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FAUNISTIC DIVERSITY AND ZOOGEOGRAPHY OF CAVE-DWELLING SPIDERS ON THE BALKAN PENINSULA

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Abstract — A total of 326 species from 115 genera and 31 families of Araneae have been established in caves of the Balkan Peninsula so far. The species are distributed in different territories as follows: Bulgaria – 99; Greece (Mainland) – 72; Greece (Insular part) – 16; Crete – 44; Croatia – 63; Serbia – 59; Bosnia – 52; Macedonia – 44; Montenegro – 44; Slovenia – 43; Albania – 10; Turkey – eight; and Romania – four species. The largest number of troglobites are encountered in the Dinaric region – 113 (39 blind), Pindus region – 32 (eight blind), Thracian-Macedonian region – 18 (four blind), Balkanid region – 13 (two blind), Danubian region — one; and North Dobruja region — four (three blind) species. The extreme richness of troglobitic spiders in these regions leads to the assumption that these were major centers of speciation and evolution of species. On the basis of their current distribution, the established 324 species can be classified into 17 zoogeographical categories, grouped into four complexes (widely distributed, European, Mediterranean, and Balkan endemics). The largest number of species belong to the group of Balkan endemics (56.5%), which are also the most characteristic and reflect the local character of the fauna. This phenomenon can be regarded as a result of the relative isolation of the mountains compared with the lowlands in the context of paleo-enviromental changes since the Pliocene. Thus, the Balkan Peninsula can be considered as the main center of speciation for the European cave fauna.

Key words: Araneae, cave-dwellers, troglobites, zoogeography, Balkan Peninsula

INTRODUCTION

The Balkan Peninsula is a region with an extremely rich and diversified cave fauna. The group of spiders is characterized by considerable species richness and also by the presence of many endemics, at both the genus and species levels. The spider fauna has been comparatively well studied due to the efforts of many araneologists from different countries. The earliest data were published by Schiødte (1847), Keyserling (1862), Pavesi (1876), Simon (1885), Kulczyński (1903, 1914), Nosek (1903, 1905), Absolon (1912), Absolon and Kratochvíl (1932, 1933), Fage (1913, 1919, 1931, 1945), Roewer (1928, 1931), Reimoser (1919, 1928, 1929), Stojićević (1929), Drensky (1931, 1936), Kratochvíl (1933, 1934, 1935, 1936, 1938 a, 1938 b, 1939, 1978), Kratochvíl and Miller (1938, 1939, 1940), and Hadjissarantos (1940). More recent publications include those

of Brignoli (1971a, 1971b, 1971c 1972, 1974a, 1974b, 1974c, 1976, 1977, 1978, 1979, 1980, 19784), Ćurčić et al. (2000, 2004), Deeleman-Reinhold (1971a, 1971b, 1976, 1977a, 1977b, 1977c, 1978a, 1978b, 1983, 1985, 1993), Deeleman-Reinhold and P. R. Deeleman (1980, 1988), Deltshev (1972a, 1972b, 1972c, 1977a, 1977b, 1978, 1979, 1980, 1983, 1993, 1996, 1999, 2000, 2003), Deltshev and Ćurčić (1997, 2002), Deltshev et al. (1996, 2003, 2007), Deltshev and Petrov (2008), Dumitrescu and Georgescu (1977, 1980, 1981), Dumitrescu and Miller (1962), Gasparo (1999, 2003, 2004a, 2004b, 2005a, 2005b, 2006), and Platnick (2008). These contributions are the result of intensive faunistic research, and the accumulation of new data is now sufficient to allow a critical zoogeographical analysis of the distribution of spiders established in the caves of the Balkan Peninsula.

STUDY AREA AND MATERIALS

The Balkan Peninsula is situated in the southeastern part of Europe. As defined here, its northern border follows the rivers Danube (including its delta), Sava, and Soča; runs through Gorizia and Monfalcone; and reaches the line of the Gulf of Trieste. Its western border follows the line of the Adriatic and Ionian coasts, including the islands. The eastern border passes to the east of the Aegean islands of Sirina, Astipalea, Amorgos, Miconos, Tinos, Andros, Skiros, Limnos, and Imros; continues along the Dardanelles; crosses the Sea of Marmara; and reaches the Black Sea coast via the Bosphorus. The southernmost points of the peninsula are Crete and the islands of Gavdos, Aiduronisi, and Kufonisi (Fig. 1).

The geographical areas and associated abbreviations used in the text are shown in Fig. 1.

Data on general zoogeographical distribution are taken mainly from Platnick (2008). The zoogeographical categories used and their abbreviations are as follows: WD - widely distributed; COS - cosmopolitan; H- Holarctic; P - Palearctic; WP - West Palearctic; ECA - European-Central Asian; E - European; MEE - Middle East-European; MSEE - Middle Southeast European; EE - East European; SE - South European; SEE - Southeast European; M - Mediterranean; EM - East Mediterranean; NM - North Mediterranean; NEM - Northeast Mediterranean; BK – Balkan; BKA - Balkan-Anatolian.

RESULTS AND DISCUSSION

Species composition - The spiders established in caves of Balkan Peninsula are represented by 326 species, included in 115 genera and 31 families (Table 1). This number was established after a critical review of all available records from the literature concerning the spiders found in caves of the Balkan Peninsula. The species are distributed in different territories as follows: Bulgaria – 99; Greece (Mainland) – 72; Greece (Insular part) – 16; Crete – 44; Croatia – 63; Serbia – 59; Bosnia – 52; Macedonia – 44; Montenegro – 44; Slovenia – 43; Albania – 10; Turkey – eight and Romania – four species. This richness, however, depends not only on the size of the

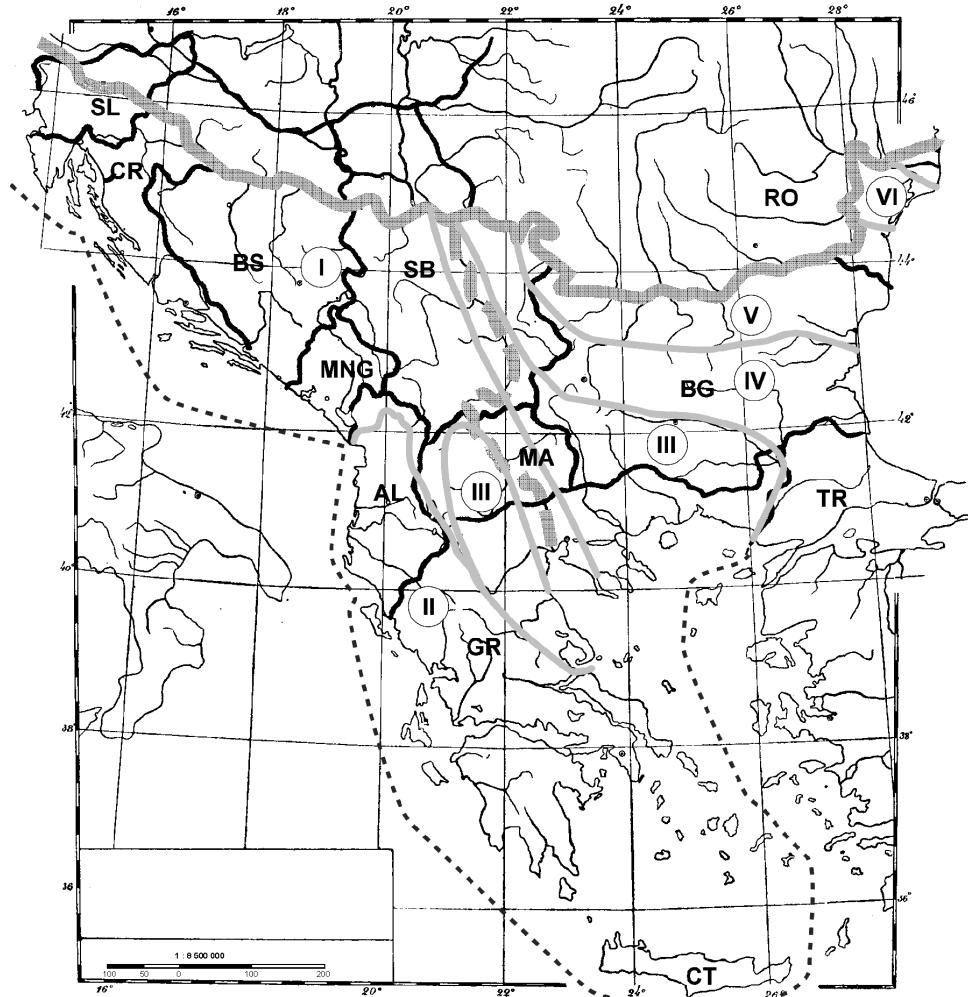


Fig. 1. Geographic Division of the Balkan Peninsula.

I - Dinaric region, II - Pindus region, III - Tracian-Macedonid region, IV - Balkanid region, V - Danubian plain region, VI - North-Dobroudzha region.

SL - Slovenia, CR - Croatia, BS - Bosnia, MNG - Montenegro, AL - Albania, GR - Greece, CT - Crete, SB - Serbia, MA - Macedonia, BG - Bulgaria, RO - Romania, TR - Turkey.

- Border between Eastern and Western part of the Balkan peninsula
- Borders of main geographic regions
- Borders of Balkan countries
- Borders of Balkan peninsula aquatory

regions, but also on the degree of exploration (Table 1). The territories of Albania and the Balkan part of Turkey have been less explored.

The genera with the most species are: *Troglohyphantes* (51), *Tegenaria* (15), *Centromerus* (13), *Histopona* (12), *Sulcia* (10), *Palliduphantes* (10), and *Leptphyphantes* (eight). The genus *Troglohyphantes* is a remarkable faunistic phenomenon, since

Table 1. Species composition of cave-dwelling spiders (Araneae) on the Balkan Peninsula

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
Cyrtidae															
<i>Cteniza moggridgei</i> O.P.-Cambridge, 1874								x					tx	NM	
<i>Cyrtocarenum grajum</i> (C. L. Koch 1836)								x	x	x			tx	BK	
Filistatidae															
<i>Filistata insidiatrix</i> (Forskoel, 1775)								x					tx	M	
Sicaridae															
<i>Loxosceles rufescens</i> (Dufour, 1820)								x	x	x			tx	COS	
<i>Scytodes thoracica</i> Latreille, 1804	x			x	x		x		x				tx	H	
Leptonetidae															
<i>Barusia insulana</i> (Kratochvíl & Miller, 1939)		x											tb	BK	
<i>Barusia maheni</i> (Kratochvíl & Miller, 1939)	x												tb	BK	
<i>Barusia korculana</i> (Kratochvíl & Miller, 1939)	x												tb	BK	
<i>Barusia hofferi</i> (Kratochvíl, 1935)		x											tb	BK	
<i>Barusia laconica</i> (Brignoli, 1974)			x	x									tb	BK	
<i>Cataleptoneta sengleti</i> (Brignoli, 1974)						x							tbb	BK	
<i>Leptonetela strinatii</i> (Brignoli, 1976)					x								tb	BK	
<i>Leptonetela andreevi</i> Deltshev, 1985						x			x				tb	BK	
<i>Leptonetela thracia</i> Gasparo						x			x				tb	BK	
<i>Leptonetela kanellisi</i> (Deeleman-Reinhold, 1971)						x			x				tb	BK	
<i>Protoleptoneta beroni</i> Deltshev, 1977	x												tb	BK	
<i>Protoleptoneta bulgarica</i> Deltshev, 1972	x	x											tb	BK	
<i>Sulcia cretica</i> Fage, 1945						x			x				tb	BK	
<i>Sulcia armata</i> Kratochvíl, 1978					x								tb	BK	
<i>Sulcia nocturna</i> Kratochvíl, 1938		x											tbb	BK	
<i>Sulcia cretica violacea</i> Brignoli, 1974						x		x	x				tb	BK	
<i>Sulcia orientalis</i> Kratochvíl, 1914	x												tb	BK	
<i>Sulcia oculta</i> Kratochvíl, 1938	x												tb	BK	
<i>Sulcia montenegrina</i> (Kratochvíl, 1938)		x						x					tb	BK	
<i>Sulcia mirabilis</i> Kratochvíl, 1938			x					x					tb	BK	
<i>Sulcia inferna</i> Kratochvíl, 1938		x					x						tbb	BK	

Table 1. Continued.

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TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Folkia haasi</i> (Reimoser, 1929)						x							tbb	BK	
<i>Folkia inermis</i> (Absolon & Kratochvíl, 1932)						x							tbb	BK	
<i>Folkia mrazeki</i> (Nosek, 1905)							x						tbb	BK	
<i>Folkia pauciaculeata</i> (Fage, 1943)						x							tbb	BK	
<i>Harpactea strinatii</i> Brignoli, 1979								x					tbb	BK	
<i>Harpactea rubicunda</i> (C.L. Koch, 1839)								x					tx	E	
<i>Harpactea pr. inserta</i> Brignoli, 1979					x								tx	BK	
<i>Harpactea babori</i> (Nosek, 1905)	x												tph	BAN	
<i>Harpactea catholica</i> (Brignoli, 1984)								x			x		tph	BK	
<i>Harpactea abantia</i> (Simon, 1884)							x						tph	BK	
<i>Harpactea corinthia</i> Brignoli, 1984							x			x			tph	BK	
<i>Mesostalita comottii</i> Gasparo, 1999						x							tbb	BK	
<i>Mesostalita Kratochvíli</i> Deeleman-Reinhold, 1971					x								tbb	BK	
<i>Mesostalita nocturna</i> (Roewer, 1931)							x				x		tbb	BAP	
<i>Minotauria fagei</i> (Kratochvíl, 1970)							x				x		tbb	BK	
<i>Minotauria attenuata</i> Kulczyński, 1903							x				x		tb	BK	
<i>Parastalita stygia</i> (Joseph, 1882)	x	x	x										tbb	BK	
<i>Rhode aspinifera</i> (Nikolić, 1963)				x									tbb	BK	
<i>Rhode subterranean</i> (Kratochvíl, 1935)				x									tbb	BK	
<i>Rhode magnifica</i> Deeleman-Reinhold, 1978						x			x				tb	BK	
<i>Rhode stalitoides</i> Deeleman-Reinhold, 1978				x									tbb	BK	
<i>Rhodera hypogaea</i> Deeleman-Reinhold, 1989							x				x		tbb	BK	
<i>Stalagzia hercegoviensis</i> (Nosek, 1905)	x	x									x		tbb	BK	
<i>Stalagzia skadarensis</i> Kratochvíl, 1970						x							tbb	BK	
<i>Stalagzia Kratochvíli</i> Brignoli, 1976							x				x		tb	BK	
<i>Stalagzia monospina</i> (Absolon & Kratochvíl, 1932)					x				x				tbb	BK	
<i>Stalita taenaria</i> Schiodte, 1847	x	x											tbb	BAP	
<i>Stalita pretneri</i> Deeleman-Reinhold, 1971				x									tbb	BK	
<i>Stalita inermisfemur</i> Roewer, 1928			x										tbb	BK	

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Stalita hadzii</i> Kratochvíl, 1934						x							tbb	BK	
<i>Stalitella noseki</i> Absolon & Kratochvíl, 1932					x								tbb	BK	
Oonopidae															
<i>Oonops mahnerti</i> Brignoli, 1974									x				tx	BK	
Mimetidae															
<i>Ero flammeola</i> Simon, 1881								x					tx	NM	
Eresidae										x			tx	E	
<i>Eresus cinnaberinus</i> (Olivier, 1789)			x							x					
Uloboridae											x		tx	COS	
<i>Uloborus plumipes</i> Lucas, 1846											x				
Nesticidae															
<i>Carpathonesticus parvus</i> (Kulczyński, 1914)				x									tb	BK	
<i>Nesticus beroni</i> Deltshev, 1973	x												tbb	BK	
<i>Nesticus beshkovi</i> Deltshev, 1979										x			tbb	BK	
<i>Nesticus cellulanus</i> (Clerck, 1758)	x	x	x	x	x	x	x	x	x	x	x	x	tph	H	
<i>Nesticus eremite</i> Simon, 1879	x		x	x	x			x	x				tb	SE	
<i>Nesticus henderickxi</i> Bosselaers, 1998										x			tbb	BK	
<i>Nesticus fagei</i> Kratochvíl, 1933			x			x							tb	BK	
<i>Nesticus speluncarium</i> Pavesi, 1873				x			x						tb	SE	
<i>Nesticus arensdorffi</i> Kulczyński, 1914				x			x						tb	BK	
<i>Typhlonesticus absoloni</i> (Kratochvíl, 1933)						x							tbb	BK	
Theridiidae															
<i>Enoplognata ovata</i> (Clerck, 1757)	x												tx	H	
<i>Episinus cavernicola</i> Kulczyński, 1897						x	x						tph	BK	
<i>Episinus maculipes</i> Cavanna, 1876	x												tx	E	
<i>Marianana mihaili</i> Georgescu, 1989	x												tb	BK	
<i>Pholcomma gibbum</i> (Westring, 1851)	x		x					x					tx	WP	
<i>Robertus frivaldszkyi</i> (Chyzer, 1894)	x												tx	SEE	
<i>Robertus lividus</i> (Blackwall, 1836)	x		x						x				tx	H	
<i>Steatoda bipunctata</i> (Linnaeus)	x												tx	H	

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Steatoda triangulosa</i> (Walckenaer, 1802)	x	x	x	x	x	x	x			x	x		tx	COS	
<i>Steatoda grossa</i> (C.L. Koch, 1838)	x				x					x	x		tx	COS	
Anapidae															
<i>Zangherella relicta</i> (Kratochvíl, 1935)							x						tb	BK	
Linyphiidae															
<i>Antrohyphantes balcanicus</i> (Drensky, 1931)	x												tb	BK	
<i>Antrohyphantes rhodopensis</i> (Drensky, 1931)	x												tb	BK	
<i>Antrohyphantes sofianus</i> (Drensky, 1931)	x												tb	BK	
<i>Caviphantes dobrogicus</i> (Dumitrescu & Miller, 1962)	x												tph		
<i>Centromerus subcaecus</i> Kulczyński, 1914							x						tb	BK	
<i>Centromerus obenbergeri</i> (Kulczyński, 1897)		x					x						tb	BK	
<i>Centromerus leruthi</i> Fage, 1933						x							tb	E	
<i>Centromerus acutidentatus</i> Deltshev, 2002	x	x	x										tb	BK	
<i>Centromerus serbicus</i> Deltshev, 2002				x									tbb	BK	
<i>Centromerus sylvaticus</i> (Blackwall, 1841)													tx	H	
<i>Centromerus cavernarum</i> (L. Koch, 1872)	x		x			x	x	x					tb	E	
<i>Centromerus silvicola</i> (Kulczyn'ski, 1887)			x										tx	E	
<i>Centromerus bulgarianus</i> (Drensky, 1931)	x												tbb	BK	
<i>Centromerus capucinus</i> (Simon, 1884)	x												tb	E	
<i>Centromerus europaeus</i> Simon, 1911					x								tbb	BK	
<i>Centromerus milleri</i> Deltshev, 1974	x									x		tbb		BK	
<i>Centromerus lataznikensis</i> (Drensky, 1931)	x	x	x										tb	BK	
<i>Diplocephalus turcicus</i> Brignoli, 1974						x			x				tx	BAN	
<i>Diplocephalus foraminifer</i> (O.P.-Cambridge, 1875)	x	x	x										tph	E	
<i>Diplocephalus cristatus</i> (Blackwall, 1833)			x										tx	E	
<i>Diplostyla concolor</i> (Wider, 1834)			x										tx	H	
<i>Dismodicus elevatus</i> (C.L. Koch, 1838)		x											tx	P	
<i>Drapetisca socialis</i> (Sundevall, 1833)			x										tx	P	
<i>Fageiella patellata</i> (Kulczyński, 1912)			x										tb	BK	

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Fageiella ensigera</i> Deeleman-Reinhold, 1974				x			x						tb	BK	
<i>Gonatium hilare</i> (Thorell, 1875)			x										tx	P	
<i>Gongylidium rufipes</i> (Linnaeus, 1758)			x										tx	P	
<i>Lepthyphantes brignolianus</i> Deltshev, 1979									x				tb	BK	
<i>Lepthyphantes beshkovi</i> Deltshev, 1979									x				tb	BK	
<i>Lepthyphantes leprosus</i> (Ohlert, 1865)	x	x	x		x			x	x		x		tph	H	
<i>Lepthyphantes centromeroides</i> Kulczyński, 1914	x	x	x	x									tb	SEE	
<i>Lepthyphantes Kratochvíli</i> Fage, 1945										x			tb	BK	
<i>Lepthyphantes magnesiae</i> Brignoli, 1979								x					tph	BK	
<i>Lepthyphantes constantinescui</i> Georgescu, 1989	x												tbb	BK	
<i>Lepthyphantes beroni</i> Deltshev, 1979									x				tb	BK	
<i>Lessertia dentichelis</i> (Simon, 1884)		x											tx	H	
<i>Linyphia triangularis</i> (Clerck, 1757)	x												tx	P	
<i>Linyphia hortensis</i> Sundevall, 1830	x												tx	P	
<i>Mansuphantes mansuetus</i> (Thorell, 1875)			x										tx	P	
<i>Megalepthyphantes collinus</i> L. Koch, 1872	x												tx	P	
<i>Meioneta affinis</i> (Kulczyński, 1898)		x											tx	P	
<i>Microctenonyx subitanicus</i> (O.P.-Cambridge, 1875)	x		x										tph	H	
<i>Microneta viaria</i> (Blackwall, 1841)	x	x	x										tph	H	
<i>Oedothorax retusus</i> (Westring, 1851)	x	x											tx	P	
<i>Oedothorax apicatus</i> (Blackwall, 1850)	x												tx	P	
<i>Palliduphantes spelaeorum</i> Kulczyński, 1914	x	x	x	x	x	x	x	x	x				tb	BK	
<i>Palliduphantes alutacius</i> Simon, 1884	x												tph	E	
<i>Palliduphantes brignolii</i> Kratochvíl, 1978						x							tb	BK	
<i>Palliduphantes byzantinus</i> Fage, 1931	x	x							x		x	x	tph	BK	
<i>Palliduphantes epaminondae</i> Brignoli, 1979								x					tb	BK	
<i>Palliduphantes istrianus</i> Kulczyński, 1914	x		x		x			x			x		tb	SEE	
<i>Palliduphantes pillichi</i> Kulczyński, 1915	x												tpph	MSEE	
<i>Palliduphantes trnovensis</i> (Drensky, 1931)	x	x	x										tb	BK	

Table 1. Continued.

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Troglolophantes polenici</i> Wiehle, 1964						x							tb	BK	
<i>Troglolophantes polyophtalmus</i> Joseph, 1881						x							tb	BK	
<i>Troglolophantes pretneri</i> Deeleman-Reinhold, 1978							x						tbb	BK	
<i>Troglolophantes helsingeni</i> Deeleman-Reinhold, 1978													tb	BK	
<i>Troglolophantes spinipes</i> Fage, 1919						x							tb	BK	
<i>Troglolophantes sketi</i> Deeleman-Reinhold, 1978						x							tb	BK	
<i>Troglolophantes roberti</i> Deeleman-Reinhold, 1978					x								tb	BK	
<i>Troglolophantes s. bosnicus</i> Kratochvíl, 1948					x								tb	BK	
<i>Troglolophantes s. noctiphilus</i> Kratochvíl, 1948					x								tb	BK	
<i>Troglolophantes s. svilajensis</i> Kratochvíl, 1948					x								tb	BK	
<i>Troglolophantes similes</i> Fage, 1919					x								tb	BK	
<i>Troglolophantes strandi</i> Absolon & Kratochvíl, 1932					x								tbb	BK	
<i>Troglolophantes scientificus</i> Deeleman-Reinhold, 1978						x							tbb	BAP	
<i>Troglolophantes cornutus</i> Deeleman-Reinhold, 1978						x							tph	BK	
<i>Troglolophantes croaticus</i> (Chyzer, 1894)					x								tb	BK	
<i>Troglolophantes d. dekkingae</i> Deeleman-Reinhold, 1978					x								tb	BK	
<i>Troglolophantes d. pauciacylindatus</i> Deeleman-Reinhold, 1978					x								tb	BK	
<i>Troglolophantes dalmaticus</i> (Kulczyński, 1914)	x					x							tb	BK	
<i>Troglolophantes diabolicus</i> Deeleman-Reinhold, 1978						x							tb	BK	
<i>Troglolophantes brignolii</i> Deeleman-Reinhold, 1978						x							tb	BK	
<i>Troglolophantes dinaricus</i> Kratochvíl, 1948						x							tb	BK	
<i>Troglolophantes draconis</i> Deeleman-Reinhold, 1978	x							x					tb	BK	
<i>Troglolophantes drenskii</i> Deltshov, 1973	x							x					tbb	BK	
<i>Troglolophantes gracilis</i> Fage, 1919							x						tb	BK	
<i>Troglolophantes roberti</i> <i>dalmatinensis</i> Deeleman-Reinhold, 1978						x							tb	BK	
<i>Troglolophantes hadzii</i> Kratochvíl, 1934					x	x							tb	BK	
<i>Troglolophantes boudewijni</i> Deeleman-Reinhold, 1974							x						tb	BK	
<i>Troglolophantes excavatus</i> Fage, 1919						x	x						tb	BAP	

Table 1. Continued.

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Pardosa agrestis</i> (Westring, 1861)		x												tx	P
Pisauridae															
<i>Pisaura mirabilis</i> (Clerck, 1757)				x										tx	P
Agelenidae															
<i>Agelena gracilens</i> C.L. Koch, 1841								x						tx	ECA
<i>Hadites tegeneroides</i> Keyserling, 1862					x	x								tbb	BK
<i>Histopona hauseri</i> Brignoli, 1972										x				tph	BK
<i>Histopona bidens</i> (Absolon&Kratochvíl, 1932)	x				x									tb	BK
<i>Histopona conveniens</i> (Kulczyński, 1914)			x	x		x								tb	BK
<i>Histopona dubia</i> (Absolon&Kratochvíl, 1932)			x	x		x								tb	BK
<i>Histopona egonpretneri</i> Deeleman-Reinhold, 1983					x									tb	BK
<i>Histopona isolata</i> Deeleman-Reinhold, 1983								x			x			tb	BK
<i>Histopona krivosijana</i> (Kratochvíl, 1935)						x								tb	BK
<i>Histopona myops</i> (Simon, 1885)							x							tph	BK
<i>Histopona tranteevi</i> Deltshev, 1978	x													tph	BK
<i>Histopona thaleri</i> Gasparo, 2005								x						tph	BK
<i>Histopona laeta</i> (Kulczyński, 1897)		x	x											tph	BK
<i>Histopona luxurians</i> (Kulczyński, 1897)					x									tx	SEE
<i>Maimuna cretica</i> (Kulczyński, 1903)								x						tx	BK
<i>Maimuna vestita</i> (C.L. Koch, 1841)							x			x				tx	EM
<i>Pseudotegenaria animate</i> (Kratochvíl&Miller, 1940)	x		x			x								tb	BK
<i>Pseudotegenaria bayeri</i> (Kratochvíl, 1934)			x			x								tb	BK
<i>Pseudotegenaria decolorata</i> (Kratochvíl&Miller, 1940)				x										tb	BK
<i>Pseudotegenaria bosnica</i> (Kratochvíl&Miller, 1940)		x	x				x							tb	BK
<i>Tegenaria picta</i> Simon, 1870														tx	WP
<i>Tegenaria schmalfussi</i> Brignoli, 1976								x			x			tb	BK
<i>Tegenaria parietina</i> (Fourcroy, 1785)	x	x	x		x				x		x			tph	WP
<i>Tegenaria pagana</i> C.L. Koch, 1841	x								x		x			tph	COS
<i>Tegenaria hauseri</i> Brignoli, 1979									x					tx	BK

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Tegenaria ferruginea</i> (Panzer, 1804)	x	x	x							x	x		tph	E	
<i>Tegenaria domestica</i> (Clerck, 1757)	x	x	x	x	x	x	x	x	x	x	x	x	tph	COS	
<i>Tegenaria dalmatica</i> Kulczyński, 1906							x		x				tph	BK	
<i>Tegenaria campestris</i> C.L. Koch, 1834				x									tx	E	
<i>Tegenaria bithyniae</i> Brignoli, 1978	x										x		tph	BAN	
<i>Tegenaria ariadnae</i> Brignoli, 1984											x		tb	BK	
<i>Tegenaria annulata</i> Kulczyński, 1912			x	x		x							tb	BK	
<i>Tegenaria agrestis</i> (Walckenaer, 1802)													tx	H	
<i>Tegenaria silvestris</i> L. Koch, 1872	x	x	x		x					x			tph	E	
<i>Tegenaria pieperi</i> Brignoli, 1979											x		tb	BK	
<i>Textrix denticulata</i> (Olivier, 1789)	x												tx	E	
Cybaeidae															
<i>Cybaeus balkanicus</i> Deltshev, 1997				x									tx	BK	
<i>Cybaeus angustiarum</i> L. Koch, 1868	x			x									tx	MSEE	
Hahnidae															
<i>Hahnia caeca</i> Georgescu, 1992	x												tbb	BK	
<i>Cicurina cicur</i> (Fabricius, 1793)	x	x	x	x		x							tph	E	
Dictynidae															
<i>Dictyna uncinata</i> Thorell, 1856	x							x		x			tx	P	
<i>Mastigusa macrophthalmia</i> (Kulczyński, 1897)			x										tx	MEE	
<i>Nigma flavescens</i> (Walckenaer, 1825)	x												tx	P	
Amaurobiidae															
<i>Amaurobius pallidus</i> L. Koch, 1868	x												tx	MSEE	
<i>Amaurobius deelemanae</i> Thaler&Knoflach, 1995										x	x		tx	BK	
<i>Amaurobius pelops</i> Thaler&Knoflach, 1991									x				tx	BK	
<i>Amaurobius ferox</i> (Walckenaer, 1825)	x												tx	H	
<i>Amaurobius fenestralis</i> (Stroem, 1768)	x												tx	E	
<i>Amaurobius strandi</i> Charitonov, 1937							x						tx	SEE	
<i>Callobius claustrarius</i> (Hahn, 1831)	x							x					tx	P	
<i>Callobius balcanicus</i> (Drensky, 1940)	x												tx	BK	

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
<i>Coelotes atropos</i> (Walckenaer, 1830)				x									tx	E	
<i>Coelotes terrestris</i> (Wider, 1834)										x			tx	NM	
<i>Eurocoelotes jurinischii</i> (Drensky, 1915)	x			x									tx	BK	
<i>Eurocoelotes drenskii</i> Deltshev, 1990		x											tx	BK	
<i>Eurocoelotes inermis</i> (L. Koch, 1855)	x			x									tx	E	
<i>Urocoras longispinus</i> Kulczyński, 1897	x												tx	SEE	
Liocranidae															
<i>Liocranum rupicola</i> (Walckenaer, 1830)	x	x	x	x	x								tph	E	
<i>Liocranum rutilans</i> (Thorell, 1875)		x	x	x	x	x	x	x	x	x			tph		
<i>Mesiotelus cyprius scopensis</i> Drensky, 1935	x												tx	BK	
<i>Agraecina christiani</i> Georgescu, 1989		x											tx	BK	
Clubionidae															
<i>Clubiona caerulescens</i> L. Koch, 1867		x											tx	P	
<i>Clubiona compta</i> C. L. Koch, 1839	x												tx	WP	
<i>Clubiona neglecta</i> O. P.-Cambridge, 1862													tx	P	
Corinnidae															
<i>Phrurolithus festivus</i> (L. Koch, 1835)	x												tx	P	
Gnaphosidae															
<i>Drassodes lapidosus</i> (Walckenaer, 1802)			x			x				x		x	tx	P	
<i>Echemus angustifrons</i> (Westring, 1862)	x												tx	E	
<i>Gnaphosa luciphuga</i> (Walckenaer, 1802)			x										tx	P	
<i>Pterotricha lentiginosa</i> (C.L. Koch, 1837)									x				tx	M	
<i>Scotophaeus blackwalli</i> (Thorell, 1871)	x												tx	COS	
<i>Zelotes femellus</i> (L. Koch, 1866)								x					tx	SEE	
<i>Zelotes oblongus</i> (C.L. Koch, 1833)								x					tx	E	
<i>Zelotes clivicola</i> (L. Koch, 1870)								x					tx	P	
<i>Zelotes apricorum</i> (L. Koch, 1876)	x												tx	E	
Philodromidae															
<i>Philodromus collinus</i> C.L. Koch, 1835							x						tx	E	

Table 1. Continued.

TAXA	RO	BG	MA	SB	BS	CR	SL	MG	AL	GR	IN	CT	TR	CAT	Z-G
Thomisidae															
<i>Synaema globosum</i> (Fabricius, 1775)								x				tx		P	
Salticidae															
<i>Evarcha falcate</i> (Clerck, 1757)										x		tx		P	
<i>Mendoza canestrinii</i> (Ninni, 1868)									x			tx		P	
<i>Philaeus chrysops</i> (Poda, 1761)								x			tx			P	
<i>Sitticus pubescens</i> (Fabricius, 1775)	x											tx		H	

out of a total of 51 species, 49 are Balkan endemics, distributed mainly in caves. Deeleman-Reinhold (1978) concluded that the present distribution and morphological diversity of *Troglhyphantes* on the Balkan Peninsula represents of a repeated processes of expansion and contraction of its range. High representation of the genera *Histopona* (11 endemics), *Sulcia* (10 endemics), *Centromerus* (eight endemics), *Tegenaria* (seven endemics), *Lepthyphantes* (six endemics), and *Palliduphantes* (five endemics) is also due to expansion in caves. A present-day example of cave penetration are the species *Lepthyphantes centromeroides* and *L. spelaeorum*, which are comparatively widespread on the Balkan Peninsula. They occur in caves, but also in the humus and ground detritus, indicating active subterranean colonization (Dedeeman-Reinhold, 1978).

Cave-dwelling spiders can be relegated to three ecological groups: troglobites – species that must spend their entire life cycle in a cave; troglophiles - species which can live their entire lives in caves, but which also occur in other environments; and trogloxenes (including accidentals) - species which utilize caves, but must leave the caves to complete their life cycle.

Troglobites often show a suite of characters associated with their adaptation to subterranean life - loss of pigment, loss of eyes, and elongation of appendages. The largest number of troglobites are encountered in the Dinaric region – 113 (39 blind), Pindus region – 32 (eight blind), Thracian-Macedonian region – 18 (four blind), Balkanid region – 13 (two blind), Danubian region — one; and North Dobruja region — four (three blind) species (Table 1). The extreme richness of troglobitic spiders in these regions leads to the assumption that these were major centers of speciation and evolution of species.

Zoogeographical analysis – On the basis of their current distribution, the established 324 species can be classified into 17 zoogeographical categories, grouped into four complexes (Balkan endemics, widely distributed, European, and Mediterranean).

Best represented is the complex of Balkan endemics, with 184 species (56.5%). The established number is high and reflects the local character of the cave fauna. The endemics are best represented in Croatia - 42, Bosnia - 38, Montenegro – 30, Greece

- 26, Crete – 25, Bulgaria – 22, and Slovenia – 21. It should be emphasized that of the 14 endemic genera established as being endemic to the Balkan Peninsula, only three (*Anthrohyphantes*, *Macedoniella*, and *Protoleptoneta*) are distributed in its eastern part. Especially interesting is the distribution of the genus *Antrohyphantes*, found only in high-altitude zones and caves of the eastern part of the region (Bulgaria). It is related to the genus *Fageiella*, endemic to caves of the western Balkans (Bosnia, Montenegro). Their allopatric distribution indicates that they had already separated before the establishment of the Vardar tectonic zone (Deltshev, 1996). This suggests that these two genera are paleoendemics. The recent cave spider fauna was formed after gradual changes in the fauna of the ancient humid Mediterranean forests. However, due to the lack of knowledge, it is difficult to determine with certainty which cave spiders endemic to the Balkans are Tertiary and which are Quaternary elements.

The complex of widely distributed species (COS+H+P+WP+ECA) comprises 74 species (22.7%). Palearctic species are dominant (12%), followed by Holarctic (5.8%), cosmopolitan (2.8%) West Palearctic (1.8%), and European-Central Asiatic (0.3%) forms. The complex includes especially widespread species associated with lowlands, buildings, caves, woodlands, and high-altitude zones of mountains. Among members of this group, characteristic of caves are *Nesticus cellulanus*, *Lepthyphantes leprosus*, *Microtenonix subitanea*, *Porrhomma convexum*, and *Tegenaria domestica*. The species *Nesticus cellulanus* and *Porrhomma convexum* are two of the most widespread taxa in the caves of Europe.

The European complex (E+MEE+MSEE+EE+SEE) includes 50 species (15.6%). European species are dominant (10.5%), followed by Southeast European (2.8%) and Middle Southeast European (1.8%). The remaining categories are represented by single species widespread mainly in mountains. Middle Southeast European (9.0%), Southeast European (9.0%), and East European (7.4%) are relatively well represented. The complex includes spiders widespread in Europe and the Balkan Peninsula which inhabit both lowlands and mountains. The most characteristic of caves are *Hoploholcus forskali*, *Centromerus cavernarum*, *Diplocephalus foraminifer*, *Lepthyphantes centromeroides*, *Palliduphantes istrianus*, *Porrhomma lativelum*, and *Porrhomma rosenhaueri*.

The last complex includes 18 species (5.5%) occurring in the Mediterranean area (M+SE+NM+EM+BAN+BAP+) or part of it. This complex forms 5.5% of the cave spider fauna of the Balkan Peninsula, but the real percentage is probably higher because some Balkan endemics have Mediterranean origin. True cavernicolous elements are *Mesostalita nocturna*, *Stalita taenaria*, *Nesticus eremita*, and *Nesticus speluncarum*.

CONCLUSION

A review of the faunistic diversity of its 326 cave-dwelling spiders shows that the Balkan Peninsula is a territory of considerable species richness. This conclusion is also supported by the existence of 184 endemic species. The uneven species richness

Table 2. Zoogeographical composition of cave-dwelling spiders (Araneae) in Balkan Peninsula.

Complexes	Chorotypes		Species	
	Classification	Code	Number	%
Widely distributed	Cosmopolitan	COS	9	2.8
	Holarctic	HOL	19	5.8
	Palearctic	PAL	39	12
	West Palearctic	WP	6	1.8
	European-Central Asiatic	ECA	1	0.3
	Total		74	22.7
European	European	E	34	10.5
	Middle-East European	MEE	1	0.3
	Middle-Southeast European	MSEE	6	1.8
	East European	EE	1	0.3
	Southeast European	SEE	8	2.8
	Total		50	15.6
Mediterranean	Mediterranean	M	4	1.2
	South European	SE	3	0.9
	North Mediterranean	NM	3	0.9
	East Mediterranean	EM	1	0.3
	Balkan-Anatolic	BAN	3	0.9
	Balkan-Apennine	BAP	4	1.2
	Total		18	5.5
Endemics	Balkan	BK	183	56.3
	Total		183	56.3

in some parts of the Balkan Peninsula is mainly due to the different degree of exploration by researchers. In the zoogeographical respect, the endemics are dominant, but elements characteristic of caves are found in all chorological complexes. The high percentage of the Balkan endemics (56.5%) suggests an important process of autochthonous speciation. Thus, the existing data suggest that the Balkan Peninsula represents one of the main centers of speciation in Europe.

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