

Original Scientific Paper

# Chara squamosa (Characeae, Charophyceae) in Serbia - insights from the taxonomic revision of the BEOU charophyte collection and recent field records

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#### ABSTRACT:

Chara gymnophylla is one of the first charophyte species reported for Serbia during the late 19th and the early 20th centuries, and at that time it was the second in terms of the frequency of its occurrence in the country. General taxonomic misinterpretations in the past resulted in the concealment of another species, C. squamosa, within the findings attributed to C. gymnophylla. In Serbia, Chara gymnophylla was treated as C. vulgaris var. gymnophylla, and as such was not listed as a species inhabiting the country. Recent improvements in the taxonomic concept for C. squamosa prompted a revision of the rich material of C. gymnophylla, C. vulgaris var. gymnophylla, C. vulgaris var. nitelloides, and C. rohlenae, deposited in the BEOU collection. The revision process was conducted concurrently with fieldwork and the collection of new material. Our study confirmed the presence of C. squamosa in Serbia for the first time. Based on numerous revised samples from the BEOU collection, as well as recently collected specimens, the species' continuous presence in Serbia since 1976 was confirmed. Chara squamosa and C. gymnophylla were thus added to the list of Characeae species inhabiting Serbia, and categorised as Critically Endangered according to the criteria outlined by IUCN. An overview of the biogeography, ecology and taxonomy of C. squamosa in Serbia is provided, particularly in relation to C. gymnophylla. The BEOU charophyte collection proved to represent a valuable and relevant resource for critical taxonomic revisions. The results presented in this study strongly encourage further studies on C. squamosa and C. gymnophylla distribution in the Balkan region and wider area in order to gain a deeper understanding of the species' ecology and the further improvement of their taxonomic concepts.

#### **Keywords:**

Charophytes, *Chara gymnophylla*, *Chara squamosa*, distribution, stoneworts, the Balkans

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### INTRODUCTION

The taxon *Chara squamosa* Desfontaines was long considered to be conspecific with *C. gymnophylla* A. Braun, resulting in the repeated misidentification of plants with a tylacanthous stem cortex which were labelled as

C. gymnophylla, or C. vulgaris L. var. gymnophylla Nyman (Krause 1997; Blaženčić 2014; Romanov et al. 2024). The recent clarification of the species concept for C. squamosa and C. gymnophylla based on their type specimens, a comprehensive review of the literature and the examination of a vast amount of herbarium mate-

rial has facilitated a solution to this taxonomical misinterpretation, finally establishing a taxonomic concept whereby C. squamosa is acknowledged as a valid taxon (Romanov et al. 2024).

Chara squamosa has been established as the legitimate name for the former taxon *C. conimbrigensis* A.G. Cunha and has been confirmed as conspecific with C. hungarica Fil. (ROMANOV et al. 2024). The distinction between C. squamosa and C. gymnophylla is possible by observing the stem cortex arrangement (i.e. tylacanthous vs. aulacanthous), while both species are characterised by a generally similar and variable habitus and the presence of mostly ecorticate branchlets with bract cells and gametangia located between at least one pair of ecorticate segments as a stable trait occurring at all branchlets exhibiting nodes. Nevertheless, the delineation of these taxa is not very straightforward or possible in all cases, as an isostichous cortex is common in both taxa, and some aulacanthous parts can be traced in plants with a predominantly tylacanthous stem cortex in the case of C. squamosa (Romanov et al. 2024). This further complicates the re-examination of herbarium material in various collections, as these details may not be clearly visible and are easily misinterpreted in pressed specimens. Collections of fresh material and further field studies are suggested to clarify the presence and distribution of *C. squamosa*. The distribution of *C. squa*mosa was found to be sparce in general, compared to C. gymnophylla. Chara squamosa was confirmed in fewer than 35 localities in the world, in Europe mainly in the Mediterranean, and outside Europe in North Africa, the Middle East (Israel) (Romanov et al. 2024), the Caucasus and Northeast China (R. Romanov, unpublished data). Considering the type locality of C. hungarica in Budapest (Hungary), associated with a thermal water spring, and identified as the northernmost reliable site for C. squamosa (Romanov et al. 2024), its occurrence between Hungary and Mediterranean seems plausible. Therefore, Serbia should be expected to be one of the areas for new localities in Europe, aligning with the suggestion that the recent record of C. rohlenae in Serbia (Blaženčić & Stevanović 2018) may actually represent the finding of C. squamosa (Romanov et al. 2019, 2024).

We conducted a targeted search of C. squamosa in the BEOU charophyte collection housed at the premises of the Institute of Botany and Botanical Garden Jevremovac in Belgrade, consisting of wet (formalin/alcohol) and herbarium specimens. The herbarium collection of charophytes in the BEOU holds some valuable and old specimens, with the earliest dating back to 1907, collected by Professor Nedeljko Košanin. Unfortunately, the oldest and first herbarium sheets of Serbian charophytes collected by Professor Josif Pančić are missing from the BEOU collection. The wet collection of charophytes in the BEOU was established by Professor Jelena Blaženčić in 1972 when the first specimens were deposited. Today, this

collection counts almost 3000 deposited specimens (2834 processed and approximately 100 yet to be processed samples), mainly from the Balkans and Europe, but also from all over the world. The vouchers for all the charophyte findings in Serbia from 1972 onwards are deposited in this collection; they are well managed and preserved, thus providing a suitable resource for revisions.

The aim of this paper is to reveal the presence and distribution of Chara squamosa in Serbia, based on the taxonomic revision of the specimens deposited in the BEOU charophyte collection and recent field data. The distribution data are discussed relative to *C. gymnophylla*.

#### MATERIALS AND METHODS

The 84 samples deposited in the BEOU collection were revised. The criteria for sample selection for revision were collection within the territory of Serbia and initial identification as C. gymnophylla, C. vulgaris var. gymnophylla, C. vulgaris var. nitelloides (A. Braun) R.D. Wood (indexed as unpublished combination C. contraria A. Braun ex Kütz. var. nitelloides (A. Braun) R.D. Wood), and C. rohlenae. The BEOU collection specimens are all preserved in 4% formalin solution, and prior to examination they were thoroughly rinsed with tap water. The taxonomic details, and specifically the aforementioned critical parameters of each sample and the newly gathered specimens (see below) were carefully examined using the stereomicroscope Nikon SMZ 745T equipped with a Dual Sight 1000 camera (Nikon, Tokyo, Japan).

The critical parameters in the revision process (summarised in Table 1) were the presence of gametangia between the ecorticate segments and the presence of the cortex on the main axes which was either prevalently aulacanthous or prevalently tylacanthous. In both cases isostichous parts were expected and tolerated, allowing for occasional aulacanthous parts in predominantly tylacanthous specimens.

The collection of new material of C. gymnophylla and C. squamosa was conducted during the 2022 and 2023 vegetative seasons. The collected plants were deposited in the BEOU collection in 4% formalin solution and on herbarium sheets and in the BIOLACHC collection in an alcohol solution (50% ethanol: glycerin, 1:1).

The IUCN status of C. gymnophylla and C. squamosa in Serbia was assessed using the application for species threat category assessment in Serbia according to IUCN criteria (NIKETIĆ 2020).

#### **RESULTS**

The revision of the BEOU collection resulted in one *C*. vulgaris, six C. contraria, nine C. contraria f. capillacea Mig., 27 C. gymnophylla and 41 C. squamosa findings.

The geographical distribution of C. gymnophylla and C. squamosa in Serbia is limited to the central and

**Table 1.** A comparative overview of the diagnostic taxonomic features of *Chara gymnophylla* and *C. squamosa* (according to Romanov *et al.* 2024 and Romanov & Becker 2024).

	Chara gymnophylla	Chara squamosa			
Main axis	Corticated. Cortex diplostichous, <b>aulacanthous to isostichous</b> , but <b>never tylacanthous</b> .	Corticated. Cortex diplostichous, <b>tylacanthous to isostichous</b> , even short <b>weakly aulacanthous parts can be present.</b>			
Branchlets	Entirely ecorticated or sometimes with 1 or 2 basal segments completely or partially corticated, but nodes with gametangia and/or bract cells between ecoritcated segments always present.	Entirely ecorticated or sometimes with 1 or 2 basal segments completely or partially corticated, but nodes with gametangia and/or bract cells between ecoritcated segments always present.			
Sexuality	Monoecious.	Monoecious.			

Table 2. An overview of the new field records of Chara squamosa (1) and C. gymnophylla (2) in Serbia.

Voucher	Locality, water body type	Date	1	2	Latitude (N)	Longitude (E)	Altitude (m)
BEOU 2881	Tara, Jagoštica, river	09/06/2023	x		43.976789	19.282665	985
BEOU 2892	Željin, Jelakci, puddle	11/07/2023	x		43.415082	20.835123	1043
BEOU 2891	Tometino Polje, puddle	08/2023	x		44.025392	20.013141	672
BEOU herbarium	Vrujci, channel	19/07/2023	x	х	44.221507	20.155631	226
BEOU 2886	Vrujci, stream	19/07/2023	x		44.222324	20.164108	243
BEOU 2885	Ljig, river arm	19/07/2023	x		44.217461	20.22656	198
BEOU 2872	Borski Stol, pond, stream, spring	29/06, 22/07/ 2022	x		44.175735	22.123561	848
BEOU 2867	Golija, Izubra, river edge	03/07/2022	x		43.423275	20.417601	1050
BIOLACHC 98	Svrljig, Okruglica village, stream	07/06/2022		х	43.378531	22.22316	428
BIOLACHC 101	Knjaževac, Rgoška Spa, pool	05/06/2022		X	43.544986	22.215662	240
BIOLACHC 102	Knjaževac, Rgoška Spa, channel	05/06/ 2022		X	43.544986	22.215662	240
BEOU 2882	Mokra Gora, Kršanje, Beli Rzav, river	07/06/ 2022		х	43.799796	19.442944	568
BEOU 2852	Sokobanja, Izgare, river	14/06/2022		х	43.630115	22.013876	457
BEOU 2837	Kladovo, Mala Vrbica	26/06/2022		х	44.600522	22.679325	75
BEOU 2835	Tara, Derventa, river	13/07/2022		х	43.943645	19.682335	407

southern regions with no findings reported in the northern area (i.e. part of the Pannonian plane - Vojvodina), with a significant overlap, particularly in the centralwestern region, while in the central-eastern Serbia C. squamosa seems to be more frequent (Fig. 1). The habitat type and ecological conditions were not retrievable for the most of the specimens in the BEOU collection, but the available data mostly refer to small and shallow waterbodies, many of which are probably contemporary, threatened and might no longer exist anymore. In several cases, the samples originated from thermal waters - Vrujci Spa, Niška Spa, Gamzigradska Spa and Zvonce Spa. In all these thermal water habitats C. squamosa was confirmed. Notably, Vrujci Spa is the only thermal spa located in western Serbia (the others are situated in east and south-east Serbia), and according to the BEOU collection revision, also the only one thermal water habitat hosting both species. This was also confirmed by the new field investigation.

The recent field work resulted in eight findings of *C. gymnophylla* and eight findings of *C. squamosa* (Table 2, Fig. 1). As stated above, both species were confirmed to cohabit the termo-mineral waters in Vrujci Spa (2023), and in other localities the species were detected independently (Table 2). The fieldwork in Vrujci Spa also indicated the vulnerability of the habitat and species, as the channel flowing through the settlement (Fig. 2a) is subjected to a strong anthropogenic influence with only two plants found at this particular locality, one being *C. gymnophylla* and the other *C. squamosa*. Downstream, the channel changes into an unregulated stream (Fig. 2b), where a small population of *C. squamosa* was de-

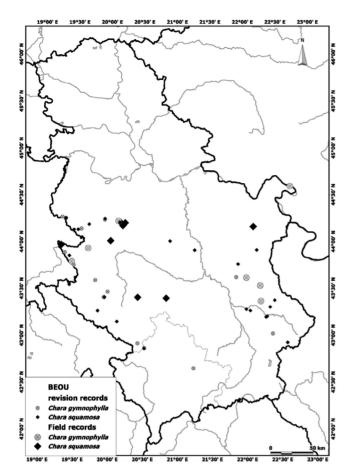


Fig. 1. The distribution of Chara squamosa and C. gymnophylla in Serbia based on revised and recent field records.

tected, along with Potamogeton nodosus Poir. Chara squamosa was also spotted near Vrujci Spa, in a small regulated channel (a branch of the Ljig River) flowing within a restaurant front yard, accompanied by Potamogeton crispus L. (Fig. 2c). Chara squamosa was found in puddles in the vicinity of the village of Tometino Polje (Fig. 2e) and on the slopes of Željin Mountain, and the edges of the rivers and streams on the Golija, Tara and Borski Stol mountains (Fig. 2d). On the Borski Stol Mountain, C. squamosa was also detected in two more localities - a pond and a nearby small spring (Fig. 2f). Chara gymnophylla was collected from the thermal mineral water in Rgoška Spa, in the streams and rivers near Svrljig, Sokobanja and Kladovo in eastern Serbia, and the streams/rivers on the Mokra Gora and Tara mountains in western Serbia (Table 2).

All the habitats of *C. squamosa* found in the recent fieldwork (Table 2, Fig. 2), with the exception of the regulated channel in Vrujci Spa, can be characterised as rather small and shallow waters with muddy/sandy bottoms. The channel flowing through the settlement of Vrujci Spa exhibited specific characteristics, the bottom was clean and covered with fine gravel, while the sides were covered with concrete panels. The channel was

about 1 m deep, but the charophytes were found growing only in substrate between the concrete panels on the channel side at a depth of about 0.5 m. Chara squamosa was generally observed growing in locations exposed to the sunlight, and in those cases when it inhabited the edges of rivers, streams and springs (in the Borski Stol, Tara and Golija mountains, Fig. 2d & f) it was found growing in semi-aquatic, i.e. transitional aquatic-terrestrial environments.

The habitus of the collected plants of C. squamosa was variable (Fig. 3), as noted in the revised material. The plants were small to medium in size, light to dark green in colour and mainly weekly/moderately incrusted with calcium carbonate. Small and compressed mosslike forms were characteristic of very shallow water and transitional aquatic-terrestrial environments (Fig. 3d & e), while medium sized forms were found growing submerged in flowing water (Fig. 3b & c). The latter exhibited moderate elongation with characteristic elongated branchlets in the older whorls. However, the apical whorls were condensed and closely spaced, giving the impression of "nest" like formations in the apical zone. The plants seem to be richly branched.

The key morphological characteristics of the C. squamosa specimens are illustrated in Figure 4. The morphological characteristics revealed with microscopy were uniform in all the revised and newly collected specimens of C. squamosa. Ecorticate branchlets were typical, as well as bract cells and gametangia between at least one pair of ecorticate segments (Fig. 4b-f). The anterior bract cells were variable in length, usually short in the condensed forms and longer in the elongated forms (Fig. 4). The gametangia were conjoined and located at a maximum of three of the lowest branchlet nodes, but usually only at one or two. Geminate oogonia were detected in a few cases. The process of gyrogonite formation was observed (Fig. 4c). The stem cortex was regular diplostichous or irregular diplo-triplostichous, slightly but mostly tylacanthous and isostichous, with an occasional aulacanthous appearance - which always proved to be isostichous on the stem cross section (Fig. 4d-f). The spine-cells were mainly papillate and solitary, but in a few cases elongated, always shorter than the axis diameter; thick and obtuse spines were observed (Fig. 4d-f). In a few specimens very rare (mostly one case per plant) rudimentary geminate spines were detected. Although in most cases the stipulodes were in double rows and rudimentary or irregularly developed, mainly longer in the upper row or the same length in both rows, better developed and longer stipulodes in the lower row were also detected (Fig. 4d-f). Starchless multicellular nodal bulbils were observed and particularly abundant in the condensed forms originating from very shallow water.

According to the IUCN criteria, both C. gymnophylla (CR: C2a(i)) and C. squamosa (CR: C2a(i); D) are classified as Critically Endangered in Serbia.

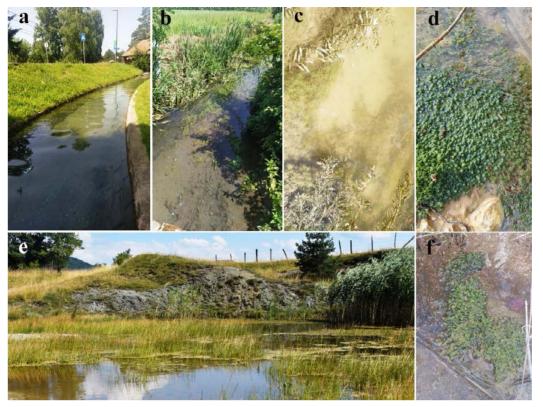


Fig. 2. The habitat types of Chara squamosa: a) Vrujci Channel, b) Vrujci Stream, c) Ljig, d) Tara, Jagoštica, e) Tometino Polje, f) Borski Stol.



Fig. 3. General habitus of the recently collected plants of Chara squamosa at the localities a) Vrujci channel, b) Vrujci Stream, c) Ljig, d) and e) Tometino Polje. Scale 1 cm.

#### **DISCUSSION**

The BEOU collection revision resulted in 41 finding of C. squamosa in the period 1976-2020, and we also reported 8 new records in 2022 and 2023, which is quite remarkable relative to the fewer than 35 localities in the world known to date (Romanov et al. 2024). Our results also showed that as a geographical region Serbia (and most probably the entire Balkan region), serves as a perfect continuum in species distribution, as previously it was considered to mainly inhabit the Mediterranean region in Europe, North Africa and the Middle East (Israel) (Romanov et al. 2024), as well as the Caucasus and Northeast China (R. Romanov, unpublished data).

Chara gymnophylla is considered a well-represented species in the Mediterranean region (ROMANOV & Becker 2024), and its distribution within the Balkans is also well recorded (e.g. TORTIĆ-NJEGOVAN 1956). At the very beginning of charophyte research in Serbia, during the late 19th and early 20th centuries, C. gymnophylla was even considered to be one of the most represented species, second only to C. vulgaris (Košanin 1907). Interestingly, Košanin (1907) described C. gymnophylla specimens collected in Serbia which included a few specimens of an unnamed form - very small, condensed, bushy and with inflated branchlet segments. Košanin (1907) also noticed that C. gymnophylla distribution in Serbia was related to hilly and mountainous regions, as our study confirms. However, since Košanin (1907), the presence of the taxon C. gymnophylla in Serbia was mainly obscured under the name C. vulgaris var. gymnophylla, and as such this species was neither listed as a species inhabiting Serbia, nor was it considered threatened in Blaženčić (2014). Considering the prolonged treatment of C. squamosa as conspecific with C. gymnophylla (e.g. Krause 1997), the presence of this species was further obscured by findings of C. vulgaris var. gymnophylla in Serbia (Fig. 1). It is interesting, however, that numerous findings of C. squamosa were also concealed under the name of *C. contraria* var. nitelloides. Finally, the suggestion made by Romanov et al. (2024) that the C. rohlenae finding in Serbia was most probably *C. squamosa*, has proven to be accurate.

Based on the IUCN criteria, we characterised both *C*. gymnophylla and C. squamosa as critically endangered (CR) in Serbia. The revision of the BEOU collection confirmed that C. squamosa was even more frequently represented in Serbia than C. gymnophylla (Fig. 1). Nevertheless, both species were frequently found forming small populations in fragile and threatened habitats. Although the data on the ecology were limited in our study, it seems that both species preferred the mountainous/hilly regions of Serbia, as no records of these species were made in the lowlands of the Pannonian plane region i.e. the northern Serbian province of Vojvodina, which has been extensively researched in Serbia over the past decades (MARKOVIĆ et al. 2023 and the references

therein). Based on this observation, the hypothesis could be proposed that geological and climatic characteristics and probably nutrient levels define the favourable habitat conditions for the development of these species. Thermal waters were recognised as specific and characteristic habitats of both species, but this was confirmed in our study only in the case of Vrujci Spa. In all the other thermal waters in Serbia, C. squamosa seems to be exclusive. TORTIĆ-NJEGOVAN (1956) also highlighted thermal waters as the habitats of specific forms of *C. gymnophylla*.

The recently observed sites of C. squamosa in Serbia (Table 1, Figs. 2 & 3) represent valuable contributions to the knowledge of the species' ecology and taxonomic characteristics. Variability in general habit was noticeable and could be linked to the habitat conditions, i.e. water depth and insolation. Although all the specimens were collected from relatively shallow water, condensed moss-like forms were associated with the very shallow water and transitional aquatic-terrestrial environments, while elongated and more robust specimens were found in completely submerged environments. These habitatrelated characteristics of the thalli were also noticed by TORTIĆ-NJEGOVAN (1956) in the case of C. gymnophylla f. sphagnoides Fil., a specific form which she reported from a few localities in former Yugoslavia. It is worth revisiting the paper written by Tortić-Njegovan (1956), as it provides a comprehensive overview of C. gymnophylla in the Balkans. The author discussed in detail the specific forms of C. gymnophylla occurring in the Balkans, highlighting the specificity and similarity of the following forms - f. subnudifolia Mig., f. sphagnoides and f. paludosa Fil. She also suggested that they could be amalgamated, noting their shared ability to thrive in transitional aquatic-terrestrial environments, and that C. rohlenae most probably also belongs to this group. According to her descriptions, all these forms could actually refer to *C. squamosa*. The parallels between our results and those obtained by TORTIĆ-NJEGOVAN (1956) suggest that C. squamosa could be more widely distributed in the Balkans.

The taxonomic characteristics of the collected specimens (Fig. 4) align perfectly with the description of C. squamosa provided by Romanov et al. (2024), adding additional value to the postulated species concept and upgrading knowledge on gyrogonite formation, phenology and reproduction. Considering both the revised and recently collected material, the specimens of C. squamosa in Serbia did not leave an impression of extremely low fertility in terms of oospore production, and reproductive specimens were detected during the entire period from June to late August (Table 2, Fig. 4). Still, the viability of the produced oospores remains unknown. Multicellular nodal bulbils were frequently exhibited in fertile C. squamosa specimens, also indicating the vegetative reproduction strategy.

Similarities and uncertainties in the taxonomy of C. squamosa and C. gymnophylla were evident, in par-

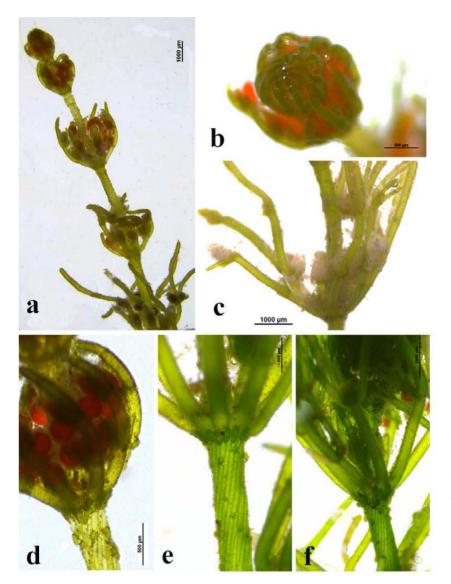


Fig. 4. The key morphological characteristic of Chara squamosa, a) apical nodes and internodes, scale 1000 µm b) the top of the apical node, ecorticated branchlets and short end cells, scale 500 µm c) the formation of gyrogonites, scale 1000 µm d) stipulodes, cortex and spines, scale 500 µm e) stipulodes, cortex and spines, scale 500 µm f) stipulodes, cortex and spines, scale 1000 µm. The plants were collected at the localities of Tometino Polje (a, b, c, d) and Vrujci (e, f).

ticular as isostichous and unrecognisable cortex types are common in both taxa. Given the variability of both species, their overlapping distribution and ecology, we still seem to be a long way off the final clarification of this taxonomic puzzle. The Balkans could represent a suitable geographical area for the revision of available herbarium material and the continuation of field studies towards the elucidation of the ecology of these species. DNA barcoding of freshly collected material could provide part of the solution in light of the contradictory results obtained to date (Schneider et al. 2016; Romanov et al. 2024), thus requiring further molecular studies.

## **CONCLUSIONS**

Our study provided a significant overview of the presence and distribution of C. squamosa in Serbia. Chara squamosa and C. gymnophylla were identified as new species of Characeae inhabiting Serbia, and based on

available recent and historical data both were categorised as Critically Endangered. Further studies on the distribution of C. squamosa and C. gymnophylla in the Balkan region and wider area are needed to enhance our understanding of their ecology. Additionally, molecular insights into the distinction between these species are required to confirm their taxonomic concept and species status.

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**REZIME** -



# Chara squamosa (Characeae, Charophyceae) u Srbiji - uvid iz taksonomske revizije kolekcije harofita u BEOU i nedavnih terenskih podataka

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Chara gymnophylla jedna je od prvih vrsta pršljenčica zabeleženih u Srbiji krajem 19. i početkom 20. veka, i tada je na našim prostorima bila druga po učestalosti javljanja. Pogrešna taksonomska tumačenja u prošlosti dovela su do toga da je još jedna vrsta, C. squamosa, bila skrivena među nalazima vrste C. gymnophylla. Chara gymnophylla je pak kasnije u Srbiji taksonomski tretirana kao varijetet - C. vulgaris var. gymnophylla, i kao takva nije bila na listama vrsta koje naseljavaju teritoriju Srbije. U skorije vreme sugerisan je novi taksonomski koncept za vrstu C. squamosa, što je podstaklo reviziju bogatog materijala C. gymnophylla, C. vulgaris var. gymnophylla, C. vulgaris var. nitelloides i C. rohlenae, deponovanih u kolekciji BEOU. Proces revizije se odvijao paralelno sa terenskim istraživanjima i prikupljanjem novog materijala. Naša istraživanja su pokazala po prvi put prisustvo vrste C. squamosa u Srbiji. Zasnovano na brojnim revidiranim uzorcima iz kolekcije BEOU, kao i uzorcima prikupljenim u novije vreme, povrđeno je kontinuirano prisustvo ove vrste u Srbiji počev od 1976. godine. Chara squamosa i C. gymnophylla su dodate na listu vrsta pršljenčica koje naseljavaju teritoriju Srbije i klasifikovane su kao kritično ugrožene (CR) prema kriterijumima IUCN. U ovom radu dat je biogeografski, ekološki i taksonomski pregled vrste C. squamosa u Srbiji, u odnosu na vrstu C. gymnophylla. Kolekcija pršljenčica BEOU se pokazala kao dragoceni i relevantni resurs za kritičke taksonomske revizije. Rezultati prezentovani u ovoj studiji snažno podstiču dalja istraživanja distribucije vrsta C. squamosa i C. gymnophylla na Balkanu i na širem području, kao korak ka daljem rasvetljavanju njihove ekologije i utemeljenju taksonomskih koncepata.

Ključne reči: Chara gymnophylla, Chara squamosa, distribucija, pršljenčice, Balkan