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The hypogean invertebrate fauna of Georgia (Caucasus)

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Information about the cave invertebrates of Georgia, Caucasus, is summarised, resulting in 43 troglo- and 43 stygobiont taxa reported from 64 caves. Species distribution analyses were conducted for 61 caves harbouring 58 invertebrate taxa, with the majority of caves (39) located in Apkhazeti (north-western Georgia). In 22 caves from central-west Georgia (Samegrelo, Imereti and Racha-Lechkhumi regions of west Georgia) 31 taxa are reported. Composition of cave fauna differed strongly between the caves in Apkhazeti and the central-west of Georgia. Only two taxa of the total 86 were shared, resulting in negligible similarity (Sørensen-Dice coefficient S_s=4.8%). Rarefaction indicated an increase in number of species with additional sampling could increase species richness from 58 to 76 for caves in Apkhazeti and from 31 to 69 for caves in central-west Georgia. These findings suggest that the low invertebrate species richness observed in caves of western Georgia is the result of insufficient sampling. A pairwise approach to analysing species co-occurrence showed ten positive spatial associations in 7 out of 86 cave species, all from Kveda Shakurani and Tsebelda caves. The species co-occurring in the same microhabitat require further study to understand their relationships.

Keywords: Cave invertebrates; distribution; endemism; diversity; Georgia

Introduction

The cave fauna of Georgia, Caucasus has been recognised as unique on a global scale, but has yet to be studied comprehensively. Altogether, 453 invertebrate species belonging to 45 orders from 18 classes and 7 phyla are recorded from 134 caves in Georgia (Barjadze et al., 2015; Antić & Makarov, 2016; Sidorov, 2016; Sidorov,& Samokhin, 2016; Turbanov, Palatov, & Golovatch, 2016; Marin, 2017; Vargovitsh, 2017; Golovatch & Turbanov, 2017, 2018; Antić, Turbanov, & Reboleira, 2018; Sidorov, Taylor, Sharina, &Gontchariv, 2018; Vinarski & Palatov, 2018). Investigations of Georgian cave invertebrates began in the 19th century (Boettger, 1879) and have dealt primarily with taxonomic, faunistic and zoogeographic topics (Barjadze et al., 2015; Turbanov et al., 2016), with information on ecology rarely receiving attention in this literature. A notable exception is an ecological contribution on the distribution and comparative analysis of the aquatic cave fauna of Apkhazeti (=Abkhazia) (Chertoprud et al., 2016). Ecological investigations of the cave fauna are hindered by the inaccessibility or at least difficult accessibility of many caves. Consequently, the existing data on the cave-dwelling invertebrates do not show a complete picture of the biodiversity of Georgian caves.

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The caves of Apkhazeti are much better investigated than the ones from the remaining Georgian karst. This is probably due to the fact that the Black Sea coastal region and the high mountainous area of the Apkhazeti were a well-known tourist destination in the former Soviet Union. In this study we compared species richness of the cave fauna of Apkhazeti with fauna of other caves of the west Georgia, southwest of the Greater Caucasus from the 19th to the 21st century. We summarise information on obligatory cave dwelling invertebrates of Georgia, estimate the number of undetected taxa (species richness), evaluate troglobitic species distributions, and assess patterns of species co-occurrence.

Material and Methods

Study area. The karstic outcrops of western Georgia along the southern slope of the Greater Caucasus mountain range extend some 325 km from the Psou River to the Ertso Lake area. The total area of the karstic rock outcrop, 4,475 km^2, covers 6.4 % of the total area of Georgia. A karstic belt with well-delineated vertical zonation is distributed from the Gagra-Gantiadi coastal area (with its submarine springs) to 2,757 m a.s.l. at the Peak of Speleologists on the Arabika Massif (Kipiani, 1974). There are 1306 known caves in Georgia (Tsikarishvili et al., 2010).

Data collection. Lists of troglobitic (i.e., terrestrial cavernicolous) and stygobitic (i.e., aquatic cavernicolous) invertebrates were compiled from literature on the Georgian cave fauna published between 1879 and 2018 in Georgian, Russian, German, French and English languages. Only eyeless cavernicolous animals that could be identified to the species level were included in the list and analysed. We did into include any undescribed troglobitic species, such as material collected in the Imereti and Samegrelo regions between 2014 and 2018. Zaitsev's (1948) study provides a baseline for our work, and includes information on the distribution of 103 animal species in 21 Georgian caves. Additionally, Birstein (1950) provided information on 115 animal species from 36 caves of western Transcaucasia, and other important information was obtained from Kobakhidze (1963), Djanashvili (1980, 1984) and Kniss (2001). Barjadze et al. (2015) provided data on 415 invertebrate taxa recorded in Georgian caves. From the literature we were able to extract data on distribution of 58 invertebrate species in 42 caves of Apkhazeti and of 31 invertebrate species in 22 caves of central-west Georgia (Imereti, Samegrelo and Racha-Lechkhumi).

The map of 61 geo-referenced caves (Figure 1) excludes three additional caves in Apkhazeti for which locations are unknown, and the fauna of these three caves is not included in the analyses. For other some caves in west Georgia with inaccurate locations given in the literature (Inchkhuri, Kveda Kvilishori, Motena, Opicho, Orpiri II, Prometheus, Sakadzhia, Sakishore, Sataplia I, Solkota, Tetra, Tsakhi, Tsivtskala and Tskaltsitela caves) we were able to correct locations for some species through field validation in 2015–2016. Geographical coordinates of some caves in Apkhazeti are provided by I. Turbanov (Borok, Russia).

Data on the distribution of 86 species from the 61 caves were used in comparative analyses as well as in the evaluation of distribution patterns and species co-occurrence.

Data processing. Data collected from the reviewed literature sources were used to create species incidence or presence-absence based matrix of database.

To measure similarity in cave species richness the abundance-type incidence Sørensen-Dice similarity index (Magurran, 2004) was used. The index was calculated by the following formula: $S_S = 2a/(2a + b + c)$ where S_S is Sørensen-Dice similarity index, *a* number of species common to both quadrats, *b* number of species unique to the first quadrat, *c* number of species unique to the second quadrat. The abundance Sørensen-Dice similarity index was calculated using software PAST 3.15 (Hammer, 2017).

The expected total number of species in caves of the reviewed regions was calculated using Chao1 estimator and species incidence-based rarefaction method. These are nonparametric estimators of species richness which are based on mark-release-recapture (MRR) type of statistical methods and estimate richness by adding a correction factor to the observed number of species (Chao & Jost, 2012). This approach enabled the comparison of different sample sizes,

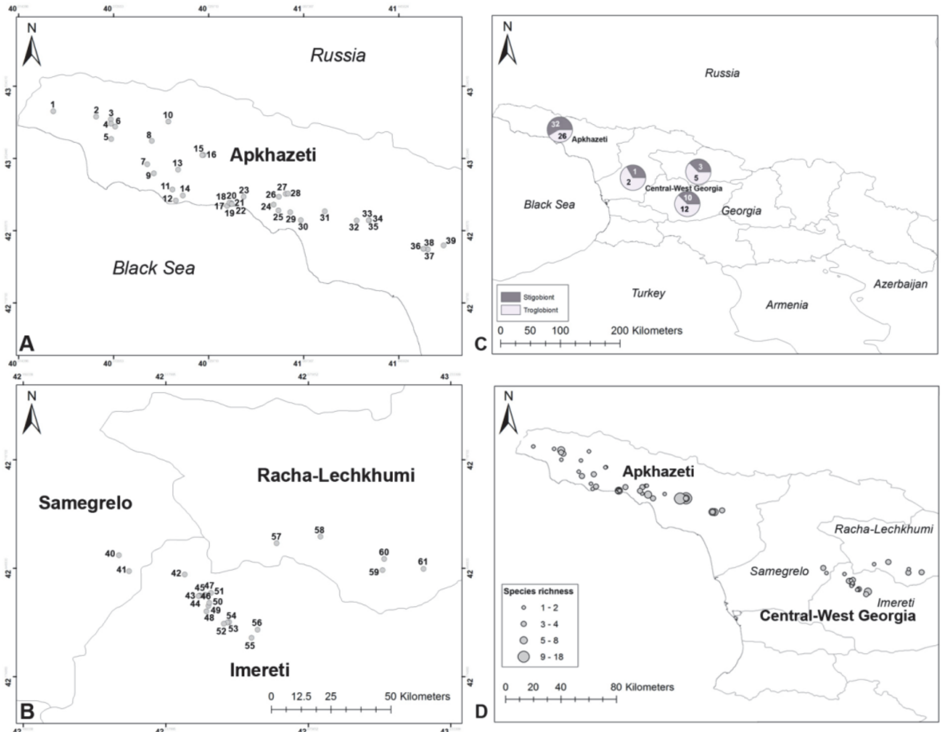

Figure 1. Locations and diversity of the reviewed caves: A) Cave locations in Apkhazeti; B) Cave locations in Central-West Georgia; C) Distribution of troglo- and stygobitic invertebrate diversity in the studied regions; D) Spatial distribution of the species richness in the caves.
Caves: 1: Jeopse Cave; 2: Kuibishevi Cave; 3: Krubera-Voronya Cave; 4: Troika Cave; 5: Orlinoe Gnezdo Cave; 6: Sarma Cave; 7: Mchishta Vokluz Cave; 8: L–24 Cave; 9: Bacha Cave; 10: Cave at Mt. Achibakha; 11: Likhni Cave; 12: Agumava Cave; 13: Tarkili Cave; 14: Chlakhe Cave; 15: Souvenir Cave; 16: Iluzia-tovliani-mejeni Cave; 17: Avidzba Cave; 18: Manikvara Cave; 19: Akhali Atoni Cave; 20: Akui Cave; 21: Aghmavali Cave; 22: Simon Kananeli Cave; 23: Anukhva (=III?) Cave; 24: Zemo Eshera; 25: Adzaba Cave; 26: Akhalsheni Cave; 27: Dasavlet Gumista Cave; 28: Guma (-Sabashvili) Cave (=Gumis I?); 29: Shroma Cave; 30: Tskaro Cave; 31: Kelasuri Cave; 32: Tsebelda Cave; 33: Zeda Shakurani Cave; 34: Shua Shakurani Cave; 35: Kveda Shakurani Cave; 36: Well Uapatyh; 37: Otapistavi Cave; 38: Abrskili Cave; 39: Well 85 m; 40: Motena Cave; 41: Inchkhuri Cave; 42: Satevzia Cave; 43: Ghliana Cave; 44: Prometheus Cave; 45: Orpiri II Cave; 46: Opicho Cave; 47: Sakadzhia Cave; 48: Tetra Cave; 49: Kveda Kvilishori Cave; 50: Zeda Kvilishori Cave; 51: Solkota Cave; 52: Sataplia IV Cave; 53: Sataplia II Cave; 54: Sataplia I Cave; 55: Tskaltsitela Cave; 56: Sapichkhia Cave; 57: Tvishi Cave; 58: Tsakhi Cave; 59: Meliis Cave; 60: Tsivtskala Cave; 61: Sakishore Cave.

extrapolating the smallest samples and comparing species diversity estimates at equal sample coverage. The analyses were done using iNEXT online software (Hsieh, Ma, & Chao, 2013) configured at 40 nodes and bootstraps with 300 replications (Zenker et al., 2015). Comparisons were done at 95 % confidence interval.

To calculate pairwise co-occurrence patterns from the community dataset the R package Cooccur (Griffith, Veech, & Marsh,2016; R Core Team, 2016) was used. This package takes a community dataset of species by site presence-absence data and classifies species pairs as having positive, negative, and random associations based on the probabilistic model of species co-occurrence (Veech, 2013).

Table 1. The distribution obligate subterranean species in caves of the Republic of Georgia. Nss/Nts – number of stygobitic vs troglobitic species; Nsf/Ntf – number of stygobitic *vs* troglobitic families. – * total species number in each animal group is lower than the sum of species numbers in all regions, because some invertebrate species are recorded from more than one region. – ** total species number of obligate cave dwelling invertebrates is lower than the sum of species numbers in all regions, because some invertebrate species are recorded from more than one region.

		CILIOPHORA	ANNELIDA	MOLLUSCA		ARTHRO-PODA												**TOTAL**
Nss/Nts		1/0	1/0	10/5		43/38												43/43
		CILIOPHORA	ANNELIDA	GASTROPODA	BIVALVIA	OSTRACODA	ISOPODA	MAXILLOPODA	AMPHIPODA	DECAPODA	PSEUDOSCORP.	PALPIGRADI	OPILIONES	CHILOPODA	DIPLOPODA	COLLEMBOLA	INSECTA	
Nsf/Ntf		1/0	1/0	2/1	1/0	1/0	0/1	3/0	3/0	1/0	0/2	0/1	0/1	0/1	0/1	0/5	0/1	13/14
Apkhazeti	Nss	1	–	8	1	–	–	5	14	3	–	–	–	–	–	–	–	32
	Nts	–	–	3	–	–	3	–	–	–	1	1	3	1	1	7	6	26
Imereti	Nss	–	–		1	1	–	5	1	2	–	–	–	–	–	–	–	10
	Nts	–	–	2	–	–	2	–	–	–	3	–	–	–	1	2	2	12
Racha-Lechkhumi	Nss	–	1	–	–	–	–	2	–	–	–	–	–	–	–	–	–	3
	Nts	–	–	–	–	–	–	–	–	–	1	–	1	–	–	1	2	5
Samegrelo	Nss	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
	Nts	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2
Total		**1**	**1**	**13**	**2**	**1**	**6***	**9***	**16**	**5**	**4***	**1**	**4**	**1**	**2**	**10**	**10**	**86****

Results

Of the 86 hypogean species recorded from 61 caves in Georgia, Caucasus (Figure 1A, B), 58 were present in caves in Apkhazeti and 31 in caves of the central part of Western Georgia: Samegrelo, Racha-Lechkhumi and Imereti (Table 1). Species richness differed significantly at a regional level (Figure 1C, D). In the caves of the central part of Western Georgia, regional species richness was low, with 3, 8 and 22 species for Samegrelo, Racha-Lechkhumi and Imereti, respectively. The Sørensen-Dice coefficient the level of similarity in biodiversity between the Apkhazeti caves and the combined group of the Imereti, Samegrelo and Racha-Lechkhumi caves, Ss=0.048, is low, with only 4.8% of the total diversity being shared between the Apkhazeti and central west Georgian cave regions.

Sample-based rarefaction and extrapolation analyses of hypogean invertebrates indicate that species richness in caves in Apkhazeti is higher than richness in central west Georgian caves. However, the probability of the increased of the diversity richness with more intensive sampling is higher in central west Georgia (Figure 2).

Doubling the number of samples would result in an estimated increase from 58 to 76 species in caves in Apkhazeti and from 31 to 69 species for caves in central west Georgia, based on Chao 1 projections. Value of Sample Cover (S.C.) index was lower

Table 2. Trend of increase of the species richness with possible future, more intensive sampling. Observed (A) and estimated with doubled sampling events (B) richness; Richness estimate by the Chao and Jost (2012) method; the estimated sample coverage for a sample of size t (S.C.); LCL = lower and UCL = upper limits of the bootstrap confidence intervals for the diversity or entropy of species richness at the probability level of 0.95 (95%); Central-west Georgia = Imereti, Racha and Samegrelo regions.

	Species richness		**S.C.**	**LCL**	**UCL**
Central-west Georgia	Observed	31	0.45	23.69	38.31
	Estimated	69.33	0.75	43.67	94.98
Apkhazeti	Observed	58	0.75	49.26	66.74
	Estimated	76.1	0.85	62.6	90.13

for caves of central west Georgian regions (Samegrelo, Imereti and Racha) than for Apkhazetian caves, indicating that available data on species richness for the central west Georgia likely falls far short of true species richness in these caves (Table 2).

Pairwise species co-occurrence analyses did not detect any negative associations between species pairs, but 10 positive associations were identified, involving 7 of the species (Figure 3).

Of the 453 invertebrate species recorded in the Georgian caves, 86 species are obligate cave dwellers (18.9% of all species): 43 of these are terrestrial (troglobionts *s.str.*) and 43 are aquatic (stygobionts) (Table S1). The troglobionts include 38 arthropod and 5 mollusk species, while stygobionts include 31 arthropods, 10 mollusks, one annelid and one ciliophora species (Table S1). Locally endemic species known from only a single cave include 32 troglobites and 21 stygobites. The family Zenkevitchiidae Sidorov, 2018 is endemic of Georgia, and the following 13 troglobitic and stygobitic genera are also endemic to Georgia: *Adaugammarus* Sidorov, Gontcharov & Sharina, 2015; *Kruberia* Sidorov & Samokhin, 2016; *Zenkevitchia* Birstein, 1940 (Amphipoda); *Lesticulus* Schileyko, 1988; *Motsametia* Vinarski, Palatov & Glöer, 2014 and *Pontohoratia* Vinarski, Palatov & Glöer, 2014 (Gastropoda); *Borutzkyella* Tabacaru, 1993*, Colchidoniscus* Borutzky, 1974 and *Mingrelloniscus* Borutzky, 1974 (Isopoda); *Troglopalites*Vargovitsh, 2012 (Collembola); *Leucogeorgia* Verhoeff, 1930 (Diplopoda); *Inotrechus* Dolzhansky & Ljovuschkin, 1989 and *Taniatrechus* Belousov & Dolzhanskij, 1994 (Coleoptera). Four troglobitic genera are endemic to the Caucasus: *Conulopolita* Boettger, 1879 (Gastropoda); *Jeannelius* Kurnakov, 1959*, Meganophthalmus* Kurnakov, 1959 and *Troglocimmerites* Ljovuschkin, 1970 (Coleoptera).

The Georgian cave fauna is still insufficiently known, with only about 10% of karst and conglomerate caves having been investigated biospeleologically. Based on our current knowledge, the most widespread obligate cave invertebrates of Georgia include *Trichoniscus aphonicus* Borutzky, 1977 (14 caves), *Zenkevitchia admirabilis* Birstein, 1940 (8 caves), *Niphargus inermis* Birstein, 1940 (8 caves), *Zenkevitchia yakovi* Sidorov, 2015 (6 caves), and *Conulopolita raddei* (Boettger, 1879) (5 caves). The remaining species have narrower distributions and are known from 1–4 caves. Species richness is highest in Kveda Shakurani Cave (18 species), and other important caves for obligate subterranean species include Tsebelda (14 species), Akhali Atoni (8 species), Otapistavi (8 species), Sapichkhia (8 species), Shroma (7 species), Abrskili (6 species), and Shua Shakurani (6 species). The remaining caves are known to contain 5 or less obligate subterranean species.

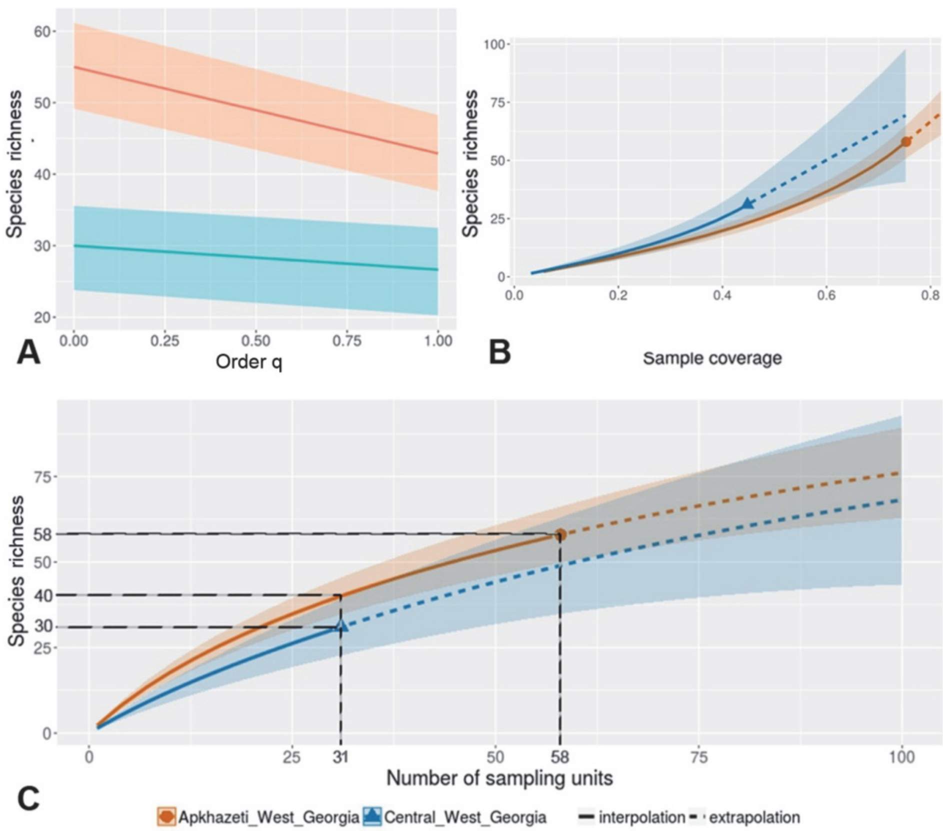

Figure 2. Prediction of potential species richness of obligate subterranean animals of the reviewed caves if sample size were increased to 100 samples. **A.** Observed diversity of invertebrate fauna in the caves in the range of analysed sample size (order indicates the diversity of order of q between 0 and 3 in increments of 0.25 [Chao & Jost, 2012]). **B.** Coverage of the taken sample. **C.** Sample-size-based rarefaction (solid curves) and extrapolation (dash curves) comparing species richness between the regions.

Discussion

Rarefaction and extrapolation analyses suggest that the existing data on the cave fauna of Georgia is incomplete. Caves in Apkhazeti are relatively well investigated biospeologically in comparison to caves in other regions of west Georgia, but even in Apkhazeti the number of cave obligate species should increase after more intensive, taxon-targeted surveys. It is difficult to validate previous published observations due to the existing political situation in Apkhazeti. Of 1306 known caves in Georgia (Tsikarishvili et al., 2010) only 10.26 % (134 caves) have been investigated biospeleologically. New species descriptions and biological study of caves not previously examined – or with only cursory investigations – should markedly increase the number of obligate cave species known from Georgia.

Of the 86 species evaluated in this study, only two – *Pilocamptus pilosus* (Douwe, 1910) (= *Echinocamptus georgevitchi*) and *Bryocamptus innominatus* Borutzky, 1940 – are shared between caves of Apkhazeti and central-west Georgian. *Pilocamptus pilosus* is widely distributed in central and eastern European countries, while *B. innominatus*

						N. inermis
					Z. yakovi	+
				T. osterloffi	+	+
			Z. admirabilis	+	0	0
		E. ljovuschkini	+	0	+	+
	N. magnus	0	0	0	+	+
T. stygios	0	0	+	0	0	0

Table 3. Matrix of species community interaction, including species pairs with positive (+), and random (0) associations based on the probabilistic model of species co-occurrence. Negative associations were not found in this study.

seems to be endemic of the Caucasus, and is also recorded from several North Caucasian caves (Turbanov et al., 2016).

Phylogenetic study of cave shrimps *Troglocaris* spp. revealed that West Balcan and Caucasian populations diverged from each other about 6–11 Ma ago (Zakšek, Sket, & Trontelj, 2007), confirming Birstein's (1950) suggestion about possible Caucasian-Dinaric speleofaunistic connection. Other invertebrates' genera are distributed in Balkans (Dinaric) and Caucasus, including leeches (*Dina* Blanchard, 1892), molluscs (*Belgrandiella* Wagner, 1927), palpigrades (*Eukoenenia* Börner, 1901) and ant-like litter beetles (*Seracamaurops* Winkler, 1925).

A review of cave biodiversity in Georgia reveals 10 positive pairwise co-occurrences between 7 of 86 (8.14%) obligate subterranean species. Six of the seven are stygobionts (5 crustaceans and 1 mollusk), and the only troglobiont is a springtail (*Troglopalites stygios* Vargovitsh, 2012) (Table 3). All seven species co-occur in Kveda Shakurani and Tsebelda caves. Further detailed investigation is necessary to understand reasons of their co-occurrence.

An animal species inventory is stated as one of the priorities in the section: "species and habitats" of the National Biodiversity Strategy and Action Plan of Georgia (NBSAP, 2005), but there are no special conservation measures, nor any legislation, established for hypogean species and biocenoses in Georgia. The following caves have status of Natural Monument: Bgheri, Didghele, Ghliana, Jortsku I, Khomuli, Melouri, Motena, Mukhura Spring, Nagarevi, Navenakhevi, Nazodelavo, Prometheus, Sakajia, Satsurblia, Solkota, Tetra, Toba I and Toba II, Tskaltsitela, Tsutskhvati caves. Besides, Sataplia I, II, III and IV caves are located at the Sataplia Strict Natural Reserve and are protected. Additionally, difficult access due to absence of roads and high altitudes to some massifs (Arabika, Bzipi = Bzybsky) in Apkhazeti, Racha, etc., ensures *de facto* protection of several caves there.

There are no publications available on conservation status of the Georgian cave dwelling invertebrates, despite the fact that 53 local endemic cavernicolous species for a single cave were identified so far. In the IUCN Red List of Threatened Species, only two species are listed, and these under Data Deficient (DD) (IUCN, 2018). Species described from Sapichkhia Cave near Kutaisi (*Trapezicandona riongessa* (Bronstein 1947), *Speocylops colchidanus* (Borutzky, 1930) and *Leucogeorgia longipes* Verhoeff, 1930)) are likely extinct due to construction of the Rioni Hydroelectric Power Station near Kutaisi, in the early 1930s.

Thirty eight caves and wells are recognised in the world as hotspots of subterranean biodiversity based on their high number of troglo- and stygobitic species, which vary from 20 to 84 cave adapted-species for each cave and well (Culver & Sket, 2000; Culver & Pipan, 2009). Culver et al. (2006) suggested the presence of potential subterranean biodiversity hotspots in the karst regions in Georgia. Such hotspot could be confirmed soon, given that 18 troglobitic species are already recorded in Kveda Shakurani Cave.

Supplementary Material

Table S1 is given as a Supplementary Annex, which is available via the "Supplementary" tab on the article's online page (http://dx.doi.org/10.1080/09397140.2018.1549789).

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Disclosure Statement

No potential conflict of interest was reported by the authors.

References

Antić, D. Ž., & Makarov, S. E. (2016): The Caucasus as a major hotspot of biodiversity: Evidence from the millipede family Anthroleucosomatidae (Diplopoda, Chordeumatida). *Zootaxa, 4211,* 1–205.

Antić, D. Ž.,Turbanov, I. S., & Reboleira, A. S. P. S. (2018): From the depths: *Heterocaucaseuma deprofundum* sp. nov., the world's deepest occurring millipede (Diplopoda, Chordeumatida, Anthroleucosomatidae) from caves in the western Caucasus. *Zootaxa, 4377,* 110–124.

Barjadze, Sh., Murvanidze, M., Arabuli, T., Mumladze, L., Pkhakadze,V., Djanashvili, R., & Salakaia, M. (2015): *Annotated list of invertebrates of the Georgia karst caves.* Tbilisi: Georgian Academic Book.

Birstein, J. A. (1950): Cave fauna of the Western Transcaucasia [in Russian]. *Zoologicheskii Zhurnal, 29*, 354–366.

Boettger, O. (1879): Neue kaukasische Hyalinia. *Jahrbücher der Deutschen Malakozoologischen Gesellschaft, 6,* 97–98.

Chao, A., &Jost, L. (2012): Coverage-based rarefaction: standardizing samples by completeness rather than by size. *Ecology, 93,* 2533–2547.

Chertoprud, E. S., Palatov, D. M., Borisov, R. R., Marinskyi, V. V., Bizin, M. S.,& Dbar, R. S. (2016): Distribution and a comparative analysis of the aquatic invertebrate fauna in caves of the western Caucasus. *Subterranean Biology, 18,* 49–70.

Culver, D., & Sket, B. (2000): Hotspots of subterranean biodiversity in caves and wells. *Journal of Cave and Karst Studies, 62,* 11–17.

Culver, D. C., Deharveng, L., Bedos, A., Lewis, J. J., Madden, M., Reddell, J. R., Sket, B., Trontelj, P., & White, D. (2006): The mid-latitude biodiversity ridge in terrestrial cave fauna. *Ecography, 29,* 120–128.

Culver, D. C., & Pipan, T. (2009): *The biology of caves and other subterranean habitats*. Oxford: Oxford University Press.

Djanashvili, R. A. (1980): Cave fauna of Georgia [in Russian}. *Georgian Caves, 8,* 88–93.

Djanashvili, R. A. (1984): Cave Fauna [in Georgian]. *Georgian Soviet Encyclopedia, 7,* 237.

Golovatch, S. I., & Turbanov, I. S. (2017): The cave millipede *Trachysphaera fragilis*Golovatch, 1976, new to the fauna of Abkhazia, western Caucasus (Diplopoda: Glomerida: Glomeridae). *Russian Entomological Journal, 26,* 101–102.

Golovatch, S. I., & Turbanov, I. S. (2018): A new cavernicolous species of the millipede genus *Typhloglomeris* Verhoeff, 1898 from western Georgia, Caucasus (Diplopoda: Glomerida: Glomeridellidae). *Russian Entomological Journal, 27,* 101–104.

Griffith, D. M., Veech, J. A., & Marsh, Ch. J. (2016): Cooccur: Probabilistic species co-occurrence analysis in R. *Journal of Statistical Software, 69,* 1–17.

Hammer, Ø. (2017): *PAST-Paleontological Statistics Version 3.15*. Oslo: Natural History Museum University.

Hsieh, T. C., Ma, K. H., & Chao, A. (2013): *iNEXT online: Interpolation and extrapolation (Version 1.0).* http://chao.stat.nthu.edu.tw/inext (Accessed on 21 August 2017).

IUCN (2018): *The IUCN Red List of Threatened Species*. Version 2018-1. www.iucnredlist.org (Accessed on 01 August 2017).

Kipiani, S. (1974): Karst of Georgia. An experience in geomorphological characteristics. Volume I. Spread, investigation and immediate tasks [in Georgian]. Tbilisi: Metsniereba Publishing House.

Kniss, V. A. (2001): *Fauna of the caves of Russia and adjacent countries* [in Russian]. Ufa: Bashkir State University Press.

Kobakhidze, D. N. (1963): Some problems and results of the investigation of Speleofauna of Georgian SSR [in Georgian]. *Caves of Georgia, 1,* 79–86.

Magurran, A. E. (2004): *Measuring biological diversity*. Oxford: Blackwell Publishing.

Marin, I. (2017): *Troglocaris (Xiphocaridinella) kumistavi* sp. nov., a new species of stygobiotic atyid shrimp (Crustacea: Decapoda: Atyidae) from Kumistavi Cave, Imereti, Western Georgia, Caucasus. *Zootaxa, 4311*, 576–588.

NBSAP (2005): National Biodiversity Strategy and Action Plan-Georgia. Tbilisi: Polygraph Ltd.

R Core Team (2016): *R: A language and environment for statistical computing.* www.R–project.org (Accessed on 21 August 2017).

Sidorov, D. A. (2016): *Zenkevitchia karamani,* a distinct new species of *admirabilis*-group (Crustacea: Amphipoda: Typhlogammaridae) from Abkhazia. *Ecologica Montenegrina, 9*, 21–30.

Sidorov, D. A.,& Samokhin, G. V. (2016): *Kruberia abchasica,* a new genus and species of troglobiont amphipods (Crustacea: Gammaridae) from Krubera Cave (Western Transcaucasia). *Arthropoda Selecta, 25,* 373–379.

Sidorov, D. A.,Taylor, S. J.,Sharina, S., & Gontcharov, A. (2018): Zenkevitchiidae fam. nov. (Crustacea: Gammaroidea), with description of new subterraneanamphipods from extremely deep cave habitats. *Journal of Natural History, 52,* 1509–1535.

Tsikarishvili, K., Barjadze, Sh., Kvavadze, E., Bolashvili, N., Djanashvili, R., & Martkoplishvili, I. (2010): Speleology of Georgia: aspects of its current situation and perspectives. *Cave and Karst Science, 37,* 73–78.

Turbanov, I. S., Palatov, D. M., & Golovatch, S. I. (2016):The state of the art of biospeleology in Russia and other countries of the former Soviet Union: a review of the cave (endogean) invertebrate fauna. *Entomological Review, 96,* 926–963, 1297–1333, 1334–1358.

Vargovitsh, R. S. (2017): Two new troglobiont *Pygmarrhopalites* species of the *principalis* group (Collembola: Arrhopalitidae) from the West Caucasus. *Zootaxa, 4250,* 23–42.

Veech, J. A. (2013): A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography, 22,* 252–260.

Vinarski, M. V., & Palatov, D. M. (2018): *Ferrissia californica*: the first record of a global invader in a cave habitat. *Journal of Natural History,* 52, 1147–1155.

Zaitsev, F. A. (1948): A review of the cave fauna of Georgia. *Trudy Instituta Zoologii GSSR, 8,* 151–173.

Zakšek, V., Sket, B., & Trontelj P. (2007) : Phylogeny of the cave shrimp *Troglocaris*: Evidence of a young connection between Balkans and Caucasus. *Molecular Phylogenetics and Evolution, 42*, 223–235.

Zenker, M. M., DeVries, P. J., Penz, C. M., Teston, J. A., Freitas, A. V. L.,& Pie, M. R. (2015): Diversity and composition of Arctiinae moth assemblages along elevational and spatial dimensions in Brazilian Atlantic Forest. *Journal of Insect Conservation, 19,* 129–140.