (Sket 1985); thus, the stygobiont component of the stream fauna may be threatened. Relations in a different kind of hypogean habitats in southern France appeared to be similar (Malard 1995). This stygobiont behaviour in the absence or presence of stygoxenes shows that stygobionts are not necessarily direct victims of pollution. Although it seems that cave animals are less susceptible to pollutants than the surface fauna (Notenboom et al. 1994), any pollution with inorganic substances as well as concentrated organic input may be deleterious for it (some cases in Dolenjsko region, SE Slovenia; Sket 1972). As K-strategists, stygobionts are in principle not able to successfully react to unpredictable short time environmental oscillations.

As larger bodies of interstitial waters are mostly formally protected as water resources for humans, their stygofauna could be automatically protected. Unfortunately, the protection areas around pumping wells are not always large enough and the chemical pollution from farming areas may penetrate entire alluvial plains; spills from road accidents and from poorly protected industrial or communal dumps are also dangerous (Malard 1995; also a number of cases in Slovenia). Even more critical is the situation in karst territories (Novak 1993) where wastes are discharged directly into streams, or to seemingly dry vertical caves, or to the fields; these may all end in subsurface streams. A cave water is not an isolated system; the whole territory of its hydrographical basin has to be protected from damage to protect its fauna (Sket 1972, 1992).

The high endemism, i.e. mostly small distribution areas, is another fact making stygobiont taxa prone to extinction. Since the protection of hypogean waters in karst areas also is in accord with the human population's firsthand interests (Sket 1972), the protection of stygobiontic species should be a very low-cost by-product.

Conclusions

The analysis of the European aquatic fauna shows that the locally high stygobiotic diversity is mainly a crustacean diversity. The rise of crustacean diversity underground seems to be mainly enabled by the absence of insects.

The stygobiotic diversity is limited: (1) by the shortage in quantity and variety of food resources that are mainly the consequence of darkness and lack of photoautotrophs; (2) by numbers of habitats and potential niches that are drastically reduced by the absence of plants but also by non-fluctuating ecological parameters, and (3) by the reduced accessibility of hypogean habitats whose contact zones with epigean habitats are mostly less extensive than among the latter ones themselves.

The overall stygobiotic diversity is supported by mutual spatial (in areas) and ecological (in niches) partitions of the hypogean environment by immigrants. The former is a consequence of endemism and the distribution barriers while the latter is caused by a more detailed specialisation of stygobionts.

The particularly high stygobiotic diversity in the wider Dinaric region (S Europe), and in Slovenia in particular, seems to be a consequence of the large karst areas as well as of its particularly turbulent geological past, which enhanced possibilities for multiple immigrations and speciation.

In the Malacostraca, taken here as a model group, the stygobios represents nearly the same number of orders or families as the whole continental hydrofauna and the same number of orders as the marine fauna. It is nevertheless dominated by the high diversity of Amphipoda and by high numbers of species within some of their genera.

The stygobiotic diversity is highly endangered by a combination of the biased composition of the underground communities, the small distribution areas of species, and their competitive inferiority in energetically (organically) enriched, i.e. polluted, environments.

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