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RESEARCH

First records of *Chara tomentosa* and *Chara papillosa* (Charophyceae) from Slovakia

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Abstract

Macroscopic charophyte algae (Charophyta / Charophyceae) are rare and threatened organisms and remain relatively poorly documented in Slovakia. In recent years, we investigated several aquatic habitats at three localities with a focus on charophyte species. Two *Chara* species, *C. papillosa* Kützing and *C. tomentosa* L., were recorded for the first time in Slovakia, and new localities of *Chara contraria* A.Braun ex Kützing, *C. globularis* Thuiller, and *Nitellopsis obtusa* (Desvaux) J.Groves were identified. In addition, the association *Charetum tomentosae* Corillion 1957 was conclusively recorded for the first time in the country.

Keywords Charophytes · Charetum tomentosae · Central Europe · Macroscopic algae · Stoneworts

Introduction

Macroscopic charophyte algae (Charophytes/Charophyceae), commonly known as stoneworts, are found on all continents except Antarctica (Wood and Imahor 1965; Krause 1997; https://www.algaebase.org/). In general, stoneworts, as true aquatic plants, prefer freshwater habitats, both lotic and lentic, and occur less frequently in brackish or saline environments. They are able to grow in both natural and artificial habitats (e.g. Schneider et al. 2015).

The European charophyte flora consists of 63 species distributed across the continent, with the highest diversity in the western and central regions. Species richness gradually decreases towards the north and east (Schubert et al. 2024). Slovakia is among the countries with relatively low charophyte species richness and limited information on their distribution. Nevertheless, 19 taxa representing three genera, *Chara* L. (11 species), *Nitella* C.Agardh (7 species), and *Nitellopsis* Hy (1 species), have been reported from the country (Hindáková et al. 2022). The most recent Checklist, based on a revision of all available herbarium specimens, showed that some species listed in previous Checklists, Red lists, or vegetation surveys (Husák 1985; Hindák and Hindáková 1998, 2001; Oťaheľová 2001; Hrivnák et al. 2019) had been included in error. For example, *Chara tomentosa* L., previously reported as a dominant species in the association *Charetum tomentosae* Corillion 1957 from southern Slovakia (Oťaheľová 2001; Hrivnák et al. 2019), was later shown, based on the critical revision of herbarium material, to be *Chara vulgaris* L. Similarly, unpublished records from other parts of Slovakia, documented by herbarium specimens stored in the Herbarium of the Slovak Academy of Sciences (SAV), were identified as other *Chara* species. Therefore, *C. tomentosa* was not included in the most recent checklist of charophytes (Hindáková et al. 2022). For the same reason, data on the occurrence of *Charetum tomentosae* in Slovakia are also incorrect.

In recent years, systematic research on charophytes has brought several noteworthy findings, including new localities of known species and the discovery of species new to Slovakia. Therefore, we aim to describe the distribution, ecology, and conservation status of two species newly confirmed for Slovakia, *Chara tomentosa* and *Chara papillosa* Kützing, as well as the plant community *Charetum tomentosae* and other charophytes in the studied localities.

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Material and methods

Chara species were studied in three localities, with particular emphasis on the target species *C. papillosa* and *C. tomentosa*.

1. Ohrady (Fig. 1a, b): The site consists of three former peat-extraction ponds located along the Ohradský kanál, southeast of the village of Ohrady in southern Slovakia (central point of the ponds: 47.9843869N, 17.7080847E, 110 m a.s.l.), area of the ponds is 9 ha, maximum depth 3 m. Macrophyte vegetation, including true aquatic plants such as *Stuckenia pectinata* (L.) Börner, *Myriophyllum verticillatum* L., *Najas marina* L., and *Utricularia vulgaris* agg., was recorded in all ponds, though with varying degrees of cover. Marsh vegetation of the *Phragmition communis* Koch 1926 alliance created the littoral zones, as well as remnants of successionally transformed fens belonging to the *Molinion caeruleae* Koch 1926 alliance (cf. Dudáš et al. 2020).
2. Senec, Slnečné jazerá ponds (Fig. 1c, d): a large gravel pit with recreational use, located on the eastern margin of the town of Senec (48.2187236N, 17.4232128E, 118 m a.s.l.), area ca 100 ha, maximum depth 12 m, dredged in 1845. Among true aquatic plants, *Myriophyllum spicatum* L., *Najas marina* L., *Stuckenia pectinata* (L.) Börner, and *Utricularia vulgaris* agg. were recorded.
3. Veľký Meder (Fig. 1e, f), gravel-ditch used as a fish pond south-eastern from the town Veľký Meder (47.8669744N, 17.7936472E, 105 m a.s.l.), area 13 ha, maximum depth 25 m. Macrophytes were limited to irregular thin reed patches along the shore due to herbivorous fish presence. *Cladophora glomerata* L., and *Chaetophora lobata* Schrank. were growing among the reeds with stoneworts.

Charophytes at the localities were intensively studied during the vegetation seasons of 2022–2025. The locations were searched from air by a drone (DJI Mini), and by hand

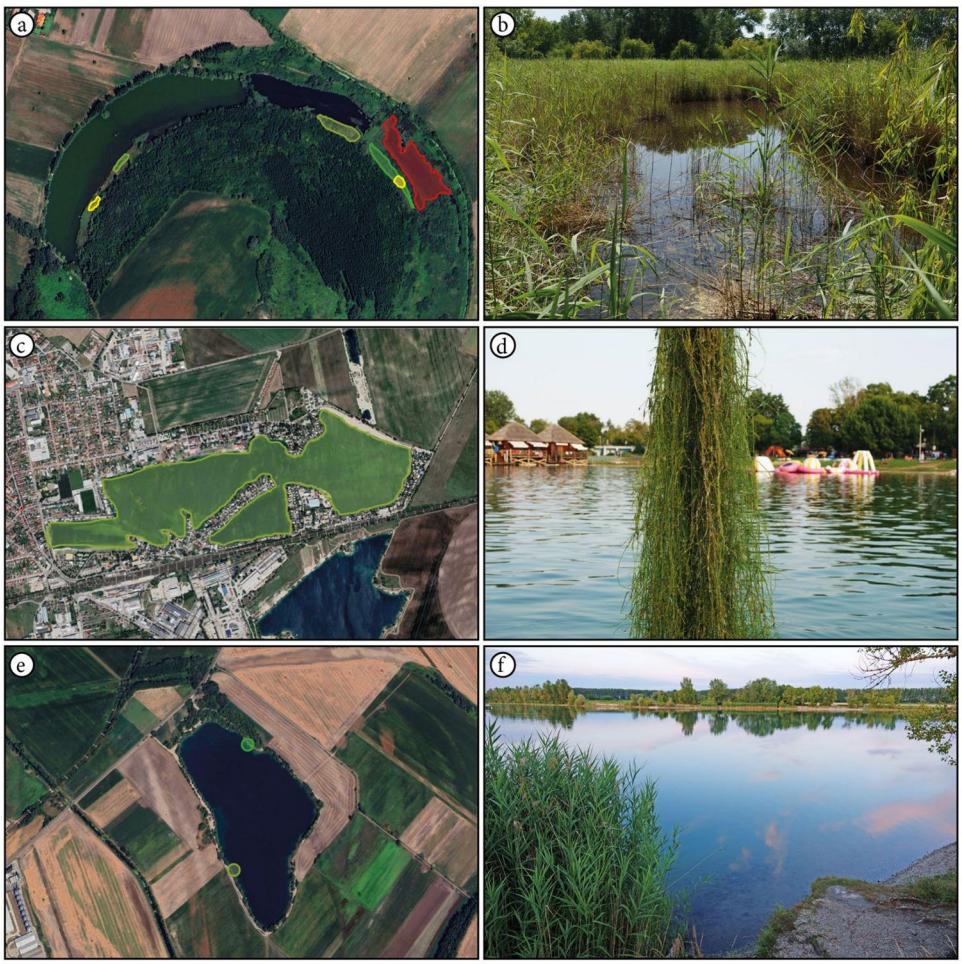

Fig. 1 Studied localities: 1, Ohrady – **a**) satellite view of Ohrady ponds with marked areas of charophyte population: *Chara contraria* (green), *Chara papillosa* (yellow), *Chara papillosa* + *Chara contraria* (light green) and *Chara tomentosa* (red), August 2024, Google Maps; **b**) habitat of *Chara papillosa* in the middle pond, 11. 7. 2025, F. Bednár; 2, Senec – **c**) satellite view of the Slnečné jazerá ponds in Senec, March 2003, Google Maps; **d**) habitat of Slnečné jazerá with *Nitellopsis obtusa* catch, 14. 8. 2024, F. Bednár; 3, Veľký Meder – **e**) satellite view of Veľký Meder pond, August 2024, Google Maps; **f**) habitat of *Chara papillosa*, 11. 7. 2024, F. Bednár

collection and by a grapnel, both from the shore and from the boat. The findings were photographically documented in the field, samples were collected and later macrophotographed in home laboratory by Canon EOS R7 and Canon EF 100/2.8 USM lens. The material was examined microscopically by Zeiss Stemi 305 and Olympus BX51 microscopes. Microscope slides were prepared from living specimens in tap water, no staining. Microphotographs were taken by Canon EOS R7 camera. Dimensions were determined from the images via a calibrated slide (Zeiss Calibration Slide Universal CG = 0, Item no.: 474029–9011-000). In addition, several ecological characteristics were evaluated in all localities. Water depth was recorded at several randomly selected locations. Water temperature, pH, conductivity, total dissolved solids (TDS), and salinity were measured in situ near water surface (water depth 5–10 cm) using a portable Thermo Scientific™ Elite PCTS meter, calibrated to Fischer NIST buffer standard solutions. The land area of the sites was measured using satellite imagery in Google Earth.

A phytosociological relevé with dominance of *Chara tomentosa* was conducted using the traditional Zurich–Montpellier approach (Westhoff and van der Maarel 1973).

The IUCN Red list Categories were applied using the IUCN guidelines [IUCN 2012a, b; 2024]. The IUCN criteria A–E were used to identify the categories for each species.

The scientific names of species follow AlgaeBase (www.algaebase.org). Herbarium specimens were pressed and are stored in the author's herbarium. In addition, specimens of *C. papillosa* and *C. tomentosa* are also deposited in the BRA herbarium. Herbarium sheets were prepared in accordance with the guidelines of The Herbarium Handbook (Royal Botanic Gardens 2019). Observations are recorded on iNaturalist: Ohrady: https://www.inaturalist.org/observations?d2=2026-01-19&nelat=47.985886882140235&nelng=17.715659255174597&subview=map&swlat=47.97991198071783&swlng=17.70055305400272&taxon_id=151788&user_id=fero&verifiable=any; Senec: https://www.inaturalist.org/observations?d2=2026-01-19&nelat=48.228848510544246&nelng=17.445298606607576&subview=map&swlat=48.208432351655645&swlng=17.39946501896109&taxon_id=151788&user_id=fero&verifiable=any; Veľký Meder: https://www.inaturalist.org/observations?d2=2026-01-19&nelat=47.875919267384006&nelng=17.805393104291856&swlat=47.859566825104885&swlng=17.784107093549668&taxon_id=151788&user_id=fero&verifiable=any; (accessed on 19. 1. 2026).

Specimens were identified using standard identification keys (Krause 1997; Urbaniak & Gąbka 2014; Schubert et al. 2024) and revised by Roman Romanov.

Results

Across the Ohrady ponds (locality 1; Fig. 1a,b), three *Chara* species were recorded: *C. contraria*, *C. tomentosa* (see also Appendix 1), and *C. papillosa* (see also Appendix 1). Each species displayed a distinct distribution pattern. *Chara contraria* A.Braun ex Kützing, *C. tomentosa* occurred mainly in the littoral zones, while *C. tomentosa* in contrast covered the entire eastern pond. *Chara contraria* was restricted to the littoral zones of both, the western and eastern ponds. In the middle pond, *C. contraria* occurred together with *C. papillosa* (Figs. 1a, 3a–d). Water was shallow (10–20 cm), under alkaline conditions and with the highest measured water conductivity (Table 1). *C. papillosa* was rare, occurring only in relatively small littoral areas of each pond (western pond: 1 m2; middle pond: 25 m^2; eastern pond: 1 m2; Fig. 1a). Similar to the previous species, it grew in shallow, alkaline water with high conductivity (Table 1). The third species, *C. tomentosa*, was the most widespread, occurring solely in the eastern pond, occupying an area of approximately 670 m, of which about 500 m^2 had more than 90% coverage throughout nearly the entire depth volume. Here, water was the deepest (0.5–3 m), and both pH and conductivity reached

Table 1 Basic ecological characteristics of water in the studied ponds

Characteristics/Locality		Date	Temperature (°C)	pH	Conductivity (µS/cm)	TDS (ppm)	Salinity (ppt)
1. Ohrady	Western pond	11.7.25	27.9	8.1	1434	1020	0.7
	Western pond puddles	5.6.25	28.5	8.6	2660	1900	1.4
	Middle pond	11.7.25	24.5	9.2	1137	808	0.6
	Eastern pond	5.6.25	25.8	8.7	732	521	0.3
2. Senec		6.9.23	22.4	9.1	905	644	0.4
		25.9.23	20.1	9.5	867	625	0.4
		6.12.23	22.4	9.1	644	644	0.4
		14.8.24	28.3	9.6	884	626	0.4
3. Veľký Meder		11.7.25	22.6	9.2	500	355	0.2

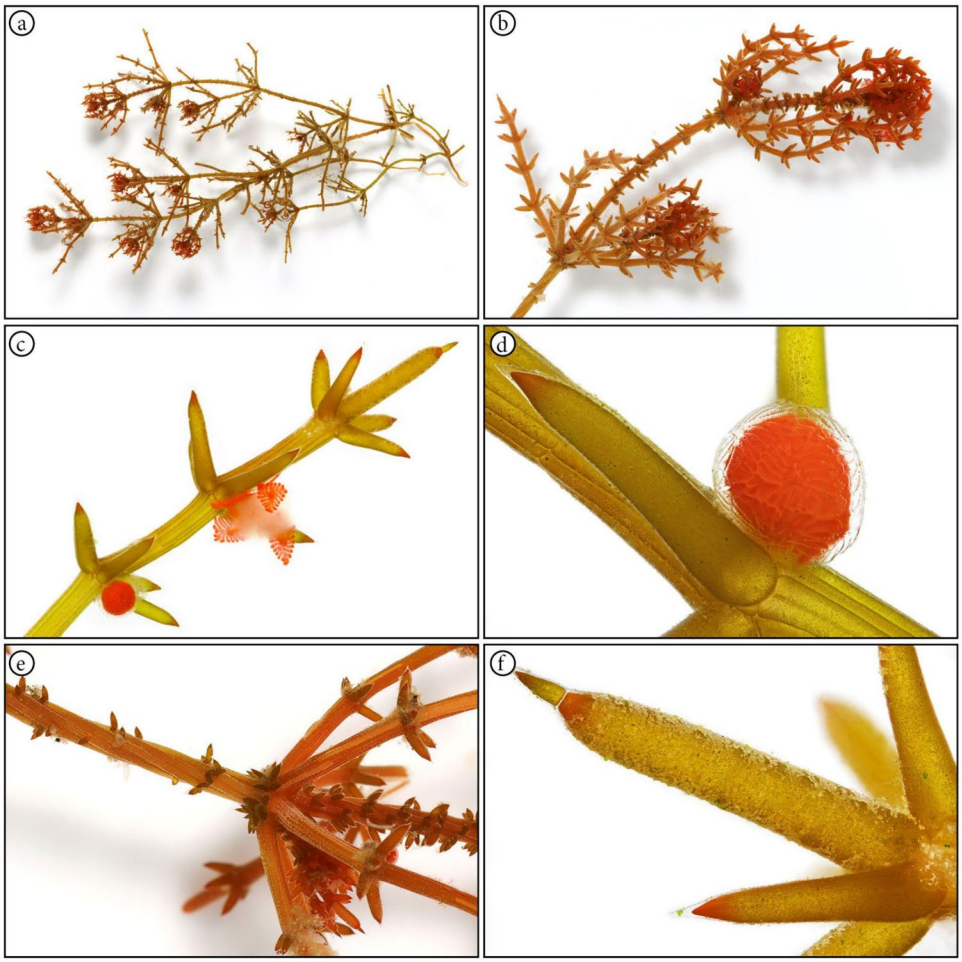

Fig. 2 *Chara tomentosa*, 1, Ohrady: **a**) general morphology, 5. 6. 2025; **b**) whorls, 14. 6. 2025; **c**) branchlet with antheridia and open shield cells, 14. 6. 2025; **d**) antheridium, 14. 6. 2025; **e**) base of a branchlet whorl with spiral cortex, spine cells and stipulodes,14. 6. 2025; **f**) branchlet terminal cell and bract cells. All photographs by F. Bednár

the lowest values among all stands (Figs. 1a, b, 2; Table 1). Typical stands of the species are represented by the following phytosociological relevé (Fig. 4):

27 May 2025, area 16 m2; herb-layer cover: 100%; stagnant water, depth 50–80 cm; author: Richard Hrivnák.

E_1: *Chara tomentosa* 5, *Phragmites australis* (Cav.) Trin. ex Steud. +.

In the locality near Senec town (2; Fig. 1c, d), *C. globularis* Thuiller, *C. hispida* L., *C. papillosa* (Fig. 3e; see also Appendix 1), and *Nitellopsis obtusa* (Desvaux) J.Groves were found; these species frequently created mixed stands forming a dense multispecific charophyte meadow, covering nearly the full bottom of the lake. All species grew across a wide range of water depths, mainly at 4–6 m below the water surface. The water was alkaline, with high transparency and relatively stable conductivity during the vegetation season (Table 1).

Chara papillosa (Fig. 3f; see also Appendix 1), *C. globularis* and *C. contraria* were recorded at the locality near Veľký Meder (3; Fig. 1e, f). Small populations of a few clumps grew in the littoral reed stands (*Phragmites australis*) along the shore in shallow water (0.2–0.5 m) with an alkaline reaction and a relatively low conductivity value (Table 1).

Given that only three localities are known in Slovakia, one of them with a very small population, we recommend the inclusion of *C. papillosa* in the Slovak Red List as Critically Endangered species (CR; B1a, 2a). Similarly, C. *tomentosa* is known from only a single locality in Slovakia, therefore we recommend listing it in the Slovak Red List as Critically Endangered (CR; B1a, 2a), as well.

Discussion

Six charophyte species were recorded in the studied area. While *C. contraria, C. globularis*, *C. hispida* and *Nitellopsis obtusa* had been previously documented in Slovakia, the other two species (*C. papillosa* and *C. tomentosa*) are reported from Slovakia for the first time (see Hindáková et al. 2022). Although *C. tomentosa* had been mentioned in Slovakia in earlier sources, a revision of the herbarium specimens revealed that these records actually belonged to

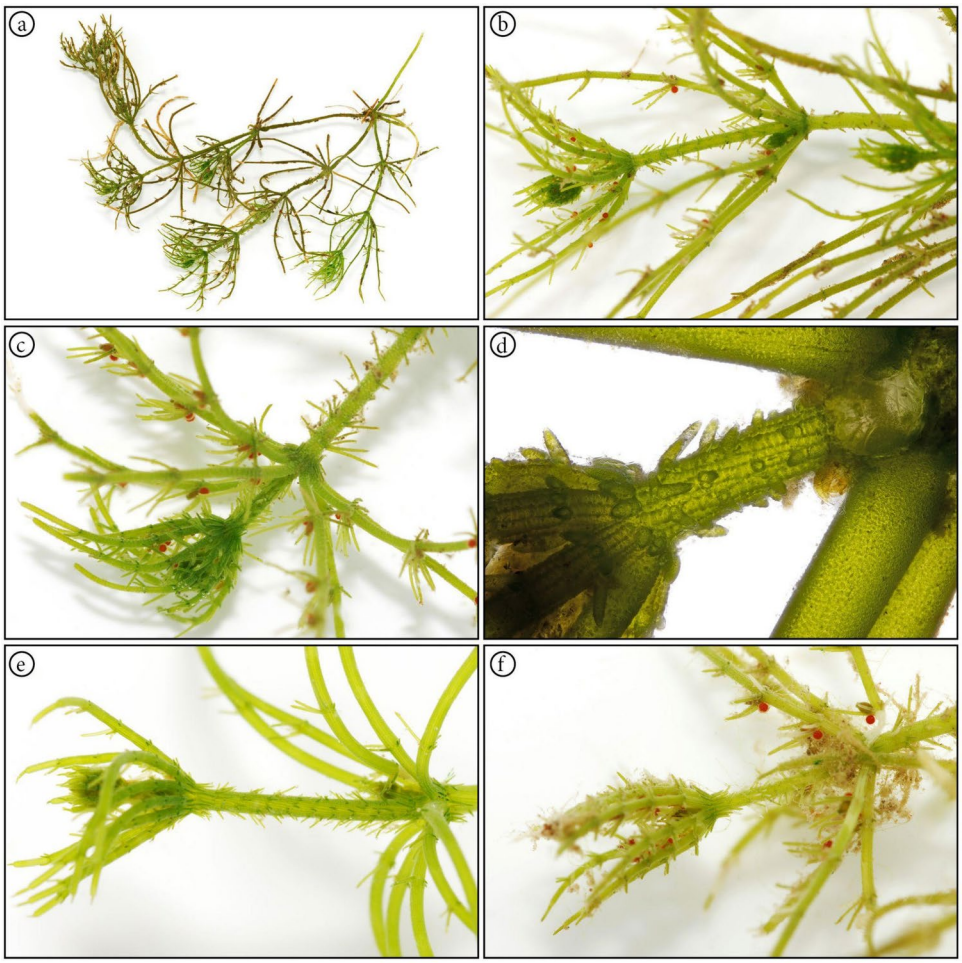

Fig. 3 *Chara papillosa*, Ohrady, 14. 6. 2025: **a**) general morphology; **b**) branch; **c**) whorl with gametangia; **d**) stem with tylacanthous cortification; **e**) plant detail from Senec, 14. 8. 2024; **f**) plant detail from Veľký Meder, 11. 7. 2025. All photographs by F. Bednár

other *Chara* species. Consequently, *C. tomentosa* was not included in the most recent charophyte checklist (Hindáková et al. 2022). Except *C. hispida* from Senec, all other species records represent new localities for Slovakia.

Chara tomentosa has formed a massive, monospecific underwater meadow near Ohrady village, covering most of the bottom of the eastern pond. The higher cover was limited to a littoral marsh species, *Phragmites australis*, which overgrew the pond margins with shallow water (Figs. 1a, 2, and 4). *Chara tomentosa* has a scattered distribution across the European continent, with more frequent records in Germany and along the Baltic coast, while recent data from areas close to Slovakia are very rare (Torn in Schubert et al. 2024). This rarity may be partly due to the species' preference for hard waters; however, it frequently grows in freshwater and tolerates a wide range of trophic conditions, water pH, electrical conductivity, and water depth (Torn in Schubert et al. 2024). The typical substrate is organic mud (Torn in Schubert et al. 2024), and in Poland, it often grows in peatland exploitation ponds (Urbaniak and Gąbka 2014). The eastern pond near Ohrady village has a similar origin, with organic mud at the bottom. The association *Charetum tomentosae* Corillion 1957, previously reported from Slovakia (Hrivnák et al. 2019) based on a misidentified dominant *Chara* species, is here published correctly for the first time from this territory. In Central Europe, this association is mainly known from Poland, where it occurs at numerous localities (Urbaniak and Gąbka 2014; Kolada 2021). In some areas, the community has even expanded over the recent decades (e.g., Kłosowski et al. 2006). Charophyte communities are generally considered competitively weak and are relatively quickly replaced by more competitive communities formed by vascular aquatic plants (Šumberová in Chytry 2011). Unlike some other charophyte species, *C. tomentosa* is a robust, medium- to large-sized plant (Urbaniak and Gąbka 2014; Torn in Schubert et al. 2024), which, under suitable ecological conditions, can be a strong competitor. Consequently, this species can survive long-term and gradually overgrow suitable habitats. The species was first documented at the locality by a photograph in 2020 (see https://floraveg.eu/vegetation/pictures/Charetea%20intermediae#image16282), but without identification to the species level. Only male plants were recorded at the locality near Ohrady, similarly to most localities across Europe, where male plants have been found more often than female plants

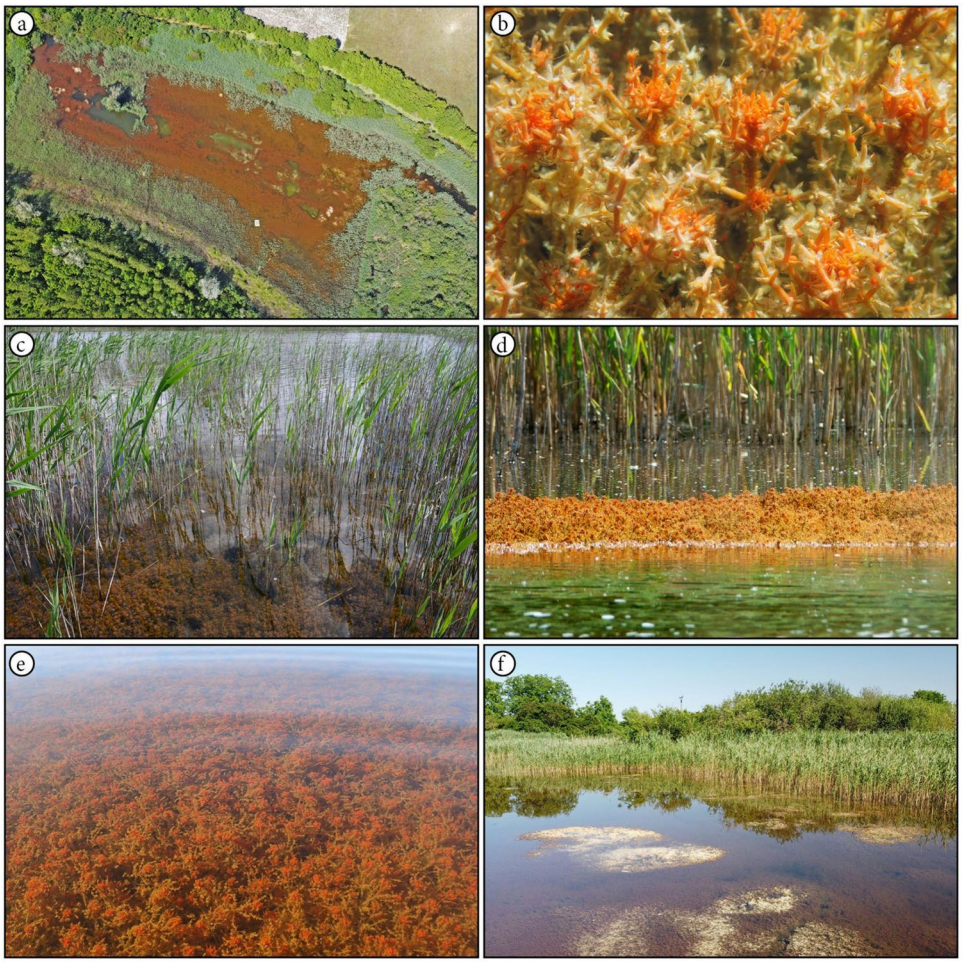

Fig. 4 *Charetum tomentosae* association near Ohrady village: **a**) aerial view, 5. 6. 2025, F. Bednár; **b**) underwater view, 14. 6. 2025, F. Bednár; **c**) habitat in littoral zone, 27. 5. 2025, R. Hrivnák; **d**) emerging plants at low level of water, 5. 6. 2025, F. Bednár; **e**) dense underwater meadow, 5. 6. 2025, F. Bednár; **f**) typical white dried *Chara* mineral incrustation at low water level, 5. 6. 2025, F. Bednár

(Torn in Schubert et al. 2024). *Chara tomentosa* is normally perennial. In autumn, the specimens break into a large number of fragments or hibernate as fully grown plants. Later, from spring to late summer, they complete the entire developmental cycle: fresh shoots emerge from the nodes or continue to grow and form antheridia and oogonia (Torn et al. 2004; Korsch 2013). It is interesting that among three separate but closely situated ponds near the village of Ohrady, a population of *C. tomentosa* was recorded only in the eastern pond. We assume this is due to the presence of the herbivorous fish, relatively frequent recreational fishing, and the physical removal of macrophytes in the other two ponds, whereas none of these activities are carried out in the eastern pond.

In Europe, *Chara papillosa* has been recorded sparsely from northern Scandinavia to the Mediterranean Sea in the south, to Russia, the Balkans in the east, and to France and Great Britain in the west (Blindow et al. in Schubert et al. 2024). In Central Europe, its distribution is generally rare, although the species has been documented in all neighbouring countries (previously as *C. intermedia* A.Braun ex Lange; Caisova and Gąbka 2009; Urbaniak and Gąbka 2014; Borisova 2016; Blindow et al. in Schubert et al. 2024). Our finding complements the known distribution and confirms the rare occurrence of the species in Central Europe. Consistent with our observations of habitat characteristics, *C. papillosa* generally prefers shallow, calcium-rich waters with neutral to alkaline pH (Caisova and Gąbka 2009; Urbaniak and Gąbka 2014; Blindow et al. in Schubert et al. 2024). *C. papillosa* belongs to the Hartmania group, a complex of coarse, diplostichous *Chara* species that are difficult to distinguish (Blindow et al. in Schubert et al. 2024). The species is threatened by eutrophication, which increases competition with other submerged plants and leads to overgrowth by filamentous algae, shading, and deoxygenation associated with algal blooms. The introduction of carp represents an additional serious threat and should be avoided at sites hosting *C. papillosa* (Blindow et al. in Schubert et al. 2024). This factor likely explains why *C. papillosa* occurs only in shallow reed zones in the fish ponds of Ohrady and Veľký Meder, whereas at Senec, a predominantly recreational site, it forms dense underwater meadows.

In addition to the newly recorded *Chara* species for Slovakia, we found four additional species belonging to

threatened charophytes: *C. globularis* (NT), *C. contraria*, *C. hispida* (VU), and the endangered (EN) *Nitellopsis obtusa* (Hindáková et al. 2022).

Chara globularis, together with *C. vulgaris*, belongs to the most frequent charophytes in Slovakia, occurring mainly in the western part of the country and less frequently in the south-eastern and northern regions (Hindáková et al. 2022; see also https://www.inaturalist.org/taxa/479829-Chara-globularis#map-tab). A similar distribution pattern is known from Europe, where the number of localities decreases from west to east. However, in contrast to its rare occurrence in the northern regions of Slovakia, the species is relatively abundant in European regions north of Slovakia (Schubert et al. 2024). This pattern is mainly related to the differences in geomorphological and environmental conditions: mountainous landscapes with a low number of suitable aquatic habitats in Slovakia versus extensive lowlands with numerous lakes and ponds in the Baltic Sea region.

Another *Chara* species, *C. hispida*, is strictly confined to lowland landscapes of south-western Slovakia and also occurs only rarely in the south-eastern part of the country (Hindáková et al. 2022; see also https://www.inaturalist.org/taxa/486266-Chara-hispida#map-tab). With the exception of the Baltic Sea region, the occurrence of this species in Slovakia represents the eastern margin of its distribution range in Central Europe (Blindow et al. in Schubert et al. 2024).

Chara contraria is commonly occurring species, distributed mainly throughout the Northern Hemisphere, but also present in South America, South Africa, and Australia. In Europe, it is similarly widespread across the entire continent (Bernhardt and Gregor in Schubert et al. 2024). Although the species is not frequently recorded in Slovakia, it is relatively common, occurring mainly in western and central parts of the country (Hindáková et al. 2022), and the number of new records has been gradually increasing (see iNaturalist: https://www.inaturalist.org/observations?place_id=8267&taxon_id=486262&verifiable=any; accessed 18 November 2025). This species inhabits a wide range of aquatic environments, and tolerates a wide range of eutrophication levels, as well as broad gradients of pH, mineral content, and water depth (Urbaniak and Gąbka 2014; Kolada 2021; Bernhardt and Gregor in Schubert et al. 2024). Similar habitat conditions to those reported for Europe have also been documented in Slovakia (Oťaheľová 2001; see also https://www.inaturalist.org/taxa/486262-Chara-contraria#map-tab).

The last charophyte species, *Nitellopsis obtusa*, has a relatively narrow distribution range in Slovakia, occurring in the lowlands of south-western Slovakia in stagnant waters of ponds and ditches (Oťaheľová 2001; Hrivnák et al. 2007; Oťaheľová et al. 2007; Dorotovičová 2013; Hindáková et al. 2022). Most localities have been recorded since 2000, which is related to intensified research on aquatic habitats (e.g. Hrivnák et al. 2007), the spread of the species to new localities, and its strong ability to colonize artificial eutrophic aquatic habitats (Pall et al. in Schubert et al. 2024). *Nitellopsis obtusa* exhibits characteristics of a superior competitor; its mass development can negatively affect other macrophytes through competition for space, light, and nutrients (Pełechaty et al. 2022; Sabovljević et al. 2024; Tomović et al. 2025). The species is rare in Central Europe, whereas more numerous localities are known from western and northern Europe (the Baltic Sea region, countries south of the North Sea, and Great Britain) (Pall et al. in Schubert et al. 2024).

The findings of new charophyte species and localities reported here is a result of two main factors. First, new intensive research by specialists has provided interesting new information. Such research has been conducted in recent years, is still ongoing, and has rapidly increased the number of charophyte discoveries in Slovakia (see iNaturalist). Second, charophytes are able to spread into new, often human-made aquatic habitats through both natural dispersal and human-mediated pathways (Schubert et al. 2024). Therefore, the number of new charophyte species recorded in Slovakia, as well as new localities of known species, is expected to increase in the future.

At present, neither *Chara tomentosa* nor *C. papillosa* are legally protected at any of the Slovak localities where they were recorded. In particular, the Ohrady pond complex represents a site of exceptional conservation value, as it currently constitutes the only confirmed locality of *C. tomentosa* in Slovakia and simultaneously hosts a population of *C. papillosa*. The coexistence of these two rare charophyte species, together with the presence of the association *Charetum tomentosae*, makes this locality unique at the national level and deserves targeted conservation attention and appropriate management to prevent habitat degradation and loss of charophyte stands. As proposed earlier in this study, based on current knowledge, both *C. tomentosa* and *C. papillosa* should be classified as Critically Endangered in Slovakia and included accordingly in the national Red List of charophytes. However, research on charophytes is ongoing, and additional localities, particularly for *C. papillosa*, may yet be identified. On the contrary, a substantial part of suitable aquatic habitats for Charales species has been studied during intensive research in recent years. Therefore, the given threat status reflects the current state of knowledge about stoneworts in Slovakia relatively well.

Appendix 1

Detailed morphological characteristics of *Chara tomentosa* and *C. papillosa* based on data from the localities in Slovakia.

Chara tomentosa from Ohrady forms dense stands of robust, yellow-green to reddish plants up to 2 m in length. The plants are encrusted and have thick, swollen spine cells and a rope-like, twisted main axis. Internodes are shorter than branchlets in the upper parts of the plant and longer in the lower parts. The cortex is tylacanthous and strongly diplostichous. Spine cells are ovoid, relatively long and swollen; stipulodes are arranged in two rows and are similar in length and appearance to the spine cells. Whorls consist of 6–7 branchlets, mostly with the last two cells ecorticated. Five to six well-developed bract cells of equal size are present. Bracteoles are similar to the bract cells and slightly more than twice as long as the antheridia. Only male plants were observed; antheridia are orange-red, placed singly at first 2–3 internodes. No bulbils were observed. See Fig. 2.

Our collected material of *C. papillosa* matches the species description (Schubert et al. 2024). Plants, light-green to olive-green colour, ranged from medium-sized, 10–20 cm (Ohrady and Veľký Meder) to robust, reaching more than 50 cm in length (Senec). Branchlets were shorter than internodes in the lower parts of the plant but longer than internodes in the upper parts. The cortex was diplostichous and tylacanthous, becoming isostichous in the lower parts, with slight spiralling observed. Spine cells were solitary but mostly arranged in groups of 2–3 (4); they were papilliform in lower parts, acute in upper parts, shorter than or as long as the main axis diameter, and occasionally longer. Stipuloids were arranged in two regular rows of nearly equal length, mostly more than half the main axis diameter to almost equal to it. Whorls consisted of 8–10 (12) branchlets, which were corticated except for the terminal cell and often the penultimate cell, the terminal cell was narrower than the apex of the penultimate cell. Bract cells were regularly arranged along the entire branchlet and spreading, with adaxial bract cells longer than abaxial ones. Two bracteoles, five times longer than antheridia. Plants monoecious, gametangia conjoined on the 3–5 lowest branchlet nodes. Oogonia and antheridia not studied in detail, mature oospores not observed. Bulbils not observed. See Fig. 3.

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Author contributions Conceptualization, Methodology, Investigation, Writing—review & editing: František Bednár, Richard. Hrivnák.

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Data availability All data are presented in iNaturalist.org.

Declarations

Competing interests The authors declare no competing interests.

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