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Stygobiotic faunal elements in spring assemblages of West Transcaucasia

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Macroinvertebrates of stygobiotic origin contributing to benthic assemblages in springs of the two regions of West Transcaucasia were investigated. The regions concerned, basins of the Khosta-Kudepsta Rivers (Krasnodarskiy krai) and Myussera Upland (Abkhazia), are well-studied and drastically different in a number of features. Frequency of occurrence, abundance and the position of stygobiotic species in the structure of crenal assemblages are given. Stygobionts dominated in 50% of cases, more often in helocrenes with variable runoff than in rheocrenes stably connected with watercourses. Stygo- and crenobiotic primary aquatic invertebrates (crustaceans and mollusks) demonstrate pronounced local endemism at the species level. Under certain circumstances spring assemblages can be considered as island ones.

Keywords: zoobenthos, crenal zone, rheocrenes, helocrenes, local endemism, *Belgrandiella*, *Niphargus*.

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Introduction

Assemblages of spring waterbodies are often built up by faunistic elements of different ecological origin. They can include oxyphilic and rheophilic groups characteristic for small rivers and brooks; ubiquitous species, characteristic for small waterbodies of any type; typical inhabitants of temporary pools; obligate crenobionts, etc. (Chertoprud, 2006). Species of stygobiotic origin carried into spring waterbodies from ground waters and possessing corresponding morphological features and adaptations (depigmentation, characteristic disproportionality of the body, etc.) are a particular group of crenal organisms. Mass introductions of stygobionts into spring assemblages usually occur in regions that have not been subject to surface glaciation in recent geological past (Chertoprud and Peskov, 2007). West Transcaucasia is one of such areas and the discussed groups is represented by crustaceans: amphipods of *Anopogammarus* (Gammaridae) and *Niphargus* (Niphargidae) genera, single species of *Synurella* (Crangonictidae), isopods *Proasellus* as well as gastropods Belgrandiellinae (Hydrobiidae), some oligochaetes (*Stylodrilus*, Rhyacodrillinae) and turbellaria (*Dendrocoelopsis*) (Turbanov et al., 2016). Stygomorphic species become dominant over specialized complexes of crenobiont amphibiotic insects in a number of spring assemblages. In this case, it is proposed to call the resulting associations troglocrenal (Chertoprud, 2010, 2011). They are known from the studied territory but described only generally (Chertoprud, 2010).

Aim of the present work was to describe composition and occurrence of stygobiotic complex of species in crenal assemblages from two large spring areas – the Khost and Kudepsta river basins (Krasnodar region, Russia) and the Myusser (Kavakluk) upland basins (Gudauta district, Abkhazia) in the Western Transcaucasia.

Material and methods

A total of 55 quantitative samples of macrobenthos collected in spring waterbodies on the territory of West Transcaucasia in 2008–2014 were studied: 27 samples taken in the Malaya and Bolshaya Khosta basins; 15 samples from Kudepsta basin; 13 samples from the territory of Myusser upland within the Pitsunda-Myusser reserve.

Samples were taken from all types of springs (rheocrenes, limnocrenes, helocrenes) from all available microbiotopes using a hydrobiological scraper (area 0.02 m^2, 0.25–1 mm mesh size) or (when sampling from waterbodies with maximum depth of several millimeters) by total collection of organisms from the substrate (stones, wet rocks, leaf litter). Sampling area was 0.1 m^2, usually. Animals were taken immediately from the scraper where bottom substrate was filtered and flushed. Samples were fixated immediately after collection with 70% ethanol.

Organisms were identified using literature containing first descriptions of species and identification keys for studied stygobiont groups (Birshtein, 1936, 1952; Martynov, 1932; Starobogatov, 1962). Mollusk preparations were done with acupuncture needles under dissecting microscope Carton TRIO 0750. Temporary glycerin preparations were used during analysis of diagnostically important structures of appendages (antennae, gnatopods, pereopods, pleopods, telson, uropods, etc.) of identified arthropods. Clarification of the integument was achieved by keeping studied objects in lactic acid solution. Preparations were studied using Olympus CX21 light microscope.

Metabolism value calculated according to the following formula (Kucheruk and Savilova, 1985):

$$D=k\cdot N^{0.25}\cdot B^{0.75},$$

where D – metabolism value, ml O_2/m^2; N – abundance of organisms, ind./m^2; B – their biomass, g; k – coefficient, specific for each group of invertebrates, was chosen as the main measure of taxon’s abundance when studying assemblage structure. We used values of k given in Alimov (1979). The intensity of metabolism is proportional to the rate of nutrition and respiration of the organism being a more adequate reflection of its role in the assemblage comparing with abundance and biomass. Since the metabolic rate of small animals is higher than that of large ones, metabolic rate increases more slowly than biomass with increasing body size.

Crenal assemblages were compared mainly using relative abundance – the share of each species in the total metabolism of the assemblage. Absolute values (total metabolism and community biomass) were also compared, but were of minor importance.

The structural hierarchy of communities was described on the basis of Ulfstrand classification (1968), developed for amphibiotic insects. The dominant species should be at least 25% of the total assemblage, subdominants – at least 10%. If the proportion of a particular taxon in the total metabolism of an assemblage was 75 percent or more, such a taxon was called superdominant.

Physical-geographic and geological features of studied areas

Choice of the study area was conditioned due to the following features. Despite their close geographical location, they differ significantly in a number of geological and hydrological characteristics (Fig. 1). The neighboring basins of the Khosta and Kudepsta rivers are located within a single biospeleological area (Birshtein and Levushkin, 1967), their valleys are washed in thick layers of limestone rocks rich in various karstic cavities, including large flooded caves. Large limestone massifs – Alec (headwaters of Malaya and Bolshaya Khosta), Vorontsovskiy (upper Kudepsta), Akhunsky (between the Khosta and Matsesta), and others (Dublyansky et al., 1985) are located here. In such conditions, spring water bodies are often directly connected with underground reservoirs, from where leaching of stigobionts occurs fairly regularly. A number of narrowly localized stygobiont endemics were described from both cave and spring reservoirs of the region (Birshtein, 1952, 1967; Martynov, 1932).

A completely different situation is observed within the Myusser Upland. In the geological sense, it is a peculiar island, separated from the southern slopes of the Bzyb and Gagra Ridges of the Greater Caucasus by a wide hollow – the Kaldkhvar corridor. The low-mountainous hilly-ridge relief with heights not exceeding 250–270 m, composed of conglomerate rocks (Bebiya et al., 1987), is characteristic. There are completely no karst relief forms (caves, craters, etc.), spring water bodies have no direct connection with groundwater. No stigobiont forms were previously known directly from the territory of the Myusser Upland.

Thus, a comparison of the crenobiont fauna (in this case, its stygobiont component) of these geologically different, but geographically close areas is of interest in the context of studying springs as island habitats, identifying potential abilities of crenal and stygobiont forms for settlement and local speciation.

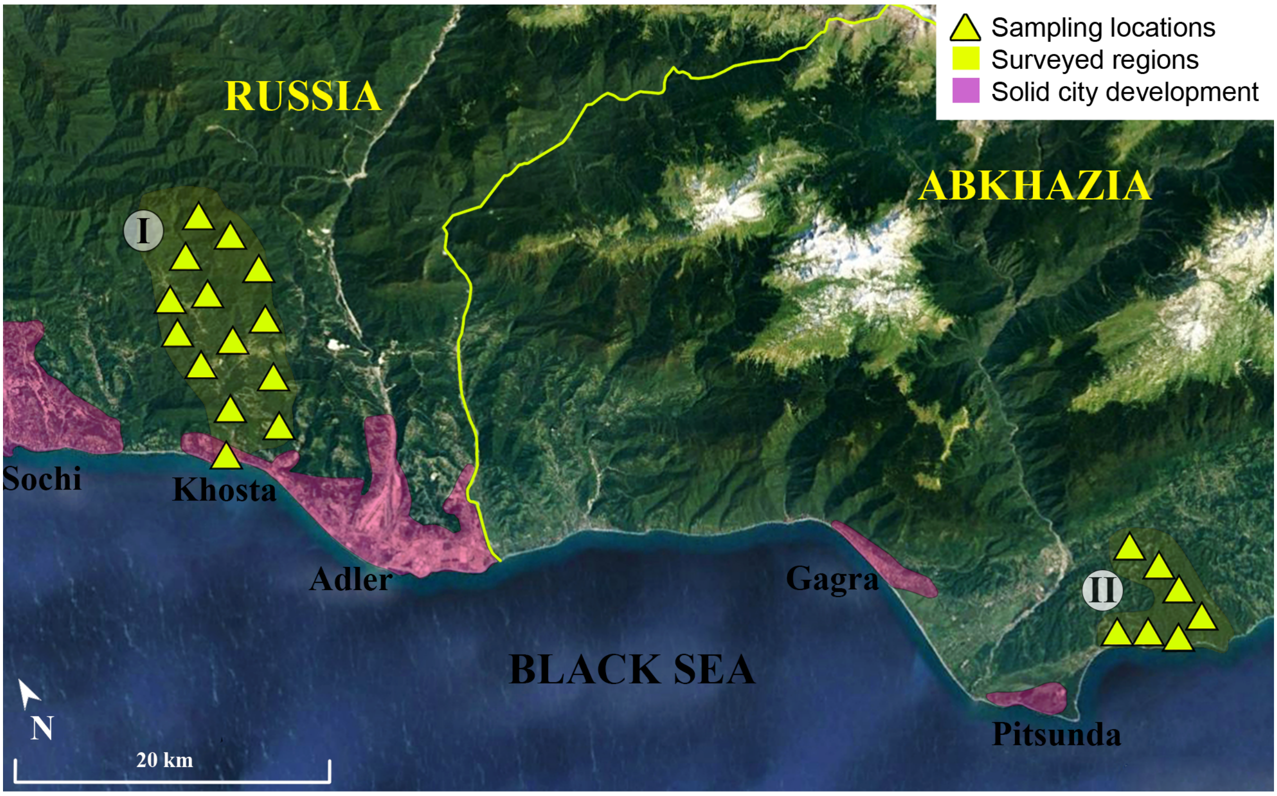

Figure 1. Map of the studied area. Roman numerals denote surveyed regions: I – Khosta and Kudepsta basins; II – Myusser Upland basin.

Results

Stygobiont invertebrates in spring assemblages: species composition and occurrence

Eight species possessing stygomorphic features linked with groundwater one way or another were found in the springs of the surveyed territory. Six species were found in springs of Khosta and Kudepsta river basins, four – in springs of Myusser Upland. Quantitative parameters of their occurrence in crenal assemblages of studied regions are given in Table 1.

Khosta and Kudepsta basins

Six species were found in this area: two species of gastropod mollusks Belgrandiellinae, three species of *Niphargus* amphipods and one species of *Proasellus* isopods.

• *Belgrandiella caucasica* Starobogatov, 1962 (Mollusca: Gastropoda: Hydrobiidae)

A species of small (shell height 1–1.5 mm) gastropods typical for spring and cave waterbodies of West Caucasus at least on the territory from Tuapse to Psou. Described from Krasnoaleksandrovskaya cave watercourse, we have also found it in Dolgaya cave and in a number of springs in the vicinity of Tuapse and Lazarevskoye (Palatov and Vinarski, 2015; Sokolova and Palatov, 2015). It is quite common (found in 52% of samples) in the spring waterbodies of the Khosta and Kudepsta basins. It is evenly spread throughout the study area - from low-mountain springs in the suburbs of the city of Khosta to springs in the headwaters of the main rivers of the region at absolute altitudes of 800–900 m. The species is quite eurybiotic, inhabiting waterbodies of various types from rheocrenes and underflow streams of mountain rivers (for instance found in the hyporhea of Mal. Khosta River) to helocrenes and barely noticeable seepages on the slopes of the valleys. Forms mass aggregations (up to 90 ind. per sample) on leaf litter and woody substrates. Despite such a large abundance, the role of this species in the total metabolism of assemblages is small (due to extremely small individual biomass) and averages 3–4%, in some cases up to 9% of the indices of community's total metabolism.

The species has significant conchological and anatomical variability. Previously considered populations were described as a separate species *B. nemethi* Schütt, 1993. However, we could not find stable differences when comparing topotypical materials of these two species (Fig. 2A, C, D), therefore *B. nemethi* is considered a junior synonym for *B. caucasica* in this work.

• *"Paladilhiopsis"* sp. (Mollusca: Gastropoda: Hydrobiidae)

Not being able to study the genital system of the male of this species (only females are present in the samples), we refrain from confidently determining its genus and species. Conchologically, it is close to *Paladilhiopsis orientalis* Starobogatov, 1962 (Fig. 2B)

Table 1. Data on the occurrence, density, and the average share according to metabolism for stygobiont species found in the composition of spring assemblages of studied regions.

Species	Occurrence, %	Average density, ind. per sample	Average share in assemblages according to metabolism, %
Khosta and Kudepsta basins			
Belgrandiella caucasica	52	19.4	3.5
«Paladilhiopsis» sp.	21	6.3	0.7
Proasellus cf. *infirmus*	38	13.7	13.5
Niphargus abchasicus	48	20.7	45
Niphargus cf. *pseudolatimanus*	31	3.9	20.3
Niphargus cf. *gurjanovae*	1	6	13.4
Myusser Upland basin			
Belgrandiella sp.	54	27.2	3
Proasellus cf. *infirmus*	31	1.5	2.8
Niphargus derzhavini	62	41.4	42.3
Niphargus cf. *gurjanovae*	15	5.5	2.4

described from Krasnoaleksandrovskaya cave. The species is relatively rare in spring waterbodies of the studied area, its occurrence is 21%. It also does not form dense aggregations, usually there are 3–4 individuals per sample, the maximum is 27 individuals in one sample (a spring in the valley of the Kudepsta river under Krasnaya Volya village). The share in the total metabolism of the assemblage, is usually below one percent, in the only case it reached 5%. The species is distributed sporadically, most often found in the springs of the middle course of the Khosta and Kudepsta rivers at an altitude of 150–200 m.

In the Transcaucasia, representatives of "*Paladilhiopsis*" genus are mainly found in cave habitats being rare in springs. Probably, all these findings are exclusively due to the occasional flushing of mollusks from the hyporheic streams. In the Khosta and Kudepsta basins "*Paladilhiopsis*" sp. was met mainly in powerful rheocrenes with a stable water discharge. Not found in helocrenes.

• *Proasellus* cf. *infirmus* (Birstein, 1936) (Crustacea: Isopoda: Asellidae)

Found individuals of *Proasellus* are morphologically close to *Proasellus infirmus* (Birstein, 1936) described from the springs of the Gumista valley (Central Abkhazia); we did not find any significant differences. However, for confident identification of the species, it is necessary to compare our specimens with type specimens of *P. infirmus*. As in the case with typical *P. infirmus*, the found populations are difficult to attribute to real stygobionts – animals are pigmented (obviously weaker than epigean *Asellus*) and have partially reduced eyes. Most likely, they are obligate crenobionts, occasionally penetrating into groundwater.

Occurrence of *Proasellus* cf. *infirmus* in the springs of the Khosta and Kudepsta basins is 38%. In about half of the cases, these crustaceans are among the dominating species complex within the assemblages, accounting for 15–25% of its total metabolism, but never becoming super dominants, that are able to suppress the accompanying amphipod species from *Niphargus* and *Gammarus* genera, completely. The highest density was recorded in the springs of the middle current of Malaya Khosta – up to 45 individuals per sample. Points of detection *P*. cf. *infirmus* in the study area are usually observed in the lower and middle currents of the main rivers, to the absolute altitude of 300 m. The species does not occur in the springs of the upper stream, in the springs on the ridges and the main large caves. It inhabits both in stable rheocrenes and helocrenal seeps.

• *Niphargus abchasicus* Martynov, 1932 (Crustacea: Amphipoda: Niphargidae)

The most widespread species of *Niphargus* in the study area, which was described from the local spring waterbodies and found here later (Levushkin, 1963). The occurrence is 48%, while in most cases the species dominates in the assemblages, accounting for 23–67% of the total abundance of metabolism. At the same time, *N. abchasicus* is unevenly distributed over the studied territory: mass finds are associated with the coastal low-mountain zone (including the city of Khosta). The occurrence decreases when moving northwards, to the headwaters of the rivers and the Alec ridge. The species almost never occurs in the spring sources of Bolshaya and Malaya Khosta and Kudepsta rivers, being replaced by *N*. cf. *pseudolatimanus* Birstein, 1952.

Observed populations correspond exactly to the diagnosis given by Martynov (1932), later updated by Derzhavin (1945) and Birshtein (1952) in terms of morphology. Nevertheless, some individuals differ possessing a larger number (3–4) of thorns on dactyles of pereopods III – VII, which quite fits into the norms of individual variability.

• *Niphargus* cf. *pseudolatimanus* Birstein, 1952 (Crustacea: Amphipoda: Niphargidae)

The species (possibly a group of species) is morphologically close to *N. latimanus* Birstein, 1952 and *N. pseudolatimanus* Birstein, 1952 described from the upper Kudepsta caves. In general, combined morphological features of spring populations have an intermediate character between these two species, somewhat approaching *N. pseudolatimanus*. But here, too, the differences are manifested in a different form of the gnatopod, smaller number of segments in antenna II and in other, mostly quantitative, features. Morphologically close populations are widespread in the West Transcaucasia – from the Khosta and Kudepsta basins to the vicinity of Tuapse and Novorossiysk (Sokolova and Chambers, 2015).

In the springs of the Khosta and Kudepsta basins, the species is found in 31% of the springs on average, often together with *N. abchasicus*, yielding to it in numbers everywhere. We did not find it in the springs of the low-mountainous seaside coastal strip: the species is mostly found in the middle and upper courses of region's main rivers (especially common in the springs of Vorontsovka village). There were springs in the upper Khosta and Kudepsta where it made up 100% of the population (up to 25 individuals per sample). In all other cases, the species was not prone to superdominance, never accounting for more than 20% of the total metabolism of the assemblage, and even less in the presence of *N. abchasicus*.

• *Niphargus* cf. *gurjanovae* Birstein, 1941 (Crustacea: Amphipoda: Niphargidae)

A species morphologically close to *N. gurjanovae* Birstein, 1941, known from the springs of Western Georgia. The latter is described only from females and not in great detail, which makes it difficult to identify individuals found reliably. We also had only females in the number of several specimens.

The species is rare in the surveyed area. Found only in four springs, three of which are located in close proximity to each other, in the upper reaches of Kudepsta river. Only in one case did the species demonstrate subdominance, accounting for 38% of the total abundance of the assemblage. In other cases, this index was at the level of 5–10%.

Thus, the springs of the Khosta and Kudepsta basins are inhabited by six species of invertebrates associated with groundwaters by their origin. Each of these species is found in all three main valleys of the region: the Kudepsta valley, Bolshaya and Malaya Khosta, but the frequency of occurrence of most species depends on the height above sea level and/or distance from the coast. In total, species of stygobiont origin dominate in the assemblages of 55% of springs. These are predominantly helocrenes and rheocrenes, with an unstable connection to a larger watercourse (river or stream). Representatives of the fairly eurybiont genus *Gammarus* (Amphipoda) dominate in 21% of springs. Most often, these are springs having a permanent connection with a larger watercourse. Amphibiotic insects form dominant complexes in 24% of cases. Usually, in springs lacking amphipods and isopods for some reason.

Myusser Upland basin

Four species have been found here: one species of gastropod mollusks of genus *Belgrandiella*, two species of *Niphargus* amphipods, one species of *Proasellus* isopod.

• *Belgrandiella* sp. (Gastropoda: Hydrobiidae)

This species is almost identical to *B. caucasica* (Fig. 2F) in terms of conchological parameters yet stably differs from the latter by at least the structure of the male reproductive system. The penis is characterized by the reduction of the lateral process typical for genus *Belgrandiella* as a whole (Fig. 2E), as well as the wider main lobe (Fig. 2G). This observation is based on the dissections of ten males.

Belgrandiella sp. was found in 54% of the surveyed springs in the Myusser Upland territory. As in the case of *B. caucasica*, this species often reached high density (up to 93 individuals per sample), but did not play a significant role in the assemblages. On average, the share of the species in the total abundance of the assemblage in metabolism was 1–4%, and up to 15% in single springs.

Belgrandiella sp. occurs in springs all over Mysra and Riapshi rivers and in the valleys of the small coastal streams of the Myusser Upland. Not found in the adjacent areas of the Bzyp lowland. Perhaps an endemic of the Myusser Upland.

• *Proasellus* cf. *infirmus* (Birstein, 1936) (Crustacea: Isopoda: Asellidae)

Morphologically identical to the populations from the Khosta and Kudepsta basins. In the springs of the Myusser Upland is less common – found in 31% of waterbodies. At the same time, almost all findings were single, the maximum was two individuals per sample. Therefore, this species does not play a significant role in the spring assemblages of the region, reaching only a few percent of the total abundance based on metabolism.

• *Niphargus derzhavini* Birstein, 1952 (Crustacea: Amphipoda: Niphargidae)

The most common *Niphargus* species in the area. Described from springs near the Olginsky grotto, in the vicinity of Adzapsh village (Otradnoye) and the town of Gagra, "Transfer" of the typical habitat of this type into the vicinity Olginskoye village, Gulripsh district of Abkhazia (Sidorov, 2014) was clearly erroneous – there are no morphologically close forms in the specified area. On the contrary, completely identical animals live in the vicinity of Gagra.

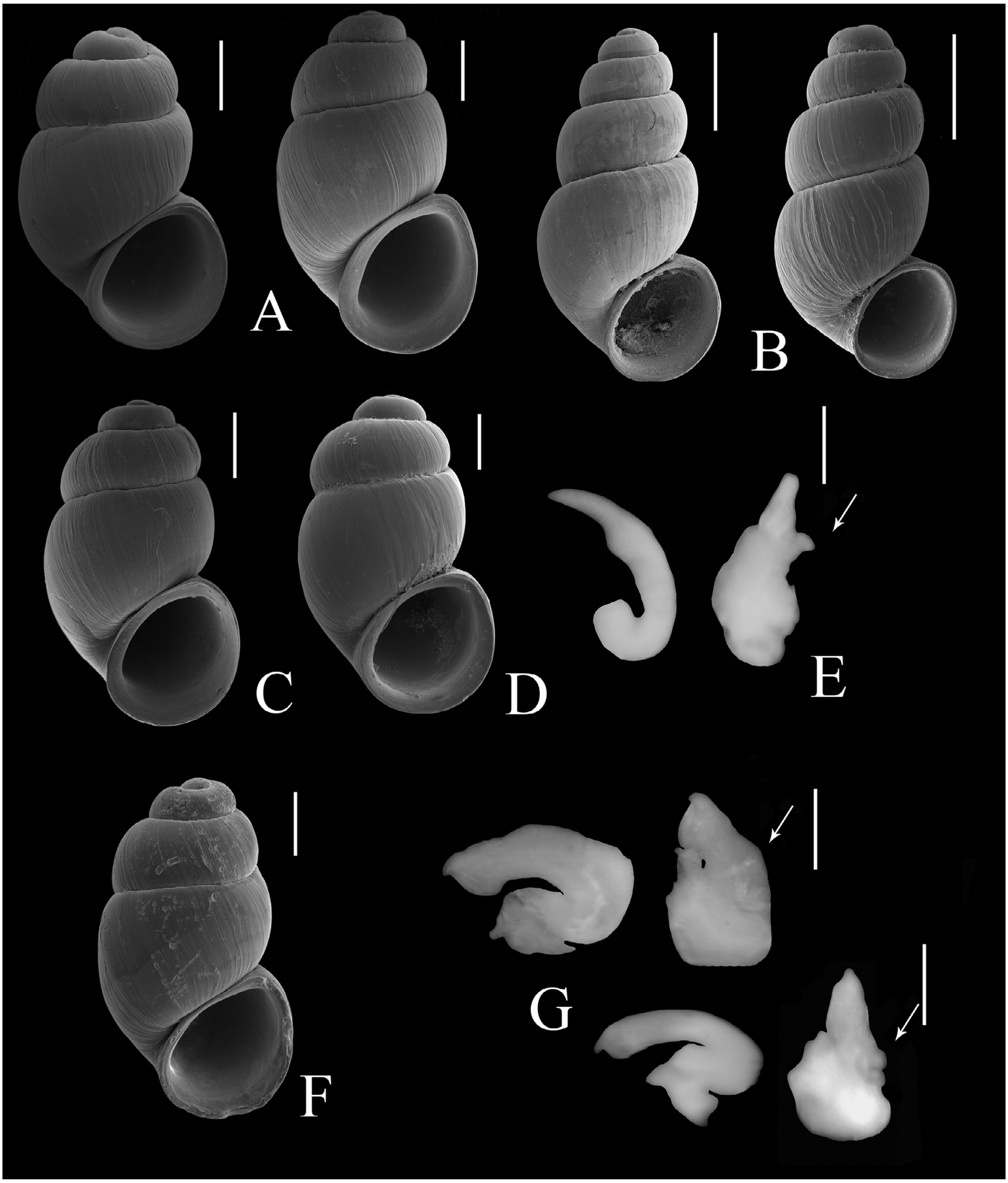

Figure 2. Belgrandiellinae from the springs of West Transcaucasia: **A** – shells of *Belgrandiella caucasica* Starobogatov, 1962, springs near the Krasnoaleksandrovskaya cave, Lazarevsky district of the city district of Sochi, Krasnodar Region, N 44°0'36.03", E 39°21'11.72", collected on 01.05.2015; **B** – shells of "*Paladilhiopsis*" sp., a spring in the valley of Kudepsta river, near the village of Krasnaya Volya, Khostinsky district of the Sochi city district of the Krasnodar Region, N 43°33'44.99 ", E 39°55'58.69", 23.02. 2009; **C** – shell of *B. caucasica* Starobogatov, 1962, spring in the valley of Malaya Khosta river, at the intersection with the road to Khleborob village, Khostinsky district of Sochi City District of the Krasnodar Region, N 43°34.871', E 39°52.428', 04.25.2015; **D** – shell of *B. nemethi* Schütt, 1993, spring seepage on the right bank of Khosta river, near SNT "Rassvet", Khleborob sett., Khostinsky district of Sochi City District of Krasnodar Region, N 43°33'0.62", E 39°53'3.44", 15.04.2008; **E** – penis of *B. caucasica* Starobogatov, 1962, a spring in the valley of Malaya Khosta river, at the intersection with the road to Khleborob village, Khostinsky district of the Sochi City district of the Krasnodar Region, N 43°34.871", E 39°52.428', 04.25.2015, side and bottom view, arrow shows a characteristic lateral process; **F** – shell of *Belgrandiella* sp., a spring on the right bank of Myussera (Mysra) river, at the mouth of the first large tributary on the left, Gudauta District, Republic of Abkhazia, N 43°11'52.30", E 40°27'0.03", 02.19.2010; **G** – penises *Belgrandiella* sp., a spring on the right bank of the river Myussera (Mysra), at the mouth of the first large tributary on the left, Gudauta district, Republic of Abkhazia, N 43°11'52.30 ", E 40°27'0.03", 02.19.2010, side and bottom views, arrow shows the absence of lateral process characteristic for *B. caucasica*. The scale segment corresponds to: **A**, **C**, **D**, **F** – 300 μm; **B** – 500 μm; **E**, **G** – 200 μm.

The occurrence of *N. derzhavini* is 62% in the springs of the region. In most cases, the species dominates in the assemblages, averaging 40–45% of the total abundance of the assemblage's metabolism. In several cases, this figure exceeded 80%. The species also forms fairly dense aggregations – from 40 to 80 individuals per sample. On the territory of the Myusser Upland, the species is widespread everywhere, in the helo- and rheocrenes, also penetrating into some springs of Lake Inkit floodplain and Bzyp plain.

• *Niphargus* cf. *gurjanovae* Birstein, 1941 (Crustacea: Amphipoda: Niphargidae)

The species is morphologically identical to the populations found in the spring reservoirs of the Khosta and Kudepsta basins. Its occurrence is relatively low in the basin of the Myusser Upland, constituting 15%. The density of populations is also small: 1–5, up to 10 individuals per sample. This species is not represented in the complex of dominants, reaching a maximum of 5% of the total metabolism of the assemblage.

Thus, the springs of the Myusser upland are inhabited by four species of invertebrates associated with groundwaters by their origin. Most of them are tied to large valleys of the upland: the valley of Mysra and Riapshi rivers, as well as the valleys of coastal streams. Only the most common stygobiont, *N. derzhavini*, is encountered in the adjacent territories of the Bzyp plain and the floodplain of Lake Inkit.

In total, species of stygobiont origin dominate in the assemblages of 52% of springs of the Myusser Upland. Genus *Gammarus* amphipods dominate in 39% of springs, complexes of crenobiont amphibiotic insects in 9% of springs.

It has long been noticed that all variants of spring assemblages can be divided into two groups: one dominated by complexes of crenal insects and the other dominated by non-insects, i.e. crustaceans and mollusks (Barquín and Death, 2006; Gray, 2005). The group of assemblages dominated by crustaceans dominates in the springs of the Western Transcaucasia, 80% versus 20%. The dominance of crustaceans of stygobiont origin is observed in 55% of cases.

Some zoogeographic patterns

Ranges of crenobiont forms are almost always larger than the ranges of typical stygobionts living in underground cavities. Many species, for example, the Caucasian *Niphargus* or *Troglocaris* are known only from one particular cave or a complex of communicating caves (Birshtein and Levushkin, 1967). Obviously, the ranges of stygobionts, which spread to the springs, are somewhat wider, but they are still inferior to real epigean forms. Thus, the range of *N. abchasicus*, as far as we know at the moment, includes only the territory squeezed between the sections of the lower reaches of Sochi and Mzymta rivers. An obviously related species, *N. derzhavini* inhabits the spring waters of the Gagra – Mysra section and, possibly, parts of the Gudauta plain. Further to the south-east, starting from Novyi Afon and at least to the Gumista river valley, spring water bodies are mostly inhabited by *N. iniochus* Birstein, 1941 (unpublished data), which was described from a creek of the cave entrance zone near the Andreyevka village (Akhalsheniya). The species of crenal gastropods and a number of other groups probably follow along the Black Sea coastline in a similar fashion. Separate endemic faunistic complexes of stygo- and crenobionts can be located on a very small area – 20–30 km^2. In particular, a similar effect has been repeatedly described for stygobiont fauna of the Balkan Peninsula (Georgiev and Hubenov, 2013; Sket, 1999). Thus, the spring areas of West Transcaucasia do indeed exhibit a certain island effect, remaining largely isolated from each other in the faunistic sense, at least at the level of non-flight primary aquatic organisms.

Conclusions

1. Stygobiont elements West Transcaucasia spring assemblages' fauna are mainly represented by crustaceans (Amphipoda and Isopoda) from *Niphargus* and *Proasellus* genera, as well as by specific gastropods of the Belgrandiellinae subfamily.

2. Stygobionts dominate in spring communities in about 50% of cases. Typically, the dominants are amphipods of genus *Niphargus*.

3. More often stygobionts dominate in helocrenes with a variable volume of flow, compared to rheocrenes, which are stably connected with watercourses. Epigean species of *Gammarus* are usually the dominant group in rheocrenes.

4. Stygo- and crenobiont primary aquatic invertebrates (crustaceans and mollusks) exhibit local species endemism. In general, spring communities can be considered as island communities under certain conditions.

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