HOTSPOTS OF SUBTERRANEAN BIODIVERSITY IN CAVES AND WELLS

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We documented 18 caves and two karst wells that have 20 or more stygobites and troglobites. Crustacea dominated the aquatic fauna. Taxonomic composition of the terrestrial fauna varied, but Arachnida and Insecta together usually dominated. Geographically, the sites were concentrated in the Dinaric Karst (6 caves). Sites tended to have high primary productivity or rich organic input from the surface, be large caves, or have permanent groundwater (phreatic water).

Dokumentirala sva 18 jam in dva kraška vodnjaka, iz katerih je znanih 20 ali vec vrst troglobiontov in stigobiontov. V vodni favni preladujejo raki. Taksonomski sestav kopenske favne je raznolik, vendar pajkovci in zuzelke skupaj navadno prevladujejo. Najvec takšnih jam (šest) je v Dinarskem krasu. Nadpovprecno so zastopane jame z lastno primarno produkcijo ali bogatim vnosom hrane s površja, obsezne jame in jame, ki vkljucujejo tudi freatsko plast.

Over the past few years, there has been a growing awareness and concern with biodiversity worldwide. Books and monographs with a focus on biodiversity have appeared (e.g., Wilson 1992; Master *et al.* 1998) and a rapidly increasing amount of information is available about patterns of biodiversity for many groups of organisms. The same can be said for the fauna of caves and other subterranean habitats. Tabulations and often lists of cave and subsurface-limited species are available for many countries in *Stygofauna Mundi* (Botosaneanu 1986) and in the multi-volume *Encyclopaedia Biospeologica* published by the Societe de Biospeologie in Moulis, France. Extensive lists of the caves and wells in which a particular subterranean species is found have been published. Prominent examples include Virginia (Holsinger & Culver 1988), the Iberian Peninsula (Belles 1987), and Slovenia (Bole *et al.* 1993). While not as well studied as temperate areas, similar information exists for many tropical regions (Peck & Finston 1993; Deharveng & Bedos 2000).

Understanding patterns of subterranean biodiversity requires an understanding of regional patterns. In general, the number of species found in any one cave or subsurface site is small relative to the number of species in the region. Cave habitats (as opposed to small cavity, interstitial habitats such as the underflow of rivers) are especially fragmented, with different species occurring in caves only a few kilometers apart. For example, of the more than 500 caves biologically investigated in West Virginia, the maximum number of obligate species in any cave is 14, but the state, with a karst area of 2500 km^2, has 76 obligate species. It is the documentation of these regional patterns and their explanation that is one of the major tasks of speleobiologists over the next several decades (Peck & Finston 1993; Sket 1999a).

Nevertheless, it is important not to neglect diversity patterns at individual sites. Even though most subterranean biodiversity results from the accumulation of different species from nearby sites, there are some outstanding examples of high biodiversity from individual caves and wells that are worth documenting. Protection and concern for the subterranean fauna of a region often begin with protection and concern for a particular cave. It is, after all, individual caves and wells that provide the building blocks for regional biodiversity.

The purpose of this short communication is to enumerate those caves and wells that are particularly rich in subterranean species and to offer some preliminary explanations for these biodiversity hotspots, both in terms of their geographic distribution and in terms of the types of sites. We use the terms troglobite for terrestrial, cave-limited species and stygobite for aquatic, cave-limited species. Stygobites also include interstitial species but they are not considered here.

METHODS AND MATERIALS

We used an arbitrary cutoff of 20 or more obligate subterranean species for a site to be included. This resulted in a manageable number of sites to enumerate, representing less than one-tenth of one per cent of the sites sampled. We limited our attention to large cavities—caves and wells that intersect large cavities. According to Curl (1964), **proper caves** are large enough for humans to enter (and proper entrances are entrances large enough for humans to enter). We restricted our attention to proper caves, whether they do or do not have proper entrances, since many wells in carbonate rock intersect proper caves that lack proper entrances. What constitutes a single cave is a matter of considerable debate and confusion. We restricted our attention to connected voids, either water- or air-filled, regardless of how many separate entrances or names

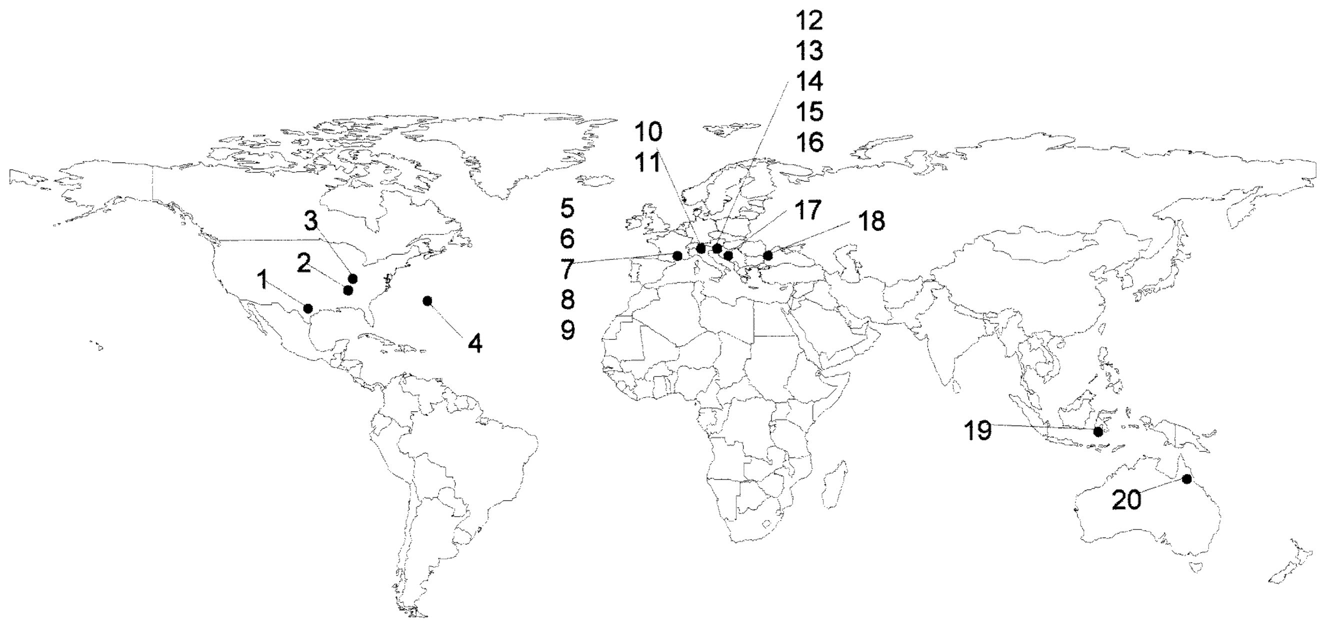

Figure 1. Location of hotspots of subterranean biodiversity: 1—San Marcos Spring, Texas; 2—Shelta Cave, Alabama; 3—Mammoth Cave, Kentucky; 4—Walsingham Caves, Bermuda; 5—Triadou Wells, France; 6—Baget/Grotte de Sainte Catherine, France; 7—Goueil di Her/Reseau Trombe, France; 8—Résurgence de Sauve/Vidourle souterrain, France; 9—Cent-fons, France; 10—Grotta dell'Arena, Italy; 11—Buso della Rana, Italy; 12—Sistem Postojna-Planina; 13—Šica-Krka Sistem, Slovenia; 14—Jama Logarcek, Slovenia; 15—Grad (Osapka Jama), Slovenia; 16—Krizna Jama, Slovenia; 17—Vjetrenica Jama, Bosnia & Hercegovina; 18: Pestera de la Movile, Romania; 19—Salukkang-Kallang/Towakkalak, Indonesia; 20—Bayliss Cave, Australia.

the cave had. We specifically excluded porous aquifers—they have been less thoroughly studied and are likely to have a pattern very different than that of proper caves. We also excluded the few known fungal parasites.

In order to generate the list, we consulted with many colleagues throughout the world with the request for information about any particular cave or well fauna. We consulted available species lists from throughout the world. An Excel file of the species list is available from the authors. We are aware of the fact that a number of caves may be missing from our list because we lack a faunal list. We also expect some species to be shown eventually not to be limited to caves. However, none of the sites enumerated here is likely to be excluded from the list owing to such changes.

Results

Eighteen caves and two wells have 20 or more obligate species. Of the 20 sites, fourteen are from Europe (five of them from Slovenia and five from France), three from North America, one from Australia, one from southeast Asia, and one from an island in the Atlantic (Fig. 1). The major taxonomic composition of these faunas is listed in Table 1. Each site is briefly described below.

San Marcos Spring, Texas, USA—This artesian spring serves as an exit point for water from the Edwards Aquifer. Two-thirds of its aquatic species are crustaceans, of which 11 are amphipods (Holsinger & Longley 1980, Table 1). Endemism is high, with 11 endemics representing 40% of the fauna. The aquifer itself is about 280 km long and 8-64 km wide. Oil and peat deposits above the aquifer may be the primary energy input into the system (Longley 1981). The aquifer is threatened by excessive drawdown, both by agricultural interests and the City of San Antonio.

Shelta Cave, Alabama, USA—Slightly over 700 m long, Shelta Cave consists of three large rooms of considerable volume that intersect permanent groundwater. Pioneering biological studies by Cooper (1975) led to the purchase of the entrance sink by the National Speleological Society. Half of the species are aquatic (Table 1). No group dominates the terrestrial fauna, but crustaceans dominate the aquatic fauna. Installation of a bat-unfriendly gate apparently led not only to a loss of bats, but to a major decline in the population sizes of the aquatic species (Hobbs & Bagley 1989; Culver 1999).

Mammoth Cave, Kentucky, USA—Mammoth Cave is the longest known cave in the world, with over 500 km of surveyed passages. Most of the cave is within the boundaries of Mammoth Cave National Park. It rivals the Postojna-Planina Cave system of Slovenia in the amount of study devoted to the biota. Major discussions of the fauna of Mammoth Cave include Packard (1888), Barr (1967), and Poulson (1992). One-third of the fauna is aquatic, two-thirds terrestrial.

Taxonomically, arachnids dominate the terrestrial fauna and crustacea dominate the aquatic fauna (Table 1). Noteworthy is the co-occurrence of five species of trechine beetles in the closely related genera *Neaphaenops* and *Pseudanophthalmus.*

Walsingham Caves, Bermuda—This complex of anchihaline caves (ones with a direct connection to the sea), including Walsingham Sink Cave, Walsingham Cave, and Tuckers Town Cave, is ~1 km long, with most of the passages submerged. With a freshwater lens and a redox boundary between fresh and saltwater, Walsingham Cave likely has considerable secondary and possibly primary productivity. The fauna is entirely aquatic and dominated by Crustacea from many orders (Sket & Iliffe 1980, Table 1). Some of the micro-crustacean species may occur outside the hypogean realm.

Triadou Wells, France—Two wells (F1 and P1) only a few meters apart in the Lez Basin in southern France at a depth of 50 m yielded a variety of stygobites, especially crustaceans (Malard *et al.* 1994, Table 1). Located in a major karst area, the wells tap a network of fissures and solution tubes beginning at a depth of ~35 m.

Baget—Sainte Catherine System, France—This subterranean system is situated in the Pyrenees, near Moulis, in the small valley of Lachein. The basin occupies an area of 13.25 km^2. The object of intense study by R. Rouch and his colleagues for more than 20 years (*e.g.,* Rouch & Danielopol 1997), three components have been extensively sampled—the outlet of the subterranean stream, a mostly flooded conduit (Aven de la Peyrere), and Grotte de Sainte-Catherine. The aquatic fauna is especially diverse, with 21 species of Crustacea (Table 1).

Goueil di Her/Reseau Trombe, France—The Trombe system is located in the Pyrenees in the Arbas Massif. The subterranean system consists of over 100 km of air- and water-filled passages, with numerous pits providing access to the submerged part of the system. The most extensively studied part of the system is Goueil di Her and its resurgence. The terrestrial and aquatic fauna are about equally diverse (Table 1), with Crustacea and Coleptera predominating.

Resurgence de Sauve and subterreanean Vidourle, France—The fountain of Sauve, near Montpelier, is the resurgence of the subterranean Vidourle River, which drains about 75 km^2 of area. The fountain is well known on account of the violence of its floods. Twenty stygobites have been collected from the watercourse, and most of these are crustaceans (Juberthie & Juberthie-Jupeau 1975, Table 1).

Cent-fons, France—The cave, which is flooded, and its resurgence are located at the southern border of the Massif Central. There are ten resurgences. The populations are diverse (Table 1) and abundant—about 16,500 crustaceans have been ejected out of the resurgence in ten weeks (C. Juberthie, pers. comm., October, 1999).

Grotta dell'Arena, Italy—This fossil cave is located in an alpine pasture (1512 m msl) and consists of a single large gallery less than 100 m long with the floor covered by large blocks of limestone. Percolating water forms some small, permanent pools at the end of the gallery. The stygobitic fauna consists of six, mostly tiny crustaceans (Table 1). Beetles and archnids dominate the richer terrestrial fauna.

Cave Buso della Rana, Italy—This large and complex cave system, with more than 20 km of passage, shows a high habitat diversity, with an alternation of inactive and active branches. A small permanent brook flows along the main passage and emerges at the entrance. During the rainy season, most of the cave may be flooded. Crustaceans dominate the aquatic fauna (Table 1). None of the terrestrial groups is particularly diverse.

Grad (*Osapska Jama), Slovenia*—The entrance is a boiling spring with 1070 m of passage accessible during the dry season. After rains, the water can rise 50 m and flood most of the cave. There is no connection with a surface stream except at the periodically emerging spring. Terrestrial fauna is largely un-investigated, and the stygobitic fauna includes 17 crustaceans (including two amphibious Oniscoidea) and among them the large cirolanid isopod *Sphaeromides virei* (Brancelj 1992, Table 1).

Krizna Jama, Slovenia—This is a hydrologically active but nevertheless beautifully decorated cave of more than 8000 m length. It is isolated from permanent surface rivers and, therefore, has very few non-stygobitic animals. The fauna is very scarce but species rich. Crustaceans (Table 1) dominate the rich aquatic fauna. Remarkable is the high number of gastropods: 2 terrestrial and 6 aquatic species have been found.

Jama Logarcek, Slovenia—A multi-level cave with a river in its deepest corridors; it measures 2300 m. It is situated close to Postojna-Planina Cave System, but with less apparent habitat diversity. Two-thirds of the fauna is aquatic, with gastropod and crustacean species predominating (Table 1). There also is an exceedingly rich epizoic ciliate protozoan fauna, described from one specimen of the bizarre isopod *Monolistra spinosissima* (Hadzi 1940).

Sistem Postojna-Planina, Slovenia—There are 17 km and 6 km of passages connected by 2 km of flooded corridors. The sinking river in the main passages is inhabited by a rich assortment of stygobites, stygophiles, and accidental surface species (Sket 1979). Hydrologically inactive parts of the system contain other aquatic and terrestrial habitats. This is the type locality of a number of "first cave" animals, including the first described troglobite, the beetle *Leptodirus hochenwarti* and the European cave salamander, *Proteus anguinus.* It also is a site of long-term ecological studies (Sket & Velkovrh 1981). Slightly over half of the species are aquatic, with a rich crustacean, snail and oligochaete fauna. Beetles dominate the terrestrial troglobitic fauna (Table 1). Some of the cave has been heavily visited by tourists since 1818.

Šica-Krka Sistem, Slovenia—Šica-Krka Sistem consists of two caves 1700 m and 250 m long, hydrologically connected by 5 km of underground flow. This sinking river is inhabited mostly by surface animals at the sink and mostly by stygobites at the resurgence. Most parts of the cave are hydrologically active and more than 70 percent of the cave fauna is aquatic, primarily crustacean (Table 1).

Table 1. Taxonomic summary of stygobites and troglobites found in the 20 caves and karst wells. See Figure 1 for their location.

Higher Groups		**San Marcos Spring TX, USA**	**Shelta Cave AL, USA**	**Mammoth Cave KY, USA**	**Walsingham Caves Bermuda**	**Triadou Wells F1 & P1 France**
AQUATIC						
Protista:	Ciliata (epizoic)					
Cnidaria						
Aschelminthes:	Nematoda					
	Rotatoria					
Nemertini						
Turbellaria:	Tricladida	1	1	2		
	Temnocephala					
Annelida:	Hirudinea					
	Oligochaeta		1			3
	Polychaeta				4	
Mollusca:		5		1	3	3
Crustacea:		18	8	11	29	28
Arachnida:	Acarina				1	
Insecta:		1				
Vertebrata:	Amphibia	2	1			
	Pisces		1			
Aquatic Subtotal		27	12	15	37	34
TERRESTRIAL						
Annelida:	Oligochaeta					
Mollusca:	Gastropoda		1	1		
Crustacea:	Isopoda		1			
Arachnida:			2	12		
Symphyla:						
Diplopoda:			1	2		
Chilopoda:						
Insecta:	Collembola		2	4		
	Coleoptera		3	5		
	Other		2	2		
Terrestrial Subtotal			12	26		
TOTAL		27	24	41	37	34

Higher Groups		**Baget—Ste. Catherine System France**	**Goueil di Her Reseau Trombe, France**	**Resurgence de Sauve Vidourle souterrain France**	**Cent-fons France**	**Grotta dell'Arena Italy**
AQUATIC						
Protista:	Ciliata (epizoic)					
Cnidaria						
Aschelminthes:	Nematoda					
	Rotatoria					
Nemertini						
Turbellaria:	Tricladida		1			
	Temnocephala					
Annelida:	Hirudinea					
	Oligochaeta	1	1			
	Polychaeta					
Mollusca:		2	1	3	1	
Crustacea:		21	11	14	20	6
Arachnida:	Acarina			3	1	
Insecta:						
Vertebrata:	Amphibia					
	Pisces					
Aquatic Subtotal		24	14	20	22	6
TERRESTRIAL						
Annelida:	Oligochaeta					
Mollusca:	Gastropoda					1
Crustacea:	Isopoda		1			1
Arachnida:		1	2			5
Symphyla:						
Diplopoda:		1	2			1
Chilopoda:						
Insecta	Collembola	3	1			
	Coleoptera	4	6			6
	Other					
Terrestrial Subtotal		9	12			14
TOTAL		33	26	20	22	20

Higher Groups		Buso della Rana Italy	Grad (Osapka Jama) Slovenia	Krizna Jama Slovenia	Jama Logarcek Slovenia	Sistem Postojna-Planina Slovenia
AQUATIC						
Protista:Ciliata (epizoic)				1	9	1
Cnidaria						1
Aschelminthes:	Nematoda					
	Rotatoria					
Nemertini						
Turbellaria:	Tricladida			1		1
	Temnocephala				3	2
Annelida:	Hirudinea					1
	Oligochaeta			6		7
	Polychaeta		1			
Mollusca:		1	1	6	7	8
Crustacea:		14	15	15	8	26
Arachnida:	Acarina					
Insecta:						
Vertebrata:	Amphibia				1	1
	Pisces					
Aquatic Subtotal		15	17	29	28	48
TERRESTRIAL						
Annelida:	Oligochaeta					
Mollusca:	Gastropoda	1		2	4	3
Crustacea:	Isopoda		2	1	1	2
Arachnida:		1		4	3	9
Symphyla:						
Diplopoda:				1	1	2
Chilopoda:						
Insecta:	Collembola			1		9
	Coleoptera	3	1	6	6	8
	Other					1
Terrestrial Subtotal		5	3	16	15	36
TOTAL		20	20	45	43	84

Higher Groups		Sica-Krka Sistem Slovenia	Vjetrenica Jama Bosnia-Herzegovina	Pestera de la Movile Romania	Salukkang Kallang Towakkalak Indoesia	Bayliss Cave N. Queensland Australia
AQUATIC						
Protista:	Ciliata (epizoic)					
Cnidaria		1	1			
Aschelminthes:	Nematoda	3		3		
	Rotatoria			2		
Nemertini			1			
Turbellaria:	Tricladida			1	1	
	Temnocephala	3	3			
Annelida:	Hirudinea		1	1		
	Oligochaeta	1		2		
	Polychaeta		1			
Mollusca:		6	8	1		
Crustacea:		12	23	7	4	
Arachnida:	Acarina					
Insecta:				1		
Vertebrata:	Amphibia	1	1			
	Pisces				2	
Aquatic Subtotal		27	39	18	7	
TERRESTRIAL						
Annelida:	Oligochaeta			1		
Mollusca:	Gastropoda	3	2			
Crustacea:	Isopoda	1	3	4	3	2
Arachnida:		2	4	10	8	5
Symphyla:				1		
Diplopoda:			3	1	3	4
Chilopoda:			1	3		1
Insecta:	Collembola		1	3	4	1
	Coleoptera	1	6	4	1	3
	Other		1	2	2	8
Terrestrial Subtotal		7	21	29	21	24
TOTAL		34	60	47	28	24

Vjetrenica Jama in Popovo polje, Bosnia and Hercegovina—This complex cave system has 7.6 km of passages, which include a number of small streams, pools, and trickles of water. There are no sinking streams but there are extensive opportunities for the import of organic debris through crevices and shafts. About two-thirds of the fauna is aquatic, and dominated by Crustacea (Pretner 1963, Sket 1999a, Table 1). Noteworthy are the amphibious catopid beetle and amphipod species that occupy rock walls covered by a film of water trickling from above (hygropetric habitat).

Movile Cave, Romania—Movile Cave is a small, mostly water filled cave near the coast of the Black Sea. Slightly more than a third of its fauna is aquatic. No one taxonomic group dominates either the aquatic or terrestrial fauna (Table 1), and the fauna, as a whole, has the remarkably high level of over 65% endemism (Sarbu 2000). Extensive chemoautotrophic production occurs in the cave system (Sarbu, Kane *et al.* 1996). The cave is threatened by extensive trash dumping in the sinkhole in which the entrance is located.

Gua Salukkan Kallang—Towakkalak, Indonesia—This immense river cave system has over 20 km of passage, a large bat population, and 25% of the obligate cave fauna is aquatic. Comprising mostly undescribed species, crustaceans predominate in the aquatic fauna and arachnids in the terrestrial cave fauna (Deharveng & Bedos 2000, Table 1).

Bayliss Cave, Australia—Bayliss Cave is a small (900 m) cave formed in lava. It is a "bad-air" cave, with up to 200 times the ambient atmospheric level of carbon dioxide (Howarth & Stone 1990), likely the result of *in situ* production of CO_2 from the oxidation of organic matter (James 1977). The cave-limited fauna is entirely terrestrial with no one group dominating (Table 1).

DISCUSSION

It is worthy reiterating that, compared to surface habitats, diversity in caves is low (Sket 1999a) and that most diversity in caves and wells is expressed regionally rather than locally. Sket (1999a) gives a variety of reasons for the low diversity compared to surface habitats, including reduced area of ecotonal regions between surface and subsurface, reduced subterranean habitat diversity, and reduced food resources. The fragmented nature of the cave habitat and restricted opportunities for dispersal keep local diversity much lower than regional diversity.

One obvious difference, even among the caves and wells listed in Table 1, is the breadth of taxonomic scrutiny. In only a scattering of caves have epizoic ciliates been collected, let alone described (Walsingham Cave and Logarèek Cave in Table 1). Likewise, microcrustaceans have not been collected from all sites; even those listed in Table 1. It seems that Copepoda in North American subterranean waters have been nearly completely ignored. Nonetheless, most of the species in all sites listed in Table 1 are easily observed and collected.

What in the way of generalities can be gleaned from the list of caves and wells with high species diversity? First, there is a remarkable concentration of sites in the Dinaric karst of Slovenia, Croatia, and Bosnia-Herzegovina, which is also the richest region of subterranean biodiversity (Sket 1999b). This is particularly evident in the stygobitic fauna. Of the ten sites with 25 or more stygobites (Table 1), six are in the Dinaric karst. France also has a concentration of sites, although, in general, diversity at these sites is slightly less than that at Dinaric karst sites. Sket (1996) points out that the Dinaric Karst in general, and the Slovenia karst in particular, is extensive in areal extent and with a rich geologic history. Poulson (1992) makes a similar argument for Mammoth Cave. Second, sites with high productivity, especially chemoautotrophy, compared to other subsurface sites are well represented. These include Washingham Cave, Movile Cave, Bayliss Cave, and San Marcos Springs. Such high productivity caves are rare. This reinforces the widely held view that caves are resource poor (*e.g.* Sket 1999a). Gua Salukkang Kallang Towakkalak and Sistem Postojna-Planina also can be counted as caves with high (secondary) productivity, but the scarcity of high diversity caves in the tropics is still a puzzle. Another example of a high diversity cave with high productivity is Cabaret Cave in Western Australia. This small cave has extensive root mats penetrating the aquatic habitat, with over 40 species in a 20 m reach of stream (Jasinska *et al.* 1996; Jasinska & Knott 2000). We did not include it in the list of hotspots because the majority of species are probably not strictly stygobitic. Nevertheless, it is a striking example of high diversity in a very small cave. Third, caves and wells that intersect the permanently saturated (phreatic) zone also are well represented. These include Movile Cave, Shelta Cave, San Marcos Spring, all six caves in the Dinaric karst, and all six caves in France. This is an especially intriguing result, and suggests that there are a great many undiscovered species at such sites. Finally, many of the caves are long caves. Seven of the caves listed in Table 1 (Mammoth Cave, Buso della Rana, Krizna Jama, Sistem Postojna-Planina, Vjetrenica Jama, Reseau Trombe, and Gua Salukkan Kallang—Towakkalak) are over 5 km long, yet less than 1% of caves are this long, at least based on U.S. cave data (Culver, unpublished). A longer cave usually means a higher number of different habitats.

More complete explanations of the patterns of subterranean biodiversity must await a more detailed regional analysis, but we hope that this report sparks an increased interest in hotspots of subterranean biodiversity.

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