

COXI based phylogenetic analysis of Caucasian clade of European *Troglocaris* (Crustacea: Decapoda: Atyidae) with the suggestion of a new taxonomic group structure

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New genetic data on Caucasian troglobiotic shrimps collected from the territory of Russia, Abkhazia and Western Georgia are presented. Based on new genetic data on the marker region of subunit I of cytochrome oxidase of mitochondrial DNA (COXI mtDNA) of Caucasian species and other taxa of European cave shrimps (*Troglocaris* s.l.) from GenBank (NCBI) database, a new generic structure is presented. Based on a significant genetic divergence of COXI mtDNA subgenera of *Troglocaris* s.l., namely *Troglocaris* s.s., *Xiphocaridinella* and *Spelaeocaris*, should be considered as separate genera while *Troglocaris* (*Troglocaridella*) *hercegovinensis* (Babić, 1922) is suggested to be transferred within Dinaric genus *Spelaeocaris* as *Speleocaris hercegovinensis* (Babić, 1922) comb. nov. Besides, *Troglocaris bosnica* shows a significant a genetic difference (at the level of the separate genus) from the remaining representatives of the genus *Troglocaris* s.s. Moreover, p-distances (COXI) of about 17% are supposed for generic separation within European *Troglocaris*-related atyid shrimps and 5% for separation of cryptic species within Caucasian *Xiphocaridinella*. A list of all known taxa of *Troglocaris*-related atyid shrimps of the European part and a discussion of the general distribution of troglobioid atyid shrimps in the Balkans and the Caucasus are presented. A new version of divergence events between Dinaric–Caucasian *Troglocaris* lineages (genera) based on new genetic data is suggested.

Keywords: phylogeny; COXI mtDNA; *Xiphocaridinella*; stygobiotic; stygobionts; shrimps; Caucasus

Introduction

Karst biocenoses due to their isolated location are especially rich in endemic species. It is very likely that each karst system has its own unique set of inhabiting species. One of the richest troglobiotic faunas in the world exists on the territory of the Southern Caucasus, followed by the cave and underground water fauna of the Balkan Peninsula. At the same time, the degree of study of the European hypogean communities obviously considerably exceeds that of the Caucasian ones. Troglobiotic higher crustaceans (Decapoda, Isopoda and Amphipoda) are the most important component of the hypogean cave ecosystems, sometimes forming them entirely. As a rule, in cave associations, crustaceans lead in number and diversity, forming the basis of the food pyramid of these communities. The relatively sparse data from the karst regions of the Caucasus indicate the extreme richness of the fauna of 37 troglobiotic crustaceans (about 50 endemic species in the Caucasus are known) (see review in Turbanov and Marin, 2015; Turbanov et al., 2016). At the moment, both the habitation of a larger number of species, and the wider distribution of this group in the Caucasus are assumed (e.g. Sadowsky, 1930; Birštein, 1939, 1948; Juzbašjan, 1940; Sendra and Reboleira, 2012; Marin and Sokolova, 2014; Marin, 2017; Turbanov et al., 2016). At the same time, subterranean fauna is characterized by a large number of endemics (local endemism), due to special ecological conditions and isolated location and low potential for dispersal (see Sket and Zakšek, 2009).

The European stygobiotic atyid shrimp genus *Troglocaris* Dormitzer, 1853 (Crustacea: Decapoda: Atyidae) is currently divided into 4 subgenera: *Spelaeocaris* Matjašić, 1956 (4 species), *Troglo-*

caridella Babić, 1922 (1 species), *Xiphocaridinella* Sadowsky, 1930 (6 species) and *Troglocaris* s. str. (4 valid species and 6 subspecies) (Zakšek et al., 2006, 2009; Sket and Zakšek, 2009; Marin and Sokolova, 2014; Marin and Turbanov, 2015; Marin 2017; Marin and Sinelnikov, 2017). The main morphological peculiarity which distinguishes *Troglocaris* from other European atyid shrimps, such as *Atyaephyra* de Brito Capello, 1867, *Dugastella* Bouvier, 1912, *Gallocaris* Sket et Zakšek, 2009 and *Typhlatya* Creaser, 1936 (Sket and Zakšek, 2009) is the length of the subapical and apical spines on the appendix masculina in males, which are significantly smaller than the diameter of the appendix masculina in all representatives of the genus *Troglocaris* (see key in Sket and Zakšek, 2009). At present, the division into subgenera does not satisfy modern morphological requirements, since most of the considered morphological features vary greatly even within the species of the same subgenus (see, for example, the length of the rostrum within the subgenus of *Xiphocaridinella* (see Marin, 2017)) and such division is mainly supported by geographical distribution.

Order Decapoda Latreille, 1802

Family Atyidae De Haan, 1849

Subfamily Typhlatyinae Holthuis, 1986

Genus *Troglocaris* Dormitzer, 1853

Subgenus *Troglocaris* Dormitzer, 1853 – distributed exclusively in the Balkans

Troglocaris (*Troglocaris*) *anophthalmus* (Kollar, 1848)

Troglocaris (*Troglocaris*) *anophthalmus anophthalmus* (Kollar, 1848)

Troglocaris (*Troglocaris*) *anophthalmus intermedia* Babić, 1922

Troglocaris (*Troglocaris*) *anophthalmus legovicii* Jugovic, Jalžić, Prevorčnik and Sket, 2012

Troglocaris (*Troglocaris*) *anophthalmus ocellata* Jugovic, Jalžić, Prevorčnik and Sket, 2012

- Troglocaris (Troglocaris) anophthalmus periadriatica* Jugovic, Jalžić, Prevorčnik and Sket, 2012
Troglocaris (Troglocaris) anophthalmus sontica Jugovic, Jalžić, Prevorčnik and Sket, 2012
Troglocaris (Troglocaris) bosnica Sket et Zakšek, 2009
Troglocaris (Troglocaris) planinensis Birštein, 1948
Troglocaris (Troglocaris) schmidti Dormitzer, 1853
Subgenus *Spelaeocaris* Matjašić, 1956 – distributed exclusively in the Balkans
Troglocaris (Spelaeocaris) kapelana Sket et Zakšek, 2009
Troglocaris (Spelaeocaris) neglecta Sket et Zakšek, 2009
Troglocaris (Spelaeocaris) prasence Sket et Zakšek, 2009
Troglocaris (Spelaeocaris) pretneri (Matjašić, 1956)
Subgenus *Troglocaridella* Babić, 1922 – distributed exclusively in the Balkans
Troglocaris (Troglocaridella) hercegovinensis (Babić, 1922)
Subgenus *Xiphocaridinella* Sadowsky, 1930 – exclusively Caucasian group
Troglocaris (Xiphocaridinella) ablaskiri Birštein, 1939
Troglocaris (Xiphocaridinella) fagei Birštein, 1939
Troglocaris (Xiphocaridinella) jusbachjani Birštein, 1948
Troglocaris (Xiphocaridinella) kutaissiana (Sadowsky, 1930)
Troglocaris (Xiphocaridinella) osterloffii Juzbašjan, 1940
Troglocaris (Xiphocaridinella) kumistavi Marin, 2017

The active study of cave shrimps in the Caucasus began in the 1930s–1950s. At the moment, 6 species of the genus *Troglocaris* (subgenus *Xiphocaridinella*) are described from the caves from the territory of the southwestern part of Russia, Abkhazia and Western Georgia, which are relicts of the freshwater fauna of the Sarmatian or Pontine seas (basins) (Sadowsky, 1930; Birštein, 1939, 1948; Juzbašjan, 1940; Sendra and Reboleira, 2012; Marin and Sokolova, 2014; Marin, 2017). This group is assumed to be much more diverse in the Caucasus than is presently known and many species will be discovered in the nearest future. Shrimps of the genus *Troglocaris* have been recorded at a depth of more than 2,000 meters in the lower siphon of Krubera Cave in Abkhazia, which at the moment is considered the deepest in the world (Sendra and Reboleira, 2012). To mark species within crustacean genera, including the *Troglocaris (Xiphocaridinella)* species complex, it is useful to use the mitochondrial cytochrome c oxidase subunit I gene marker (COI), as one of the most informative markers for population and species-level genetic studies (Avise, 1993). At the same time, data on the Caucasian clade are not numerous and special criteria are needed for recognition of species and genera within this group of atyid cave shrimps.

Material and methods

This paper presents an attempt to evaluate the genetic diversity on the marker region of subunit I of cytochrome oxidase of mitochondrial DNA (COXI mtDNA) of troglobiotic shrimps of the genus *Troglocaris* and representatives of the genus from the Caucasus based on available collections and new collected material. For the Caucasian clade freshly collected topotypic material was used, which allowed us to obtain genetic data that had not previously been reported for this genus – *Troglocaris (Xiphocaridinella) kutaissiana* Sadowsky, 1930 (Tskaltsitela Cave, Western Georgia), *Troglocaris (Xiphocaridinella) fagei* Birštein, 1939 (New Athos Cave, Abkhazia), *Troglocaris (Xiphocaridinella) jusbachjani* Birštein, 1948 (Agura River, Sochi, Russia), *Troglocaris (Xiphocaridinella) ablaskiri* Birštein, 1939 (Abrskila Cave, Abkhazia) and *Troglocaris (Xiphocaridinella) osterloffii* Juzbašjan, 1940 (the Lower Shakuran Cave, Abkhazia) and *Troglocaris (Xiphocaridinella) kumistavi* Marin, 2017 (Prometheus (Kumistavi) Cave, Western Geor-

gia). The name "*Troglocaris birsteini* Muge, Zueva et Ershov, 2001", proposed for the species reported from Otapa Cave, should be considered as nomen nudum (Franjević et al., 2010). All collected material is deposited in the collection of the Laboratory of Ecology and Morphology of Marine Invertebrates of the Institute of Ecology and Evolution. A. N. Severtsov RAS (Moscow). Species names and a modern taxonomic position are given according to the international database of the World Register of Marine Species (WoRMS) and the Marine Species Identification Portal.

To resolve the taxonomy of cryptic diversity of species complex fragments of the mitochondrial gene coding for cytochrome oxidase c subunit I (COI) as one of the most popular markers for population genetic studies (Avise, 1994, 2000) were amplified and compared. Total genomic DNA was extracted from pleopods or abdominal muscle tissue using the innuPREP DNA Micro Kit (AnalitikJena, Germany) following the manufacturer's protocol. The mitochondrial marker COI was amplified with the help of «PCR Core» (Isogene Lab., Moscow) using the universal primers LCO1490 (5'-ggtaacaaatcataaaatgg-3') and HC02198 (5'-taaacttcagggtgaccaaaaatca-3') (Folmer et al., 1994). PCR products were performed on amplifier «Tercik DNA Technology» under the following conditions: initial denaturation at 94 °C for 2 min followed by 40 cycles of 95 °C for 2 min, 59°C for 45 s, and 72 °C for 1.5 min, followed by chain extension at 72 °C for 7 min. The volume of 20 μL of reaction mixture contained 5 μL of total DNA, 10 μL of PCR Diluent and 2.5 μL of each primer. Synthesis of the full-length fragment was performed at an annealing primer temperature 59 °C during 45 seconds. The amplification products were separated by using gel electrophoresis of nucleic acids on a 2% agarose gel in 1xTBE, and then stained and visualized with 0.003% EtBr using imaging UV software. The resulting PCR products were sequenced in both forward and reverse direction on the basis of "EuroGen" (Moscow, Russia). Uniformity of sequences obtained was performed using the program BioEdit v. 5.0.9. The resulting markers of COXI gene of mtDNA with 598 bp long section were used for further phylogenetic analysis. The received nucleotide alignments of COI gene were used to construct the phylogenetic relations (tree) in MEGA 7.0 using k-nearest neighbor's algorithm (k-NN, Neighbor-Joining method) and Maximum-likelihood algorithm. Uncorrected pairwise genetic distances (p-distance) were calculated based on COI sequences using MEGA 7.0. Data on "molecular clocks" are used according to Zakšek et al. (2006) calculated for *Troglocaris* s.s. as well as Knowlton et al. (1993) and Knowlton & Weigt (1998) suggested for shrimps of the genus *Alpheus* (Crustacea: Decapoda: Alpheidae) as sequence divergence rate of about 1.4–2.4% per MYA for COXI gene marker.

Results

All known Caucasian *Xiphocaridinella* species are strictly restricted to certain karst cave ecosystems showing significant genetic divergence between known species (Table 1), which is usually not less than 5%. At the same time, the interspecies genetic variability within populations is very low (Table 2). Relatively high variability within *Troglocaris (Xiphocaridinella) fagei* is explained by mixture of three separate populations from the closely spaced New Athos, Habu and Mchishta caves, while variability within population from each of caves is similar to other species, being about 0.003 substitutions per 100 nucleotides.

Table 1

Uncorrected pairwise genetic (COXI) distances between known Caucasian species of subgenus *Xiphocaridinella* (asterisk indicates minimum values of p-distances)

Species	<i>X. kutaissana</i>	<i>X. kumistavi</i>	<i>X. ablaskiri</i>	<i>X. osterloffii</i>	<i>X. fagei</i>
<i>X. kumistavi</i>	0,058 ± 0,010*	–	–	–	–
<i>X. ablaskiri</i>	0,112 ± 0,014	0,099 ± 0,013	–	–	–
<i>X. osterloffii</i>	0,120 ± 0,014	0,108 ± 0,013	0,103 ± 0,014	–	–
<i>X. fagei</i>	0,120 ± 0,014	0,107 ± 0,014	0,106 ± 0,014	0,100 ± 0,013	–
<i>X. jusbachjani</i>	0,109 ± 0,014	0,104 ± 0,015	0,104 ± 0,015	0,108 ± 0,014	0,064 ± 0,010*

Table 2

Uncorrected pairwise genetic (COXI) distances within studied populations of known Caucasian species of subgenus *Xiphocaridinella* (asterisk indicates minimum values of p-distances)

Species	Uncorrected pairwise genetic
<i>Xiphocaridinella fagei</i>	0,014 ± 0,003*
<i>X. kutaissana</i>	0,0006 ± 0,0006*
<i>X. ablaskiri</i>	0,003 ± 0,001
<i>X. jusbachiani</i>	0,002 ± 0,001
<i>X. osterloffii</i>	0,003 ± 0,0015
<i>X. kunistavi</i>	0,0009 ± 0,0008*

Uncorrected pairwise genetic (COXI) distances (p-distances) between subgenera of *Troglocaris* s.l. (Table 3; Fig. 1) show well supported divergences with p-distances not less than 17–20%. The division of the subgenus *Spelaeocaris* and *Troglocaridella* for the Dinaric group is not justified on the basis of available molecular data. The genetic subdivision between subgenera of *Troglocaris* s.l. is similar to generic level divergence between *Galocaris* and *Troglocaris* s.s. (Table 3). The data obtained clearly support the monophylety of *Xiphocaridinella* and *Troglocaris* s.s. while *Spelaeocaris* represents a paraphyletic taxon (Fig. 1).

Discussion

The genetic subdivision between subgenera of *Troglocaris* s.l. is similar to generic level divergence between *Galocaris* and *Troglocaris*.

Table 3

Uncorrected pairwise genetic (COXI) distances between subgenera of *Troglocaris* s.l. and outgroup atyid shrimp genera (asterisk indicates minimum values of p-distances)

Species	<i>Troglocaris</i>	<i>Troglocaris bosnica</i>	<i>Speleocaris</i>	<i>Troglocaridella</i>	<i>Xiphocaridella</i>	<i>Atyaephyra</i>	<i>Dugatella</i>	<i>Galocaris</i>
<i>Troglocaris bosnica</i>	0,153 ± 0,024*	—	—	—	—	—	—	—
<i>Speleocaris</i>	0,217 ± 0,024	0,222 ± 0,024	—	—	—	—	—	—
<i>Troglocaridella</i>	0,243 ± 0,024	0,241 ± 0,025	0,169 ± 0,024*	—	—	—	—	—
<i>Xiphocaridella</i>	0,214 ± 0,024	0,225 ± 0,024	0,189 ± 0,025*	0,207 ± 0,024	—	—	—	—
<i>Atyaephyra</i>	0,265 ± 0,027	0,261 ± 0,029	0,295 ± 0,027	0,322 ± 0,031	0,275 ± 0,020	—	—	—
<i>Dugatella</i>	0,264 ± 0,022	0,279 ± 0,026	0,287 ± 0,024	0,308 ± 0,026	0,296 ± 0,017	0,275 ± 0,018	—	—
<i>Galocaris</i>	0,200 ± 0,025*	0,213 ± 0,023	0,276 ± 0,025	0,295 ± 0,026	0,255 ± 0,020	0,257 ± 0,025	0,260 ± 0,021	—
<i>Typhlatya</i>	0,275 ± 0,023	0,264 ± 0,020	0,260 ± 0,023	0,290 ± 0,023	0,289 ± 0,018	0,255 ± 0,023	0,288 ± 0,019	0,235 ± 0,016

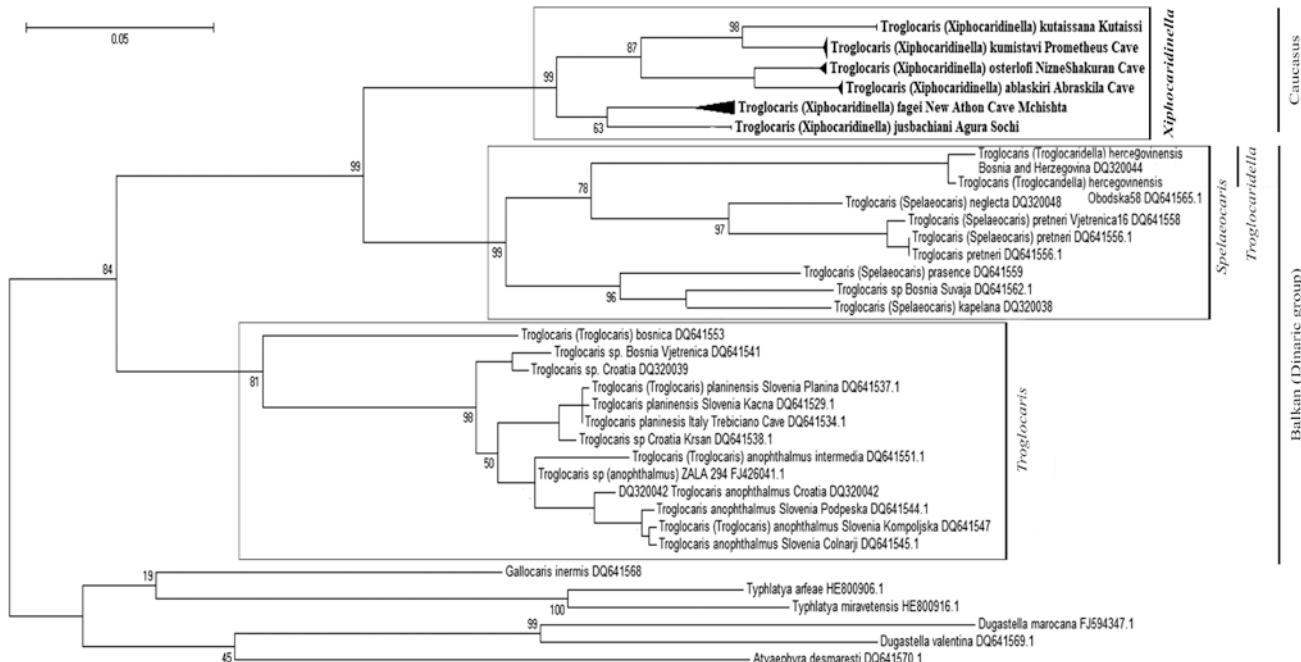


Fig. 1. The evolutionary tree of *Troglocaris* s. l. based on COXI gene marker obtained using the Maximum-Likelihood method based on the Kimura 2-parameter model

Similar morphological variability in the armature of the rostrum in the carapace is known from the Caucasian *Xiphocardinella* currently including 6 valid species known from the Russian part of the Caucasus (Krasnodar Territory), Abkhazia and Western Georgia. *Xiphocardinella jusbaschjani* known exclusively from the Agura River (Sochi, Russia) shows an extremely short (reduced) unarmed rostrum and the absence of supraorbital or suborbital teeth on the carapace. This has even led to the transfer of the species to the genus *Typhlatya* (D'Udekem D'Acoz, 1999). Five remaining species of *Xiphocardinella* show a varying pattern of armature of the rostrum from unarmed in *X. fagei* (Marin and Sokolova, 2015) to strongly armed dorsally and ventrally in *X. kumistavi* (Marin, 2017). Anyway, *X. jusbaschjani* strictly belongs to the genus *Xiphocardinella* by other morphological features and present genetic data (Table 1; Fig. 1). Thus, the armature of the rostrum and the presence of supraorbital or suborbital teeth on the carapace could not be considered as morphological features of the generic level. Moreover, extreme variations of the length of the rostrum and supraorbital teeth within the genera *Troglocaris* and *Xiphocardinella* and even populations of *Troglocaris*-related shrimps has been shown (Zakšek et al., 2007; Jugovic et al., 2010, 2011, 2012; Marin, 2017), even suggesting the theory of the influence of predators such as cave salamander *Proteus anguinus* Laurenti, 1768 (Amphibia: Caudata: Proteidae) (Jugovic et al., 2011). The obtained genetic data clearly support the monophylety of *Xiphocardinella* and *Troglocaris* while *Spelaeocaris* represent a paraphyletic taxon (Fig. 1).

It is obvious that representatives of modern genera *Troglocaris*, *Spelaeocaris* and *Xiphocardinella* were descended from a common ancestor which lived in the ancient Sea of Paratethys. The hypothesis of the recent split (about 6–11 million years ago) between the Caucasian and Dinaric cave shrimps of the Paratethys relict (Zakšek et al., 2006) supports the idea of a closer relationship between the subgenus *Spelaeocaris* and *Xiphocardinella* than with the Dinaric group, which we also believe is correct on the basis of our research. Besides, it is possible to suggest two separate divergence events between within Dinaric–Caucasian *Troglocaris* lineages (genera), which occurred about 9–15 MYA (ancestors of *Troglocaris* separated from *Spelaeocaris*–*Xiphocardinella*) and about 8–13 MYA when ancestors of *Spelaeocaris* separated from *Troglocaris* vs single split about 6–11 MYA suggested by Zakšek et al. (2006).

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