

Cladocera (Crustacea: Branchiopoda) in lowlands of the Ciscaucasian Region, European Russia

Cladocera (Crustacea: Branchiopoda) низменностей Северного Кавказа, европейская часть России

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КЛЮЧЕВЫЕ СЛОВА: ветвистоусые ракообразные, фауна, Евразия, зоогеография, Евразия, Азовское море, Черное море.

ABSTRACT: Paradoxically, attention of experts on cladoceran biogeography is focused in Russia on the Arctic zone, Far East and Siberia, while Caucasus and Ciscaucasia are studied inadequately. The aim of this communication is to analyse the cladoceran fauna of lowlands of the Ciscaucasian Region to determine general regularities of their distribution, i.e. to reveal local biodiversity hotspots of the region. In total, 171 qualitative samples from 155 water bodies are analysed where 57 species of Cladocera are recorded. All taxa are assigned to the following geographic faunistic complexes: (1) widely distributed Eurasian (WE), (2) southern tropical (ST), (3) Mediterranean-Ponto-Caspian endemic (EN), (4) arid (AR) complex; and two artificial groups: (5) widely distributed non-revised taxa (WS) and (6) eastern (possibly, anthropogenic) invaders (IS). Distribution of faunistic complexes between two main biotopes in Taman and Other Ciscaucasia is significantly different: it is relatively similar for benthic + littoral (BP) species, but very different among the planktonic species (PL). Among PL species in the Taman sub-region, the portion of EN, IS and AR species is significantly higher and rate of WE and WS is significantly lower as compared to the Other Ciscaucasia. To date we have no explanation for such specificity of the Taman region. Also we cannot discuss the endemism hotspots of the Ciscaucasia and even Caucasus concerning the Cladocera, moreover, no one cladoceran taxon is regarded as an endemic of the Caucasus. The cladoceran studies need to be continued in this region.

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РЕЗЮМЕ: Парадоксальным образом внимание специалистов по биogeографии кладоцер в России сосредоточено на Арктической зоне, Дальнем Востоке и Сибири, а Кавказ и Предкавказье изучены недостаточно. Целью данного исследования является анализ фауны ветвистоусых ракообразных (Cladocera) низменностей Предкавказья для установления общих закономерностей их распространения, т.е. выявления локальных очагов биоразнообразия региона. Всего проанализирована 171 качественная проба из 155 водоемов, в которых зарегистрировано 57 видов Cladocera. Все таксоны отнесены к следующим географическим фаунистическим комплексам: (1) широко распространенный евразийский (WE), (2) южный тропический (ST), (3) средиземноморско-пonto-каспийский эндемичный (EN), (4) аридный (AR); и двум искусственным группам: (5) широко распространенные нерезионные таксоны (WS) и (6) восточные (возможно, антропогенные) вселенцы (IS). Распределение фаунистических комплексов между двумя основными биотопами в Тамани и в остальном Предкавказье существенно различается: оно относительно сходно для бентосных + литоральных (BP) видов, но сильно различается для планктонных видов (PL). Среди видов PL в Таманской подобласти доля видов EN, IS и AR значительно выше, а доля WE и WS значительно ниже, чем в остальном Предкавказье. На сегодняшний день у нас нет объяснения подобной специфике Таманского субрегиона. Также мы не можем обсуждать очаги эндемизма Предкавказья и даже Кавказа в отношении Cladocera,

тем более, что ни один таксон ветвистоусых не считается эндемиком Кавказа. Исследования кладоцер в этом регионе необходимо продолжать.

Introduction

Biodiversity of continental waters apparently is studied irregularly among different invertebrate taxa, even in “well-studied” Eurasia. If we have adequate knowledge of the species composition of fishes, amphibia, mollusks and some insects in many regions of Russia [Kantor, Sysoev, 2005; Bogutskaya *et al.*, 2008; Novoselov, 2020; Bolotov *et al.*, 2020; Vinarski *et al.*, 2021; Simonov *et al.*, 2022], micro-crustaceans attract less attention by hydrobiologists. Water fleas (Crustacea: Cladocera) represent a dominant group of microscopic animals in continental water bodies of different types [Dumont, Negrea, 2002], and many publications on their ecology appear each year [Lampert, 2011; Lares *et al.*, 2022], but publications on their fauna and taxonomy are much more rare. Moreover, strong changes in the taxonomy of many macrotaxa [Van Damme, Dumont, 2008; Korovchinsky, 2018; Sinev, 2020] compromise use of previously obtained data for subsequent ecological and biogeographical analyses.

Paradoxically, attention of experts on cladoceran biogeography is concentrated in Russia on the Arctic zone [Novichkova, Chertoprud, 2015; Chertoprud, Novichkova, 2021], Siberia [Burmistrova, Ermolaeva, 2013; Afonina *et al.*, 2019; Chertoprud *et al.*, 2022] and Far East [Kotov *et al.*, 2011a,b; Kotov, Sinev, 2011; Garibian *et al.*, 2019; Kotov *et al.*, 2021]. In contrast, the European part of Russia is not studying intensively, except for revealing non-indigenous cladocerans, which are tasks of many special publications (see review by Kotov *et al.* [2022]). All available taxonomic information on the cladocerans of the whole of North Eurasia was summarized by Korovchinsky *et al.* [2021] but still some regions are studied inadequately.

It is well-known that Caucasus is an important hotspot of biodiversity and endemism of the terrestrial [Griffin, 1999; Myers *et al.*, 2000; Krever *et al.*, 2001; CEPF, 2018] and freshwater [Katouzian *et al.*, 2016; Parvizi *et al.*, 2019; Marin *et al.*, 2021] animals, but we have no idea if it is true for Cladocera? Again, recent information on the Cladocera of Georgia and Azerbaijan is scarce [Alekhperov, Taptiqova, 2021; Taptiqova, 2022]; studies of the water fleas of Armenia are more numerous [Krylov *et al.*, 2016; Malin *et al.*, 2021] but lacking any taxonomic revisions. Ciscaucasia (covering several Russian Federation regions) is among inadequately studied territories, although studies on the Cladocera were started there many years ago [Sowinsky, 1891; Schiklejew, 1929; Kalita, 1930; Kudelina, 1930; Tauson, 1936] and are continued recently [Dementiev, 2015; Karnaukhov, Zlotnikov, 2017; Bondareva, 2019].

During previous years, numerous samples were collected in the Ciscaucasian Region, but they were used

only in few taxonomic trans-Eurasian studies at the time. The aim of this communication is to analyse the cladoceran fauna of the Ciscaucasian Region to determine general regularities of the cladoceran distribution, i.e. to reveal local biodiversity hotspots of the region.

Material and Methods

Samples were collected in the Ciscaucasian Region from late March to earlier October of 2004–2021 by team of the Laboratory of aquatic communities and invasions of A.N. Severtsov Institute of Ecology and Evolution of Russian Academy of Sciences or by our colleagues from IEE RAS, or from other institutes using plankton nets and dip nets of various designs with a mesh size of no more than 50 μm . A single total sample was taken from each small water body; a single sample from pelagic zone and 1–2 samples from the littoral zone were taken from each large water body. An altitude effect on the cladoceran fauna [Dumont, Negrea, 2002; Korovchinsky *et al.*, 2021] leads to a situation when mountain regions have their own specific traits, so we excluded from our analysis all the samples from water bodies above 500 m a.s.l. to avoid an altitude effect on the regularities of a horizontal distribution of the taxa. Therefore, our study concerns lowlands only.

In total, 171 qualitative samples from 155 water bodies (Fig. 1) were analysed by the protocol described in Garibian *et al.* [2021]. All specimens identified to genus level (juveniles, ephippia of the Anomopoda, deformed specimens, separate body parts) were excluded from our analysis. Initial distribution of each species in the Ciscaucasian Region was visualized in Quantum GIS Ver. 3.28 (<https://qgis.org/en/site/>). Initial data on the water bodies and cladoceran records are available at the Open Science Framework portal (<https://doi.org/10.17605/OSF.IO/QR7HS>).

Linear Regression Model (OLS method, the permutation test on correlation (R^2) using 9999 replicates) was applied to reveal a relation between the number of species detected, and environmental variables in a whole dataset: latitude, longitude, altitude (remember that all of them were located below 500 m a.s.l.!) of the locality where each sample was taken, and approximate area of the water body (in square meters, identified using images from Yandex Satellite Map, www.yandex.ru, accessed on 1 June 2023). Data were z-transformed (value of the water body surface square also was log-transformed) and added to Linear Regression Model with Monte-Carlo tested p -values.

Each water body was assigned to either temporary or permanent group, based on a description made by a sample collector or on the satellite image of the studied area by Yandex Satellite Map; both methods permit identifying obvious signs of complete drying at some phases of the water body seasonal cycle. Roadside ditches, drying oxbows, rice fields, all puddles and tanks were automatically assigned to temporary water bodies. All other water bodies were assigned to the permanent group.

Based on a provisional analysis of the distribution maps of each taxon, all the localities were subdivided into two sub-regions:

(1) “Taman” within the following boundaries (Fig. 1): latitude 44.5–45.5 °N, longitude 36.6–39.5 °E; including floodplain and delta of the Kuban, the town of Krasnodar and the Krasnodar reservoir, the Azov Sea and Black Sea coasts including Novorossiysk.

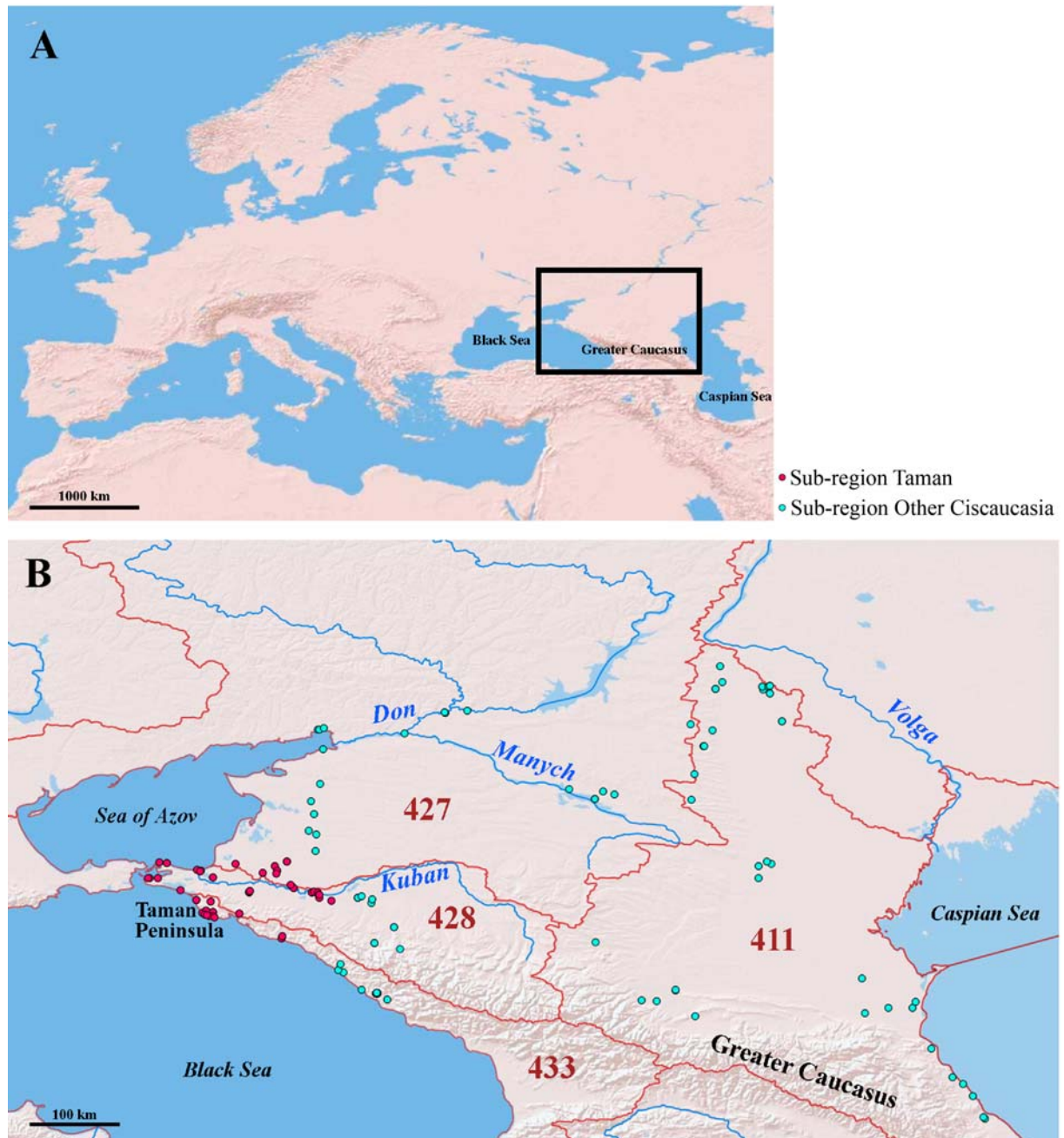


Fig. 1. Maps: A — of Europe; B — of studied region with sampling points. Brown lines and numbers represent borders and numbers of Ecoregions according to Abell *et al.* [2008]. Base map here and below is the ESRI Shaded Relief layer in Pseudo-Mercator projection (https://server.arcgisonline.com/ArcGIS/rest/services/World_Shaded_Relief/MapServer/tile/{z}/{y}/{x}).

Рис. 1. Карта: А — Европы; В — исследуемого региона с точками отбора проб. Коричневые линии и цифры представляют собой границы и номера экорегионов согласно Abell *et al.* [2008]. Базовая карта здесь и ниже — слой Shaded Relief ESRI в псевдо-Меркаторской проекции (https://server.arcgisonline.com/ArcGIS/rest/services/World_Shaded_Relief/MapServer/tile/{z}/{y}/{x}).

(2) “Other Ciscaucasia” sub-region, where the rest of the samples were assigned (Table 1).

The number of water bodies and the number of records belonging to each water body type were calculated for each sub-region separately. An empirical randomized species accumulation curve depending on the sampling effort (the number of samples analyzed) was constructed for Taman and Other Ciscaucasia sub-regions in the EstimateS9.1 pack-

age [Colwell, Elsensohn, 2014] with five different non-parametric species estimators: Chao1, Chao2, Jackknife1, Jackknife2, and Bootstrap separately for the species from the sub-regions. Bootstrap was found to be the best model (among five) according to the minimum dispersion of predicted values for each step.

All species were subdivided into planktonic (PL) and benthic + phytoplanktonic (BP) according to Korovchinsky *et*

Table 1. Information on the sub-regions used in this study: number of water bodies, number of identifications and information on their belonging to particular Freshwater Ecoregions according to Abell *et al.* [2008].

Таблица 1. Информация о субрегионах, изученных в данном исследовании: число водоемов, число находок и информация об принадлежности последних к конкретным пресноводным экорегионам согласно Abell *et al.* [2008].

Sub-region	No. of identifications	Water bodies, total	Water bodies, temporary	Water bodies, permanent
Taman	162	53	15	38
Other	276	102	43	59
Ciscaucasia				
Total	438	155	58	97

Sub-region	No. of species recorded	No. of records in temporary water bodies	No. of records in permanent water bodies	Freshwater Ecoregion
Taman	45	24	138	427, 428, 433
Other	42	99	177	411, 427, 428, 433
Ciscaucasia				
Total	57	123	315	411, 427, 428, 433

Table 2. Species found in two sub-regions and their belonging to planktonic or benthic+phytoplous group and geographic faunistic complex.

Таблица 2. Виды, обнаруженные в двух субрегионах, и их принадлежность к планктонной или бентосной-фитофильной группе и географическому фаунистическому комплексу.

Taxon	Taman	Other Ciscaucasia	Faunistic complex	Planktonic/ benthic + phytoplous
<i>Acroperus angustatus</i> Sars, 1862	+	+	WE	BP
<i>Acroperus harpae</i> (Baird, 1834)	+	+	WE	BP
<i>Alona quadrangularis</i> (O.F. Müller, 1785)	+	+	WE	BP
<i>Alonella excisa</i> (Fischer, 1854)	+	+	WS	BP
<i>Alonella exigua</i> (Lilljeborg, 1853)	+	+	WS	BP
<i>Bosmina coregoni</i> Baird, 1857	+		WE	PL
<i>Bosmina longirostris</i> (O.F. Müller, 1776)	+	+	WS	PL
<i>Ceriodaphnia laticaudata</i> P.E. Müller, 1867		+	WS	PL
<i>Ceriodaphnia pulchella</i> Sars, 1862		+	WS	PL
<i>Ceriodaphnia reticulata</i> (Jurine, 1820)	+	+	WS	PL
<i>Chydorus ovalis</i> Kurz, 1875	+		WE	BP
<i>Chydorus sphaericus</i> (O.F. Müller, 1776)	+	+	WE	BP
<i>Coronatella elegans</i> (Kurz, 1875)	+	+	AR	BP
<i>Coronatella rectangula</i> (Sars, 1861)	+	+	WS	BP
<i>Daphnia cucullata</i> Sars, 1862	+	+	WE	PL
<i>Daphnia curvirostris</i> Eylmann, 1887	+	+	WE	PL
<i>Daphnia longispina</i> O.F. Müller, 1776		+	WS	PL
<i>Daphnia magna</i> Straus, 1820	+	+	AR	PL
<i>Daphnia obtusa</i> Kurz, 1874	+	+	WS	PL
<i>Daphnia pulex</i> Leydig, 1860	+	+	WS	PL
<i>Daphnia similis</i> Claus, 1876	+	+	EN	PL
<i>Daphnia sinensis</i> Gu, Xu, Li, Dumont et Han, 2013	+		AR	PL
<i>Diaphanosoma dubium</i> Manuilova, 1964	+	+	IS	PL
<i>Diaphanosoma macrophthalmum</i> Korovchinsky et Mirabdullaev, 1995	+	+	IS	PL
<i>Diaphanosoma orghidani</i> Negrea, 1982	+		WE	PL
<i>Diaphanosoma mongolianum</i> Uéno, 1938	+		WE	PL
<i>Disparalona rostrata</i> (Koch, 1841)	+	+	WE	BP
<i>Dunhevedia crassa</i> King, 1853	+	+	ST	BP

Table 2 (continued).
Таблица 2 (продолжение).

Taxon	Taman	Other Ciscaucasia	Faunistic complex	Planktonic/ benthic + phytophilous
<i>Flavalona costata</i> (Sars, 1862)		+	WS	BP
<i>Graptoleberis testudinaria</i> (Fischer, 1851)	+	+	WS	BP
<i>Ilyocryptus agilis</i> Kurz, 1874		+	WS	BP
<i>Leydigia acanthocercoides</i> (Fischer, 1854)	+		WE	BP
<i>Macrothrix dadayi</i> Behning, 1941		+	EN	BP
<i>Macrothrix hirsuticornis</i> Norman et Brady, 1867		+	WS	BP
<i>Macrothrix laticornis</i> (Jurine, 1820)	+		WE	BP
<i>Megafenestra aurita</i> (Fischer, 1849)		+	WE	PL
<i>Moina belli</i> Gurney, 1904	+		AR	BP
<i>Moina brachiata</i> (Jurine, 1820)	+	+	WE	PL
<i>Moina lipini</i> Smirnov, 1976	+	+	WE	PL
<i>Moina macrocopa</i> (Straus, 1820)	+		WE	PL
<i>Moina micrura</i> Kurz, 1874	+		WS	PL
<i>Moina salina</i> Daday, 1888	+	+	AR	PL
<i>Ovalona cambouei</i> (Guerne et Richard, 1893)		+	ST	BP
<i>Oxyurella tenuicaudis</i> (Sars, 1862)	+	+	WE	BP
<i>Phreatalona protzi</i> (Hartwig, 1900)		+	WE	BP
<i>Pleuroxus aduncus</i> (Jurine, 1820)	+	+	WS	BP
<i>Pleuroxus laevis</i> Sars, 1862	+		WE	BP
<i>Pleuroxus quasidenticulatus</i> (Smirnov, 1996)	+	+	ST	BP
<i>Pleuroxus truncatus</i> (O.F. Müller, 1785)		+	WE	BP
<i>Prendalona guttata</i> (Sars, 1862)	+		WS	BP
<i>Scapholeberis mucronata</i> (O.F. Müller, 1776)	+	+	WS	PL
<i>Scapholeberis smirnovi</i> Garibian, Neretina, Taylor et Kotov, 2020	+	+	ST	PL
<i>Sida crystallina</i> (O.F. Müller, 1776)	+	+	WE	BP
<i>Simocephalus exspinus</i> (De Geer, 1778)	+	+	WS	BP
<i>Simocephalus mixtus</i> Sars, 1903	+		WS	BP
<i>Simocephalus vetulus</i> (O.F. Müller, 1776)	+	+	WS	BP
<i>Tretocephala ambigua</i> (Lilljeborg, 1901)		+	AR	BP
Total	45	42	57	57

al. [2021], and the number of records belonging to each biotope was calculated for each sub-region. In order to estimate how the species belonging to different biotopes were distributed over temporary and permanent water bodies, we excluded from our analysis 49 samples with a single species record.

For further analysis, all the taxa were assigned to the following geographic faunistic complexes based on literature information on their distribution summarized by Koro-chinsky *et al.* [2021] (Table 2):

- 1) widely distributed Eurasian (WE);
 - 2) southern tropical (ST);
 - 3) Mediterranean-Ponto-Caspian endemic (EN);
 - 4) arid (AR) complex;
- and two artificial groups:
- 5) widely distributed non-revised taxa (WS);
 - 6) eastern (possibly, anthropogenic) invaders (IS).

The diagrams visualizing number of species belonging to each faunistic complex in each sub-region, and with differentiation by two biotopes (plankton vs. benthos+litoral), were constructed. Non parametric Mann-Whitney test [Mann, Whitney, 1947] was used to check the differences in average

number of PL and BP species per water body in permanent and temporary water bodies in all studied sub-regions.

All calculations and visualization of the graphs are performed in the STATISTICA 12 statistical analysis package (www.statsoft.com) and PAST 4.11 package [Hammer *et al.*, 2001].

Finally we have applied the scheme of Ecoregions according to Abell *et al.* [2008] realized in the FEOW [2023] website. Our samples belonged to the following Ecoregions: 411 — Western Caspian Drainages; 427 — Don; 428 — Kuban and 433 — Western Trans-Caucasia. Diagram representing the rate of the records belonging to each faunistic complex in each Ecoregion was provided. Fisher's exact *p* (based on network algorithm of Mehta & Patel [1986]) for frequency tables of faunistic complexes in different Ecoregions is used, because conventional Chi squared test with Monte-Carlo permutation *p* doesn't work for zero-level cells.

Results

In total, 438 cladocerans belonging to 57 species were recorded. We have provided here the maps for

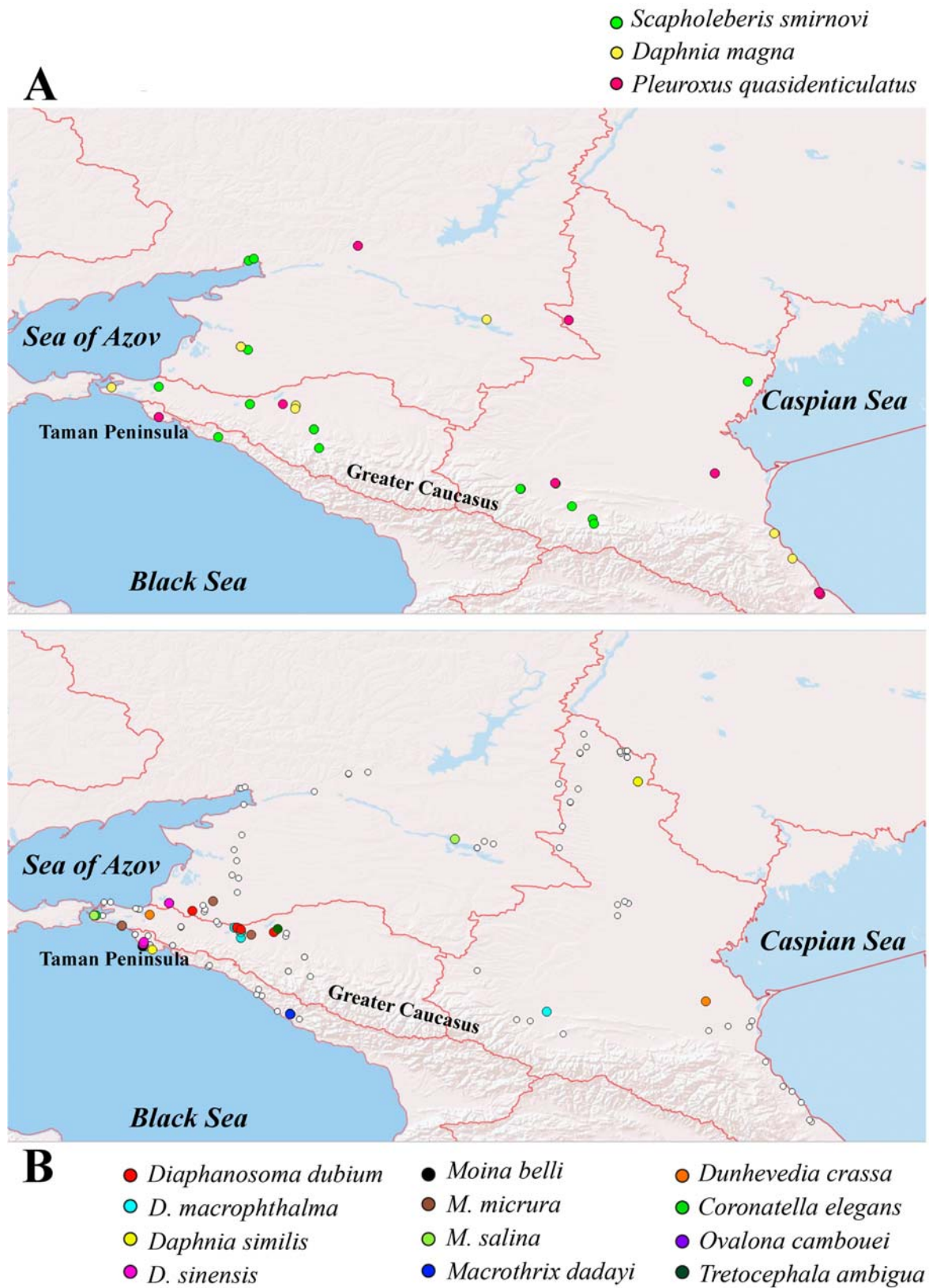


Fig. 2. Localities where species belonging to EN and AR faunistic complexes were found: A — regularly distributed through whole territory; B — concentrated in the Taman sub-region.

Рис. 2. Местонахождения видов, принадлежащих к фаунистическим комплексам EN и AR: А — равномерно распределенных по всей территории; В — сконцентрированных в Таманском субрегионе.

Table 3. Regression coefficients for environmental variables and number of species per water body in a whole dataset.
Таблица 3. Коэффициенты регрессии для переменных окружающей среды и количества видов на водоем во всем наборе данных.

	Coefficient	Standard error	t	p	R ²
Constant	2.83	0.19	15.11	0.000	
Longitude	0.18	0.20	0.91	0.363	0.016
Latitude	-0.12	0.19	-0.62	0.537	0.002
Altitude	-0.14	0.21	-0.66	0.508	0.010
Water body square	0.28	0.21	1.34	0.182	0.027

Table 4. Mean number of BP and PL species in permanent and temporary water bodies.
Таблица 4. Среднее число видов BP и PL в постоянных и временных водоемах.

	Water bodies	BP species (n±SD)	PL species (n±SD)
Permanent	74	2.72±2.44	1.22±1.30
Temporary	32	1.81±1.51	1.25±0.88
Total	106	2.44±2.24	1.23±1.19

only some taxa distributions, while for most taxa the distribution was more or less regular through whole the region under consideration (Fig. 2A), or they were too rare for an adequate statistical analysis. But analysis of such maps has resulted in the conclusion that AR and EN taxa were concentrated just in the Taman Peninsula, the Kuban Delta and their vicinities (Fig. 2B).

No environmental variable demonstrated a significant influence on the number of species found per water body as the regression model showed a low power and a low significance (multiple R=0.193, adjusted R²=0.011, F=14.453 with 4 and 150 degrees of freedom, permutation $p=0.218$), coefficients of the model are presented in Table 3. But Bivariate regression model with a log-transformed value of the water body square alone, demonstrated a small positive influence on the number of species detected (R=0.164, R²=0.027, $t=2.057$, $p=0.041$), as common for species richness and square of ecosystem [Preston, 1962].

Biotopes were varying in species abundances; 32 species belonged to BP (benthic + phytophilous) and 25 species belonged to PL (planktonic) groups. Their average numbers per water body were not equal in permanent and temporary water bodies (Table 4). Non parametric Mann-Whitney test demonstrated that average number of PL species per water body did not differ in permanent and temporary waters, but number of BP species was significantly larger in permanent waters (Table 5). Moreover, the Taman sub-region demonstrated even more definite pattern of the biotope differences (permanent vs. temporary water bodies) (Table 6).

Among 57 species, 30 were found in both sub-regions, 15 species were recorded in Taman only, and 12 species were found outside of the Taman sub-region only. Estimated (by Bootstrap method) species number was 53.64±1.63 for Taman and 48.09±1.24 for Other

Ciscaucasia (Fig. 3). These values were close enough to observed species numbers to consider the species diversity in two sub-regions reasonably well-studied.

The portion of records belonging to different faunistic complexes in the Taman and Other Ciscaucasia was relatively similar (Fig. 4A), although a portion of IS and AR was somewhat higher in Taman. Such similarity in the faunistic composition was provided by a higher portion of BP species per water body (Fig. 4B), for which such differences were minimal between two sub-regions. In contrast, distribution of faunistic complexes between two main biotopes in sub-regions (Fig. 5A–D) was significantly different: it was relatively similar for the BP species, but very different among the PL species: χ^2 test for equal distribution gave the following values: $p=0.6956$ for BP and $p=0.0002$ for PL. Indeed, among PL species in the Taman sub-region the portion of EN, IS and AR species was significantly higher and rate of WE and WS was significantly lower as compared to the Other Ciscaucasia. Just plankton made the Taman sub-region specific for cladoceran biogeography.

The portion of records of different faunistic complexes in each Ecoregion by Abell *et al.* [2008] is represented in Figure 5E. In general, it was similar in different Ecoregions, although the rate of IS is somewhat higher in Ecoregion 433, and the rate of EN higher in Ecoregion 411.

Table 8 shows a proportion of different faunistic complexes in different Ecoregions. Fisher's exact p test demonstrated that composition of the faunistic complexes had significant difference in parts of Ecoregions 427 and 428 belonging to two different Ciscaucasian sub-regions. Ecoregion 433 (Western Trans-Caucasia) had no significant difference in proportions of faunistic complexes in Taman and Other Ciscaucasia sub-regions (Table 7).

Table 5. Significance of the differences between the number of PL and BP species in permanent and temporary water bodies by non parametric Mann-Whitney test.
 Таблица 5. Результаты проверки различий между числом PL и BP видов в постоянных и временных водоемах по всему региону с помощью непараметрического теста Манна-Уитни.

	Rank Sum Permanent	Rank Sum Temporary	U	Z	p-value
PL species	3837.0	1834.0	1062.0	-0.839591	0.401138
BP species	4295.5	1375.5	847.5	2.315757	0.020572
	Z adjusted	p-value	Valid N Permanent	Valid N Temporary	
PL species	-0.881927	0.377817	74	32	
BP species	2.376778	0.017465	74	32	

Table 6. Results of the non parametric Mann-Whitney test of difference between the number of PL and BP species in permanent and temporary water bodies by two subregions.
 Таблица 6. Результаты проверки различий между числом БФ и ПЛ видов в постоянных и временных водоемах двух субрегионов с помощью непараметрического теста Манна-Уитни.

	Sub-region	Rank Sum Permanent	Rank Sum Temporary	U	Z	p-value
BP species	Other	1559.0	719.0	419.0	1.268435	0.204644
PL species	Other	1424.0	854.0	478.0	-0.496912	0.619251
Number of species	Other	1548.0	730.0	430.0	1.124591	0.260763
BP species	Taman	688.0	92.0	56.0	2.365068	0.018027
PL species	Taman	598.0	182.0	102.0	-0.765169	0.444171
Number of species	Taman	698.0	82.0	46.0	2.712873	0.006671
	Sub-region	Z adjusted	p-value	Valid N Permanent	Valid N Temporary	
BP species	Other	1.314923	0.188537	43	24	
PL species	Other	-0.525521	0.599221	43	24	
Number of species	Other	1.165458	0.243835	43	24	
BP species	Taman	2.412160	0.015859	31	8	
PL species	Taman	-0.796894	0.425513	31	8	
Number of species	Taman	2.801313	0.005090	31	8	

Discussion

Preliminary conclusions on the Cladocera of the Ciscaucasian Region were made by Behning [1941] who typified the water bodies of Caucasus, Ciscaucasia and Transcaucasia and even subdivided the cladocerans into several faunistic groups: (1) boreal forms, (2) subtropical forms, (3) eastern invaders (probably from Middle Asia), (4) old forms, (5) forms of unknown origin (either old relicts or recent invaders due to human activity). Note that such groups by Behning [1941] could be regarded as direct analogues to our faunistic complexes, moreover, most these groups fully conform to the latter.

Subsequent publications on the Cladocera of this region did not reveal any remarkable traits of the Cla-

docera biodiversity distribution. They were focused on specific small subregions and even water bodies, without attempts to make their comparative analysis and form a summarizing checklist, except for Dementiev [2015], who formed a representative list of the Cladocera of Central Ciscaucasia. Based on his own original records during tens of years, he listed many more species relative to our list, but some of his identifications concerned regions above 500 m a.s.l., some other records are dubious, and some records need to be rechecked based on new original samples. At the same time, we believe that our list is not a final one, but ideas on the cladoceran distribution regularities revealed here should not be changed after adding more to the analysis.

Subdivision of Ecoregions according to Abell *et al.* [2008] does not work well for the Cladocera (as it

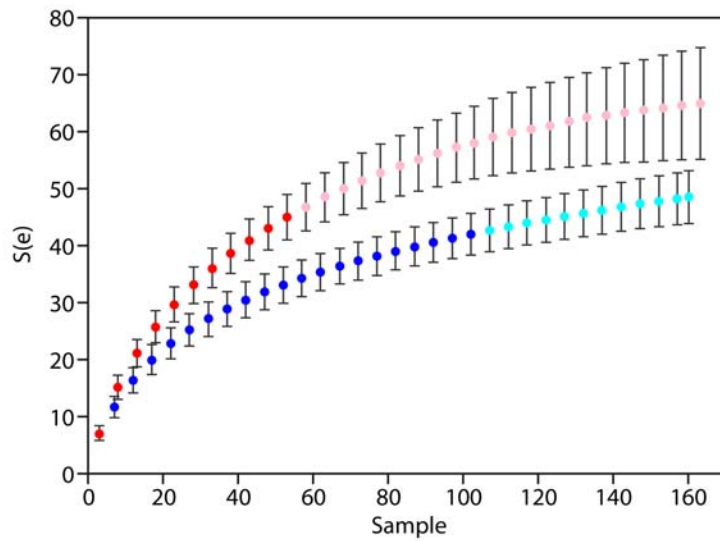


Fig. 3. Randomised species accumulation curve for Taman (red) and Other Ciscaucasia (blue) with 95% confidence interval bounds.
 Рис. 3. Рандомизированная кривая накопления видов для Тамани (красный цвет) и остального Предкавказья (синий цвет) с границами доверительного интервала в 95%.

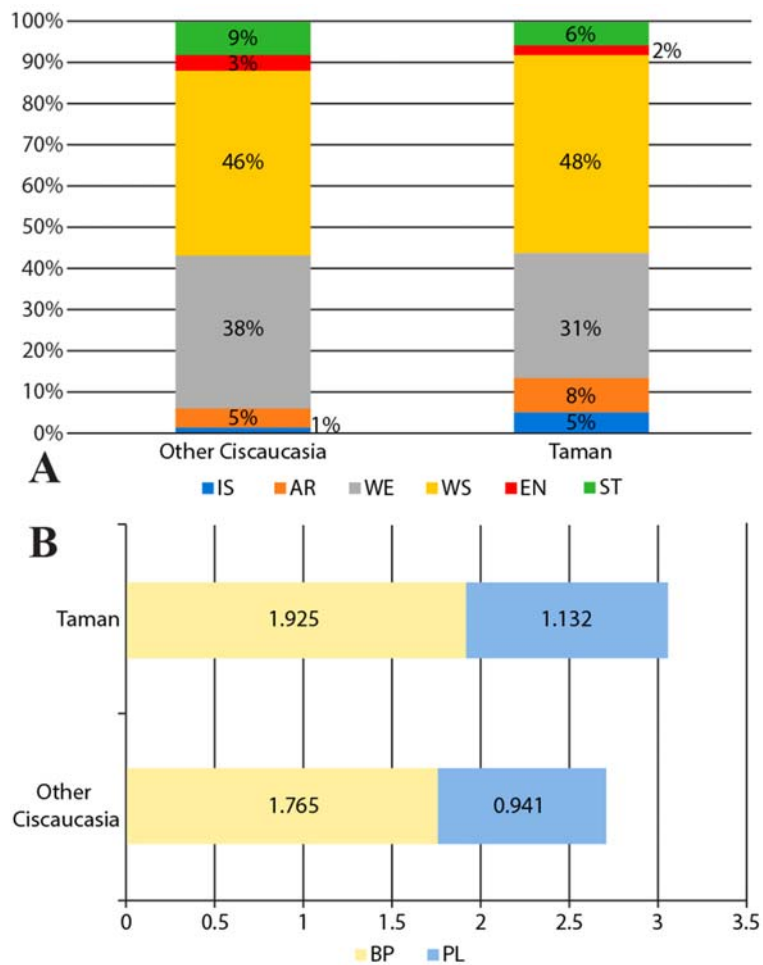


Fig. 4. A — portion of PL and BP taxa per water body in each subregion; B — an average number of PL and BP taxa per a water body in two sub-regions (B).
 Рис. 4. А — доля находок таксонов PL и BP на каждый водоем в каждом субрегионе; В — среднее число находок таксонов PL и BP на водоем в двух субрегионах.

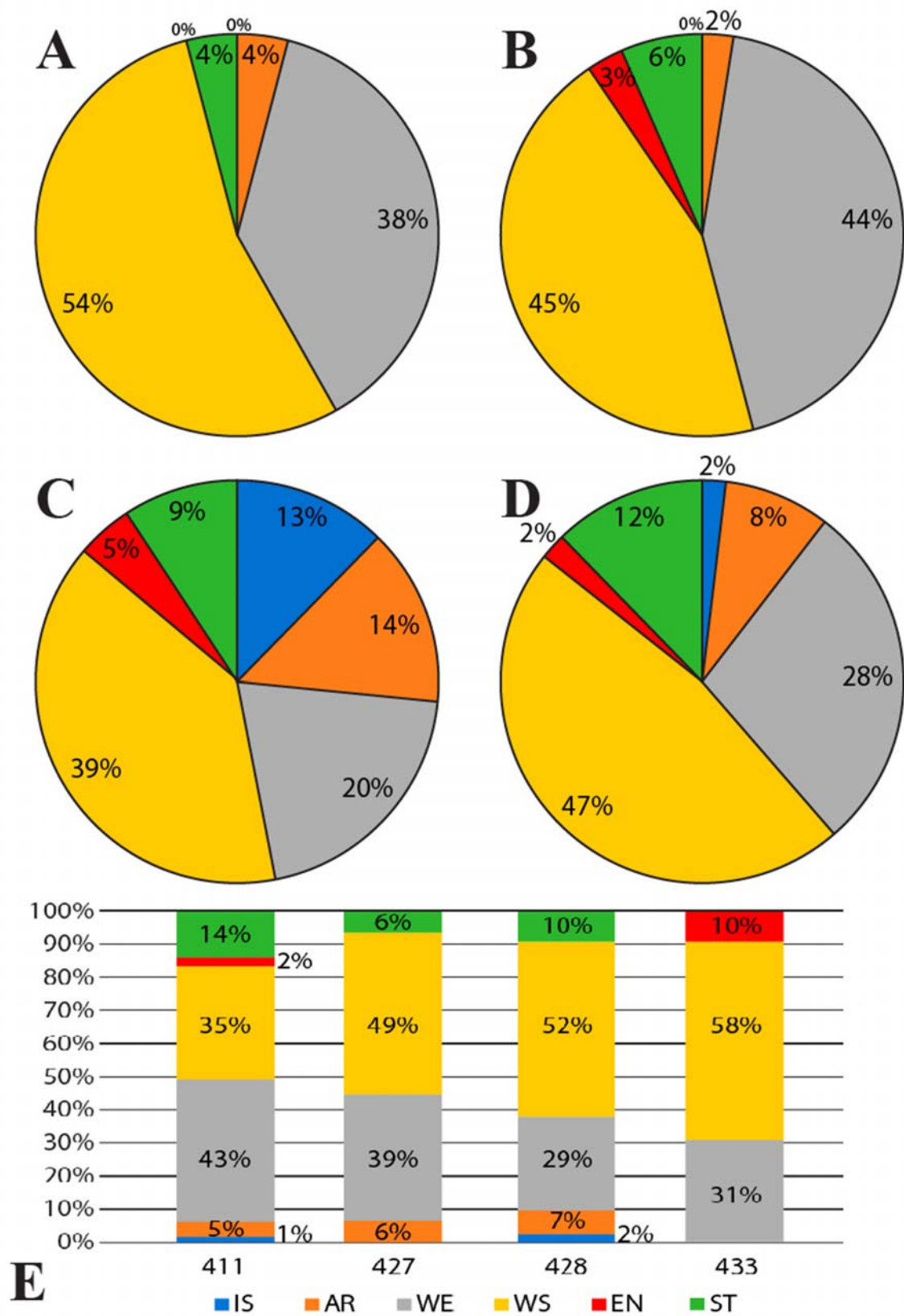


Fig. 5. Faunistic composition in two sub-regions: A — Taman, BP; B — Other Ciscaucasia, BP; C — Taman, PL; D — Other Ciscaucasia, PL; E — faunistic composition in four Ecoregions of Ciscaucasia according to Abell *et al.* [2008].

Рис. 5. Состав фауны двух субрегионов: А — Таманского, ВР; В — Остального Предкавказья, ВР; С — Тамань, РЛ; D — Остальное Предкавказье, РЛ; E — состав фауны в четырех экорегионах Предкавказья по Abell *et al.* [2008].

Table 7. Percentage distribution of records belonging to different faunistic complexes in the parts of Ecoregions according to Abell *et al.* [2008] falling into different sub-regions identified in this study (Taman / Other Ciscaucasia) and *p* values of Fisher's exact test to distinguish between distributions.

Таблица 7. Процентное распределение находок, принадлежащих фаунистическим комплексам в частях Экорегиионов по Абелю и др. (Abell *et al.* [2008]), попадающих в разные субрегионы, выделенные в этом исследовании (Тамань / Прочее Предкавказье), и значения *p* точного теста Фишера для различия распределений.

Ecoregions	411	427	428	433
IS	0 / 1	4 / 0	8 / 2	0 / 0
AR	0 / 4	16 / 6	5 / 7	10 / 0
WE	0 / 44	32 / 39	32 / 29	28 / 31
WS	0 / 35	48 / 49	51 / 52	44 / 58
EN	0 / 2	0 / 0	0 / 0	6 / 10
ST	0 / 14	0 / 6	5 / 10	12 / 0
Fisher's exact <i>p</i>	1.0000	0.1581	0.2680	0.0107

was previously demonstrated by us for several regions of the Far East of Eurasia [Kotov *et al.*, 2022; Krolenko *et al.*, 2023]. Moreover, even the specific zone (a potential hotspot) of biodiversity, and a possibly specific region in terms of the Cladocera zoogeography — Taman Peninsula and its vicinities — covers some portions of territories of three different Ecoregions (427, 428, 433). But please take into consideration that we did not study the Volga Delta, which is known as a source of specific cladoceran taxa, i.e. thermophilous species of a tropical origin [Smirnov, 1971].

Earlier Kotov [2016] proposed to subdivide all the cladoceran taxa of North East Asia into seven geographic faunistic complexes = “groups of species with similar, or sometimes different, recent geographic distributions, but with similar centers of differentiation and dispersion in the past” [Krolenko *et al.*, 2023]. Such subdivision was used for Far Eastern cladocerans, where only four complexes are found: widely distributed Eurasian (WE); East Asian + North American = “Beringian” (EAA); Far Eastern endemic (EA); southern tropical (ST), plus the aforementioned artificial group of widely distributed non-revised taxa (WS). This subdivision permits several interesting conclusions on the history of faunistic changes in the Far East during the Late Pleistocene [Garibian *et al.*, 2021; Kotov *et al.*, 2022; Krolenko *et al.*, 2023]. An important conclusion was made concerning a different age of the complex differentiation: if Boreal WE and EAA complexes were differentiated in Late Pleistocene, EA taxa have an old-Pre-Pleistocene origin, being geographic, and sometimes phylogenetic, relicts [Kotov *et al.*, 2021, 2022]. Unfortunately, the age of differentiation of ST is unknown to date. Just old endemic taxa monopolized the water bodies of the Far East and prevented penetration of the Boreal taxa south and tropical taxa north, preventing faunal mixing and shaping the Boreal/Tropical transitional zone. We expect to find such a zone in Europe also. But the set of faunistic complexes must be re-evaluated, i.e. because “Bering-

ian” (EAA) and endemic Far Eastern (EA) species are absent, while other faunistic elements are present there. In this article, we have made a first attempt to adapt the scheme of Kotov [2016] to European Boreal/Tropical transition zone.

The situation in Ciscaucasia is made more complicated by a recent anthropogenic influence on the water bodies, namely, intensive rice cropping in the region. Presumable eastern invaders (IS), *Diaphanosoma dubium* and *D. macrophthalma*, are associated just with the rice fields [Korovchinsky, 2018; Kotov *et al.*, 2022]. Moreover, just the Kuban is a region where some other freshwater alien species, first of all fishes, were introduced from East Asia due to improper human activity, i.e. during a deliberate introduction of the species “helpful” for aquaculture [Artaev *et al.*, 2021; Karabanov *et al.*, 2021; Makhrov *et al.*, 2023]. We found that possibly alien species from the genus *Diaphanosoma* make a significant portion from the records of planktonic cladocerans in the Taman-Kuban region. Presence of such IS species makes a zoogeographic analysis more complicated.

But we believe that our initial attempt to subdivide all the cladoceran taxa of the Ciscaucasian Region was relatively successful, although it was not reinforced by the phylogeographic studies to date. Referring to the East Asia as a possible analog of the Caucasian territory, we can hypothesize that the Ciscaucasian Region represents the northernmost portion of the transitional zone between Boreal (WE) and Tropical (ST) fauna. Behning [1941] correctly concluded that just Boreal taxa are predominant in the Ciscaucasia, while several Boreal taxa are already rare there and fully absent in more southern regions. At the same time, a contribution of the tropical (“subtropical” in Behning, [1941]) taxa (ST) to the Ciscaucasian fauna is minimal. The core of the Boreal/Tropical transitional zone is located south, probably in Transcaucasia, Turkey and the Mediterranean region; the latter is also a well-known zone of cladoceran endemism [Korovchinsky, 2006]. We can roughly hypothesize that this zone is very wide

latitudinally, similar to that in the Far East of Eurasia [Garibian *et al.*, 2021; Krolenko *et al.*, 2023].

Our provisional separation of an independent arid faunistic complex (AR) must be checked by new faunistic and phylogeographic studies. Previously such studies have demonstrated that the inhabitants of the “Arid Belt of Eurasia” are, at least partly, represented by the Pre-Pleistocene relicts [Kotov *et al.*, 2022; Hamza *et al.*, 2023]. Therefore, EN and AR could represent a single complex of old relicts shaping the transitional zone between Boreal and Tropical faunas. Such a situation is relatively similar to that in the Far East [Kotov *et al.*, 2022; Krolenko *et al.*, 2023], but an arid belt is absent in the latter region.

Why is the Taman Peninsula (and its vicinities) a specific region for microscopic crustaceans? This question could not immediately be answered, but recently some evidence of a specific status and a biogeographic role of this region and its surroundings are obtained for other groups of the freshwater invertebrates like unionid bivalves [Tomilova *et al.*, 2020] or nyphargid amphipods [Marin, Palatov, 2023]. Several authors suggested that an ancient glacial refugium existed in the Northern Black/Azov Sea Lowland [Lyubas *et al.*, 2023; Marin, Palatov, 2023], and such an idea agrees with our conclusion on a specific cladoceran fauna in this region. Moreover, the Taman Peninsula is located in front of the Crimean Peninsula, and the latter is also regarded as the hotspot of freshwater biodiversity [Birstein, 1961; Mamos *et al.*, 2016; Lantushenko *et al.*, 2022]. But note that to date no one local endemic species of cladocerans was found in Crimea. The Kerchinsky Strait, 4.5–15 km width, could be crossed by any water bird (carrying resting eggs of freshwater invertebrates on the feathers and in the food mass in the gut, see [Green, Figuerola, 2005; Viana *et al.*, 2016]) by a single non-stop flight. But, again, fauna of Crimea is inadequately studied, and our idea on a Crimean influence to Taman fauna is a hypothesis only.

To date we have no explanation for the difference between planktonic and benthic/littoral groups of taxa in their faunistic composition. While benthos/littoral of Taman (and its vicinity) and that of other Ciscaucasian territories is similar, the plankton of the former is specific: it contains a high proportion of the endemic (EN), “arid” (AR) and “eastern” (IS) taxa. At the same time, there is no evidence that the Taman region has a wider range of water body types as compared to other Ciscaucasia.

To date we cannot discuss the endemism hotspots of the Ciscaucasia and even Caucasus concerning the Cladocera, moreover, no one cladoceran taxon is regarded as an endemic of the Caucasus. It apparently reflects our poor knowledge on the cladocerans from this region rather than its mediocrity in part of the biogeographic affinities. All endemics species found here (EN) are endemics of the Mediterranean-Ponto-Caspian region rather than local endemics. Behning [1941: p. 77] reached the same conclusion more than

80 years ago, and the situation has not changed since that time. Our study is a next step towards understanding the regularities of cladoceran biodiversity in the region. We believe that our list is not final one, and such studies need to be continued.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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