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ZOOGEOGRAPHICAL FRESHWATER DIVISIONS OF THE CAUCASUS AS A PART OF THE WEST ASIAN TRANSITIONAL REGION

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ABSTRACT

The Caucasus, together with Anatolia, Mesopotamia, internal Iranian and Afghan drainages form a region of extremely high heterogeneity and transitional character between the "true" Holarctic, Sino-Indian and African regions *sensu* Berg (e.g. 1934, 1949). Its zoogeographical delineation is therefore of considerable interest. The goal of this study was to analyse zoogeographical affinities of the Caucasian ecoregions in terms of fish distribution and estimate the rank of the zoogeographical boundaries between the Caucasus and the drainages of north-eastern Europe (eastern Baltic, Dnieper, Don and Volga), and between the Caucasus and the Iranian basins. Based on a beta-diversity index and cluster analyses of lists of taxa (over 500) by the ecoregions, it is shown that faunas of the true freshwater fishes of the Caucasus displays a clear boundary with the eastern Europe, and that the ecoregions of the Ciscaucasia and the Transcaucasia exhibit striking dissimilarities from each other and from the Middle East basins. The Caucasus and neighbouring drainages of the southern coasts of the Black and Caspian seas are merged into the Caucasian Province which is included into the West Asian Transitional Region *sensu* Bănărescu (1991). The results also support delineation of six zoogeographical subdivisions, defined as districts of the Caucasian Province, namely, the West Ciscaucasian District, West Transcaucasian District, East Ciscaucasian District, East Transcaucasian District, the North Anatolian District, and Urmia District.

Key words: biogeography, Caucasian Province, distribution, ecoregions, freshwater fishes, palaeohydrography, West Asian Transitional Region

ЗООГЕОГРАФИЧЕСКИЕ ПРЕСНОВОДНЫЕ РЕГИОНЫ КАВКАЗА КАК ЧАСТЬ ЗАПАДНОАЗИАТСКОЙ ПЕРЕХОДНОЙ ОБЛАСТИ

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РЕЗЮМЕ

Кавказ вместе с Анатолией, Месопотамией и внутренними бассейнами Ирана и Афганистана образует чрезвычайно гетерогенный выдел переходного характера между Голарктикой, Сино-индийской и Африканской областями в понимании Берга (1934, 1949). Таким образом, зоогеографическое районирование Кавказа вызывает значительный интерес. Целью данной работы было проанализировать зоогеографические отношения кавказских экорегионов на основании распространения рыб и оценить ранг границ между Кавказом и лежащими к северу палеарктическими бассейнами, с одной стороны, и между Кавказом и внутренними иранскими бассейнами, с другой. На основании индексов сходства и кластерного анализа списков таксонов бесчелюстных и рыб (более 500) показано, что фауны истинно-пресноводных речных рыб Кавказа демонстрируют выраженную границу с севера, а экорегионы Предкавказья и Закавказья обнаруживают резкие отличия как друг от друга, так и от лежащих к югу Малой Азии и Среднего Востока. Предложено выделить Кавказскую провинцию, объединяющую Кавказ и прилежащие речные бассейны южных берегов

Черного и Каспийского морей, и отнести ее к Западноазиатской переходной области в понимании Бэнэреску (Bănărescu 1991). Результаты подтверждают выделение шести зоогеографических округов в пределах предлагаемой Кавказской провинции: Западнопредкавказского, Западнозакавказского, Восточнопредкавказского, Восточнозакавказского, Североанатолийского и Урмийского.

Ключевые слова: биогеография, Кавказская провинция, распространение, экорегионы, пресноводные рыбы, палеогидрография, Западноазиатская переходная область

INTRODUCTION

The topography of the Caucasus comprises the Greater Caucasus Range (with the highest peak being Mountain Elbrus at 5.642 m), the Lesser Caucasus Mountain Chain (to 4.000 m), the South Caucasian Uplands (covering parts of Asia Minor, Armenian, and Iranian uplands), and the Transcaucasian Depression, between the Greater Caucasus Range and the Lesser Caucasus Mountain Chain. The northern boundary of the Caucasus as a geographical unit is distinct and corresponds with the historical boundary along the Kumo-Manych downfold. The broad North Caucasus Plain lies in the north, the eastern part of which is below sea level. The main ridge is oriented in a nearly east-west direction and practically closes the space between the Black and the Caspian seas, dividing the Caucasus into two main geographical areas commonly called Ciscaucasia and Transcaucasia. The system of rivers flowing north and south are formed respectively, and, in their turn, have within them water drainages of the western and the eastern parts of Ciscaucasia and Transcaucasia.

The global scheme of zoogeographical regions has been changing since it was first proposed by Wallace (1876). In most zoogeographical classification the Caucasus lies within the Palaearctic or the Eurasian region (e.g. Wallace 1986; Darlington 1957; Cox 2001), or the Holarctic if the Palaearctic and the Nearctic are combined. Differently, Smith (1983), based on the occurrences of mammal families, considerably shifted the south-western border of the Palaearctic. He included the whole circum-Mediterranean area and south-west Asia overlapping the Caucasus and the Middle East, into the Afro-Tethyan Region. According to Kreft and Jetz (2010), the mammal species-level boundary between Africa *sensu lato* and the Palaearctic goes along the main Caucasian Range while on the family and genera levels the Palaearctic does include the Caucasus and Asia Minor.

Berg (1932, 1934, 1940, 1949) developed a scheme of zoogeographical regionalisation of the Palaearctic based on distribution of freshwater fishes, where the Palaearctic was considered as an informal term overlapping four zoogeographical units – a part of Holarctic and three transitional regions, Mesopotamian, Syrian, and Manchurian. In this scheme, the Caucasian fresh waters lie within the Mediterranean Subregion ("Der mediterranen Subregion" in Berg (1932)) of the Holarctic Region and encompass parts of the Ponto-Caspian-Aral Province ("Die Ponto-Kaspi-Aralische Provinz" in Berg (1932)) in the Black Sea District ("Der Schwarzmeer-Distrikt" in Berg (1932)) and the Caspian District ("Der kaspische Distrikt" in Berg (1932)), neighbouring the Fore-Asian, Mesopotamian, and Iranian provinces (Fig. 1A). Thus, the most high-rank zoogeographical border in the area under consideration, according to Berg, is that one between the provinces, separating drainages of the Black and Caspian seas from endorheic basins of Asia Minor and Iran. The Black Sea District is subdivided, in its turn, into the Northern Aegean, Danubian-Kubanian, and Colchis-Anatolian subdistricts, the two latter ones partly covering the western Caucasus area. The Caspian District is subdivided into the Volga and Kura-Persian subdistricts, partly encompassing the eastern Caucasus area as seen in the maps in Berg (1932, 1934, 1949).

Bănărescu (1960, 1991) emphasised the specific zoogeographical nature of the area and delimited a single transitional region, the West Asian Transitional Area, thus widening Berg's transitional Mesopotamian and Syrian regions to include southern Anatolia, entire Near East, central and southern Iran, and parts of Afghanistan. Bănărescu (1991) did not include the Caucasus (rivers belonging to the Black Sea and Caspian Sea basins) into his West Asian Transitional Area though he did not specifically discuss the matter.

Starobogatov (1970) based on mollusc distribution, included the whole Caucasian region into his

Euro-Siberian Subregion. A new scheme of biogeographical delineation of the Eurasian fresh waters was recently published based on the macrobenthic faunas – insects of the orders Ephemeroptera, Odonata, Plecoptera, Hemiptera, Coleoptera and Trichoptera, and Malacostraca, Gastropoda and Bivalvia (Chertoprud 2010). It differs from the Starobogatov's scheme mainly by a higher rank of the border between the Japanese and Amur faunas, and emphasising the affinity of the both to the Palaearctic rather than Oriental Region. Important is the separation of Western Asia and Middle East from the European-Siberian Region.

A new map depicting the global biogeographical regionalisation of Earth's freshwater systems was published (Abell et al. 2008); this map of freshwater ecoregions is based on the distributions and compositions of freshwater fish species and incorporates major ecological and evolutionary patterns. The European and Middle East ecoregions include, among others, Western Caspian Drainages (Abell et al. 2008: ecoregion 411), Kuban' (ecoregion 428), Northern Anatolia (ecoregion 430), Western Transcaucasia (ecoregion 433), Kura-South Caspian Drainages (ecoregion 434), Orumiyeh (ecoregion 445). A logical and practical extension of the delineations was the compilation of fish species lists for each ecoregion. Information on the ecoregions of the former USSR and adjacent countries, including those in the Caucasus and neighbouring areas, are presented in the Internet (available at www.feow.org) and in a separate paper (Naseka and Bogutskaya 2007). In this paper, a species/genera/family presence/absence matrix was compiled for a hierarchy of hydrographic units, and cluster analysis and ordination techniques (Primer v.6 statistics software) were employed to assess biotic similarities among hydrographic units and to identify major faunal breaks.

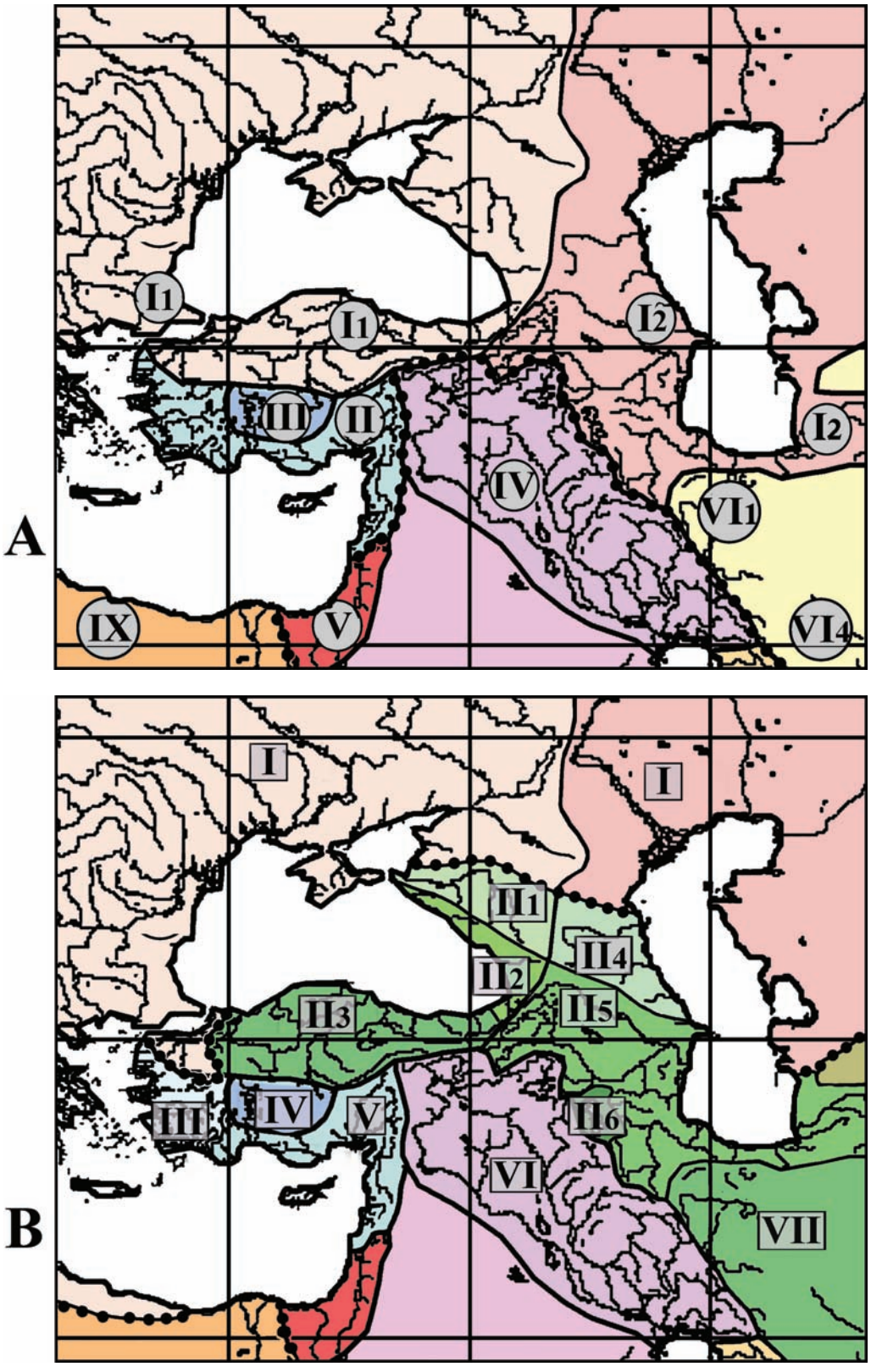
The main goal of this study was to analyse zoogeographical affinities of the Caucasian ecoregions based of fish distribution, delineated in the previous papers (Naseka and Bogutskaya 2007; Abell et al. 2008).

MATERIAL AND METHODS

Recent revisions or summarising publication on different taxonomic groups of Palaearctic fishes were used for taxonomic assignment used in the list of taxa in consideration (e.g. Perdices et al. 2003; Bogutskaya and Naseka 2004; Naseka et al. 2005; Boldyrev and Bogutskaya 2007; Kottelat and Freyhof 2007; Neilsen and Stepien 2009; Bogutskaya and Coad 2009; Prokofiev 2009; my unpublished data).

Geographical distribution of taxa (presence/absence data by drainage basin) – from family to subspecies or Evolutionary Significant Unit (ESU)/Operational Significant Unit (OSU) – from the eastern Baltic basin, Black Sea and Caspian Sea basins, and adjacent areas of Turkey and Iran were analysed. Methodology of the use of ESU and OSU was discussed in an earlier paper (Naseka and Bogutskaya 2007). The principal sources for these data are material deposited at the Zoological Institute of the Russian Academy of Sciences (Saint Petersburg), in Kalmyk State University (Elista), Sochi National Park (Sochi), Natural History Museum (Vienna), Zoological Institute and Museum of Hamburg University, Canadian Museum of Nature (Ottawa) collections, uncatalogued collections and observations from a number of expeditions to the drainage areas of the Kuban' (2001, 2006), West Transcaucasia (2001, 2006–2008), East Transcaucasia (2007, 2008), to the Lower Don and Lower Volga (2002), Northern Azov region and the Crimea (2002, 2003), East Ciscaucasia (2004, 2008), and critically analysed data from extensive existing literature (e.g. Aleksandrov 1927; Barach 1941; Abdurakhmanov 1962; Elanidze 1983; Emtyl' 1997; Emtyl' and Ivanenko 2002; Kottelat and Freyhof 2007; Coad 2010).

To assess biotic similarities among hydrographic units and to identify major faunal breaks, geographical distribution of native (indigenous) taxa was employed based on standard presence-absence data by ecoregions using agglomerative hierarchical cluster analyses (UPGMS [group average]). The beta-sim index (β_{sim}) (measure of co-occurrence or distance coefficient) were used which fulfils the species richness independence criterion (Kreft and Jetz 2010). The β_{sim} is defined as $1-a / [\min(b, c)+a]$, where a is the number of species present in both zoogeographical units compared (shared species), and b and c are the numbers of species unique to each of the two zoogeographical units; it varies between 0 (low dissimilarity, identical species lists) and 1 (high dissimilarity, no shared species) (Kreft and Jetz 2010). This coefficient is the same as the one used by Chertoprud (2010) if substracted from 1 [$1- \beta_{sim} = a / S_{min}$, where a is the number of shared species and S_{min}


A
I1
I1
I2
III
II
I2
IV
VI1
IX
V
VI4
B
I
I
III1
II4
II2
II5
II3
III
IV
V
II6
VI
VII

is the number of species in the less numerous fauna among two compared]. Calculations of the indices were done with StatistiXL 1.80 (*www.statistixl.com*) and PRIMER 6 (Clarke and Gorley 2006) software. PRIMER 6 was also used for evaluation of taxonomic dissimilarity based on Gamma*, a measure based on a natural extension of Bray-Curtis dissimilarity on presence/absence data, i.e. the complement of Sørensen S_8 (Clarke and Gorley 2006); Gamma* is (to within a constant) the Taxonomic Distance (TD) of Izsak and Price (2001). For the clustering of regions (PRIMER 6), the group average (UPGMA) method was used for it is an agglomerative hierarchical clustering having consistently the best performance (Kreft and Jetz 2010).

RESULTS

The list of native taxa includes 508 taxa (from family to ESU/OSU level) from the following river drainages and lake basins: eastern Baltic Sea basin (from Zapadnaya Dvina to Neva); Dnieper and South Bug; Don and other rivers of the Sea of Azov (Molochnaya, Berda, Obitochnaya, Kalmius, Mius); Kuban'; Volga, Ural, Emba; Kuma, Terek, Sulak, Samur, rivers in Azerbajdjan to the north of the Main Caucasus Ridge Sumgait [Sumqayitcay] River inclusive; rivers of the Black Sea coast in Russia from Sukko rivulet (north of Novorossiysk) in the north, Mzymta, Psou; Bzyb', Kodori, Inguri, Rioni, lakes Abrau and Paliastomi; Coruh, Yesil Irmak, Kizil Irmak, Sakarya; Tuz, Beysehir and Aksehir lake basins; Aksu, Göksu, Seyhan, and Ceyhan rivers, lakes Egridir and Burdur; Lake Sevan, Kura-Aras drainage; Safid River [Sefid Rud]; Lake Van; Lake Urmia [Orumiyeh=Reza'iyeh] and other Iranian endorheic basins. Data for separate drainage basins are compiled mainly according to the ecoregions (zoogeographical divisions) revealed earlier (Abell et al. 2008) with few exceptions as explained below).

Description of ecoregions

West Ciscaucasia (428 Kuban' Ecoregion in Abell et al. 2008: 409). The area includes only one river drainage, River Kuban' with major tributaries the Laba, Belaya, Teberda, Bolshoy Zelenchuk, and Malyy Zelenchuk rivers. The Greater Caucasus Mountain Range dominates the eastern side of the ecoregion with elevations rising over 4800 m. In total, 58 native species/ESU/OSU historically occurred in the Kuban' (deltaic limans exclusive) belonging to 47 genera of 15 families. Eleven species and ESU/OSU are endemic for the Kuban': *Alburnoides kubanicus* Berg, 1932, *Barbus kubanicus* Berg, 1912, *Chondrostoma kubanicum* Berg, 1914, *Eudontomyzon* cf. *mariae, Gobio kubanicus* Vasil'eva et Vasil'ev, 2004, *Romanogobio parvus* Naseka et Freyhof, 2004, *R. pentatrichus* Naseka et Bogutskaya, 1998, *Squalius aphipsi* (Aleksandrov, 1927), *Sabanejewia kubanica* Vasil'eva et Vasil'ev, 1988, *Phoxinus* sp., *Ponticola* cf. *constructor*.

East Ciscaucasia (411 Western Caspian Drainages Ecoregion in Abell et al. 2008: 409). The area includes rivers of the Caspian basin from Kuma in the north down to Sumqayitcay and some alpine lakes of the Great Caucasus. In the north, the Chornyye Zemly Desert, isolated lakes and marshes lie adjacent to the Kuma River drainage. This area also includes the Vostochnyy Manych River, which is now a partly dried and isolated drainage connected in its upper section with the Kalaus River (part of the Don River drainage). The main rivers are Kuma, Terek with tributaries Gizeldon, Ardon, Urukh, Malka, Argun' and Sunzha, Sulak formed from the confluence of the rivers Avarskoye Koisu and Andiyskoye Koisu, and Samur. The area also includes a number of mountainous lakes, e.g. Lake Kezenoi-Am which is 426 m deep. There are 52 native species/ESU/OSU in the region belonging to 41 genera of 14 families; nine of them are endemic: *Alburnoides gmelini* Bogutskaya et Coad, 2009, *Barbatula barbatula caucasica* (Berg, 1898),

Fig. 1. Scheme of zoogeographic delineation of: A, south-western Holarctic Region and neighbouring regions, from Berg (1940: fig. 20). *Holarctic Region*: Mediterranean Subregion: I–Ponto–Caspian–Aral Province: I_1–Black Sea District, I_2–Caspian District; II–Mediterranean Province; III–Central Anatolian Province; VI–Iranian Province: VI_1–Teheran District, VI_4–Fars District. *Mesopotamian Transitional Region*: IV–Mesopotamian Province. *Syrian Transitional Region*: V–Syrian Province. *African Region*: IX; B, same territory, new zoogeographical regionalisation: *Holarctic Region*: I–Ponto–Caspian Province. *West Asian Transitional Region*: II–Caucasian Province: II_1–West Ciscaucasian District, II_2–West Transcaucasian District, II_3–North Anatolian District, II_4–East Ciscaucasian District, II_5–East Transcaucasian District, II_6–Urmia District; III–West Anatolian Province; IV–Central Anatolian Province; V–South Anatolian Province; VI–Mesopotamian Province; VII–Iranian Endorheic Province.

Table 1. Degree of endemism of species/ESU/OTU in Caucasian ecoregions, North Anatolia, Urmia Lake and Iranian endorheic basins. Numbers of ecological groups as in the text and Table 2.

	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia Lake	Iranian endorheic basins
Native freshwater, brackish water, euryhaline, and migratory fishes (groups 1–10)							
Number of species/ESU/OTU	58	63	67	52	73	13	40 (up to 44)
Endemic	19%	29%	16%	17%	37%	54%	32.5% (up to 39%)
True freshwater fishes (groups 1, 4 and 5)							
Number of species/ESU/OSU	26	26	21	18	38	12	39 (up to 43)
Endemic	38%	60%	57%	39%	68%	58%	33% (up to 39%)

Barbus ciscaucasicus Kessler, 1877, *Chondrostoma oxyrhynchum* Kessler, 1877, *Gobio holurus* Fowler, 1976, *Ponticola* cf. *cyrius* (as *Neogobius constructor* or 'Caucasian river goby' in literature), *Romanogobio ciscaucasicus* (Berg, 1932), *Sabanejewia caucasica* (Berg, 1906), *Salmo ezenami* Berg, 1948.

West Transcaucasia (433 Western Transcaucasia Ecoregion in Abell et al. 2008: 409). The area includes river drainage areas and lakes of the Black Sea coast in Russia, Georgia, and Turkey from the Sukko rivulet (north of Novorossiysk) to the Yesil Irmak River basin. The primary waterbodies in the ecoregion include lakes Abrau and Paliastomi, and the Mzymta, Psou, Bzyb', Kodori, Inguri, Rioni, Coruh, Yanbolu Dere, and Melet Irmari rivers. In total, 63 native species and subspecies/ESU/OSU historically occurred in the West Transcaucasia (including some doubtful records) belonging to 45 genera of 17 families. The largest number of species/ESU/OSU, 49, occurs in the Rioni. In rivers of the Black Sea coast in Russia (the Psou inclusive), there are 41 species/ESU/OSU. Eighteen species/ESU/OSU from 63 occurring in the whole region are endemic for it: *Alosa tanaica palaeostomi* (Sadovsky, 1934), *Barbus artvinicus* Kamensky, 1899, *B. rionicus* Kamensky, 1899, *Capoeta banarescui* Turan, Kottelat, Ekmekci et Imamoglu, 2006, *C. ekmekciae* Turan, Kottelat, Kirankaya et Engin, 2006, *Chondrostoma colchicum* Derjugin, 1899, *Clupeonella abrau* (Maliatsky, 1928), *Cobitis satunini* Gladkov, 1935 (the range is not clear, may be also distributed in North Anatolia), *Lampetra lanceolata* Kux et Steiner, 1872 (the range is not clear, may be also distributed in North Anatolia), *Lethenteron ninae* Naseka, Tuniyev et Renaud, 2009, *Phoxinus colchicus* Berg, 1910 (the range is not clear, may be also distributed in North Anatolia), *Ponticola constructor* (Nordmann, 1840), *P. rizensis* (Kovačić et Engin, 2008), *P. rhodioni* (Vasil'eva et Vasil'ev, 1994), *P. turani* (Kovačić et Engin, 2008), *Rhodeus colchicus* Bogutskaya et Komlev, 2001, *Salmo coruhensis* Turan, Kottelat et Engin, 2010, *S. rizensis* Turan, Kottelat et Engin, 2010.

North Anatolia (430 Northern Anatolia Ecoregion in Abell et al. 2008: 409), a region which comprises the drainages of north-central and western Anatolian Turkey, from the Sakarya basin in the west to the Kizil and Kelkit basins in the east. Sakarya, Kizil Irmak, Kelkit, and Yesil Irmak rivers are the largest rivers wholly within Anatolia/Turkey. The region contains about 67 species/ESU/OSU belonging to 50 genera from 20 families (distribution of same taxa, e.g. *C. satunini, L. lanceolata, R. colchicus* need

Table 2. List of taxa of *true freshwater fishes* by ecoregions used for the biogeographical analysis. ? – presence needs confirmation; +? – species identification doubtful.

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
PETROMYZONTIDAE	+	+	+	+	+	+					
***Eudontomyzon* Regan, 1911**		+	+		+	+					
Eudontomyzon mariae (Berg, 1931)		+	+								
Eudontomyzon cf. *mariae*					+						
***Lampetra* Bonnaterre, 1788**	+			+							
Lampetra lanceolata Kux et Steiner, 1972						+					
Lampetra planeri (Bloch, 1784)	+			+							
***Lethenteron* Creaser et Hubbs, 1922**						+					
Lethenteron ninae Naseka, Tuniyev et Renaud, 2009						+					
CLUPEIDAE				+							
***Clupeonella* Kessler, 1877**				+							
Clupeonella tscharchalensis (Borodin, 1896)				+							
CYPRINIDAE	+	+	+	+	+	+	+	+	+	+	+
ACHEILOGNATHINAE	+	+	+	+		+	+		+		
***Rhodeus* Agassiz, 1832**	+	+	+	+		+	+		+		
Rhodeus amarus (Bloch, 1782)	+	+	+	+							
Rhodeus colchicus Bogutskaya et Komlev, 2001						+	+?				
Rhodeus sp. 1									+		
BARBINAE	+	+		+	+	+	+	+	+	+	+
***Barbus* Cuvier, 1816**	+	+			+	+	+	+	+	+	+
Barbus artvinicus Kamensky, 1899						+					
Barbus barbus (Linnaeus, 1758)	+	+									
Barbus ciscaucasicus Kessler, 1877								+			
Barbus cyri De Filippi, 1865									+	+	
Barbus escherichii Steindachner, 1897							+				
Barbus goktschaicus Kessler, 1877									+		
Barbus kubanicus Berg, 1912					+						
Barbus cf. *lacerta*											+

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Barbus rionicus Kamensky, 1899						+					
***Capoeta* Valenciennes, 1842**						+	+		+	+	+
Capoeta aculeata (Valenciennes, 1844)											+
Capoeta baliki Turan, Kottelat, Ekmekci et Imamoglu, 2006							+				
Capoeta banarescui Turan, Kottelat, Ekmekci et Imamoglu, 2006						+					
Capoeta buhsei Kessler, 1877											+
Capoeta capoeta (Gueldenstaedt, 1773)									+	+	+
Capoeta damascina (Valenciennes, 1842)											+
Capoeta ekmekciae Turan, Kottelat, Kirankaya et Engin, 2006						+					
Capoeta fusca Nikolskii, 1897											+
Capoeta sevangi De Filippi, 1865									+		
Capoeta sieboldii (Steindachner, 1864)						+	+				
***Carasobarbus* Karaman, 1971**											+
Carasobarbus luteus (Heckel, 1843)											+
***Luciobarbus* Heckel, 1843**				+					+	+	+
Luciobarbus barbulus (Heckel, 1849)											+
Luciobarbus mursa (Gueldenstaedt, 1773)									+	+	+
Luciobarbus pectoralis (Heckel, 1843)											+
CYPRININAE	+	+	+	+	+	+	+	+	+		+
***Carassius* Jarocki, 1822**	+	+	+	+	+	+	?	+			
Carassius carassius (Linnaeus, 1758)	+	+	+	+	+	+	?	+			
***Cyprinion* Heckel, 1843**											+
Cyprinion milesi (Day, 1880)											+
Cyprinion tenuiradius Heckel, 1849											+
Cyprinion watsoni (Day, 1872)											+
***Garra* Hamilton, 1822**											+

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Garra persica Berg, 1913											+
Garra rossica (Nikolskii, 1900)											+
Garra rufa (Heckel, 1843)											+
GOBIONINAE	+	+	+	+	+	+	+	+	+	+	
***Gobio* Cuvier, 1816**	+	+	+	+	+	+	+	+			
Gobio brevicirris Fowler, 1976			+								
Gobio caucasicus Kamensky, 1901						+	+				
Gobio gobio (Linnaeus, 1758)	+	+									
Gobio holurus Fowler, 1976								+			
Gobio kubanicus Vasil'eva et Vasil'ev, 2004					+						
Gobio sarmaticus Berg, 1949		+									
Gobio volgensis Vasil'eva, Mendel, Vasil'ev, Lusk et Lusková, 2008	+			+							
***Romanogobio* Bănărescu, 1961**		+	+	+	+			+	+	+	
Romanogobio albipinnatus (Lukasch, 1933)				+							
Romanogobio belingi (Slastenenko, 1934)		+									
Romanogobio ciscaucasicus (Berg, 1932)								+			
Romanogobio macropterus (Kamensky, 1901)									+		
Romanogobio parvus Naseka et Freyhof, 2004					+						
Romanogobio pentatrichus Naseka et Bogutskaya, 1998					+						
Romanogobio persus (Günther, 1899)										+	
Romanogobio tanaiticus Naseka, 2001			+								
LEUCISCINAE	+	+	+	+	+	+	+	+	+	+	+
***Acanthalburnus* Berg, 1916**									+	+	
Acanthalburnus microlepis (De Filippi, 1863)									+		
Acanthalburnus urmianus (Günther, 1899)										+	
***Alburnoides* Jeitteles, 1861**	+	+	+	+	+	+	+	+	+	+	+

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Alburnoides bipunctatus (Bloch, 1782)	+										
Alburnoides eichwaldii (De Filippi, 1863)									+		
Alburnoides cf. *eichwaldii*									+		
Alburnoides fasciatus (Nordmann, 1840)						+	+				
Alburnoides gmelini Bogutskaya et Coad, 2009								+			
Alburnoides kubanicus Berg, 1932					+						
Alburnoides namaki Bogutskaya et Coad, 2009											+
Alburnoides petrubanarescui Bogutskaya et Coad, 2009										+	
Alburnoides qanati Coad et Bogutskaya, 2009											+
Alburnoides rossicus Berg, 1924		+	+	+							
Alburnoides sp. 1											+
***Alburnus* Rafinesque, 1820**	+	+	+	+	+	+	+	+	+	+	+
Alburnus alburnus (Linnaeus, 1758)	+	+	+	+	+						
Alburnus atropatenae Berg, 1925										+	
Alburnus escherichii Steindachner, 1897							+				
Alburnus filippii Kessler, 1877									+		
Alburnus hohenackeri Kessler, 1877								+	+		
Alburnus mossulensis Heckel, 1843											+
***Chondrostoma* Agassiz, 1832**	+	+	+	+	+	+	+	+	+		+
Chondrostoma angorense Elvira, 1987							+				
Chondrostoma colchicum Derjugin, 1899						+					
Chondrostoma cyri Kessler, 1877									+		
Chondrostoma kubanicum Berg, 1914					+						
Chondrostoma nasus (Linnaeus, 1758)	+	+									
Chondrostoma orientale Bianco et Bănărescu, 1982											+
Chondrostoma oxyrhynchum Kessler, 1877								+			
Chondrostoma regium (Heckel, 1843)											?
Chondrostoma variabile Jakovlev, 1870			+	+							

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
***Leucalburnus* Berg, 1916**									+		
Leucalburnus satunini (Berg, 1910)									+		
***Leucaspius* Heckel et Kner, 1858**	+	+	+	+	+			+	+		
Leucaspius delineatus (Heckel, 1843)	+	+	+	+	+			+	+		
Leucaspius delineatus caucasicus Coad, 1995									+		
***Leuciscus* Cuvier, 1816**	+	+	+	+							
Leuciscus danilewskii (Kessler, 1877)			+								
Leuciscus idus (Linnaeus, 1758)	+	+	+	+							
Leuciscus leuciscus (Linnaeus, 1758)	+	+	?	+							
***Petroleuciscus* Bogutskaya, 2002**		+	+		+	+	+			+	+
Petroleuciscus borysthenicus (Kessler, 1859)		+	+		+	+	+				
Petroleuciscus esfahani Coad et Bogutskaya, 2010											+
Petroleuciscus gaderanus (Günther, 1899)										+	
Petroleuciscus persidis (Coad, 1981)											+
Petroleuciscus ulanus (Günther, 1899)										+	
***Phoxinus* Rafinesque, 1820**	+	+	+	+	+	+	+				
Phoxinus colchicus Berg, 1910						+	+?				
Phoxinus phoxinus (Linnaeus, 1758)	+	+	+	+							
Phoxinus sp.					+						
***Rhynchocypris* Günther 1889**		+		+							
Rhynchocypris percnurus (Pallas, 1814)		+		+							
***Pseudophoxinus* Bleeker, 1860**									+		
Pseudophoxinus atropatenus (Derzhavin, 1937)									+		
Pseudophoxinus sojuchbulagi (Abdurakhmanov, 1950)									+		
***Rutilus* Rafinesque, 1820**	+	+	+	+	+	+	+	+	+		
Rutilus rutilus (Linnaeus, 1758)	+	+	+	+	+	+	+	+			
Rutilus rutilus schelkovnikovi Derzhavin, 1926									+		
***Squalius* Bonaparte, 1837**	+	+	+	+	+	+	+	+	+	+	+
Squalius aphipsi (Aleksandrov, 1927)					+						

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Squalius cephalus (Linnaeus, 1758)	+	+	+	+							
Squalius orientalis (Nordman, 1840)					+	+		+	+	+	+
Squalius pursakensis (Hankó, 1925)							+				
SCHIZOTHORACINAE											+
***Schizothorax* Heckel, 1838**											+
Schizothorax pelzami Kessler, 1870											+
TINCINAE	+	+	+	+	+	+	+	+	+		
***Tinca* Cuvier, 1816**	+	+	+	+	+	+	+	+	+		
Tinca tinca (Linnaeus, 1758)	+	+	+	+	+	+	+	+	+		
COBITIDAE	+	+	+	+	+	+	+	+	+		+
***Cobitis* Linnaeus, 1758**	+	+	+	+	+	+	+		+		+
Cobitis linea (Heckel, 1849)											+
Cobitis melanoleuca gladkovi Vasil'ev et Vasil'eva, 2008			+	+	+						
Cobitis satunini Gladkov, 1935						+	?				
Cobitis cf. *satunini*									+		
Cobitis simplicispina Hankó, 1925							+				
Cobitis splendens Erk'akan, Atalay-Ekmekçi et Nalbant, 1998							+				
Cobitis taenia Linnaeus, 1758	+	+	+	+							
Cobitis tanaitica Bacescu et Maier, 1969		+	+		+						
***Misgurnus* La Cepède, 1803**	+	+	+	+	+						
Misgurnus fossilis (Linnaeus, 1758)	+	+	+	+	+						
***Sabanejewia* Vladykov, 1929**		+	+	+	+			+	+		
Sabanejewia aurata (De Filippi, 1863)								?	+		
Sabanejewia cf. *aurata*											
Sabanejewia baltica Witkowski, 1994		+									
Sabanejewia cf. *bulgarica*			+								
Sabanejewia caspia (Eichwald, 1838)				+					+		

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Sabanejewia caucasica (Berg, 1906)								+	+		
Sabanejewia kubanica Vasil'eva et Vasil'ev, 1988					+						
NEMACHEILIDAE	+	+	+	+	+	+	+	+	+	+	+
***Barbatula* Linck, 1790**	+	+	+	+	+	+		+			
Barbatula barbatula (Linnaeus, 1758)	+	+	+	+	+						
Barbatula barbatula caucasica (Berg, 1898)								+			
***Oxynoemacheilus* Banarescu et Nalbant, 1966**					+		+	+	+	+	+
Oxynoemacheilus angorae (Steindachner, 1897)						+	+				
Oxynoemacheilus araxensis (Banarescu et Nalbant, 1978)									+		
Oxynoemacheilus banarescui (Delmastro, 1982)							+				
Oxynoemacheilus bergi (Gratzianov, 1907)									+		
Oxynoemacheilus bergianus (Derzhavin, 1934)									+		+
Oxynoemacheilus brandtii (Kessler, 1877)									+		
Oxynoemacheilus farsicus (Nalbant et Bianco, 1998)											+
Oxynoemacheilus lenkoranensis (Abdurakhamanov, 1962)									+	+	
Oxynoemacheilus merga (Krynicki, 1840)					+			+			
Oxynoemacheilus persus (Heckel, 1849)											+
***Paracobitis* Bleeker, 1863**									+		+
Paracobitis cyri (Berg, 1910)									+		
Paracobitis iranica Nalbant et Bianco, 1998											+
Paracobitis malapterura (Valenciennes, 1846)									+		
***Paraschistura* Prokofiev, 2009**											+
Paraschistura bampurensis (Nikolskii, 1900)											+
Paraschistura sargadensis (Nikolskii, 1900)											+
***Seminemacheilus* Banarescu et Nalbant, 1995**							+				+
Seminemacheilus lendlii (Hankó, 1925)							+				

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Seminemacheilus tongiorgii Nalbant et Bianco, 1998											+
SISORIDAE							+				
***Glyptothorax* Blyth, 1860**							+				
Glyptothorax sp.							+				
OSMERIDAE	+			+							
***Osmerus* Linnaeus, 1758**	+			+							
Osmerus eperlanus (Linnaeus, 1758)	+			+							
COREGONIDAE	+			+							
***Coregonus* Linnaeus, 1758**	+			+							
Coregonus maraenoides Polyakov, 1874	+										
Coregonus pallasii Valenciennes, 1848	+										
Coregonus vessicus Drjagin, 1933				+							
THYMALLIDAE	+			+							
***Thymallus* Cuvier, 1829**	+			+							
Thymallus thymallus (Linnaeus, 1758)	+			+							
SALMONIDAE	+			+		+		+	+	+	+
***Hucho* Günther, 1866**				+							
Hucho taimen (Pallas, 1773)				+							
***Salmo* Linnaeus, 1758**	+			+		+		+	+	+	+
Salmo aestivalis Fortunatov, 1926									+		
Salmo danilewskii Gul'elmi, 1888									+		
Salmo ezenami Berg, 1948								+			
Salmo gegarkuni Kessler, 1877									+		
Salmo ischchan Kessler, 1877									+		
Salmo rizenziz Turan, Kottelat et Engin, 2010						+					
Salmo sp. 1										+	
Salmo sp. 2											+

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
LOTIDAE	+	+	+	+					?		
***Lota* Oken, 1817**	+	+	+	+					?		
Lota lota (Linnaeus, 1758)	+	+	+	+					?		
CYPRINODONTIDAE							+				+
***Aphanius* Nardo, 1827**							+				+
Aphanius isfahanensis Hrbek, Keivany et Coad, 2006											+
Aphanius persicus (Jenkins, 1910)											+
Aphanius sophiae (Heckel, 1849)											+
MASTACEMBELIDAE											+
***Mastacembelus* Scopoli, 1777**											+
Mastacembelus mastacembelus (Banks et Solander, 1794)											+
COTTIDAE	+	+		+							
***Cottus* Linnaeus, 1758**	+	+		+							
Cottus koshewnikowi Gratzianov, 1907	+			+							
Cottus microstomus Heckel, 1837		+									
Cottus cf. *poecilopus*	+										
PERCIDAE	+	+	+	+	+	+	+	+	+		
***Gymnocephalus* Bloch, 1793**	+	+	+	+	+			+			
Gymnocephalus acerina (Gueldenstaedt, 1775)		+	+								
Gymnocephalus baloni Holcík et Hensel, 1974		+									
Gymnocephalus cernua (Linnaeus, 1758)	+	+	+	+	+			+			
***Perca* Linnaeus, 1758**	+	+	+	+	+	+	+	+	+		
Perca fluviatilis Linnaeus, 1758	+	+	+	+	+	+	+	+	+		
GOBIIDAE		+	+	+	+	+	+	+	+		
***Benthophilus* Eichwald, 1831**			+								
Benthophilus durrelli Boldyrev et Bogutskaya, 2004			+								
***Ponticola* Iljin, 1927**					+	+		+	+		

Table 2 (*continued*)

Taxa	Eastern Baltic	Dnieper and South Bug	Don	Volga	West Ciscaucasia	West Transcaucasia	North Anatolia	East Ciscaucasia	East Transcaucasia	Urmia	Endorheic Iran
	1	2	3	4	5	6	7	8	9	10	11
Ponticola constructor (Nordmann, 1840)						+					
Ponticola cf. *constructor*					+						
Ponticola cyrius (Kessler, 1874)									+		
Ponticola cf. *cyrius*								+			
Ponticola rhodioni (Vasil'eva et Vasil'ev, 1994)						+					
Ponticola rizensis (Kovačić et Engín, 2008)						+					
Ponticola turani (Kovačić et Engín 2008)						+					
***Proterorhinus* Smitt, 1899**		+	+	+	+	+	+				
Proterorhinus semilunaris (Heckel, 1837)		+									
Proterorhinus sp. 1						+	+				
Proterorhinus sp. 2			+		+						
CHANNIDAE											+
***Channa* Scopoli, 1777**											+
Channa gachua (Hamilton-Buchanan, 1822)											+

clarification; this species may be absent from North Anatolia); at least 11 of them are endemic: *Alburnus escherichii* Steindachner, 1897, *Aphanius villwocki* Hrbek et Wildekamp, 2003, *A. danfordii* (Boulenger, 1880), *Aphanius* cf. *danfordii*, *Chondrostoma angorense* Elvira, 1987, *Barbus escherichii* Steindachner, 1897, *Cobitis simplicispina* Hankó, 1925, *C. splendens* Erk'akan, Atalay-Ekmekçi et Nalbant, 1998, *Glyptothorax* sp., *Seminemacheilus lendlii* (Hankó, 1925), *Squalius pursakensis* (Hankó, 1925).

East Transcaucasia (434 Kura-South Caspian Drainages and 446 Caspian Highlands ecoregions in Abell et al. 2008: 409). In a zoogeographical sense, this name is applied to the Kura-Aras drainage, rivers of the Lenkoranskaya (Talyshskaya) lowland flowing from the slopes of the Talyshskiy [Talysh] Ridge, and rivers in the Lesser Caucasus. The main rivers in the region include the Kura with tributaries Araks [Aras, Araxes], Razdan [Zanga], Aragvi, Iori, Alazani, Chrami, Atstev [Akstafa], Arpa, then Vilyashchay, Lenkoran', and Safid Rud. The eastern border of this region (the border with the Hari Rud and Murghab, and the Amu Darya historical watershed in general) needs to be further investigated; it is tentatively accepted here that the East Transcaucasia extends further eastward to include the Atrek (450 Turan Plain Ecoregion in Abell et al. 2008: 409). The fish faunas of drainages from Kura to Safid are very close. Historically, 73 native species and subspecies/ESU/OSU belonging to 44 genera of 14 families have been reported in the region. Twenty-seven are endemic: *Acanthalburnus microlepis* (De Filippi, 1863), *Alburnoides eichwaldii* (De Filippi, 1863), *Alburnoides* cf. *eichwaldii* (from Safid Rud), *Alburnus filippii* Kessler, 1877, *Aspius aspius taeniatus* (Eichwald, 1831), *Barbus goktschaicus* Kessler, 1877, *Blicca bjoerkna transcaucasica* Berg,

1916, *Capoeta sevangi* De Filippi, 1865, *Chondrostoma cyri* Kessler, 1877, *Cobitis* cf. *satunini* (as *C. satunini* in literature; probably not the same species as *Cobitis satunini* from the Black Sea basin), *Leucalburnus satunini* (Berg, 1910), *Paracobitis cyri* (Berg, 1910), *P. malapterura* (Valenciennes, 1846), *Ponticola cyrius* (Kessler, 1874), *Pseudophoxinus atropatenus* (Derzhavin, 1937), *P. sojuchbulagi* (Abdurakhmanov, 1950), *Rhodeus* cf. *amarus, Romanogobio macropterus* (Kamensky, 1901), *Rutilus rutilus schelkovnikovi* Derzhavin, 1926, *Salmo ischchan* Kessler, 1877, *S. aestivalis* Fortunatov, 1926, *S. danilewskii* Gul'elmi, 1888, *S. gegarkuni* Kessler, 1877, *Oxynoemacheilus bergi* (Gratzianow, 1907), *O. bergianus* (Derzhavin, 1934), *O. brandtii* (Kessler, 1877), *O. lenkoranensis* (Abdurakhamanov, 1962).

Urmia [Orumiyeh] Lake (445 Orumiyeh Ecoregion in Abell et al. 2008: 409) basin is considered to be isolated from the Kura drainage since only relatively recently, in the post-glacial epoch. However, the fauna of the basin is comparatively poor and very peculiar, containing only 13 species and ESU/OSU in 12 genera from 4 families, Cyprinidae being the most numerous. Seven of them are endemic: *Acanthalburnus urmianus* (Günther, 1899), *Alburnoides petrubanarescui* Bogutskaya et Coad, 2009, *Alburnus atropatenae* Berg, 1925, *Petroleuciscus gaderanus* (Günther, 1899) [a questionable synonym of *P. ulanus*], *Petroleuciscus ulanus* (Günther, 1899), *Romanogobio persus* (Günther, 1899), *Salmo trutta* cf. *caspius*.

Iranian Endorheic Basins (447 Namak, 448 Kavir & Lut deserts, 449 Esfahan, 702 Helmand-Sistan ecoregions in Abell et al. 2008: 409) which are flanked by the Alborz [Elburz] Mountains to the north, the Zagros Mountains to the south-west and eastern part of the Plateau of Iran to the east include some major basins: Namak Lake basin, Dasht-e Kavir, Esfahan, Kor River, Sirjan, Lake Maharlu, Kereman Na'in, Dasht-e Lut, Hamun-e Jaz Murian. Many rivers and lakes are brackish and support a limited fauna. Terminal salt lakes are fishless (Coad 2010). The fishes of the region comprise 40 species/ESU/OSU in 21 genera belonging to seven families, mainly Balitoridae and Cyprinidae. Thirteen species are endemic for the region: *Alburnoides namaki* Bogutskaya et Coad, 2009, *A. qanati* Coad et Bogutskaya, 2009, *Alburnoides* sp. (Esfahan), *Aphanius isfahanensis* Hrbek, Keivanny et Coad, 2006, *A. persicus* (Jenkins, 1910), *A. sophiae* (Heckel, 1849), *Capoeta buhsei* Kessler, 1877, *Chondrostoma orientale* Bianco et Bănărescu, 1982, *Cyprinion tenuiradius* Heckel, 1849, *Oxynoemacheilus persus* (Heckel, 1849), *Paracobitis iranica* Nalbant et Bianco, 1998, *Petroleuciscus esfahani* Coad et Bogutskaya, 2010, *Salmo* cf. *caspius* (Namak). There are at least four taxa (local forms) still undescribed or non-re-established: *Chondrostoma* cf. *regium*, *Alburnus* cf. *mossulensis*, *Capoeta* cf. *damascina* 1 [available names *amir* Heckel, 1849, *niger* Heckel, 1849, *rostratus* Keyserling, 1861], *Capoeta* cf. *damascina* 2 [available name *Scaphiodon saadii* Heckel, 1849]. In general, northern endorheic basins, such as the Namak, demonstrate a larger number of species shared with the Caspian basin that those in the south, such as the Kor River, with clear affinities with drainages of the Persian Gulf and the Arabian Sea.

The relative numbers of endemic species and ESU/OSU are summarised in Table 1. As can be seen, the relative number of endemic forms within the Caucasian area is comparatively high, varying between 16 and 54%. In the Volga, Ural, and Emba drainage basins with their river deltas, there occurred at least 78 native species and subspecies/ESU/OSU in 54 genera belonging to 18 families; only two of them are endemic: *Romanogobio albipinnatus* (Lukasch, 1933) and *Coregonus vessicus* Dryagin, 1932. In the Don River drainage and neighbouring rivers of the Sea of Azov (Kuban' excusive), there are 66 native species/ESU/EOU in 50 genera of 15 families; endemic are *Benthophilus durrelli* Boldyrev et Bogutskaya, 2004, *Leuciscus danilewskii* (Kessler, 1877), *Gobio brevicirris* Fowler, 1976, and *Romanogobio tanaiticus* Naseka, 2001. Most genera and species belong to taxa widely distributed in drainages of both the Ponto-Caspian basin and basins of the North and Baltic seas and the Arctic basins.

Each of the Caucasian, Anatolian and Iranian regions is characterised by vertical zonation among the fish assemblages. Quite distinct are successive species assemblages: in high mountainous (alpine) sections the brook trout (riverine forms of *Salmo*) is the only species. In lower mountainous sections down to the foothill zone, other rheophilous species appear in addition to the trout (species of the genera *Squalius* Bonaparte, 1837, *Barbus* Cuvier, 1816, *Chondrostoma* Agassiz, 1832, *Alburnoides* Jeitteles, 1861). Downstream, in piedmont to lowland sections, species of the genera *Gobio* Cuvier, 1816, *Romanogobio* Bănărescu, 1961 and *Phoxinus* Rafinesque, 1820 often predominate. The lower reaches are mostly inhabited

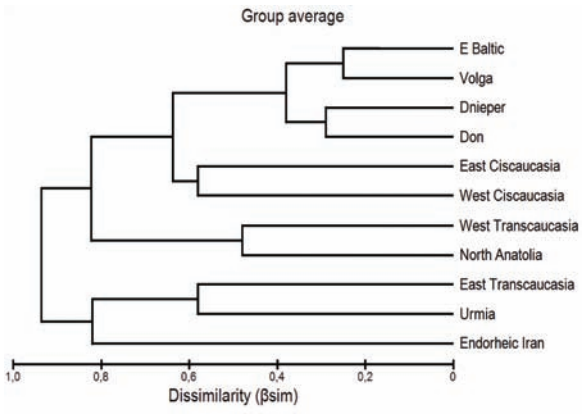


Fig. 2. Dendrogramme resulting from group average hierarchical clustering of fish assemblages by ecoregions based on β_{sim} dissimilarity matrix at the level of species.

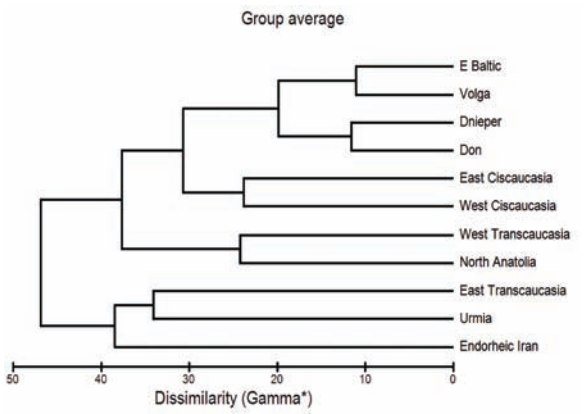


Fig. 3. Dendrogramme resulting from group average hierarchical clustering of fish assemblages by ecoregions based on Gamma* resemblance measure; weights: determined by taxon richness in master data (species 26,657, genus 52,319, family 65,654, order 100).

Table 3. β_{sim} (pairwise among ecoregions); 1 – Eastern Baltic (Zapadnaya Dvina to Neva), 2 – Dnieper and South Bug, 3 – Don and rivers of northern coast of Sea of Azov, 4 – Volga, Ural and Emba, 5 – West Ciscaucasia, 6 – West Transcaucasia, 7 – North Anatolia, 8 – East Ciscaucasia, 9 – East Transcaucasia, 10 – Urmia, 11 – Endorheic Iran. Only *true freshwater fishes* (groups 1, 4 and 5: Table 2; explanations in text) are included into analysis.

	1	2	3	4	5	6	7	8	9	10	11
1											
2	0.32										
3	0.47	0.29									
4	0.25	0.40	0.32								
5	0.65	0.58	0.57	0.62							
6	0.85	0.81	0.85	0.85	0.77						
7	0.86	0.81	0.86	0.86	0.81	0.48					
8	0.67	0.67	0.67	0.67	0.58	0.72	0.83				
9	0.89	0.90	0.89	0.87	0.85	0.88	0.90	0.67			
10	1.00	1.00	1.00	1.00	0.92	0.92	1.00	0.92	0.58		
11	1.00	1.00	1.00	1.00	0.96	0.96	1.00	0.94	0.89	0.75	

by phytophilous species, which are typical inhabitants of slow flowing rivers and stagnant waters.

The fish taxa inhabiting fresh and brackish waters under consideration can be classified using the combined terminology of Kessler (1877) and Myers (1938, 1949, 1951) in the following way (Naseka and Bogutskaya 2009) though some species can be defined in terms of this grouping only rather conventionally: 1. primary freshwater: freshwater (may be accidental in brackish water); 2. primary freshwater: semi-anadromous; 3. primary/secondary freshwater: anadromous; 4. secondary freshwater: freshwater; 5. primary marine: freshwater (= vicarious); 6. primary marine: brackish water; 7. primary marine: euryhaline (= sporadic); 8. primary marine: accidental; 9. primary marine: anadromous; 10. primary marine: catadromous. Exclusively (true) freshwater taxa are only those in the ecological groups 1, 4, and 5 (Table 2). These fishes occur in specific fluvial, often mountainous, habitats, cannot tolerate increased salinity, do not go into deltaic and coastal waters, and their dispersal through the lower reaches is thus hampered

and unlikely. Fishes of the groups 2, 3, and 6–10 include species of the genera *Caspiomyzon* Berg, 1906, all Acipenseridae, *Clupeonella* Kessler, 1877 [*C. tscharchalensis* (Borodin, 1896) exclusive], *Alosa* Linck, 1790, *Anguilla* Schrank, 1798, two species of *Luciobarbus* Heckel, 1843, species of the former genus *Chalcalburnus* Berg, 1933 (such as *Alburnus chalcoides* Güldenstädt, 1772 and *Alburnus leobergi* Freyhof et Kottelat, 2007), *Abramis brama* (Linnaeus, 1758), *Aspius aspius* (Linnaeus, 1758), *Blicca bjoerkna* (Linnaeus, 1758), *Leuciscus idus* (Linnaeus, 1758), *Rutilus rutilus heckelii* (Nordman, 1840), *Rutilus caspicus* (Yakovlev, 1879), species of the subgenus *Pararutilus* Berg, 1912 (*Rutilus frisii* (Nordman, 1840) and *Rutilus kutum* (Kamensky, 1901)), *Scardinius erythrophthalmus* (Linnaeus, 1758), *Pelecus cultratus* (Linnaeus, 1758), species of the genera *Ballerus* Heckel, 1843, *Vimba* Fitzinger, 1873, *Cyprinus* Linnaeus, 1758, *Babka* Iljin, 1927, *Benthophiloides* Beling et Iljin, 1927, *Caspiosoma* Iljin, 1927, *Knipowitschia* Iljin, 1927, *Mesogobius* Bleeker, 1874, *Neogobius* Iljin, 1927, *Pomatoschistus* Gill, 1863, *Percarina* Nordman, 1840, and *Sander* Oken, 1817, and some species of *Coregonus* Linnaeus, 1758, *Benthophilus* Eichwald, 1831, *Ponticola* Iljin, 1927 and *Proterorhinus* Smitt, 1900. The ecological conditions permitted species of these groups to have extensive ranges spreading through coastal sea waters that allowed genetic exchange. These taxa are not given in Table 2 and excluded from the discussion below.

Thus, in contrast to Berg (1934, 1940, 1949), in this paper the categories of anadromous, semi-anadromous, and euryhaline fishes are not used for the zoogeographical delineation of freshwater regions. If only exclusively freshwater species (ecological groups 1, 4, and 5 defined above, Table 2) are taken into account, it can be seen that the relative number of endemic taxa becomes much higher, varying between 38 and 68% in the Caucasian ecoregions (Table 1). These data support distinctness of these zoogeographical divisions at the species level. The Volga and Don contain 30 and 28 true freshwater taxa, the majority of which are very widely distributed Palaearctic ones (Table 2) with only 6% and 11% endemic, respectively. All the Caucasian ecoregions lack such widely distributed taxa of presumably northern origin as *Thymallus thymallus* (Linnaeus, 1758), two *Leuciscus* species, species of *Romanogobio albipinnatus* species-group, *Cottus gobio* species-group, and *Misgurnus fossilis* (Linnaeus, 1758).

Table 3 presents the β_{sim} dissimilarity matrix for fish assemblages by the ecoregions. The eastern Baltic, Dnieper with South Bug, Don with rivers of the northern coast of the Sea of Azov, Volga, Ural and Emba demonstrate relatively low indices (low dissimilarity) when compared to each other, from 0.25 to 0.47, while the β_{sim} indices are much higher for all pairwise comparisons of these ecoregions to any of the other basins. Distance between the Kuban' (Western Ciscaucasia) and adjacent Don and Volga are at the level of 0.57 and 0.42, respectively. The distance between the Eastern Ciscaucasia and the Volga is 0.67. It can be seen form Table 3 that all Caucasian ecoregions are highly dissimilar especially in the south from the Main Caucasian Ridge.

Dendrogrammes constructed based on the two approaches yielded remarkably similar topologies (Fig. 2, 3). A primary split occurred between a group consisting of assemblages of the East Transcaucasia, Urmia, and endorheic Iranian basins and a group of all other ecoregions. The latter deeply split into the West Transcaucasia+North Anatolia and the rest, which is further split into the Ciscaucasia and the northern ecoregions. The group average hierarchical clustering based on both the β_{sim} dissimilarity matrix and the Gamma* resemblance measure at the level of species revealed four major clusters relatively deeply separated.

The two Ciscaucasian divisions are closest to the Baltic-Don-Dnieper-Volga cluster due to, mostly, the presence (in Kuban') of *Eudontomyzon* Regan, 1911, and the absence of *Capoeta* Valenciennes, 1842 and the majority of nemachelids. The following genera are distributed in the Caucasus and further southwards being absent from the Volga and the Don: *Acanthalburnus* Berg, 1916, *Barbus, Capoeta, Glyptothorax* Blyth, 1860, *Leucalburnus* Berg, 1916, *Oxynoemacheilus* Bănărescu et Nalbant, 1966, *Paracobitis* Bleeker, 1863, *Pseudophoxinus* Bleeker, 1860, *Paraschistura* Prokofiev, 2009, and *Seminemacheilus* Bănărescu et Nalbant, 1995. The genera shared by these ecoregions and the Volga and Don are *Alburnoides, Alburnus, Barbatula* Linck, 1790, *Chondrostoma, Gobio*, *Petroleuciscus* Bogutskaya, 2002, *Romanogobio, Sabanejewia* Vladykov, 1929, and *Squalius*. The genera present in the Volga and/or Don but absent from the Caucasus are *Coregonus* Linnaeus, 1758, *Cottus* Linnaeus, 1758, *Hucho* Günther, 1866, *Leuciscus* Cuvier, 1816, *Osmerus* Linnaeus, 1758, and *Thymallus* Cuvier, 1829.

DISCUSSION

The data presented above on presence/absence of the taxa of different taxonomic rank belonging to three groups of true freshwater fishes provide a good support for a conclusion that the Caucasian drainages form a biogeographical division well separated from the areas located in the north. This conclusion is different from the opinion of Berg (1934, 1940, 1949), who divided the Caucasian area only meridionally, along to the border between the Black Sea and Caspian Sea watersheds. He merged the Kuban' with the Don, the Dnieper, the Dniester and the Danube into a single subdistrict, the Danubian-Kubanian, for he found no principal faunistic differences between these river drainages.

It may be supposed that Berg (1934, 1940, 1949) and later Bănărescu (1960, 1991) overestimated the significance of the presence of many widely spread Ponto-Caspian fishes in their evaluation of affinities between the Palaearctic zoogeographical units adjacent to the Black Sea and Caspian Sea basins. The almost circum-Pontic or circum-Caspian distribution of many diadromous and brackish water species tolerant to increased water salinity at least at some stages of their life cycle was made possible by the palaeohistory of the Ponto-Caspian basin. Miscellaneous geological data on the glacial history (summarised in e.g. Chochia and Evdokimov 1993) suggest that the recent distribution of the semi-anadromous and salinity-tolerant species is mostly the result of the Pleistocene events determined by connection of the lower reaches of the rivers as a consequence of strong regressions of the sea (e.g. Turkanian, Venedian, Chelekenian, Atelian) and the low salinity of coastal waters at river mouths and estuaries. It may be even concluded that the majority of Cyprinidae and Percidae most likely have foraged in the sea and spawned in estuaries and deltas of the Ponto-Caspian basin since Late Sarmatian time, i.e. 8.3–10 million years ago (MYA).

The other reason is the development of taxonomic concepts. For example, re-evaluation of taxonomic status of a number of Kubanian forms and description of new species dramatically changed the concept of the Kubanian (West Ciscaucasian) fish fauna. The West Ciscaucasia differs from the Don and adjacent drainages, i.e. from the most part of the Ponto-Caspian-Aral Province *sensu* Berg, by a high local endemism (38% of the true freshwater fluvial species), the absence of the genera *Cottus* and *Leuciscus,* and the presence of the Middle Eastern genus *Oxynoemacheilus* and a barb, *B. kubanicus,* which is deeply diverged from the *Barbus barbus* clade (Kotlik et al. 2004). *Barbus barbus* (Linnaeus, 1758) occurs in the Dnieper and further westward but is absent from Volga and Don. A similar argumentation supports the boundary between the East Ciscaucasia and the Volga drainage. The East Ciscaucasia is characterised by a high local endemism (39% of native true freshwater species), the absence of the genera *Cottus* and *Leuciscus,* the presence of the genera *Oxynoemacheilus* and an endemic barb, *B. ciscaucasicus,* which forms, together with *B. kubanicus*, a basal lineage for the Caucasian-Middle Eastern clade within the genus *Barbus* (Kotlik et al. 2004). There is no one species exclusively shared by the East Ciscaucasia and the Volga. This supports a hypothesis on a relatively ancient age of the Caucasian fish fauna and its origin from the southern branch of the Oligocene East Asian fauna – Internal Asian fauna *sensu* Sychevskaya (1986). The hypothesis can be further confirmed by data on a long geological history of the Caucasus summarised in a number of publications (e.g. Blazhniy 1954; Gorelov 1961, Safronov 1961, 1967, 1972; Gerasimov 1966; Zubakov 1974; Fedorov 1978; Svitoch 1991; Chochia and Evdokimov 1993; Rögl 1999; Reid and Orlova 2002; Popov et al. 2004, 2006). The fundamental reorganisation of the Tethyan Realm in the Cenozoic (Late Eocene) was caused by the African / Apulian / Arabian-Eurasian continent-continent collision starting during the Eocene. This resulted in the uplift and emergence of the evolving Alpine chains from the Pyrenees in the west to the Lesser Caucasus-Alborz Mountains-Kopetdagh island arcs in the east. With respect to palaeogeography, the collision resulted in the break-up of the Tethyan Realm (Early Oligocene, 34–37 MYA) into southern (circum-Mediterranean) and northern (Paratethyan) domains, as well as in their strong fragmentation and an increase in biogeographical differentiation in the course of time. A more complete isolation of the Paratethys in combination with moderately warm, humid climate conditions and episodes of a considerable regression of the sea took place in the Late Oligocene (29–24 MYA). During the Oligocene first cyprinids colonised Europe via the Russian Land in the north of the Turan Sea. In mid-Chokranian time (Early Middle Miocene 16–15 MYA) an unstable land bridge intermittently connected the Greater Caucasus Island with Anatolian

land and Africa. Since Late Middle Miocene (12–11 MYA) the Iranian and Anatolian land became connected. River drainages were formed flowing into the southern Eastern Paratethys. The Eastern European Platform was a lowland with many rivers flowing into the northern Eastern Paratethys.

As a result of expansion of elevations in the area of the Greater Caucasus, a large massif of insular land was formed. On this single Caucasian island an ancient river network began taking shape, its formation probably completed in the Miocene time for the earliest remains of freshwater animals discovered in the Caucasus are dated to the Miocene. In the Middle Miocene (8.5–7.0 MYA) the Caucasian island gradually rose and became a peninsula adjoining the Fore-Asian massif. The Caucasus had been a peninsula till the Latest Miocene 6.1–5.7 MYA. The Early Pontian basin was strongly enlarged, especially by transgression along its northern and eastern margins. A pronounced regression started at the beginning of the Late Pontian (Portaferrian and Babadzhanian), and the Ciscaucasian Strait was closed, connecting the Caucasus to the northern shore of the Euxinian-Caspian. The drastic regression during the Balakhanian was followed by a major (the largest one in the history of the Eastern Paratethys) transgression (Akchagylian, around 3.4–1.8 MYA) which resulted in a separation of the Caucasus from the northern land again. The Caspian and Euxinian basins had repeated interconnections through Pleistocene until, probably, as recently as Late Khvalynian.

The hydrographic network of the system of the Kuban' River and rivers of the East Ciscaucasia appeared as early as the Miocene, on the primary surface of the northern slope of the Caucasian ridge. They had a major longitudinal direction with deviation westwards and eastwards in the lower reaches of the rivers, in accordance with the submersion of the areas of the Kuban' and Tersky downfolds. Later, the western and eastern hydrographic nets gradually extended in conjunction with raising the uplands and with regression of the waterbodies that occupied both depressions. At that time, left-bank tributaries of the Kuban' River, the Laba, Belaya, and others fell into the shallow freshwater or brackish water basin, which existed in the north from the Caucasus Range as discussed above. In the Middle Quaternary time the elevation of the Stavropol Upland brought about a final draining of the land and an abrupt deviation of the Kuban' River south-westwards. Such a change in direction of the Kuban' River led to its connection with streams which are now its left-bank tributaries. The process of differentiation of water flows and their localisation in recent valleys in the lower reaches of the Kuban' and Terek was completed only in the Upper Quaternary. During all the periods mentioned, the Kuma-Manych Depression, dried or filled with water, was a distinct geographical frontier of the northern Caucasus.

The zoogeographical border which goes along the Kuma-Manych Depression was also revealed based on distribution of mammals (Smith 1983) and almost 9000 species of Eurasian invertebrates (Chertoprud 2010). In the latter paper, this border delimits the European-Ob' Subregion and the Western Asian Subregion (Chertoprud 2010). The Caucasus (unit number 12 in Chertoprud 2010: Fig. 4) is separated from Central and Eastern Europe and the Urals at the β_{sim} level of 0.58, 0.69 and 0.65, respectively (the indices re-calculated from Chertoprud 2010). This level of distances well coincides with 0.57–0.67 found in this study for the two Ciscaucasian ecoregions (Table 3). Chertoprud (2010) considers these values as representing 'striking separation' between areas, which are worth delineating at the level of subregion. He divides Palaearctic Region in a number of subregions, Western Asian Subregion inclusive. The latter one is divided into the Caucasian Province and the Asia Minor Province though their exact borders are not clearly depicted, and are not brought into correlation with river drainage basins. Therefore, the data of Chertoprud illustrate the biogeographical affinities of the Caucasus and the Euro-Siberian area. Results of the present paper based on fish distribution confirm a high rank boundary between the Caucasus and the rest of Palaearctic.

CONCLUSIONS

Thus, the comparison of dissimilarity indices and clustering supported by the data on palaeohistory, give reasons to conclude that the border between the Caucasus and the Volga and Don drainages deserves a high biogeographical rank. The Caucasus, as defined here (West Ciscaucasia+West Transcaucasia+East Ciscaucasia+East Transcaucasia), does not belong to the Ponto-Caspian-Aral Province *sensu* Berg. Indeed, it should be merged with the West Asian Transitional Area *sensu* Bănărescu (1991). For keeping a consistency of hierarchical zoogeographical units used by

Berg, I would suggest to name the transitional area as the West Asian Transitional Region (Fig. 1b). This further develops the ideas of Berg (1934, 1940) who recognised the Mesopotamian Transitional Region and the Syrian Transitional Region though the transitional region as defined here is much larger.

This interpretation cannot reflect the whole clustering pattern, which is the common case for transitional biogeographical zones (Vermeij 1991). As the cluster analysis revealed, the Caucasian ecoregions are highly dissimilar (Fig. 3, 4). β_{sim} indices vary between 0.58 and 0.88 (Table 3). Very deep dissimilarity is between the East Transcaucasia (the Kura being the main drainage) and the rest of the Caucasus. Very distinct are the West Ciscaucasia and the West Transcaucasia (β_{sim}=0.77). The North Anatolia and the Urmia Lake basin display some affinities to the West Transcaucasia and the East Transcaucasia, respectively. A pronounced specificity of the North Anatolia is the presence of the genera *Glyptothorax* (Sisoridae) and *Aphanius* (Cyprinodontidae), typical for basins further southwards. The β_{sim} at the level of 0.48 does not permit to merge the North Anatolia with the West Transcaucasia as it is done by Berg (1932, 1934, 1940, 1949) who included the whole eastern and southern coast of the Black Sea into the Colchis-Anatolian District. A departure from the Berg's scheme should be also done for the Urmia Lake basin, which is considered here as a distinct district because of its unique endemic fauna; it is not included into the East Transcaucasia (Fig. 1b).

The North Anatolia and the Urmia are combined here with the four Caucasian areas into the Caucasian Province of the West Asian Transitional Region. I further propose to give the West Ciscaucasia, West Transcaucasia, East Ciscaucasia, East Transcaucasia, North Anatolia and Urmia Lake, characterised by a similar degree of endemism, as defined above, an equal biogeographical rank, the rank of district in the Caucasian Province, namely, the West Ciscaucasian District, the West Transcaucasian District, the East Ciscaucasian District, the East Transcaucasian District, the North Anatolian District, and the Urmia District (Fig. 1b).

The difference of the Caucasian Province from the endorheic basins of Iran is very high. The same is probably true if the endorheic Iranian basins are compared with the Tigris-Euphrates drainage (Coad 2010). However, relationships within Iranian endorheic basins other than the Urmia need further study.

Though there can be no perfect biogeographical regionalisation that satisfies all aspects of historical and ecological biogeography (Kreft and Jetz 2010), the results of this study may be useful for interpretation of broad-scale fish distribution patterns in Europe and West Asia and contribute to the understanding of the biogeographical status of the Caucasian fish fauna.

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