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AQUATIC MACRO-INVERTEBRATE FAUNA OF CAVES OF SAMEGRELO-ZEMO SVANETI AND IMERETI, WESTERN GEORGIA, CAUCASUS: TROGLOBIOTIC AND EPIGEAN SPECIES COMPLEXES

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The fauna of cave-dwelling aquatic macro-invertebrates in western Georgia has been very poorly studied. Only few papers have been devoted to the taxonomy of individual groups of cavernicolous organisms. In addition, no analysis of the structure of aquatic assemblages has ever been attempted. The present work describes the invertebrate fauna of five caves of western Georgia, the checklist comprising 17 species of troglobionts with 11 new species to be described elsewhere. Trogloniles and troglonenes include eight species each. Two main types of ecofaunistic complexes have been revealed in the caves. The first complex is troglobionts, the second one comprises epigeal macro-invertebrates and is composed of two ecological variants: rheophilic and xylophilic. The latter variant has been observed only in the Kumistavi Cave which is equipped for tourist visits. The remains of wood construction material caught in cave rivers and creeks are occupied by troglonenic insects. Both artificial illumination and exogenous material brought inside from the surface render the anthropogenic impact that helps epigeal amphibiotic insect larvae colonize subterranean habitats. The compositions of troglobionts from different caves overlap for an average of 25% of the total number of species, the lists of trogloniles shared 75% species, while the troglonenes are completely specific to each cavity. The total fauna of aquatic invertebrates differs greatly between the caves, even when these were located at a distance of 10–20 km from each other.

Keywords: Caucasus, western Georgia, troglobiotic macro-invertebrates, amphibiotic insects

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Caves represent a unique habitat characterized by the constancy of environmental conditions, lack of light, scarce food resources and isolation of separate cave systems. (Ljovuschkin, 1975; Simões et al., 2015).

The fauna of stygobiotic organisms inhabiting groundwater bodies is known to be of a high degree of endemism and having morphological and physiological adaptations to the underground environment (Birstein, 1950; Botosaneanu, 1986; Culver, Pipan, 2013; Wilkens et al., 2000 etc.). Species diversity and abundance of troglobionts are largely determined by previous climate and the conditions under which formation of karst cavities took place (Birstein, Borutzky,

1950; Culver, Pipan, 2013). However isolated caves may appear, they are not entirely insular systems. In the grotto parts of caves and in watercourses seeping from the surface one can observe a contact between the troglobiotic and epigeal faunas (Chertoprud et al., 2016).

Within Transcaucasia, diverse forms of karst relief are most pronounced in Georgia and the part of Krasnodar Krai in Russian Federation. These karst territories belong to the speleoprovince of the Greater Caucasus attributed to Crimean-Caucasian speleoregion (Dublyansky et al., 1987). In these areas one can find

a large number of caves of different origin and degree of exploration by speleologists and speleobiologists.

The extent of exploration of the troglotrophic fauna is relatively low and varies between different regions of Georgia (Birstein, 1950; Barjadze et al., 2015). The largest number of researches dealt with caves located on the territory of Abkhazia (Chertoprud et al., 2016; Kniss, 2001; Turbanov et al., 2016), currently having a disputed territory status. The adjacent areas of Western Georgia (Samegrelo-Zemo Svaneti and Imereti districts) are less studied (Barjadze et al., 2015). There are data on troglotrophic fauna of about 20 caves located in these areas, among which the largest are Belaya, Tskhatsiteli, Sataplia, Gogoleti (Ljovuschkin, 1966; Djanashvili, 1971; Kniss, 2001). For these caves some facts are known about several groups of troglotrophic macrozoobenthos: amphipods (Birstein, 1933; Birstein, Ljovuschkin, 1970; Jusbashian, 1942; Lagidse et al., 1974 etc.), gastropods (Palatov, Sokolova, 2016; Grego et al., 2017; Vinarski et al., 2014), shrimps of the family Atyidae (Marin, 2017, 2017a). However, the information presented in some of these works has become outdated. This fully applies to a few early morphological descriptions of amphipods (Birstein, 1933; Birstein, Ljovuschkin, 1970), which, obviously, need to be supplemented. Descriptions of gastropods based only on the shell morphology without involvement of the reproductive system's features (Grego et al., 2017) also leave open the possibility to clarify their taxonomic status.

Against the background of poor information about the fauna of this region, ecology and assemblages' structure of troglotrophic fauna in the Western Georgia are almost completely undescribed. There are no studies that would include all taxa of aquatic invertebrates inhabiting an individual cave system. Studies describing the structure of cave benthic assemblages were conducted only in Abkhazia and Krasnodar Krai (Russian Federation) (Chertoprud et al., 2016; Ljovuschkin, 1975).

This paper presents an analysis of aquatic fauna in five caves of Samegrelo-Zemo Svaneti and Imereti (Western Georgia) regions. There have been three aims of this study: (1) making an inventory of the species diversity of freshwater invertebrates; (2) identifying the main species complexes of benthic cave-dwelling animals; and (3) revealing the main environmental factors that facilitate the introduction of the epigean fauna into cave communities. The latter issue is extremely relevant, since the detection of epigean species in cave ecosystems can be both a consequence of natural processes and the result of anthropogenic influence (Marinskiy et al., 2015).

MATERIAL AND METHODS

Explored area

Our investigation was conducted in Megrelo-Rachinsky speleoregion (Dublyansky et al., 1987) at the area between the Suram Ridge and the Inguri River valley (Western Georgia). The material was collected in four small and one large horizontal caves in Samegrelo-Zemo Svaneti and Imereti regions during the first couple of weeks of February 2017. All cave water bodies had low water levels in that time, so the flood effects were absent. The locations of the examined caves are shown on Fig. 1.

Samegrelo-Zemo Svaneti region

(1) *Martvili municipality* (district). Samples were taken in the karst caves Motena and Jortsku. Motena Cave is located at an altitude of 452 m above sea level. The studied part of the cave has a length of just over 120 m and ends with a lake with a siphon leading to a remote part of the cave. The material was collected in the lake, in a stream flowing from it and also in rimstone pools. Cave Jortsku is the highest of all the caves studied; it is situated at an altitude of 661 m above sea level. The length of the inspected part of the cave totals about 140 m. There are two streams of different origin in the cave. One of them is fed by groundwater, and the other is largely filled by runoff from the surface. Samples were gathered in both streams, as well as downstream in their merger.

(2) *Chkhorotsku municipality* (district). The material was collected in Shurubumu and Garakha Caves. Shurubumu Cave is located at an altitude of 309 m above sea level and has a length of about 100 m. This cave contains a large number of rimstone pools and puddles, in which samples were taken. Garakha Cave is located in conglomerate rocks at an altitude of 192 m above sea level. The total length of the studied cave's passages is about 150 m. Two streams flow in the cave, one of them is largely fed by runoff from the surface through cracks and pores. The material was collected both in each of the streams and downstream at their confluence.

Imereti region

(3) *Tsqaltubo Municipality* (district). Sampling was carried out in Kumistavi cave (the Cave of Prometheus), a huge (of nearly 1 mln m³ volume) karst cave with several large halls; its elevation equals to 100 m above the sea level. There are lakes in four of the halls, and small puddles and streams scattered almost all over the cave. The material was collected in four halls, three of which are visited by organized tourist groups.

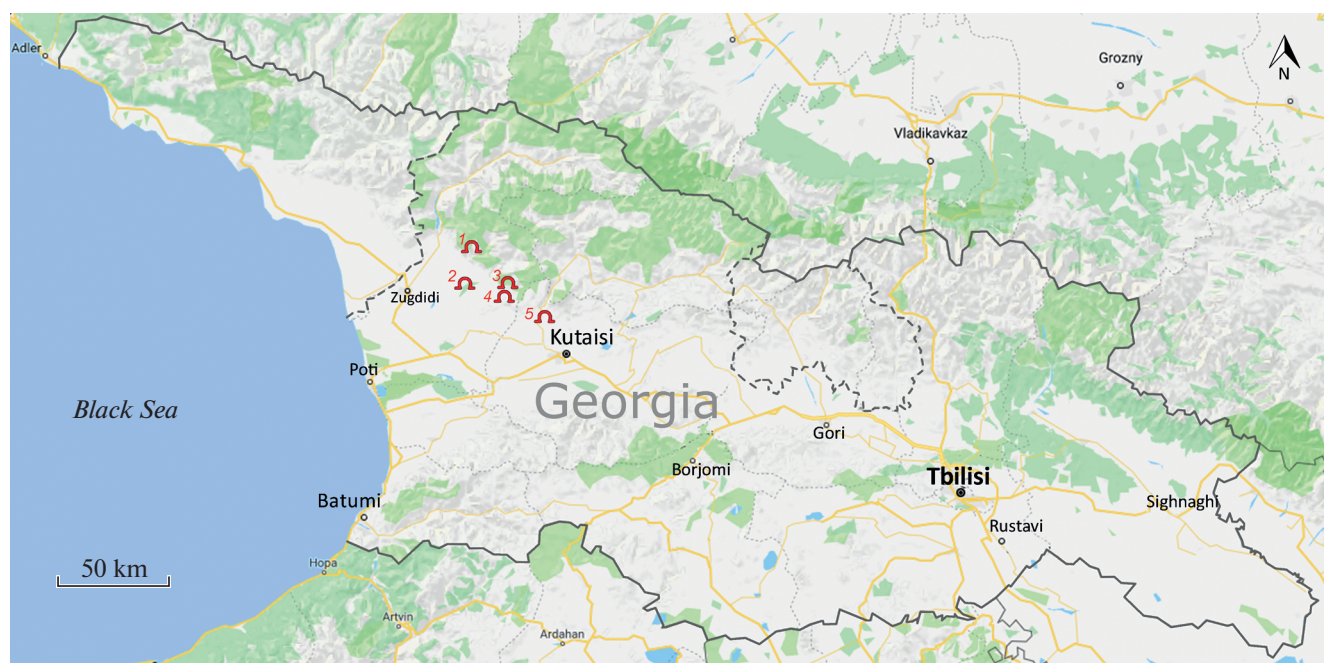


Fig. 1. Map of the concerned region of Western Georgia. Caves: 1 – Motena, 2 – Jortsku, 3 – Shurubumu, 4 – Garakh, 5 – Kumistavi.

Anthropogenic impact

Tourists mostly visit Kumistavi Cave (Djamrishvili et al., 1989), which has two short route passes. Total length of the cave totals 11 km with 1 km accessible to visitors. The cave is supplied with tourist trails, bridges, and illumination in at least 60% of the tourist part. Shurubumu Cave is visited by tourists in summer, but significantly less often than the former one, and is not equipped with artificial illumination. Motena and Jortsku Caves as well as Garackha Cave are only occasionally visited by local people.

Sampling strategy

Semi-quantitative macrobenthos sampling was undertaken in all of the caves. Samples of macrobenthos were taken with an hemispherical scraper with an area of 0.02 m² and a mesh size of 1 mm. Each sample included organisms pooled from five to ten scrapers depending on the type of soil and biotope. Since the number of scrapers taken for individual samples was different, comparing the number of organisms per area unit between particular samples was impossible. This method of sampling was used because the distribution density of organisms in cave biotopes can be extremely low. As a result, it is not always possible to determine in advance the optimal sample area. For example, with a sampling area of 0.1 m², in some cave biotopes the number of organisms will be high, while in others it will be zero. However, in the selection of semi-quantitative samples it is possible to compare the relative (percentage) abundance of organisms in different

samples, which allows us to make conclusions about the structure of dominance. All collected macrobenthos organisms were preserved in 90% ethanol.

Sampling stations were set in transects along the streams from the deepest halls to the entrance (grotto) area. The transects comprised three stations in short caves, Motena, Jortsku and Shurubumu, and five in the longest Garakha Cave (Fig. 2B–E). In Kumistavi Cave, which has only an artificial outlet to the surface besides a few cracks in the vaults of some halls, five sampling stations were established (Fig. 2A). The stations thus covered all the main types (streams, ponds and lakes) of cave water bodies.

At all the stations, the basic hydrological (width, depth, flow rate, type of sediments) and hydrochemical (water temperature, mineralization (total dissolved solids), pH) parameters of water bodies were determined using portable instrument of HANNA (HI 98129). The mean values of temperature and hydrochemical characteristics of the cave water bodies are presented in Table 1.

Taxonomy

To identify the species, we used reference material being kept in the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) and the Zoological Museum of the Moscow State University. Identification keys are only known for the Caucasian representatives of *Niphargus* (Birstein, 1952), the family Zenkevitchiidae (Sidorov et al., 2018), as well as for troglotactic molluscs (Starobogatov, 1962). However,



Fig. 2. Maps of the studied caves. Sampling stations are marked by red points. *a* – Kumistavi (accordingly Imereti Caves Protected Areas Tours Trails, 2014), *b* – Motena Cave (accordingly Petrov et al., 1991), *c* – Shurubumu Cave (accordingly Gergedava Pichkhaia, 2009), *d* – Jortsku Cave (accordingly Gergedava Pichkhaia, 2009), *e* – Garakha Cave (accordingly Petrov, Komarov, 1991).

due to the high probability of new species encounters, in some cases no precise identification was possible based on these publications. Moreover, information was used from taxonomic and faunistic articles on cave gastropods (Palatov, Sokolova, 2016; Vinarski et al., 2014), amphipods (Birstein, Ljovuschkin, 1970) and the shrimp *Xiphocaridinella* (Marin, 2017; 2018).

Ecological groups

The traditional classification of cave invertebrate fauna into troglobionts, troglaphils and troglloxenes, have recently become the subject of discussions. This is due to the ambiguous interpretation of the characters of these ecological groups by different authors (Racovitza, 1907; Holsinger, Culver, 1988; Sket,

Table 1. The mean values of temperature and hydrochemical characteristics of water bodies in the studied caves

Characteristic	Cave						
	Motena	Jortsku		Shurubumu	Garakha		Kumistavi
		stream of underground water	stream of surface water		stream of underground water	stream of surface water	
Temperature, °C	11	11	8.5	12.9	11	8.9	14.4
Mineralization, ppm (total dissolved solids)	112	110	113	143	129	135	148.7
pH	9.4	8.9	8.6	8.8	8.8	8.5	8.5

2008). In this paper, we commit to the concept of Trajano and Carvalho (2017). According to the scheme of differentiation of ecological groups proposed by them, troglobionts can be distinguished from troglaphiles by morphological adaptations evolved to cave habitat (absence of eyes, depigmentation, elongated limbs, etc.). Specific morphological adaptations of troglobionts limit their penetration into terrestrial communities, rendering them vulnerable to sighted predators and, for a number of groups, subject to negative effects of ultraviolet radiation (Fišer et al., 2014).

Troglophiles in turn differs from troglonexes by possessing of ecological adaptations to life in underground cavities: the ability to fully incorporate underground trophic chains depleted of organic matter, the completion of a full cycle of development in cave conditions.

Statistical analysis

Species diversity. An analysis of species diversity in the study stations used the Shannon-Weaver index (Shannon, Weaver, 1963). This index is applicable to assess community structure and takes into account both the number of species in a sample and the extent of their domination (% of total organisms abundance). The Shannon-Weaver index (H) is less dependent on the sample volume. In addition, this index is sensitive to changes in the abundance of rare species.

Comparing of caves faunas. Pairwise similarity of the species composition from different samples in one cave was evaluated using the Czekanowski index (D) for normalized percentage (%) data (Magurran, 2004):

$$D(x, y) = \sum_{i=1} \min(X_i, Y_i), \quad (1)$$

where X_i , Y_i are the proportion of individuals belonging to each species of all individuals found in samples X and Y , respectively.

The similarity in faunal composition between the caves was estimated using the Kulczynski index (K) for presence/absence data (Clarke, Gorley, 2006):

$$K(x, y) = (a/(a+b) + a/(a+c))/2, \quad (2)$$

where a is the number of common species in fauna groups x and y ; and b and c are the numbers of species restricted to one of the groups. This index is independent of joint absence and moderately sensitive to the difference in the total length of the compared lists, making it useful for potentially insufficient or fragmentary data. It is often used for ecological and biogeographic analyses of isolated islands faunas (Murray et al., 2002).

RESULTS

Species richness and diversity

The water bodies of the studied caves were found to be inhabited by 34 taxa of aquatic invertebrates occurring in subterranean and grotto habitats (Table 2).

The observed fauna includes 17 troglolobiotic taxa: one taxon of Turbellaria (the genus *Dendrocoelum* Ørsted 1843), one leech (Hirudinea) (*Dina* Blanchard 1892); seven taxa of molluscs: Gastropoda ('*Paladilhiopsis*' Pavlovic 1913, '*Geyeria*' Wagner 1914) and Bivalvia (the subgenus *Euglesa* Jenyns 1832); eight taxa of crustaceans: Isopoda (*Asellus* Geoffroy 1762, *Ligidium* Brandt 1833), Amphipoda (*Niphargus* Schiödt 1849, *Synurella* Wrzesniowski 1877, *Adaugammarus* Sidorov, Gontcharov, Sharina 2015, *Zenkevitchia* Birstein 1940) and Decapoda (*Xiphocaridinella* Sadowsky 1930). At least 11 of these troglolobiotic invertebrates are undescribed or poorly described: *Dendrocoelum* sp., '*Paladilhiopsis*' sp., '*Paladilhiopsis*' sp. 4 sensu Palatov, Sokolova 2016, '*Paladilhiopsis*' sp. 5 sensu Palatov, Sokolova 2016, '*Geyeria*' sp. 2 sensu Palatov, Sokolova 2016, '*Geyeria*' sp. 4 sensu Palatov, Sokolova 2016, *Euglesa* (*Casertiana*) sp.; crustaceans *Ligidium* sp., *Zenkevitchia* sp., *Synurella* sp., *Xiphocaridinella* sp. So many new species discovery is not unusual for cave fauna (Ficetola et al., 2019).

In a number of cases, an unambiguous identification of species was problematic, since the descriptions, that were made long ago, are not detailed enough and do not allow a thorough comparison of organisms. As cave fauna is known to be characterized by a high level of local endemism (Birstein, Ljovuschkin, 1970), de-

Table 2. The list of aquatic macroinvertebrates from the five caves examined

Species	Cave				
	Motena	Jortsku	Shurubumu	Garakha	Kumistavi
Turbellaria					
¹ * <i>Dendrocoelum</i> sp.	+				
Oligochaeta					
² <i>Emblocephalus velutinus</i> (Grube 1879)		+	+	+	
² <i>Haplotaxis gordioides</i> (Hartmann 1821)			+		
² <i>Eisenia</i> sp.			+		
Hirudinea					
¹ <i>Dina</i> cf. <i>ratschaensis</i> Kobakhidze 1958	+				
Gastropoda					
¹ * <i>Paladilhiopsis</i> sp.				+	
¹ * <i>Paladilhiopsis</i> sp. 4 sensu Palatov, Sokolova 2016		+			
¹ * <i>Paladilhiopsis</i> sp. 5 sensu Palatov, Sokolova 2016					+
¹ * <i>Geyeria</i> sp. 2 sensu Palatov, Sokolova 2016		+			
¹ * <i>Geyeria</i> sp. 4 sensu Palatov, Sokolova 2016					+
Bivalvia					
¹ * <i>Euglesa</i> (<i>Casertiana</i>) sp.					+
¹ <i>Euglesa</i> (<i>Euglesa</i>) cf. <i>personata</i> (Malm 1855)		+			
Isopoda					
¹ * <i>Ligidium</i> sp.				+	
² <i>Asellus</i> cf. <i>monticola fontinalis</i> Birstein 1936		+			+
Amphipoda					
¹ <i>Niphargus</i> cf. <i>borutzkyi</i> Birstein 1933	+		+		+
¹ <i>Niphargus</i> sp. (juv. or female)		+		+	
¹ <i>Adaugmarus revazi</i> (Birstein, Liovushkin 1970)	+	+			
¹ * <i>Zenkevitchia</i> sp.			+		
¹ * <i>Synurella</i> sp.				+	
² <i>Gammarus komareki imeretinus</i> Birstein 1933		+		+	+
Decapoda					
¹ <i>Xiphocaridinella kumistavi</i> Marin 2017					+
¹ <i>Xiphocaridinella shurubumu</i> Marin 2018			+		
¹ * <i>Xiphocaridinella</i> sp.	+				
Insecta					
Ephemeroptera					
³ <i>Electrogena zimmermanni</i> (Sowa 1984)				+	
Plecoptera					
³ <i>Leuctra</i> sp.					+
Coleoptera					
³ <i>Agabus bipustulatus</i> (Linnaeus 1767)					+
³ <i>Dryops lutulentus</i> (Erichson 1847)					+
² * <i>Hydraena</i> sp.	+				
² <i>Limnius colchicus</i> Delève 1963	+			+	+
Trichoptera					
³ <i>Lype phaeopa</i> (Stephens 1836)					+
³ <i>Lithax incanus</i> (Hagen 1859)	+				
Diptera					
² <i>Metriocnemus</i> sp.	+				
³ <i>Paraphaenocladus</i> sp.			+		
³ <i>Cnetha</i> sp.				+	
Total number of species	9	8	7	9	12

¹ Troglonbionts, ² troglonbionts, ³ troglonbionts, * undescribed taxa.

scriptions of species from other regions of Georgia and Russia are likely to give information only on the attribution of the organism to a particular group of species. A further molecular genetic analysis of the collected material will make it possible to clarify the identification of leeches, molluscs and crustaceans.

Eight species of the found aquatic invertebrates are troglophilic: three Oligochaeta species (*Haplotaxis gordioides* (Hartmann 1821), *Embolecephalus velutinus* (Grube 1879), *Eisenia* sp. Michaelsen 1900), two species of crustaceans: Isopoda (*Asellus* cf. *monticola fontinalis* Birstein 1936) and Amphipoda (*Gammarus komareki imeretinus* Birstein 1933 and three Insecta (*Hydraena* sp. Kugelann 1794, *Limnius colchicus* Delève 1963, *Metriocnemus* sp. van der Wulp 1874). Of these, *E. velutinus*, *A.* cf. *monticola fontinalis*, *G. komareki imeretinus* and *L. colchicus* are the most common. The amphibiotic beetle *L. colchicus* is noted in caves at the stages of both larvae and adults, which confirm its association with subterranean biotopes. The beetle *Hydraena* sp. discovered in the grotto of Motena Cave is new to science and possesses troglomorphic adaptations (partial depigmentation and reduction of eyes) (Dr. A.A. Prokin, pers. comm.).

Trogloxenes are represented by amphibiotic insects typical of epigean reservoirs. They were noted in the reservoirs in the grotto areas as well as in the distant parts of the caves (tens or hundreds of meters far from the entrance). In total, eight taxa of insects have been identified. Among the insects Coleoptera, Diptera and Trichoptera were presented by two species. In addition, Ephemeroptera and Plecoptera were represented by a single species each. The most distant from the entrance (more than 200 m) were the beetles' imago (*Agabus bipustulatus* (Linnaeus 1767), *Dryops lutulentus* (Erichson 1847)) and larvae of caddisflies (*Lype phaeopa* (Stephens 1836)) found in Kumistavi Cave. This cave is a touristic site complete with wooden paths and lights that illuminate its most interesting formations. It was on the large snags and sunken board remnants brought into the cave for building that all the insects listed above were noted. In particular, the caddisfly *L. phaeopa* is a specific xylophilic taxon that constructs galleries on the surface of the wood.

The highest species richness was observed in the largest cave, Kumistavi (twelve species), while the lowest was in Shurubumu Cave, whose studied passages are as short as 100 m. Faunas of the other three caves varied from eight to nine species. The highest faunal diversity was also found in Kumistavi Cave (value of Shannon-Weaver index (H) = 2.3). In relatively small cavities, irrespective of their hydrology, the diversity was naturally lower ($H = 1.8 \pm 0.26$).

Structure of cavernicolous species complexes

Two main types of species complexes of aquatic macroinvertebrates have been identified in the caves

studied. Their main structural distinction is the different contribution of troglobionts, larvae and adult individuals of amphibiotic insects and the epigean amphipod *G. komareki imeretinus*.

(1) *Troglobiotic species complex* inhabits parts of cave remote from the entrance to several meters. The most common invertebrates here are various species of gastropods '*Paladilhiosis*' and the shrimps *Xiphocardinella*, as well as the amphipods *Niphargus* cf. *borutzkyi* Birstein 1933, *Adaugammarus revazi* (Birstein, Liovushkin 1970) and *Synurella* sp. The structure of dominance in different types of troglobiotic assemblages of the studied caves is tabulated (Table 3). The diversity and abundance of troglobionts vary considerably between distinct cave biotopes. In particular, the fauna of rimstone pools with clay bottom usually consists exclusively of *Niphargus* and oligochaetes. Another notable fact is the specifics of the faunal composition in cave creeks formed due to the flow of surface water (observed in Garakha and Jortsku Caves). The water temperature in such streams was several degrees lower than that of streams feeding mainly on groundwater (Table 1). In addition, flood waters often wash into the caves amphibiotic larvae of insects from the epigean biotopes. The combination of these two factors contributes to the formation of species complexes including both typically troglobiotic and troglophilic/trogloxenic species. The similarity of samples from streams of different origin evaluated using the Czekanowski's index is relatively low and amounts to 0.41 in Garakha Cave and 0.22 in Jortsku Cave.

(2) *Epigean species complex* have two ecological variants.

First *rheophilic species complex* recorded in the watered grotto parts of Motena and Garakha Caves. This complex includes exclusively troglloxenic and troglphilic taxa occurring and often abundant on stones and pebble in surface streams. In Motena Cave the grotto part was clearly dominated by the caddisflies *Lithax incanus* (Hagen 1859) constituting 80% of the total abundance. In grotto area of Garakha Cave the most prominent species was *G. komareki imeretinus* (92% of the total abundance) which is characteristic of both cave and epigean biotopes.

Second *xylophilic species complex* formed on atypical for underground biotopes wood substrates in Kumistavi Cave, which undergoes substantial anthropogenic changes. The main dominant was the typical of cave and spring assemblages troglphilic isopod *A.* cf. *monticola fontinalis* that reached 52% of the total number. Subdominants were the larvae of amphibiotic insects: caddisflies *L. phaeopa* (24%) and *Leuctra* sp. (14%). Although being remote more than 200 m from the entrance, this species assemblage is almost 40% composed of troglloxene amphibiotic insects that have invaded the cave ecosystem.

In the caves, where surface and underground waters confluent together, troglobiotic and epigean spe-

Table 3. Characteristics of different types of troglobiont assemblages from caves examined

Cave	Water body		
	stream with waters from the surface (Water temperature: 8.7°C; flow velocity: 0.2 m/s; bottom sediments: sandy-pebble ground)	stream with ground waters (Water temperature 11–14°C; flow velocity: 0.2 m/s; bottom sediments: sandy-pebble ground)	rimstone pools with stagnant water (Water temperature 15°C; flow velocity: 0 m/s; bottom sediments: clay)
Motena	—	<i>Xiphocaridinella</i> sp. 1 (41) <i>Niphargus</i> cf. <i>borutzkyi</i> (35) other species (24)	—
Jortsku	<i>Embolocephalus velutinus</i> (20) ' <i>Paladilhioipsis</i> ' sp. 4 (25) <i>Euglesa</i> (<i>Euglesa</i>) cf. <i>personata</i> (15) <i>Asellus</i> cf. <i>monticola fontinalis</i> (15) <i>Gammarus komareki imeretinus</i> (13) other species (24)	<i>Adaugammarus revazi</i> (78) other species (22)	—
Shurubumu	—	<i>Xiphocaridinella shurubumu</i> (60) <i>Niphargus</i> cf. <i>borutzkyi</i> (12) other species (28)	—
Garakha	' <i>Paladilhioipsis</i> ' sp. (49) <i>Synurella</i> sp. (28) <i>Electrogena zimmermanni</i> (14) other species (9)	<i>Synurella</i> sp. (50) ' <i>Paladilhioipsis</i> ' sp. (33) other species (17)	—
Kumistavi	—	<i>Xiphocaridinella kumistavi</i> (86) <i>Niphargus</i> cf. <i>borutzkyi</i> (6) other species (6)	<i>Niphargus</i> cf. <i>borutzkyi</i> (100)

Relative abundances (%) of dominant species are presented. Dash — 'community absent'.

cies complexes mixed after junction of streams beds. Different ecological groups of organisms inhabited biotops together. However, troglobiont crustaceans (*Niphargus*) lived in interstitial space, and epigeic (*Gammarus*) — on surface of sediments. The length of areas with mixed fauna was short due to the morphology of caves (Fig. 2).

Comparative analysis of the faunas

The faunistic lists of troglobionts were largely specific to individual caves. The portion of shared troglotic species between faunas of different caves varied from 20 to 40%. The only exception was Garakha Cave inhabited by a completely unique fauna. The most widespread were the amphipods: *N. cf. borutzkyi* (Motena, Shurubumu and Kumistavi Caves), *A. revazi* (Motena and Jortsku Caves).

The species composition of troglonetic insects dwelling in a grotto zone or settled in remote cave assemblages was unique to individual caves. No species of troglonetics was found in more than one of the caves studied.

The similarity between the troglonetic species complex from different underground cavities is most profound and ranges from 33 to 100%. Oligochaete

E. velutinus, amphipod *G. komareki imeretinus* and *L. colchicus* beetle were recorded from three different cavities each. The isopod *A. cf. monticola fontinalis* was found in two caves (Jortsku and Kumistavi). The remaining troglonetic taxa were found only in single cavities.

In whole, the overlap of taxonomic lists of aquatic macroinvertebrates from different caves does not exceed 33% (on average $23 \pm 7\%$). The similarity of taxonomic lists from different caves calculated on the basis of qualitative (presence/absence) data by the Kulchinsky (K) index is extremely low and does not exceed, on average, 17.2 ± 7.4 . Even cave faunas located at a distance of 10–20 km from each other (for example, Motena and Jortsku Caves or Garakha and Shurubumu Caves) differ profoundly ($K = 12.6 \pm 0.14$).

DISCUSSION

Main characteristics of troglonetic fauna

The composition of the groundwater macroinvertebrates of the Samegrelo-Zemo Svaneti and Imereti regions (Megrelo-Raci, Imereti and Central-Megrelian speleoregions) includes almost all of the main subterranean groups typical of the Western Caucasus

(Chertoprud et al., 2016). However, some taxonomic groups are not as diverse in the region as in the north-western part of the Caucasian Range (Novorossiysk-Tuapse, Greater Sochi, Gagra-Bzybysky and Gumishkhino-Panavsky speleoregions). For example, this fully applies to the species richness of cave planarians, bivalves, shrimps and amphipods (Marin 2017a; Turbanov et al., 2016). However, this fact is obviously caused by the poor knowledge of the underground cavities of the region rather than by real depletion of fauna. There is scarce information about troglobiotic fauna of Samegrelo-Zemo Svaneti and Imereti regions in comparison with Abkhazia and Krasnodar Krai of the Russian Federation (Kniss, 2001; Barjadze et al., 2015). According to contemporary catalogs of cave fauna, the last two regions were the main focus of biospeological researches in the Southern slope of the Greater Caucasus in the last decade.

In our material, all main groups of the Caucasian troglobionts were found, except Syncarida. The total number of recognized troglobiotic taxa is 17 (Table 2). The most diverse were Crustacea (Decapoda, three species; Amphipoda, four species; Isopoda, one species) and Gastropoda (family Hydrobiidae, 4 species), which are dominant in the groundwater of the western Caucasus. Comparatively high rates of species richness of troglobiotic Crustacea and Hydrobiidae are typical of Mediterranean regions with relatively wet coastal climate such as the Croatian coast (Jalžić, Pavlek, 2013). The fauna of Samegrelo-Zemo Svaneti and Imereti regions, and Georgia as a whole, is highly specific and includes presumably more than 90% endemic species. Frequently troglobiotic species are restricted to individual cave systems (Palatov, Sokolova, 2016; Vinarski et al., 2014). Almost every cave studied by a biospeologist extends the faunal list by several taxa, which are new to the region and/or science. For example, according to our data, in the five explored caves at least 12 undescribed species were recognized (Table 2).

The faunas of caves and epigeal habitats differ significantly in species richness within the major taxa of high rank. For example, crustaceans and molluscs make up the core of the aquatic cave fauna of Georgia constituting nearly 45 and 34% of total species number respectively (original data; Birstein, 1933; Birstein, Ljovuschkin, 1970; Jusbashian, 1942; Lagidse et al., 1974; Marin, 2017; Palatov, Sokolova, 2016; Vinarski et al., 2014 etc.). In the fauna of dense grounds of epigeal watercourses, Insecta predominates (80% of the total species number) while Crustacea and Mollusca make up only 7 and 4% respectively (Palatov, Chertoprud, 2018). This difference in allocation of species number by higher taxa is partially accounted for the history of cavernicolous fauna's formation, since many of its groups originated in the sea (Birstein, Borutzky, 1950). For example, this refers to the families Niphargidae and Atyidae (Birstein, Borutzky, 1950; Kabat, Hershler, 1993). Probably, the high diversity of crustaceans characteristic of marine

biotopes (Vinogradov, 1977) is also reflected in cave assemblages. Grotto cave zones, located at a junction of different environmental conditions, represent areas of the closest interaction between the epigeal and underground faunas of different evolutionary history and type of adaptation to habitat conditions (Fišer et al., 2014).

Ecological groups

Among aquatic macroinvertebrates collected in the five caves studied in Georgia, 17 are troglobionts and eight are troglonexes and troglaphiles (Table 2).

Troglobionts

This ecological group was mainly represented by molluscs (seven species) and crustaceans (eight taxa). Single specimens of oligochaetes *Dendrocoelum* sp. and leeches *Dina* cf. *ratschaensis* were noted in the stream and rimstone pools of Motena Cave. Five species of gastropods and two species of bivalve molluscs were found in the three caves and were strictly specific to individual cavities. In Jortsku and Kumistavi Caves, two species of gastropods and one species of bivalve molluscs were recorded in each. It is worth noting that genera of molluscs in both caves were common ('*Paladilhiosis*', '*Geyeria*' and '*Euglesa*'), but at the species level the faunas differed. In Garakha Cave only one '*Paladilhiosis*' sp. was recorded. The shrimp *Xiphocaridinella* (3 taxa) was also strictly confined to the individual caves Motena, Shurubumi and Kumistavi. It is interesting that in the lakes of Kumistavi Cave the shrimps of different ages were caught, what emphasizes that the species completes its life cycle in the reservoirs of the studied cave part rather than being washed out from remote karst cavities inaccessible to researchers.

All the shrimps in Kumistavi Cave belonged to the same species *Xiphocaridinella kumistavi* Marin 2017, what was confirmed by both molecular genetic and morphological analyses (Marin, 2017). In the caves of Gulrypshsky region of Abkhazia (Gumishkhinsko-Panavsky speleorion), contrarily, two different shrimp species commonly occurred in one cave (Marin, 2017a). All of them were adults with no developed sexual products (Marin, 2018) that indirectly indicates these species used to live and reproduce in other cavities (possibly not yet found) and are swept by floods into a cave under study.

Isopods *Ligidium* sp. were met in the rimstone dams of Garakha Cave. This species belongs to the semi-aquatic terrestrial fauna, and accidentally occurs in benthic samples. The troglobiotic amphipods were represented by four species; among them, only *Synurella* sp. (Garakha Cave) and *Zenkevitchia* sp. (Shurubumu Cave) are unique to individual caves. The others, *N. cf. borutzkyi* and *A. revazi* were record-

ed from several caves: Motena, Shurubumu, Kumistavi and Motena, Jortsku, respectively.

The wider ranges of cave amphipods able to penetrate into groundwater through interstitial capillaries (Culver, Pipan, 2008; Culver et al., 2006), compared to other groups of stygobionts, were noted earlier for the fauna of cave systems of Abkhazia (Chertoprud et al., 2016). The cited preliminary analysis of stygobiotic fauna's distribution by the examined Abkhazian caves confirmed a high local endemism of the slow-moving Hydrobiidae gastropods occupying the surface of stony substrates, as well as of the motile but large benthoplanktonic shrimps. In contrast, some subterranean Amphipoda species demonstrated wide distribution.

Trogloxenes

The absence of common troglloxenic insects in the five studied caves is probably due to they inhabit cave biotopes random (according Souza-Silva et al., 2012). Caucasus region have high species richness of macrozoo benthos in epigean habitats. More than 300 species constitute the fauna of aquatic macroinvertebrates inhabiting the streams and rivers of the Eastern Black Sea region; amphibiotic insects make up 86% of the total species list (Palatov, 2018). Thus, the probability that in different underground cavities will inhabit similar species from total regional pool is low.

Another way for epigean insects to penetrate into the underground cavities is drift with surface waters flowing into cave reservoirs. Probably, this is how the larvae of Ephemeroptera (*Electrogena zimmermanni* (Sowa 1984)) and Diptera (*Cnetha* sp.) fell into Garakha Cave. Both of these species are abundant in the surface streams of the region; since that individual specimens are likely to be carried away by the flow.

The third variant of colonization of caves by troglloxenic insects is directly related to the anthropogenic factor. Imago insects can fly into cavities that have artificial lighting and then lay eggs on non-typical for cave communities substrates that are poorly populated by trogllobiotic fauna (Marinskiy et al., 2015). Presumably, this is the way the imago beetles *A. bipustulatus* and *D. lutulentus* appeared in Kumistavi Cave, as well as the larvae of *Leuctra* sp. and *L. phaeopa*.

Troglophile

The species complexes of trogllophiles are quite similar in different subterranean cavities. For example, in the caves Garakha, Jortsku and Kumistavi, there are no trogllophilic macroinvertebrates specific to these cavities. The high ability of this ecological group to spread between individual caves is due to the fact that its representatives can live in both epigean and underground biotopes (Trajano, Carvalho, 2017).

In particular, the four species that are most widely distributed in the studied caves illustrate this. Very abundant in the epigean assemblages, *G. komareki imeretinus* penetrates into the caves both through grotto parts and by drifting with flood waters. The dispersal ability of the trogllophilic beetle *L. colchicus*, having a flying long-lived imago stage, is high and thus this species is not restricted to individual river valleys (Palatov, 2018). *A. cf. monticola fontinalis*, the isopod characteristic of spring reservoirs, and the creek oligochaet *E. velutinus* are able to penetrate caves through the subterranean waters and hypotelminorheic habitats.

Factors determining the structure of trogllobiont assemblages

The structure, geology and localization of caves

The species richness and abundance of cave-dwelling aquatic invertebrates often depend on the cave morphology (Simões et al., 2015). For the faunas under comparison the most significant factor was the size of the cavity (Chertoprud et al., 2016; Culver et al., 2003; Culver et al., 2004; Ferreira, 2004; Souza-Silva et al., 2011). The highest diversity was observed in the long caves such as Kumistavi Cave. Its fauna was the richest and included twelve taxa. Species list of the four other caves, smaller than Kumistavi by a factor of more than ten, included from seven to nine species. This corresponds with the previously reported positive correlation between species richness and cave volume (Culver et al., 2004; Simões et al., 2015).

Probably, the composition of the trogllobiotic fauna can be affected by the rocks in which the cave lies. That assumption is based on the fact that the fauna of the conglomerate cave Garakha has no common trogllobionts with the other four limestone caves (Table 3). Among the trogllobionts of Garakha Cave *Synurella* sp. and '*Paladilhopsis*' sp. dominated. It is worth to report that the genus *Synurella*, typical of cave biotopes and springs, was found in that cave only. However, the *Xiphocaridinella* shrimps, common in caves of the region, were absent. Perhaps, the factor determining the faunal differences is the higher density of conglomerate rocks compared to the limestone easily eroded by water (Dunham, 1962). Large number of karst microcavities and passages makes limestone caves more accessible for fauna. Caves formed in conglomerates are, in contrast, more isolated. This assumption requires further detailed verification.

The shrimps were also absent in the most high-mountain cave, Jortsku (661 m above sea level). The absence of the genus *Xiphocaridinella* in cavities located in high-altitude areas of the Caucasus was noted by biospeleologists in a number of caves on the Arabica plateau (more than 2000 m above sea level): Sarma, Troika, Eagle's Nest and Krubera-Voronja (Sendra, Reboleira, 2012; Sidorov et al., 2014). All *Xiphocaridi-*

nella species found in this region up to this day live in caves located at heights below 500 m a. s. l. (Anosov, 2016; Barjadze et al., 2015; Chertoprud et al., 2016; Marin, 2017, 2017a etc.). High-mountain caves are characterized by lower water temperatures which can prevent the development of relatively warm-water invertebrates. Perhaps, low dispersal abilities also hamper shrimps in occupying high-altitude areas. However, this assumption needs further verification and more data from different caves.

The hydrological type of cave water bodies

The community structure significantly depended on the hydrological type of water bodies and on the diversity of microhabitats in cave aquatic environment. Species richness is higher in the caves with streams and rivers in comparison with those with stagnant ponds (Simões et al., 2015). In the caves where rivers flow, there is a high air humidity favorable for troglotic fauna inhabiting the near-water biotopes (Souza-Silva et al., 2012, 2012a). In addition, river waters often bring detritus, which is one of the main food resources in cave trophic web. In the studied caves of Western Georgia, there are four main types of water bodies: 1) lakes; 2) rimstone pools; 3) rivers and streams feeding on groundwater; 4) streams formed mainly due to the flow of water from the surface. In each of these types of reservoirs its own specific complex of species occurred. It is noted that the higher the variety of hydrological types of reservoirs in a cave, the higher diversity of its fauna of aquatic invertebrate is. Thus, the fauna of Kumistavi Cave, which includes rimstone pools, lakes, rivers and streams, is 1.5 times as rich as the fauna of Shurubumu Cave containing only rimstone pools and a stream.

In the fauna of rimstone pools the oligochaetes and amphipods *Niphargus* were most abundant while in standing water a shrimp *Xiphocaridinella* is the most characteristic; it is numerous in the lakes of Motena and Kumistavi Caves. In creeks influenced by water flow from the surface, troglophilic and troglone species frequently dominate. It is along such creeks that many of the epigean species fall into caves during the flood (Souza-Silva et al., 2012).

On the dense grounds of streams feeding on groundwater, the cave Gastropoda are usually common (Vinarski et al., 2014). Among all groups of troglonites, amphipods are the most eurybiotic. The same species of *Niphargus* can occur in water bodies of various hydrological types. The ability to populate various biotopes and, having reached a high number, to transform an indigenous assemblage, is also known for the epigean representatives of these invertebrates (Chertoprud, 2014).

Anthropogenic pressure

A preliminary assessment of the anthropogenic influence was made in Kumistavi Cave. This cave was equipped with artificial light and tourist paths relatively recently (about 10 years ago) (Imereti Caves Protected Areas Tours Trails 2014). The anthropogenic impact on this cave is significantly lower than on the New Athos Cave, whose reservoirs contain coins and plastics (Chertoprud et al., 2016). However, in the river flowing through the cave, pieces of construction debris (boards and large snags) are regularly found. Large pieces of wood are usually absent in caves not visited by humans, and present an uncharacteristic biotope for troglonite fauna (Marinskiy et al., 2015). In Kumistavi Cave, a multi-species complex of troglonitic amphibiotic insects was discovered to inhabit wood substrates. The most common were the larvae of *L. phaeopa* and *Leuctra* sp. Probably, the imago of these species flew into the underground cavity being attracted by light lamps and, having found a suitable wood substrate, laid eggs on it. Thus, both artificial illumination and external substrates brought from the surface serves as good examples of anthropogenic impact that promotes amphibiotic insect larvae to move upstream from the surface to caves, colonize the subterranean habitats and replace the troglonites. This phenomenon was observed earlier in Abrskila Cave (Abkhazia) (Chertoprud et al., 2016). Thus, for the preservation of cave communities in a pristine state it is necessary to introduce a restriction on the nature management of individual cave systems or even karst massifs.

Factors regulating the penetration of troglonites into cave communities

At first glance, it seems obvious that the main factor determining the possibility of penetration of the epigean fauna into underground reservoirs is the extent of their isolation from the surface. The larger the size of cave entrance and the closer waterbodies are to the grotto part, the easier troglonites can enter (Simões et al., 2015). The observed relation between width of entrance and number of species can be due to the fact that large entrances probably function as "windows" that facilitate the colonization of hypogean systems by external invertebrates (Ferreira, Marques, 1998; Prous et al., 2004). In addition, regular flood events can contribute to the appearance of epigean species in underground biotopes. However, it turns out that actually this factor does not play a decisive role for faunas of the Caucasian caves (Chertoprud et al., 2016). In underground cavities having large entrances with watered grotto parts affected by regular seasonal flooding, massive introduction of troglone species, however, does not occur. Faunistic lists of aquatic invertebrates of the caves Lower Shakuranskaya, Abrskila, Otap's Head (Abkhazia) and Motena (Western Georgia) provide an example of it (Cherto-

prud et al., 2016). This fact indicates the existence of some additional barriers that prevents highly mobile troglobiotic amphibiotic insects to colonize caves.

One of the probable but poorly understood factors limiting the penetration of epigean species into underground cavities is the presence of competitive or predatory interactions between troglobiotic and troglloxenic fauna. This can be manifested in a competition for food resources, strictly limited in cave habitats (Simões et al., 2015), as well as in direct feeding of some species on others (Fišer et al., 2014). In partially illuminated grottoes of caves the epigean species are supposed to have an advantage, and in the remote cave parts morphologically adapted trogllobiont species (Trajano, Carvalho, 2017) should be under favorable conditions.

Indeed, the complementarity of the distribution of trogllobionts and troglloxenes was reported for a few caves of Abkhazia (Chertoprud et al., 2016). The distribution of the main cave dominants, shrimp of the genus *Xiphocaridinella* and amphipods *Niphargus*, almost does not overlap with the distribution of the complex of amphibiotic insects (Birstein, 1950; Chertoprud et al., 2016). It ought to be noticed that many trogllobionts have behavioral and physiological reactions allowing them to avoid illuminated areas. For example, a number of cave amphipods were shown to have a negative phototaxis (Fišer et al., 2016). Some species of crustaceans (some Ostracoda and Amphipoda) possessing fine chitinous exoskeleton do not tolerate exposure to sunlight (Ginet, 1960; Maguire, 1960). Light intensities of the order of 1/20th that of normal sunlight are sufficient to kill troglobiotic ostracods (Maguire, 1960).

There is a reason to suggest that, in the absence of light, representatives of the true cave fauna exert pressure on the troglloxenes that enter the cavity (Fišer et al., 2010). This type of interaction can be especially pronounced in the case of dominant species. Amphipods represent such a widespread and numerous component of cave communities (Birstein, Borutzky, 1950). Analysis of the contents of the intestinal tract of *Niphargus* showed that they are indeed able to eat epigean larvae of mayflies living in grotto parts (Fišer et al., 2010). Probably, cave amphipods can also consume eggs laid in underground watercourses by adults of amphibiotic insects and thereby preventing their development.

The existence of the direct competitive relationship between the epigean and cave amphipods has not yet been confirmed (Luštrik et al., 2011). It is assumed that this may be due to the spatial divergence of species of different ecological groups between biotopes. For example, the syntopic occurrence of the troglobiotic *Niphargus* and troglphilic *Gammarus* was noted in Jortsku Cave. It is worth mentioning that in the epigean watercourses the high abundance of amphipods correlates with a decrease in the abundance of

other benthic organisms (Chertoprud, 2014). This fact confirms that other macroinvertebrates undergo predation by amphipods and suffer from competition for food resources.

Another factor promoting the penetration of troglloxene species into caves can be anthropogenic impact of artificial lighting, introduction of nonspecific substrates and destruction of the natural troglobiotic fauna as a result of mechanical or chemical actions. For instance, in Abkhazian Abrskila Cave the presence of lighting combined with an increase in the mechanical load on the watercourse (change of the bottom relief) correlated with a sharp decrease in trogllobiont abundance (Marinskiy et al., 2015). The lamp light attracts winged stages of insects which, if there are suitable substrates, can lay eggs here. A similar situation was noted for Kumistavi Cave. It has been shown that troglloxenes can replace troglobiotic organisms in case of destruction of the troglobiotic fauna (Notenboom et al., 1994). It is also worth noting that the caves of Russian north (Arkhangelsk region), where the specific trogllobiont fauna was destroyed by periodic glaciations (Birstein, Ljovuschkin, 1976), colonization of cave reservoirs with troglloxenic and troglphilic species was also registered (Chertoprud et al., 2011).

In addition to the factors above, both species composition and abundance of troglloxenes penetrating a cave are influenced by the hydrological characteristics of water bodies: bottom sediment character, flow velocity and temperature. The hydrochemistry of epigean and underground waters of a particular region is usually akin (Culver, Pipan, 2009), since the epigean watercourses are heavily fed by groundwater.

Thus, given the variety of factors determining the degree of introduction of the epigean fauna into cave communities, troglloxenes-trogllobionts distribution in each underground cavity should be analyzed individually. To more completely understand the ecosystem processes, further accumulation of factual material and conduct of behavioral experiments are needed. That would also facilitate revealing of factors that regulate the taxis of individual species and an assessment of the interspecific interactions between macroinvertebrates of different ecological groups.

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ФАУНА ВОДНЫХ МАКРОБЕСПОЗВОНОЧНЫХ ПЕЩЕР САМЕГРЕЛО-ЗЕМО СВАНЕТИИ И ИМЕРЕТИИ (ЗАПАДНАЯ ГРУЗИЯ): ТРОГЛОБИОНТНЫЕ И ЭПИГЕЙНЫЕ ВИДОВЫЕ КОМПЛЕКСЫ

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Фауна пещерных водных макробеспозвоночных Западной Грузии изучена очень слабо. Только немногие исследования посвящены таксономии отдельных групп пещерных организмов. Анализ структуры водных сообществ пещер никогда ранее не проводился. Настоящая работа описывает фауну беспозвоночную пяти пещер Западной Грузии. Общий список организмов включал 17 видов троглобионтов, из них 11 являлись потенциально новыми для науки. Троглофильные и троглоксенные организмы составляли по восемь таксонов. В пещерах были отмечены два типа экофаунистических комплексов. Первый комплекс состоял из троглобионтов, а второй — включал эпигейных беспозвоночных и имел два экологических варианта: реофильный и ксилофильный. Последний вариант отмечен только в пещере Кумистави, оборудованной для посещений туристами. Остатки древесных строительных материалов в пещерных водотоках, были заселены троглоксенными насекомыми. Искусственное освещение и субстраты, занесенные в подземные воды с поверхности, создавали благоприятные условия для вселения эпигейных насекомых. Состав троглобионтов из разных пещер был сходен в среднем на 25% от общего числа видов, списки троглофилов были общие на 75%, а троглоксены оказались полностью специфичны для каждой полости. В целом, фауны водных беспозвоночных из разных пещер, даже находящихся на расстоянии 10–20 км одна от другой, имели значительные различия.

Ключевые слова: Западная Грузия, троглобионтные макробеспозвоночные, амфибиотические насекомые