NAT. CROAT. | VOL. 35 | No 2 | 0 - 0 | ZAGREB | December 31, 2026

This work is licensed under a Creative Commons Attribution 4.0 International License

original scientific paper/izvorni znanstveni rad
DOI 10.20302/NC.2026.35.32

ON THE EVOLUTION AND OCCURRENCE OF THE CROATIAN FAIRY SHRIMP, *CHIROCEPHALUS CROATICUS* STEUER, 1898 (CRUSTACEA: ANOSTRACA)

JOSIP SKEJO[1,*], MARIJANA VUKOVIĆ[2,*] & NIKOLA TVRTKOVIĆ[3,*]

[1]Faculty of Science, Zagreb University, Croatia (e-mail: jskejo@biol.pmf.hr; https://orcid.org/0000-0002-2554-4499)
[2]Croatian Natural History Museum, Zagreb, Croatia (e-mail: marijana.vukovic@hpm.hr; https://orcid.org/0009-0001-1806-6134)
[3]Croatian Biospeleological Society, Zagreb, Croatia (e-mail: nikolatvrtkovic71@gmail.com; https://orcid.org/0000-0002-1775-0292)

Skejo, J., Vuković, M. & Tvrtković, N.: On the evolution and occurrence of the Croatian fairy shrimp, *Chirocephalus croaticus* Steuer, 1898 (Crustacea: Anostraca). Nat. Croat., Vol. 35, No. 2, _____, 2026, Zagreb.

The presence of a rare endemic fairy shrimp *Chirocephalus croaticus* Steuer, 1898 in the intermittent karst lake Blata (= Begovac) near Plaški in Lika (Croatia) was confirmed in 2004 for the first time since type series collection in 1895. We discuss the distribution of this species in the northwestern Dinaric Alps, and clarify the misunderstandings regarding the location of that lake. A preliminary phylogenetic analysis based on mitochondrial COI sequences, confirmed Daday's 1910 opinion about the taxonomic position within the Europe-endemic *C. (spinicaudatus*) species group, basal within the genus, and also including *C. spinicaudatus* and *C. chyzeri*. Species status of *C. croaticus* must furthermore be tested with additional mitochondrial and nuclear markers on larger samples. Besides, we recommend a field study including monitoring of the Croatian population, in order to determine its seasonal dynamics, and conservation measures, including the management of (one of) the last Croatian natural montane intermittent karst lake habitat.

Key words: type locality, Blata, intermittent lake, *Chirocephalus (spinicaudatus*), threatened species, extinction, phylogeny

Skejo, J., Vuković, M. & Tvrtković, N.: O evoluciji i pojavnosti hrvatskog škrgonošca, *Chirocephalus croaticus* Steuer, 1898 (Crustacea: Anostraca). Nat. Croat., Vol. 35, No. 2, _____, 2026, Zagreb.

Prisutnost rijetkog endemičnog račića škrgonošca (*Chirocephalus croaticus* Steuer, 1898) u povremenom krškom jezeru Blata (= Begovac) kraj Plaškog u Lici (Hrvatska) potvrđena je 2004. godine po prvi put nakon prikupljanja tipske serije 1895. godine. U ovom radu raspravljamo o rasprostranjenosti ove vrste u sjeverozapadnim Dinaridima i razjašnjavamo nesporazume vezane oko lokacije tog jezera. Preliminarna filogenetička analiza temeljena na sekvencama mitohondrijskog gena za podjedinicu I citokrom c oksidaze (COI) potvrdila je Dadayevo mišljenje iz 1910. godine o taksonomskom položaju unutar kompleksa *C. (spinicaudatus*), bazalnog u rodu i endemičnog za Europu, a koji također uključuje vrste *C. spinicaudatus* i *C. chyzeri*. Status vrste *C. croaticus* potrebno je dodatno preispitati filogenetičkom analizom temeljenom na dodatnim mitohondrijskim i jezgrinim biljezima na većem uzorku. Uz to, preporučujemo terenska istraživanja koja uključuju monitoring hrvatske populacije kako bi se utvrdila njezina sezonalnost, kao i mjere očuvanja, uključujući upravljanje jednim od posljednjih (a možda i posljednjim) od hrvatskih prirodnih gorskih povremenih krških jezera.

Ključne riječi: tipski lokalitet, Blata, periodično jezero, *Chirocephalus (spinicaudatus*), ugrožene vrste, izumiranje, filogenija

*all authors are of equal contribution

INTRODUCTION

The ancient crustacean group of fairy shrimps (Anostraca) has been known since the Paleozoic and inhabits inland waters, including freshwater and salt ponds or pools, puddles, and intermittent lakes (GUERIAU *et al*., 2016; MARRONE *et al*., 2017; WALOSSEK, 1999). They produce special resting eggs that ensure the survival of populations when water bodies dry out or freeze solid (BRENDONCK, 1996; MURA, 2001; BRENDONCK & DE MEESTER, 2003), and are important in the species dispersal by birds (ROGERS, 2013; NAGANAWA *et al*., 2019). The interest of this paper is the second largest anostracan genus, Holoarctic *Chirocephalus* Prévost, 1803 (suborder Anostracina, family Chirocephalidae, subfamily Chirocephalinae), currently including 54 described species and 2 subspecies (CATALOGUE OF LIFE, 2026), and many undescribed (BOUMENDJEL *et al*., 2024). The genus is in need of a taxonomic revision (ROGERS & SOUFI, 2013), because the current species groups (BRTEK, 1995) have been loosely defined and have never been systematically tested by phylogenetic methods. The genus is divided into five species groups (BRTEK, 1995), four of which are present in Europe, and these are (1) *C. (spinicaudatus*) group, whose species (e.g. *C. spinicaudatus, C. chyzeri, C. slovacicus, C. croaticus*) share basally widened male antenna II; trilobate antennal appendage; spinose basomedial branch of the antenna II; and female genital and postgenital segments laterally armed with spines (DADYKIN *et al*., 2026), (2) *C. (diaphanus)* group, whose species (e.g., *C. algeriensis, C. marchesonii, C. ruffoi, C. salinus, C. sibyllae*) share antennal morphology in males (MURA 2001), (3) *C. (bairdi*) group, whose species are characterized by ornamented thoracic, genital and/or abdominal metameres and a characteristic male antenna II, with the distal article bearing a relatively small basal apophysis and several tubercles, including, among others, *C. bairdi* and *C. kerkyrensis* (COTTARELLI *et al*., 2010), and (4) *C. (pristicephalus)* species group, including for example *C. carnuntunus* and *C. josephinae*, whose species are characterized by a single-lamellar male antennal appendage, a distinct basomedial projection on the distal article of antenna II, and generally unarmed female genital and abdominal segments (ROGERS & SOUFI, 2013).

A little over 130 years ago, on 9th and 23rd June 1895, the Austrian malacologist Rudolf Sturany collected 20 adult males and 15 adult females of emerald-green fairy shrimps, 1.5–2 cm long, northwest of the Plitvice Lakes, in the intermittent Blata Lake (*Blata See*) in Croatia (Fig. 1). The eminent Austrian carcinologist Adolf Steuer described these specimens, deposited in the collection of the Natural History Museum Vienna, as a new variety, namely '*Chirocephalus diaphanus* Prev. var. *croatica* n. var.' (STEUER, 1898). While describing this variety, Steuer sent one specimen to the Austro-Hungarian zoologist of Slovak origin Dr. Kornel Chyzer, who subsequently forwarded it to the Hungarian carcinologist of Romanian origin Dr. Eugen von Daday (Jenő Deési Daday), Anostraca specialist, in order to compare it to the collection in the Budapest Museum. According to STEUER (1898), Daday informed him that he considered the examined specimen to belong to "*Branchipus diaphanus* var. *chyzeri*", rather than representing a new variety. Nevertheless, Steuer proceeded with its description as *C. diaphanus* var. *croatica*. Twelve years later, in the monograph on Anostraca, DADAY (1910) treated *C. chyzeri* as a variety of *C. spinicaudatus* and likewise reassigned *C. diaphanus var. croatica* to the same taxon, recognizing them respectively as '*C. spinicaudatus* var. *chyzeri*' and '*C. spinicaudatus* var. *croatica*'. BRTEK (1966) elevated Steuer's taxon to species level, i.e., *C. croaticus*, but SKET & BRANCELJ (1992) still reported its occurence in a puddle near intermittent Cerkniško jezero Lake (Fig. 1, later destroyed), as well as in the intermittent Palško jezero Lake near Pivka, under the name "*C.* cf. *spinicaudatus croatica*". BRANCELJ & GORJANC (1999) furthermore recorded its presence in larger number in another intermittent lake near Pivka, Petelinjsko jezero Lake, Slovenia (Fig. 1).

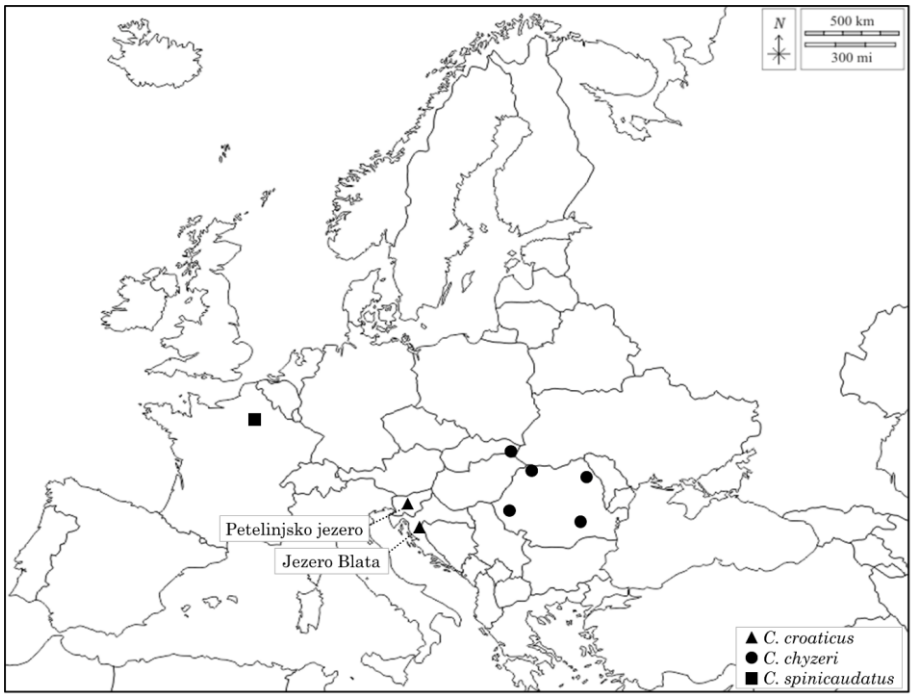


Fig. 1. Provisional distribution of the species belonging to *Chirocephalus* (*spinicaudatus*) group, considered in our analysis: *C. croaticus* (triangles, Croatia and Slovenia); *C. chyzeri* (dots, Romania and Slovakia); *C. spinicaudatus* (square, France).

BRANCELJ & GORJANC (1999) suggested *C. croaticus* placement in the *C. spinicaudatus* species group based on the presence, size, shape, and distribution of spines on the female abdominal segments, but have also concluded that the species within this group (*C. spinicaudatus*, *C. chyzeri*, *C. slovacicus*, and *C. robustus*) are difficult to distinguish morphologically, partly due to morphological variability within the species; and suggested that additional analyses would be required to clarify their taxonomic status. The same was concluded by MURA (2001) based on the resting egg morphology. MURA (2001) assigned *C. croaticus* to *C. (spinicaudatus)* species group based on morular appearance of the egg, which are almost identical to *C. spinicaudatus, C. chyzeri* and *C. slovacicus*. Two other members of the *C. (spinicaudatus)* species group—*C. povolnyi*, and *C. bobrinskii*—have much less ornamented egg surface than the aforementioned species (MURA, 2001; DADYKIN *et al*., 2026).

Nowadays, Steuer's variety '*C. diaphanus* var. *croatica*' has been accepted as *C. croaticus*, a member of the *C. (spinicaudatus*) species group, as evidenced in the works of BELK & BRTEK (1995), BRTEK & THIÉRY (1995), BRANCELJ & GORJANC (1999), MURA (2001), ROGERS (2013), and most recently, during the review of this paper, DADYKIN *et al*. (2026).

Chirocephalus croaticus is considered a rare and threatened species endemic to the northwestern Dinaric Alps of Slovenia and Croatia (SKET, 1996). Based on the data from Slovenia, the species has been assessed as Vulnerable on global level by the IUCN (criteria B1+2bcde) (SKET, 1996). In Croatia the species is listed as Critically Endangered (OFFICIAL GAZZETTE, 2013) following an assessment by Croatian carcinologists (GOTTSTEIN *et al*., 2013: B1ab/I,II,III, IV/+2ab/I,II,III,IV/), although without detailed locality information. Several studies (PETROV & MARINČEK, 1991; BRANCELJ & GORJANC, 1999; PIPAN, 2005) expressed doubts about the species' existence in Croatia after 1895.

The aim of this study is (1) to discuss the precise location of the type locality of *C. croaticus*, (2) to present previously unpublished record of this species from Croatia, and,

finally, (3) to determine, on the basis of COI sequence data, which species are most closely related to *C. croaticus*, and to which species group it belongs phylogenetically.

MATERIAL AND METHODS

Locus typicus and unpublished investigation

The type locality of *C. croaticus* Steuer, 1898 — the karst polje with the intermitent Lake Blata (Fig. 2a, b) — lies on a plateau at the 487–700 m a.s.l. near the road between Plaški and Saborsko in the Mala Kapela Mountain, northwest of the Plitvice Lakes National Park, as correctly stated by STEUER (1898). In 2004, the Croatian Natural History Museum (*Hrvatski prirodoslovni muzej*) began investigations in the Croatian part of the Dinaric karst. During this project we had the opportunity to visit the periodic Blata Lake once a month, from spring to winter. We documented the fauna of the lake throughout the sampling period; however, these data have unfortunately never been published in a scientific paper, only as an exhibiton catalogue (TVRTKOVIĆ *et al*., 2009).



Fig. 2. Two different phases of the lake Blata; A – high water (March 2021); B – drying out (May 2021) (photo: Suzana Pinjuh).

Phylogenetic analysis

In order to determine the phylogenetic position of *C. croaticus* within the genus *Chirocephalus*, a dataset was compiled including 40 COI-5P sequences of all sequenced *Chirocephalus* species and related genera (REMIGIO & HEBERT 2000; KETMAIER *et al*. 2003; JEFFERY *et al*., 2011; RENIERS *et al*., 2013; COTTARELLI *et al*., 2017; NAGANAWA *et al*., 2020; DENG *et al*., 2021; BOUMENDJEL *et al*., 2024; KITANO *et al*., 2024) from NCBI GenBank and BOLD Systems. Altogether, 33 sequences belong to *Chirocephalus* members, representing 13 described and 6 undescribed species (BOUMENDJEL *et al*., 2024), while the remaining seven sequences belong to members of the genera *Artemiopsis*, *Eubranchipus*, *Galaziella*, and *Polyartemiella*, which were used as outgroups. All sequences, together with their accompanying information, are listed in Tab. 1. Although a sequence of *C. chyzeri* (Daday, 1890) (EVER049-24) is included in our dataset, we did not find this sequence reported in any previously published study; all other sequences included in the dataset have been previously reported in the literature.The sequences were imported into MEGA12 (TAMURA *et al*., 2021; KUMAR *et al*., 2024) and aligned using Clustal algorithm (THOMPSON *et al*., 1994). After the alignment, sequences were trimmed to a length of 440 bp (of which 246 conserved sites, 194 variable sites, 167 parsimony-informative sites, and 27 singletons), corresponding to the length of the *C. croaticus* sequence from Slovenia, in order to retain only regions homologous to this sequence for subsequent analyses. The trimmed alignment was exported in FASTA format and used for all downstream phylogenetic analyses in MEGA12. The best-fitting nucleotide substitution model was selected in MEGA12 using the built-in model selection based on the lowest Akaike Information Criterion (AICc) and identified as General Time Reversible (GTR+G+I), AICc = 8555.123 (TAVARÉ, 1986). Phylogenetic relationships were subsequently reconstructed using the Maximum Likelihood (ML) method under this model, and nodal support was assessed based on 1000 bootstrap replicates. In addition, a Maximum Parsimony (MP) phylogram with a statistical support based on 1000 bootstrap replicated was reconstructed in order to compare the topological congruence between the two approaches. For MP, Subtree-Pruning-Regrafting (SPR) has been used as the search method.

Pairwise sequence divergence between the species was estimated as uncorrected p-distance, calculated as the proportion of nucleotide differences per site between sequences, using MEGA12 (KUMAR *et al*., 2024) after each species of *Chirocephalus* was annotated as a group. For ease of interpretation, divergence values are reported as percentages (p-distance × 100) (Tab. 2).

Tab. 1. List of Anostraca: Chirocephalidae COI-5P sequences used in the phylogenetic part of this study. Presented are the accession number (source of all sequences is NCBI, except for *C. chyzeri,* which is from BOLD), country of origin, and the corresponding reference. Species identifications follows the system presented in BOUMENDJEL *et al*. (2024).

Species	Accession	Country	Reference
Artemiopsis stefanssoni Johansen, 1921	AF209062	Canada	REMIGIO & HEBERT, 2000
Chirocephalus algeriensis Boumendjel *et al*., 2024	OP596277	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus bairdi (Brauer, 1877)	KY399030	Israel	COTTARELLI *et al*., 2017
Chirocephalus chyzeri (Daday, 1890)	EVER049-24	Slovakia	BOLD systems
Chirocephalus croaticus Steuer, 1899	KY399032	Slovenia	COTTARELLI *et al*., 2017
Chirocephalus diaphanus Prévost, 1803	OP597704	France	BOUMENDJEL *et al*., 2024
Chirocephalus diaphanus Prévost, 1803	OP597706	France	BOUMENDJEL *et al*., 2024
Chirocephalus diaphanus Prévost, 1803	JX990347	France	RENIERS *et al*., 2013

Species	Accession	Country	Reference
Chirocephalus diaphanus Prévost, 1803	JX990339	Netherlands	RENIERS *et al*., 2013
Chirocephalus diaphanus Prévost, 1803	OP597703	France	BOUMENDJEL *et al*., 2024
Chirocephalus diaphanus Prévost, 1803	JX990358	France	RENIERS *et al*., 2013
Chirocephalus diaphanus Prévost, 1803	OP597701	France	BOUMENDJEL *et al*., 2024
Chirocephalus kerkyrensis Pesta, 1936	JN246503	Albania	KETMAIER *et al*., 2003
Chirocephalus kerkyrensis Pesta, 1936	JN246505	Italy	KETMAIER *et al*., 2003
Chirocephalus kerkyrensis Pesta, 1936	JN246526	Greece	KETMAIER *et al*., 2003
Chirocephalus marchesonii Ruffo & Vesentini, 1957	JN246530	Italy	KETMAIER *et al*., 2003
Chirocephalus ruffoi Cottarelli & Mura, 1984	AY188999	Italy	KETMAIER *et al*., 2003
Chirocephalus salinus Daday, 1910	OP595376	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus salinus Daday, 1910	OQ588790	France	BOUMENDJEL *et al*., 2024
Chirocephalus salinus Daday, 1910	OP595372	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus salinus Daday, 1910	OP595368	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus salinus Daday, 1910	OP595378	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus sanhadjaensis Boumendjel *et al*. 2018	OP596279	Algeria	BOUMENDJEL *et al*., 2024
Chirocephalus sarpedonis Cottarelli *et al*., 2017	KY399031	Turkey	COTTARELLI *et al*., 2017
Chirocephalus sp1.	OP599900	Morocco	BOUMENDJEL *et al*., 2024
Chirocephalus sp2.	JX990360	Bulgaria	RENIERS *et al*., 2013
Chirocephalus sp3.	AY189000	Sardinia	KETMAIER *et al*., 2003
Chirocephalus sp4.	AY188996	Italy	KETMAIER *et al*., 2003
Chirocephalus sp5.	JX990344	Spain	RENIERS *et al*., 2013
Chirocephalus sp5.	JX990335	Spain	RENIERS *et al*., 2013
Chirocephalus sp6.	JX990338	Portugal	RENIERS *et al*., 2013
Chirocep	JX990337	Portugal	RENIERS *et al*., 2013
Chirocephalus spinicaudatus Simon, 1886	OP596276	France	BOUMENDJEL *et al*., 2024
Chirocephalus sibyllae Cottarelli & Mura, 1975	AY189001	Italy	KETMAIER *et al*., 2003
Eubranchipus bundyi Forbes 1876	JN233927	Canada	JEFFERY *et al*., 2011
Eubranchipus grubii Dybowski, 1860	OP596274	France	BOUMENDJEL *et al*., 2024
Eubranchipus uchidai (Kikuchi, 1957)	LC778728	Japan	KITANO *et al*., 2024
Galaziella baikalensis Naganawa & Orgiljanova, 2000	LC469605	Russia: Baikal	NAGANAWA *et al*., 2020
Galaziella graziellae (Rogers, 2013)	MW822919	China: Tibet	DENG *et al*., 2021
Polyartemiella hazeni (Murdoch, 1884)	AF209063	USA: Alaska	REMIGIO & HEBERT, 2000

RESULTS

Notes on the type locality of *C. croaticus*

Three different names for the intermittent lake Blata (N45.025824, E15.405441) can be found on maps and in the literature. The first is Lake Blata (Blata See, *Jezero Blata*) (STEUER, 1898; HIRC, 1900; NATURAVIVA, 2021); while the second is Lake Begovac (*Jezero Begovac*) (POLJAK, 1922; TVRTKOVIĆ *et al*., 2009; GOOGLEMAPS, 2025). GAVAZZI (1904) recorded both names. A rare third name, Blaćansko Lake (*Blaćansko jezero*), is used by the Municipality of Saborsko (Općina Saborsko, 2020; https://saborsko.hr/jezero-blata). In numerous scientific papers, however, the *locus typicus* has been incorrectly reported: either as Blatačko jezero Lake on Bjelašnica Mountain in Bosnia and Herzegovina (PETROV & MARINČEK, 1991), or as a small lake in southern Croatia (BRANCELJ & GORJANC, 1999), or as a locality in the lower course of the Neretva River in Croatia (PIPAN, 2005).

The average surface area of the lake is ca 80 ha, with an average depth of 3–4 m, while maximum values reach ca 220 ha and 16 m depth, during the extremely flooding season (GAVAZZI, 1904) (Fig. 2). Northwest of the lake lies the settlement of Blata, whereas Begovac village is situated to the southeast.

Chirocephalus croaticus rediscovery on *locus typicus*

During our visit in June 2004, just before the water stagnates and sinks back into the karst underground, the lake contained numerous tadpoles of the common toad, *Bufo bufo* (Linnaeus, 1758), and was visited by many migratory black-headed gulls, *Larus ridibundus* (Linnaeus, 1766), which may act as vectors for the dispersal of fairy shrimp resting eggs during their spring migration to northern Europe. The tadpoles and gulls were observed in July, as well, when we found adult fairy shrimps.

On a single occasion, that being on the sunny day of July 14th, M. Vuković and N. Tvrtković observed and, with entomological net, collected 15 adult emerald green specimens of *C. croaticus* near the shallow lake shore. Twelve specimens are deposited in the Crustacean Collection of the Croatian Natural History Museum under the inventory number 1431. The locality name on the collection label was designated as 'Begovac Lake' (TVRTKOVIĆ *et al*., 2009) following POLJAK (1922).

During our visit to Velika pećina cave in 2004, Blata jezero lake was, as is typical in August, dry. Because the intermittent lake is hydrologically connected to the cave systems and drains through it, the cave waters' fauna forms part of the same ecosystem as *Chirocephalus croaticus*. In the first cave pool, we observed nocturnal European weatherfish, *Misgurnus fossilis* (Linnaeus, 1758), a strictly protected species (OFFICIAL GAZZETTE, 2013) the only fish species known from Lake Blata (POLJAK, 1922), which may represent a potential predator of *C. croaticus*.

Phylogenetic analysis

Chirocephalus croaticus is reconstructed as sister to *C. chyzeri* in both Maximum Likelihood (bootstrap support, BS = 65), and in Maximum parsimony analyses (BS = 93). In the distance matrix (Tab. 2), difference between *C. croaticus* and *C. chyzeri* is 1.14%. Together, these are recovered as sister to *C. spinicaudatus,* and the distance in the matrix towards *C. spinicaudatus* is 4.32% in *C. croaticus,* and 4.55% in *C. chyzeri*. The bootstrap node support for these three species, representing the *C. (spinicaudatus)* species group, is 100. *Chirocephalus (spinicaudatus)* species group is characterized by numerous synapomorphic substitutions of COI-5P, resulting in a long ancestral branch.

On the other hand, *C. (diaphanus*) group containing *C. salinus, C. sibyllae, C. algeriensis, C. ruffoi, C. diaphanus* and at least five underscribed species (sp2, sp3, sp4, sp5, sp6), has very good support in ML phylogeny (BS 94), and relatively good in MP phylogeny (BS 75). Relationships between the species of the *C. (diaphanus)* species group are not well supported. Genetic differences within *C. (diaphanus*) species group range from 1.82% between *C. ruffoi* and *C.* sp4, up to 21.36% between *C. spinicaudatus* and *C.* sp3 (Tab. 2).

Species *C. sanhadjaensis, C. marechsonii, C. bairdi, C. sarpedonis,* and *C. kerkyrensis* do not belong to any of the species groups and their relationships towards other species are not well supported by bootstrap values in any of the analyses (Fig. 3). *Chirocephalus sarpedonis* has the smallest genetic distance towards *C. kerkyrensis* (10.98%), and is same is true for *C. bairdi* towards *C. kerkyrensis* (12.35%) (Tab. 2).

Tab. 2. Pairwise sequence divergence between groups, expressed as percentages and calculated as uncorrected p-distance.

C. chyzeri	*C. spinicaudatus*	*C. sibyllae*	*C. bairdi*	*C. sarpedonis*	*C. salinus*	*C. diaphanus*	*C. ruffoi*	*C. algeriensis*	*C. kerkyrensis*	*C. marchesonii*	C. sp1	C. sp2	C. sp3	C. sp4	C. sp5	C. sp6	*C. sanhadjaensis*	
1	**4**	**19**	**15**	**15**	**18**	**15**	**17**	**14**	**15**	**16**	**16**	**16**	**21**	**17**	**17**	**15**	**14**	***C. croaticus***
	5	19	15	15	19	15	18	15	16	17	15	17	20	17	17	14	14	*C. chyzeri*
		20	16	15	19	17	19	16	16	18	17	17	21	18	18	16	15	*C. spinicaudatus*
			16	15	14	12	12	13	12	16	15	12	15	10	10	11	14	*C. sibyllae*
				13	15	15	15	14	12	14	13	14	17	14	13	13	13	*C. bairdi*
					16	14	14	14	11	16	16	16	18	14	14	12	12	*C. sarpedonis*
						11	12	10	14	15	15	12	16	12	11	11	14	*C. salinus*
							9	8	11	15	13	10	13	9	8	7	13	*C. diaphanus*
								8	13	16	15	10	7	2	8	10	14	*C. ruffoi*
									11	15	12	10	12	8	9	9	12	*C. algeriensis*
										13	14	13	15	11	11	11	11	*C. kerkyrensis*
											16	16	20	16	15	15	14	*C. marchesonii*
												14	18	14	14	13	13	C. sp1
													15	10	10	10	14	C. sp2
														5	12	13	17	C. sp3
															7	9	13	C. sp4
																7	14	C. sp5
																	12	C. sp6

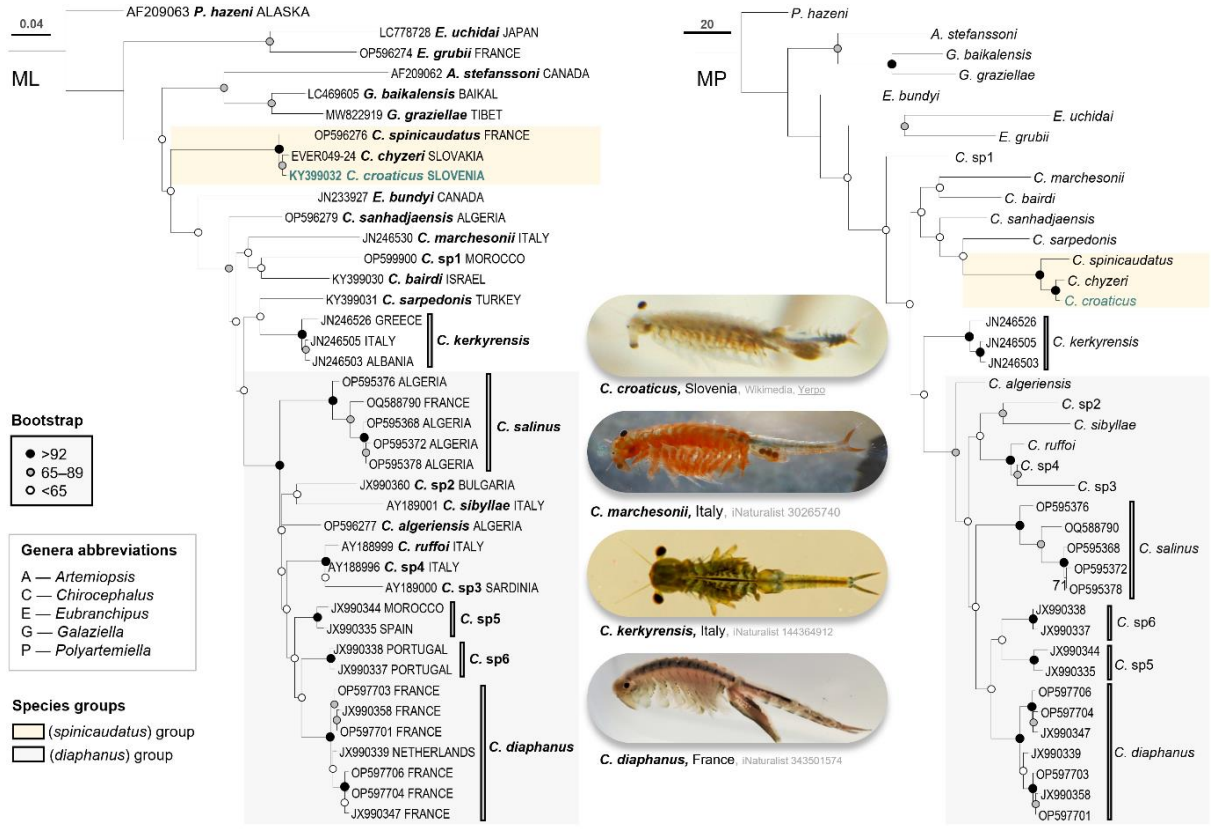


Fig. 3. Phylogenetic relationships within Chirocephalidae inferred from COI-5P sequences. Left: Maximum likelihood (ML) phylogram reconstructed using GTR+G+I model (highest log likelihood -4,188.22 tree is shown). Bootstrap was calculated on 1000 replicates. Right: Maximum parsimony (MP) phylogram (length = 910, CI = 0.349451, RI = 0.575931), with bootstrap calculated on 1000 replicates. Marked in yellow is *Chirocephalus (spinicaudatus)* species group.

DISCUSSION

Previous authors have held conflicting views regarding the exact taxonomic placement of *C. croaticus*, with some assigning it to the *C.* (*spinicaudatus*) species group as a variety of *C. spinicaudatus* (DADAY, 1910) and others to the *C.* (*diaphanus*) species group (STEUER, 1898). Although it is well established that the mitochondrial COI gene is not optimal for resolving deeper phylogenetic relationships above the species level, it can still provide useful signals at shallower evolutionary depths (BRENNAN *et al*., 2017; MARCUS, 2018). Closely related species tend to exhibit more similar COI sequences than more distantly related taxa (HEBERT, 2003; WARD *et al*., 2005; PENTINSAARI *et al*., 2020; KASALO *et al*., 2023).

Despite being based on a shorter alignment (440 bp compared with 632 bp in BOUMENDJEL *et al.* (2024)), our phylogenetic analyses recovered a largely congruent topology. As expected, several nodes received lower statistical support than in BOUMENDJEL *et al*. (2024), most likely due to the shorter sequence used in the present study. Similar to BOUMENDJEL *et al.* (2024), the *C. (diaphanus)* species group, comprising *C. algeriensis*, *C. diaphanus*, *C. ruffoi*, *C. salinus*, *C. sibyllae*, *C.* sp2, *C.* sp3, *C.* sp4, *C.* sp5, and *C.* sp6, was recovered as a relatively well-supported clade. Likewise, *C. diaphanus* was reconstructed as sister to *C.* sp6, whereas *C. ruffoi*, *C.* sp3, and *C.* sp4 formed a well-supported clade. In agreement with BOUMENDJEL *et al.* (2024), *Chirocephalus kerkyrensis* was recovered as sister to the *C. (diaphanus)* species group. The placement of *C. sanhadjaensis*, *C. marchesonii*, and *C.* sp1 differed slightly from that reported by BOUMENDJEL *et al*. (2024); however, these relationships received low statistical support in our analyses and therefore cannot be interpreted with confidence. Unlike BOUMENDJEL *et al.* (2024), we also included *C. bairdi* and *C. sarpedonis* in our analyses, although their phylogenetic relationships were likewise not recovered with strong statistical support. BOUMENDJEL *et al.* (2024) recovered *C. spinicaudatus* as sister to all other species included in their analysis. It should be noted, however, that their phylogenetic analysis did not include *C. croaticus* and *C. chyzeri*, so basically, *C. (spinicaudatus*) species group has been recovered as sister to the studied *Chirocephalus* species, just as in our analysis.

In this context, our results clearly indicate that *C. croaticus* belongs to the *C. (spinicaudatus)* species group, together with *C. spinicaudatus* and *C. chyzeri*. *Chirocephalus bobrinskii* from Pamir of Tajikistan in Central Asia has been found to belong to this group as well and has been reconstructed as sister to *C. croaticus* and *C. spinicaudatus* (DADYKIN *et al*., 2026). *Chirocephalus spinicaudatus* has been recently rediscovered only on five locations near the *locus typicus* (Fig. 1) (RABET & CART, 2002), and is regarded a species endemic to France. On the other hand, *C. chyzeri* is known to inhabit 14 sites in the Pannonian and the Pontic parts of Romania (Fig. 1) (BĂNĂRESCU *et al*., 1998; DEMETER & STOICESCU, 2008), as well as in northern Banat, Pannonian part of Slovakia (DEVÁNOVÁ *et al*., 2024, 2026) in 28 sites in the area close to the *locus typicus*.

The genetic divergence between *C. croaticus* and *C. chyzeri* is only about 1% in the COI gene (Tab. 2), whereas their divergence from *C. spinicaudatus* is approximately 4–5% (Tab. 2). This pattern is consistent with a comparatively recent divergence between *C. croaticus* and *C. chyzeri*, although the available data do not allow the timing of this divergence to be inferred. At the same time, the *C.* (*spinicaudatus*) group appears to represent a deeply divergent lineage, as indicated by its long branch and clear separation from the remaining lineages in the phylogenetic analyses (Fig. 3), as already shown by BOUMENDJEL *et al*. (2024). Molecular distinctiveness is coupled with clear morphological synapomorphies, in external morphology, but also in egg morphology (MURA, 2001).

On the other hand, it seems that species assigned to the *C.* (*diaphanus*) species group—here defined in more conservative manner than in BRTEK (1995) (Fig. 3) and not including *C. marchesonii*—diverged well before the last glacial maximum (CLARK *et al*., 2009; EHLERS *et al*., 2011; KRIJGSMAN *et al*., 2024) and survived the Pleistocene glaciations in multiple (sub)refugia along the Iberian, Apennine, and Balkan peninsulas (RENIERS *et al*., 2013). Overall, the genus *Chirocephalus*, as defined morphologically (BRTEK & MURA, 2000), does not exhibit a simple or clear-cut division into species groups as previously assumed (BRTEK, 1995). The COI phylogeny shows once again (see COTTARELLI *et al*., 2017) that, in addition to the *C.* (*spinicaudatus*) and *C.* (*diaphanus*) groups—which also require revisions—many species cannot be confidently assigned to either group by analysing COI.

An additional point worth considering is the remarkably low genetic divergence between *C. croaticus* and *C. chyzeri*. In the present dataset, COI sequence divergence between them (~1%) falls well within the range typically observed among populations of a single species. Indeed, in other cases within the genus (e.g., *C. diaphanus*, *C. salinus*, *C. kerkyrensis*), divergences below 3% consistently correspond to intraspecific variation rather than distinct species, except in the case of *C.* sp4 and *C. ruffoi* (~2%) (Fig. 3). This raises the possibility that *C. croaticus* and *C. chyzeri* may not represent distinct species, but rather subspecies or junior synonyms. However, such a taxonomic conclusion would require additional evidence from longer mitochondrial and/or nuclear DNA sequences, morphology, and broader geographic sampling before any formal revision can be proposed. Future phylogeographic analyses of *Chirocephalus* should therefore include multiple specimens per species, particularly for *C. chyzeri* and *C. croaticus*, to enable robust assessments of intraspecific genetic variation and species boundaries.

The presence of a flock of *Larus ridibundus* at Blata Lake suggests a potential role of this species in the dispersal of fairy shrimp resting eggs, both during spring migration from the Danube and Tisza river systems toward northeastern Europe and during autumn migration to wintering areas along the Adriatic coast, the westernmost part of the eastern Mediterranean (KRALJ *et al*., 2013).

After reports by Slovenian authors (BRANCELJ & GORJANC, 1999; PIPAN, 2005; KIRN, 2020; JUGOVIC & JEKLAR, 2021), and based on multi-year observations and sampling conducted in different seasons, the population of *C. croaticus* in the Petelinsko jezero Lake (Slovenia) appears to be stable, having been regularly observed in large numbers throughout all seasons between 1998 to 2018. In contrast, in Croatia only two evidence of this officially Critically Endangered species exist. BRANCELJ & GORJANC (1999) noted that "*at the moment, there is no information on the status of the population from the type locality*". With the present study, we aim to supplement the list of important species from this site within the Croatian ecological network (intermitent Blata Lake, HR2000594). Currently, the only species listed as important for protection at the site is plant *Chouardia litardierei* (Breistr.) Speta (= *Scilla litardieri*) (NATURAVIVA, 2021), endemic for the Dinaric Alps, and listed as Near Threatened (KOVAČIĆ & STAMENKOVIĆ, 2014) and protected by EU Habitats Directive.

It is curious that *C. croaticus* might be the most endangered relic freshwater crustacean species in Croatia, but is, sadly, still neglected by all financed national or regional nature protection projects. *Chirocephalus croaticus* should definitely have been considered in the recent plans for the future touristic concepts for the area of Blata Lake (ANONYMOUS, 2024), commissioned by the municipality of Saborsko, on whose territory the lake is located.

In conclusion, *C. croaticus* belongs to *C. (spinicaudatus*) species group (the same was concluded by DADYKIN *et al.* (2026) during the revision of our study), and not to *C.* (*diaphanus*)

species group, as defined in BOUMENDJEL *et al*. (2024) and in this study (**Fig. 3**). There is still lack of sequenced western, southern and eastern European *Chirocephalus* representatives, especially from the western Alps, Dinaric Alps, Northern Macedonia, Pontic and the Pannonian region (KETMAIER *et al*., 2012; RENIERS *et al*., 2013; ROGERS, 2013), thus, in future it will be interesting to see *C. croaticus* position within a more taxon-rich analysis.

Besides including additional mitochondrial and nuclear phylogenetic markers for all populations of *C. croaticus*, as well as several geographically isolated populations of *C. chyzeri*, a systematic field study of the populations in Blata Lake is also needed. Such a study should integrate analyses of morphological variability, measurements, seasonal dynamics monitoring, and recommendations for conservation and management.

ACKNOWLEDGMENTS

We are very grateful to Mrs Suzana Pinjuh for kindly providing photographs of Lake Blata; to the curator of the CNHM Crustacean Collection, Dr. Irena Grbac, for sharing the inventory number; and to Dr. Martina Podnar (CNHM) for retrieving the *C. chyzeri* COI sequence data from the BOLD database. We would like to sincerely thank the two reviewers whose insightful comments and valuable suggestions significantly contributed to the quality of our work. Lake Blata was visited during the PIN/MATRA project "Dinaric Alps Rare Habitats and Species Conservation Project" in collaboration with the Royal Dutch Society for Nature Conservation, and the "Karst Ecosystem Conservation Project" – WB-GEF grant.

Received May 15, 2026

REFERENCES

ANONYMOUS, 2024: Idejno rješenje uređenja prostora uz jezero Blata, Općina Saborsko. Vitaprojekt, pp 1–52. https://plitvickedoline.hr/wp-content/uploads/2024/10/Idejno-rjesenje-uredenja-jezera-Blata.pdf.

BĂNĂRESCU, P. M., STOICESCU, A. & NEGREA, Ş., 1998: The lower crustacea from the temporary pools of the Banat (south-western Romania). Analele Banatului, Şt. Nat. **4**, 145–164.

BELK, D. & BRTEK, J., 1995: Checklist of the Anostraca. Hydrobiologia **298**, 315–353.

BOUMENDJEL, L., AMAROUAYACHE, M., BONILLO, C., SORBA, L., BAGNI, T. & RABET, N., 2024: Phylogenetic analysis of *Chirocephalus* (Branchiopoda: Anostraca), with the description of a new species from Algeria. Biologia **79**(2), 495–518.

BRANCELJ, A. & N. GORJANC, N., 1999: On the presence of *Chirocephalus croaticus* (Steuer, 1899) in an intermittent lake in SW Slovenia. Hydrobiologia **412**, 25–34.

BRENDONCK, L., 1996: Diapause, quiescence, hatching requirements: what we can learn from large freshwater branchiopods (Crustacea: Branchiopoda: Anostraca, Notostraca, Conchostraca). Hydrobiologia **320**(1), 85–97.

BRENDONCK, L. & L. DE MEESTER, L., 2003: Egg banks in freshwater zooplankton: evolutionary and ecological archives in the sediment. Hydrobiologia **491**, 65–84.

BRENNAN, I. G., BAUER, A. M., VAN TRI, N., WANG, Y. Y., WANG, W. Z., ZHANG, Y. P. & MURPHY, R. W., 2017: Barcoding utility in a mega-diverse, cross-continental genus: keeping pace with *Cyrtodactylus* geckos. Scientific Reports **7**(1), 5592.

BRTEK, J., 1966: Einige Notizen zur Taxonomie der Familie Chirocephalidae Daday, 1910. Annot. Zool. Bot. (Bratislava) **33**, 1–65.

BRTEK, J., 1995: Some notes on the taxonomy of the family Chirocephalidae (Crustacea, Branchiopoda, Anostraca). Zborník Slovenského Národného Múzea, Prírodné Vedy **41**, 3–15. Slovenského Národného Múzea, Prírodné Vedy, 41, 3–15.

BRTEK, J., & MURA, G., 2000: Revised key to families and genera of the Anostraca with notes on their geographical distribution. Crustaceana **73**(9), 1037-1088. https://doi.org/10.1163/156854000505083.

BRTEK, J. & THIÉRY, A., 1995: The geographic distribution of the European branchiopods (Anostraca, Notostraca, spinicaudata, Laevicaudata). Hydrobiologia **298**(1), 263–280.

CATALOGUE OF LIFE, 2026: Genus *Chirocephalus* Prévost, 1803 Available at https://www.catalogueoflife.org/data/taxon/3NBH (accessed 27 July 2026).

CLARK, P. U., DYKE, A. S., SHAKUN, J. D., CARLSON, A. E., CLARK, J., WOHLFARTH, B., MITROVICA, J. X., HOSTETLER, S. W. & MCCABE, A. M., 2009: The last glacial maximum. Science **325**(5941), 710–714.

COTTARELLI, V., AYGEN, C. & MURA, G. 2010: Fairy shrimps from Asiatic Turkey: Redescription of *Chirocephalus tauricus* Pesta, 1921 and descriptions of *Chirocephalus algidus* sp. nov. and *Chirocephalus brteki* sp. nov. (Crustacea, Branchiopoda, Anostraca). Zootaxa **2528**(1), 29–52.

COTTARELLI, V., MURA, G., IPPOLITO, G. & MARRONE, F., 2017: *Chirocephalus sarpedonis* sp. nov. (Branchiopoda, Anostraca, Chirocephalidae) from Turkey questions the monophyly of the traditional *Chirocephalus* species-groups. Hydrobiologia **801**(1), 5–20.

DADAY, E. VON, 1910: Monographie Systématique Des Phyllopodes Anostracés. Annales des sciences naturelles. Zoologie et biologie animale, pp. 91–486.

DADYKIN, I. A., PEREBOEV, D. D., ROGERS, D. C. & KOTOV, A. A., 2026: Redescription of *Chirocephalus bobrinskii* (Alcock, 1898) (Anostraca: Chirocephalidae) with special attention to somatic sensillar armature. Nauplius **34**, e20260606.

DEMETER, L. & STOICESCU, A., 2008: A review of the distribution of large branchiopods (Branchiopoda: Anostraca, Notostraca, Spinicaudata, Laevicaudata) in Romania. North-Western Journal of Zoology **4**(2), 203–223.

DENG, Z., CHEN, Y., MA, X., HU, W. & YIN, M., 2021: Dancing on the top: phylogeography and genetic diversity of high-altitude freshwater fairy shrimps (Branchiopoda, Anostraca) with a focus on the Tibetan Plateau. Hydrobiologia **848**(10), 2611–2626.

DEVÁNOVÁ, A., ZAVADIL, V. & KAUTMAN, J., 2024: Žábronožka slovenská ještě stále nevyhynula/The Slovak fairy shrimp is not yet extinct. Živa **6**, 334–336.

DEVÁNOVÁ, A., KAUTMAN, J., MOCK, A. *et al.*, 2026: Temporal and spatial dynamics of large branchiopods in Slovakia: updated distribution and conservation implications. Hydrobiologia. https://doi.org/10.1007/s10750-026-06133-y

EHLERS, J., GIBBARD, P. L. & HUGHES, P. D. (Eds.), 2011: Quaternary glaciations-extent and chronology: a closer look. (Developments in Quaternary Sciences; Vol. **15**). Elsevier.

GAVAZZI, A., 1904: Die Seen des Karstes. Abhandlungen der K.K. Geographischen Gesellschaft in Wien **5** (1903/04), 54–136 + VII Tafeln + XV Karten.

GOOGLEMAPS, 2025: Jezero Begovac. Available at www.google.com/maps/search/jezero+begovac (accessed September 9, 2025).

GOTTSTEIN, S., HUDINA, S., LUCIĆ, A., MAGUIRE, I., TERNJEJ, I. & ŽGANEC, K., 2013: *Chirocephalus croaticus* Steuer, 1899 (HRCP001900). In: Crveni popis Hrvatske. https://crvenipopis.haop.hr/preglednik/1900. Zavod za zaštitu okoliša i prirode Ministarstva gospodarstva i održivog razvoja. Accessed October 10, 2025. (Red List of Croatia, in Croatian).

GUERIAU, P., RABET, N., CLÉMENT, G., LAGEBRO, L., VANNIER, J., BRIGGS, D.E.G., CHARBONNIER, S., OLIVE, S. & BÉTHOUX, O., 2016: A 365-Million-Year-Old Freshwater Community Reveals Morphological and Ecological Stasis in Branchiopod Crustaceans. Current Biology **26**(3), 383–390, https://doi.org/10.1016/j.cub.2015.12.039.

HEBERT, P. D., 2003: Biological identifications through DNA barcoding. Proceedings of the Royal Society of London. Series B: Biological Sciences **270**, 313–321.

HIRC, D., 1900: Lika i Plitvička jezera. Tiskara Rijeka, Rijeka (reprint 1996), pp 1-163. (Lika and Plitvička jezera lakes, in Croatian).

JEFFERY, N. W., ELIAS-GUTIERREZ, M. & ADAMOWICZ, S. J., 2011: Species diversity and phylogeographical affinities of the Branchiopoda (Crustacea) of Churchill, Manitoba, Canada. PLoS One **6**(5), e18364.

JUGOVIC, J. & JEKLAR, M., 2021: A seasonal dynamics and population status of the steno-endemic karst fairy shrimp *Chirocephalus croaticus* (Steuer, 1899) (Branchiopoda, Anostraca) from Slovenia. Crustaceana **94**(5), 529–549. https://doi.org/10.1163/15685403-bja10075

KASALO, N., SKEJO, J. & HUSEMANN, M., 2023: DNA barcoding of pygmy hoppers—The first comprehensive overview of the BOLD Systems' data shows promise for species identification. Diversity **15**(6), 696.

KETMAIER, V., ZARATTINI, P., DE MATTHAEIS, E., COBOLLI, M. & MURA, G., 2003: Intra-and inter-specific relationships in the six Italian species of the fairy shrimp genus *Chirocephalus*: combining allozyme and mtDNA data. Journal of Zoological Systematics and Evolutionary Research **41**(4), 276–285.

KETMAIER, V., MARRONE, F., ALFONSO, G., PAULUS, K., WIEMANN, A., TIEDEMANN, R., MURA, G. 2012: Mitochondrial DNA regionalism and historical demography in the extant populations of *Chirocephalus kerkyrensis* (Branchiopoda: Anostraca). PLoS One **7**(2), e30082

KIRN, T., 2020: Occurrence of fairy shrimp (*Chirocephalus croaticus*) in the lake Petelinjsko jezero during the 2005-2008-2014 period. Natura Sloveniae **22**(1), 29–32.

KITANO, T., TABATA, M., TAKAHASHI, N., HIRASAWA, K., IGARASHI, S., HATANAKA, Y., OOYAGI, A., IGARASHI, K. & UMETSU, K., 2024: Integrating mitochondrial and nuclear genomic data to decipher the evolutionary history of *Eubranchipus* species in Japan. Molecular Phylogenetics and Evolution **194**, 108041.

KOVAČIĆ, S. & STAMENKOVIĆ, V., 2014: *Chouardia litardierei* (Breistr.) Speta (HRCP003740). In: „Crveni popis divljih vrsta Hrvatske". Available at: https://crvenipopis.haop.hr/preglednik/3740. Zavod za zaštitu okoliša i prirode Ministarstva gospodarstva i održivog razvoja,. DOI: https://doi.org/10.71545/aw0z-0v80. Accessed October 9, 2025.

KRALJ, J., BARIŠIĆ, S., TUTIŠ, V. & ČIKOVIĆ, D., 2013: Atlas selidbe ptica Hrvatske (Croatian Bird Migration Atlas). Hrvatska Akademija Znanosti i Umjetnosti, Zavod za Ornitologiju, Zagreb. 265 pp.

KRIJGSMAN, W., ROHLING, E. J., PALCU, D. V., RAAD, F., AMARATHUNGA, U., FLECKER, R., FLORINDO, F., ROBERTS, A. P., SIERRO, F. J. & ALOISI, G., 2024: Causes and consequences of the Messinian salinity crisis. Nature Reviews Earth & Environment **5**(5), 335–350.

KUMAR, S., STECHER, G., SULESKI, M., SANDERFORD, M., SHARMA, S. & TAMURA, K., 2024: MEGA12: Molecular Evolutionary Genetic Analysis Version 12 for Adaptive and Green Computing. Molecular Biology and Evolution **41**(12), https://doi.org/10.1093/molbev/msae263.

MARCUS, J. M., 2018: Our love-hate relationship with DNA barcodes, the Y2K problem, and the search for next generation barcodes. AIMS genetics **5**(01), 001–023.

MARRONE, F., ROGERS, D. C., ZARATTINI, P. & NASELLI-FLORES, L., 2017: New challenges in anostracan research: old issues, new perspectives and hot topics. Hydrobiologia **801**(1), 179–185.

MURA, G., 2001: Morphological diversity of the resting eggs in the anostracan genus Chirocephalus (Crustacea, Branchiopoda). Hydrobiologia **450**(1), 173–185.

NAGANAWA, H., NAUMOVA, E. Y., DENIKINA, N. N., KONDRATOV, I. G., DZYUBA, E. V. & IWASAWA, A., 2019: Does the dispersal of fairy shrimps (Branchiopoda, Anostraca) reflect the shifting geographical distribution of freshwaters since the late Mesozoic? Limnology **21**(1), 25–34.

NATURAVIVA, 2021: Povremeno jezero Blata. Available at naturaviva.hr/povremeno-jezero-blata/, accessed September 9, 2025 (Intermittent lake Blata, in Croatian).

OFFICIAL GAZZETTE, 2013: Pravilnik o strogo zaštićenim vrstama (Republike Hrvatske) Narodne Novine **144**, narodne-novine.nn.hr/clanci/sluzbeni/full/2013_12_144_3086.html (Ordinance on strictly

protected species, in Croatian).

PENTINSAARI, M., BLAGOEV, G. A., HOGG, I. D., LEVESQUE-BEAUDIN, V., PEREZ, K., SOBEL, C. N., VANDENBRINK, B. & BORISENKO, A., 2020: A DNA barcoding survey of an Arctic arthropod community: implications for future monitoring. Insects **11**(1), 46.

PETROV, B. & MARINČEK, M., 1991: On the Anostraca (Crustacea) of Yugoslavia. Hydrobiologia **21**(2), 267–272.

PIPAN, T., 2005: Fauna of the Pivka intermittent lakes. Acta Carsologica **34**(3), 650-659. https://doi.org/10.3986/ac.v34i3.256.

POLJAK, J., 1922: Periodičko jezero Blata. (Intermittent lake Blata). Glasnik Hrv. prir. društva **34**, 71-78. (Intermittent lake Blata, in Croatian)

RABET, N. & CART, J.F., 2002: Rediscovery of the French endemic *Chirocephalus spinicaudatus* Simon, 1886 from France (Crustacea: Anostraca). Anostracan News **10**(1).

REMIGIO, E. A. & HEBERT, P. D., 2000: Affinities among anostracan (Crustacea: Branchiopoda) families inferred from phylogenetic analyses of multiple gene sequences. Molecular Phylogenetics and Evolution **17**(1), 117–128.

RENIERS, J., VANSCHOENWINKEL, B., RABET, N. & BRENDONCK, L., 2013: Mitochondrial gene trees support persistence of cold tolerant fairy shrimp throughout the Pleistocene glaciations in both southern and more northerly refugia. Hydrobiologia **714**(1), 155–167.

ROGERS, D.C., 2013: Anostraca Catalogus (Crustacea: Branchiopoda). The Raffles Bulletin of Zoology **61**(2), 525–546.

ROGERS, D.C., & SOUFI, M., 2013: A new species of *Chirocephalus* (Crustacea: Anostraca) from Iran. Zootaxa **3609**(3), 319–326.

SKET, B., 1996: *Chirocephalus croaticus*. The IUCN Red List of Threatened Species. https://dx.doi.org/10.2305/IUCN.UK.1996.RLTS.T4661A11069616.en. Accessed April 04 2025.

SKET, B. & BRANCELJ, A., 1992: Rdeči seznam ogroženih sladkovodnih nižjih rakov (Entomostraca: Anostraca, Cladocera, Copepoda, Ostracoda) v Sloveniji The Red List of Freshwater Entomostraca (Anostraca, Cladocera, Copepoda, Ostracoda) in Slovenia. Varstvo narave: revija za teorijo in prakso varstva naravne dediščine **17**, 165–172.

STEUER, A., (1898)1989: Die Entomostraken der Plitvicer-Seen und des Blata-Sees (Croatien), gesammelt von Dr. R. Sturany (1895). Ann. d. k. k. Nat. Hofmus. **13**(2–3), 159-188 + Tafel VI-VIII.

TAMURA, K., STECHER, G. & KUMAR, S., 2021: MEGA11: molecular evolutionary genetics analysis version 11. Molecular biology and evolution **38**(7), 3022–3027.

TAVARÉ, S., 1986: Some Probabilistic and Statistical Problems in the Analysis of DNA Sequences. Lectures on Mathematics in the Life Sciences **17**, 57–86.

THOMPSON, J. D., HIGGINS, D. G. & GIBSON, T. J., 1994: CLUSTAL W: improving the sensitivity of progressive multiple sequence alignment through sequence weighting, position-specific gap penalties and weight matrix choice. Nucleic acids research **22**(22), 4673–4680.

TVRTKOVIĆ, N., TOPIĆ, J., LACKOVIĆ, D., JALŽIĆ, B. & M. VUKOVIĆ, 2009: Priroda krških polja Dinarida. (Nature of Dinaric Alps karst poljes) - katalog izložbe, Hrvatski prirodoslovni muzej, Zagreb, pp 80. (Nature of Dinaric Alps karst poljes, exhibition catalogue, in Croatian).

WALOSSEK, D., 1999: On the Cambrian Diversity of Crustacea. In SCHRAM, F. & VON VAUPEL KLEIN, C. (Eds.): Crustaceans and the Biodiversity Crisis. Pp. 3–27. DOI: https://doi.org/10.1163/9789004630543_003

WARD, R. D., ZEMLAK, T. S., INNES, B. H., LAST, P. R. & HEBERT, P. D., 2005: DNA barcoding Australia's fish species. Philosophical transactions of the royal society B: biological sciences, **360**(1462), 1847–1857.