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VEGETATION CLASSIFICATION

Calliergonetea megalophylli – a new class of bryophyte vegetation

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ABSTRACT

The new class Calliergonetea megalophylli **cl. nov.** is described for submerged and amphibious bryophytic vegetation of lakes and other enclosed water bodies with slow water exchange, with organic and organic-mineral substrates. The structure of the class is represented by a new order Calliergonetalia megalophylli **ord. nov.**, two alliances Calliergonion megalophylli **all. nov.** and Charo strigosae–Scorpidion scorpioidis **all. nov.** and 6 associations. The range of the class covers the tundra and boreal zones and southward to the mountainous regions of the Holarctic. The cenoflora of the class is characterized, its boundaries in composition, structure and ecology with other classes of aquatic and mire vegetation, where mosses occupy a significant place, are outlined.

Keywords: aquatic bryophyte vegetation, Braun-Blanquet classification, lakes, Calliergonetea, Calliergonetalia, European North, Altai

РЕЗЮМЕ

Тетерюк Б.Ю., Лавриненко О.В., Киприянова Л.М. Calliergonetea megalophylli – новый класс бриофитной растительности. Описан новый класс Calliergonetea megalophylli **cl. nov.** для погруженной и амфибиотической бриофитной растительности озер и других замкнутых водоемов с медленным водообменом, с органическими и органо-минеральными субстратами. Структура класса представлена новым порядком Calliergonetalia megalophylli **ord. nov.**, двумя союзами Calliergonion megalophylli **all. nov.** и Charo strigosae–Scorpidion scorpioidis **all. nov.** и 6 ассоциациями. Ареал класса охватывает тундровую и бореальную зоны и южнее – горные районы Голарктики. Приведена характеристика ценофлоры класса, очерчены его границы в составе, структуре и экологии от других классов водной и болотной растительности, где значимы мохообразные.

Ключевые слова: водная моховая растительность, классификация по Браун-Бланке, озера, Calliergonetea, Calliergonetalia, Европейский Север, Алтай

In plant communities of hydromorphic habitats bryophytes are often edificators and occupy sometimes large areas (Krajina 1933, von Hübschmann 1971, Dierßen 1982, Marstaller 1987, 2001, 2006, Baisheva 2010, Lavrinenko et al. 2016, Lapshina et al. 2022).

To date, there are two approaches to syntaxonomy of bryophyte-dominated communities (Berg et al. 2016). The first is synusial (merocoenotic) (Berg et al. 2016), in which the bryophyte layer is treated as an independent bryocoenosis. In such cases, vascular plants are not included in the relevés, only the biotope in which the described bryocoenosis (bryosynusia) is formed is given. The area of relevés in this case is from 1 to several dm^2 (Berg et al. 2016). According to the requirements of the International Code of Phytosociological Nomenclature (ICPN) (Theurillat et al. 2021), this approach is legitimate when using floristic-sociological criteria when making relevés and their processing. Using this approach, almost all syntaxa of bryophyte-dominated communities included in EuroVegChecklist2 (Mucina et al. 2016) have been described. The second approach is phytocenotic (holocenotic) (Berg et al. 2016), in which the entire species composition of communities, including both vascular and cryptogamous plants, is considered in the relevants. The area of relevés is usually a few m^2. The decision on the syntaxonomic status of communities is based on the presence and abundance of diagnostic species of the class.

Communities dominated by bryophytes and involving vascular plants in hydromorphic ecotopes are most often considered within the classes Scheuchzerio palustris–Caricetea nigrae Tx. 1937 (Krajina 1933, Dierßen 1982, Lavrinenko et al. 2016, Lapshina et al. 2022), Montio–Cardaminetea Br.-Bl. et R. Tx. ex Klika et Hadač 1939 (Bardat & Hauguel 2002, Baisheva et al. 2004, Peterka et al. 2023), Utricularietea intermedio–minoris Den Hartog et Segal 1964 (Bardat & Hauguel 2002, Matuszkiewicz 2008 ect.), Lemnetea minoris O. de Bolòs et Masclans 1955 (Bardat & Hauguel 2002), Littorelletea uniflorae Br.-Bl. et Tx. ex Westhoff et al. 1946 (Bardat & Hauguel 2002), Platyhypnidio–Fontinalietea antipyreticae Philippi 1956 (Taran 1997, Baisheva et al. 2004, Taran et al. 2005, Taran & Tyurin 2006 ect.).

The only class that unites exclusively aquatic bryophyte communities according to modern syntaxonomic reviews (Marstaller 2006, Mucina et al. 2016: EuroVegChecklist2) is the class Platyhypnidio–Fontinalietea antipyreticae. Since Krajina (1933) and somewhat later Koch (1936) described aquatic bryophyte communities as independent syntaxa of higher rank (orders and alliances), their syntaxo-

nomic content has been repeatedly supplemented and corrected (Schwickerath 1944, Waldheim 1944, von Krustenstjerna 1945, Poelt 1954, Hertel 1974, Plămădă 1974, Geissler 1976, Drehwald & Preising 1991 etc.). Both authors (Krajina 1933, Koch 1936) did not describe an independent class for aquatic bryophyte communities. This was later done by Philippi (1956). He presented a generalized system of aquatic moss communities of the southern Schwalzwald (Germany) as a first step in the analysis of this vegetation type. In this paper, Philippi united the aquatic bryophyte communities into one new class, but did not give it a verbal characterization. He proposed to distinguish orders by altitudinal gradient and water pH values: Brachythecietalia plumosi Philippi 1956 – acidic water communities of the high mountain belt; Leptodictietalia riparii Philippi 1956 – communities of alkaline waters of foothill and plain areas; Platyhypnidietalia rusciformis Philippi 1956 – communities of lowland rivers and streams. Based on this syntaxonomic structure of the class, it can be characterized as an integration of bryophyte communities in cold running waters, usually on mineral, less often organic-mineral substrates. The proposal of von Hübschmann (1957) to divide aquatic bryophyte communities into four independent classes on the basis of altitudinal principle, expressed a little later, did not find support, because it was essentially a repetition of the system of bryophyte communities of watercourses presented by Philippi (1956).

The study of the vegetation of water bodies of the European North of Russia and the Altai Mountains, as well as the analysis of numerous publications allowed us to identify communities of aquatic bryophytes, the syntaxonomic status of which is either not reflected in the currently existing generalized classification reviews of both European (von Hübschmann 1986, Marstaller 2006, Mucina et al. 2016) and Russian (Korotkov et al. 1991, Ermakov 2012) phytosociologists, or reflected erroneously.

To date, the syntaxonomic hierarchy of aquatic bryophyte communities in standing and low-flow reservoirs has not been developed. In this paper, new associations and high syntaxa are described for aquatic bryophyte communities in lentic ecosystems.

MATERIAL AND METHODS

Study area

Relevés were made at 9 sites (Fig. 1, Table 1) in the European North of Russia and the Altai Mountains. Climate data in the table 1 are characterized from the Climate Data (2025).

Sampling and data analysis

Geobotanical studies of aquatic bryophytes were carried out in the north of the European part of Russia – in the Nenets Autonomous Area and the Komi Republic, as well as in the south of Siberia – in the Republic of Altai and Altai Territory (Fig. 1). The material for syntaxonomic analysis was 44 relevés, performed by the authors in the summer (July – August) from 2005 to 2024. Three relevés taken from publications of other authors (Podbielkowski 1967, Taran 1997, Taran & Tyurin 2006) were also included in the analysis.

The survey was carried out according to standard methodologies. Hydro-botanical rakes were used during the works. In relatively deep lakes (5–7 m) in Altai, scuba diving equipment and a GoPro 9 camera were used to describe and photograph underwater plant communities.

Relevés were made within homogeneous contours of bryophyte vegetation on plots from 4 to 25 (60) m^2 in the European North. The area of studied mosses stands at depths below 5 m varied from 9 to 100 m^2 in the Altai. All species of cryptogamous and vascular plants at the

Table 1. Characterization of the authors' study areas

No. and name of study site	Zone / subzone	Landscape	MAT, °C	Mean (max) July – mean (min) January tempetrature, °C	MAP, mm
1. Pechora River Delta and adjacent tundra localities: Lovetskii Isl. in the Pechora Bay, eastern part of the Malozemelskaya tundra (Nenets Ridge), western part of the Bolshezemelskaya tundra (Bolvanskii Nose Cape, Ortina, Severnaya and Yachey River basins) (Nenets Autonomous Area)	Subarctic / typical and southern tundra (Aleksandrova et al. 1989)	Floodplain, hilly plain (Aleksandrova et al. 1989)	- 2.3	13 (30) – -17 (-45)	550
2. The south-eastern part of the Bolshezemelskaya tundra (Nenets Autonomous Area)	Subarctic / southern tundra (Aleksandrova et al. 1989)	Upland hilly plain (Aleksandrova et al. 1989)	- 5.5	12 (30) – -18 (-45)	700
3. The Polar Ural (Komi Republic)	Subarctic / southern tundra (Aleksandrova et al. 1989)	Mid-mountains of subalpine type (Gladkova 1977)	-5.3	14 (31) – -22 (-48)	825
4. The Subpolar Ural (Komi Republic)	Boreal / northern taiga (Aleksandrova et al. 1989)	Mid-mountains (Gladkova 1977)	- 3.0	15 (34) – -19 (-35)	744
5. The Middle Timan (Komi Republic)	Boreal / northern taiga (Aleksandrova et al. 1989)	Upland plain with ridges and hills (Gladkova 1977)	-0.2	16 (35) – -16 (-46)	676
6. The upper Pechora River basin (Komi Republic)	Boreal / northern taiga (Aleksandrova et al. 1989)	Smooth, flat-topped uplands (up to 786 m a.s.l.), stretched meridionally (Gladkova 1977)	0.3	17 (35) – -17 (-50)	712
7. The middle Vychegda River basin (Komi Republic)	Boreal / middle taiga (Aleksandrova et al. 1989)	Gently sloping plain (150 (200) m a.s.l. (Gladkova 1977)	1.7	18 (34) – -14 (-46)	700
8. Kolyvanskii Ridge of Altai (Altai Territory) is a mountain range in the northwest Altai Mountains	Boreal / south taiga (Kuminova 1960)	Low-mountains (500–600 m a.s.l.) (Kuminova 1960)	2.8	18 (38) – -14 (-50)	877
9. The Mountain Altai (Ulaganskii district, Republic of Altai)	Boreal / south taiga (Kuminova 1960)	Plateau, 1800–2100 m a.s.l., deeply dissected by river erosion (Kuminova 1960)	-2.3	15 (28) – -21 (-32)	681

plots are included in the relevés. The material was collected and analyzed according to the Braun-Blanquet's phytosociological approach (Westhoff & van der Maarel 1973) taking into account phytocenotic (holocenotic) approach in studying bryophyte communities (Berg et al. 2016). The cover of each species in a plant community was assessed by the old Braun-Blanquet's scale (Becking 1957): "r" – extremely rare; "+" – rare with low cover; "1" – cover up to 5 %; "2" – 5–25 %; "3" – 25–50 %; "4" – 50–75 %; "5" – 75–100 %. Estimates of species abundance in the papers of other authors have retained the original. The constancy of the species in the tables (for 5 and more relevés) is given on a percentage scale (%): I – > 0–20, II – 21–40, III – 41–60, IV – 61–80, V – 81–100. Diagnostic (dominant) and constant species were established when distinguishing syntaxa of association level and above (Chytrý 2011). Additional information includes depth, mechanical composition, and type of substrate on which communities form.

When processing relevés, the integrated botanical information system IBIS was used (Zverev 2007). Clustering of relevés (all species are included in the analysis) was performed by the cluster analysis (Ward's method), detrended correspondence analysis (DCA) ordination and assessment of ecological conditions of habitats in the PAST 4.03 package (Hammer et al. 2001).

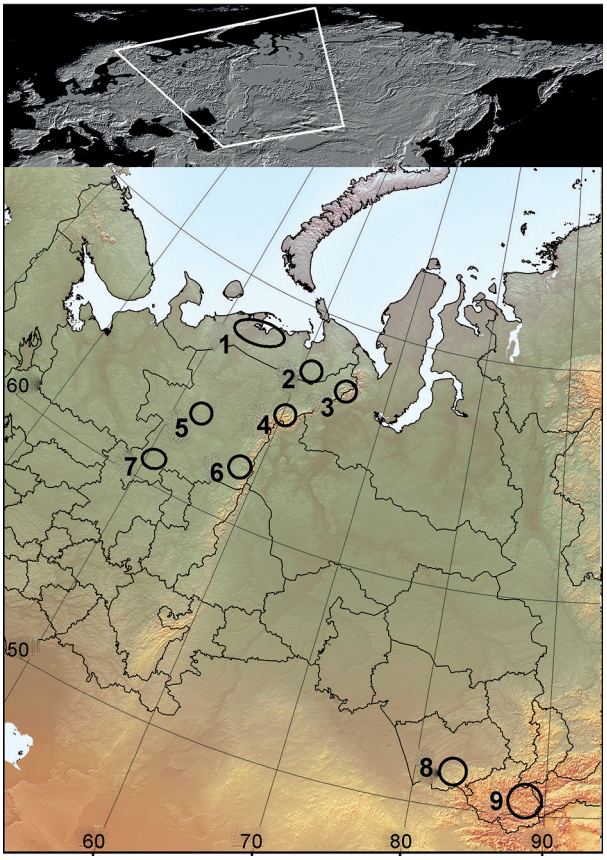

Figure 1 Study sites: 1 – Pechora River delta and adjacent Malozemelskaya and Bolshezemelskaya tundra localities (Nenets Ridge, Bolvanskii Nose Cape, Ortina, Severnaya and Yachey rivers basins; 2 – the south-eastern part of the Bolshezemelskaya tundra; 3 – the Polar Ural; 4 – the Subpolar Ural; 5 – the Middle Timan; 6 – the upper Pechora River basin; 7 – the middle Vychegda River basin; 8 – Altai Territory (Kolyvanskii ridge); 9 – the Mountain Altai (Ulaganskii District)

Measurement of water hydrogen index (pH) and its salinity (TDS) during fieldwork was carried out using a portable conductometer HANNA-98129.

Plant identification has been carried out and confirmed for mosses by O.M. Afonina (Komarov Botanical Institute RAS – BIN), G.V. Zheleznova (Institute of Biology Komi SC UB RAS – IB Komi SC) and E.Z. Baisheva (Ufa Institute of Biology UFRC RAS – UIB UFRC), for macrophytes – by A.A. Bobrov (Papanin Institute for Biology of Inland Waters RAS – IBIW).

The nomenclature of taxa of vascular plants, is given according to the World Flora Online (WFO 2025), mosses – the annotated checklist of bryophytes (Hodgetts et al. 2020), algae – Listing the World's Algae (Guiry & Guiry 2025).

The new syntaxonomic units are named according to the International Code of Phytosociological Nomenclature (ICPN) (Theurillat et al. 2021). Authors of syntaxa are given in the text at first mention and in Prodromus.

RESULTS

Based on the analysis of the summary table of relevés of moss communities of standing and slow-flowing water bodies, 6 associations divided into 2 alliances were identified (Table 2). Relevés grouped in associations reflect real combinations of species and form well-differentiated groups on the cluster tree and in DCA ordination analysis (Fig. 2A, B).

All. Calliergonion megalophylli Lavrinenko ex Teteryuk, Lavrinenko et Kipriyanova all. nov. hoc loco

Holotypus: ass. Calliergonetum megalophylli Lavrinenko et D'yachkova 2021 (Lavrinenko & D'yachkova 2021: P. 39 (rel. L54) and P. 37–38 (Table 2, syntaxon 2)).

Name-giving taxon: *Calliergon megalophyllum* Mikut. (Bryoth. Balt. No. 141. 1908).

Diagnostic species: *Calliergon megalophyllum*, *Drepanocladus aduncus*, *Sarmentypnum exannulatum*, *S. trichophyllum*.

Synonym: Calliergonion megalophylli O. Lavrinenko in Lavrinenko, Lavrinenko, Tsyvkunova et D'yachkova 2024 all. prov. (Art. 3b ICPN).

Description. Submerged (up to 1 m deep) and amphibious bryophyte vegetation in the shallow, well-warmed meso- and eutrophic lakes of various origins, enclosed water bodies and permanently watered depressions of relief in tundra and boreal zones of the Holarctic and in tundra and forest belts of mountains of South Siberia.

Ass. Sarmentypnetum trichophylli Lavrinenko et D'yachkova 2021 mut. Lavrinenko, Lavrinenko, Tsyvkunova et D'yachkova 2024 (Table 2, rel. 1–10; Fig. 3A, B)

Name-giving taxon: *Sarmentypnum trichophyllum* (Warnst.) Hedenäs (J. Hattori Bot. Lab. No. 100: 133. 2006).

Synonym: Warnstorfietum trichophylli Lavrinenko et D'yachkova 2021 nom. inept. (ICPN Art. 45).

Description. Submerged (up to 1 m deep) communities of *Sarmentypnum trichophyllum* in the lakes and other water bodies with slow water exchange.

Composition. Diagnostic species: *Sarmentypnum trichophyllum* (dominant). Mosses of medium to large size (10–15, up to 20 cm long) form single-species stands. Macrophytes are found occasionally (*Sparganium hyperboreum*) and once (*Hippuris vulgaris*) with low abundance. Total number of taxa registered in association is 3: 2 herbs and 1 moss; 1–2 species in communities.

Table 2. Syntaxa of the new class Calliergonetea megalophylli in the European North and the Altai Mountains

Alliance	Calliergonion megalophylli																																						Charo strigosae–Scorpidion scorpioidis								Constancy and abundance					
Association	Sarmentypnetum trichophylli (a)										D. a. (b)			Calliergonetum megalophylli (c)								Myriophyllo sibirici–Sarmentypnetum exannulati (d)																		C. g.–C. g. (e)				C. s.–S. s. (f)									
Relevé area, m²	16	12	6	10	25	30	4	15	4	6	75	4	0.25	25	9	9	25	18	8	5	9	10	10	10	28	10	10	60	10	6	40	20	10	16	10	10	10	10	25	100	50	100	50	9	100	9	30						
Substrate	sa-si	si	sa	sa	sa-si	sa-p	si	sa-si	si	si	–	si	–	sa-si	sa-si	sa	sa	sa-si	sa-si	si	c-si	s-si	si	c	si	si	c-si	si	sa-s	sa	si	s-si	c-si	sa-si	p-si	sa-si	si	si	p-si	s-si	s-si	s-si	s-si	si	–	si	sa						
Water depth, cm	70	60	50	50	60	50	70	40	70	70	40	0	50	40	50	10	5	10	100	50	30–150	70	10	0	100	90	60	40	90	30	80	40	50	20	10	100	100	70	40	110	50	370	500	360	300	140	22						
Cover total, %	80	90	100	100	100	100	100	100	100	100	100	90	100	100	100	100	100	0	100	100	100	35	90	100	100	90	100	90	80	100	100	100	100	100	100	100	100	100	90	100	100	90	100	50	90	80	100						
herbs	0	0	0	0	0	0	<1	<1	1	10	1	1	–	20	<1	5	<1	<1	0	20	5	<1	1	0	<1	1	1	<1	5	10	10	<1	10	15	3	7	10	3	10	<1	<1	0	0	<1	<1	<1	<1						
mosses	80	90	100	100	100	100	100	100	100	90	100	90	–	90	100	100	100	100	100	90	100	35	90	100	100	90	100	90	70	100	90	100	100	100	100	100	85	100	90	100	100	85	100	55	90	80	100						
Number of taxa	1	1	1	1	1	1	2	2	2	2	9	10	4	5	4	6	2	4	1	4	7	3	7	1	3	2	2	3	3	4	5	3	3	6	6	4	7	7	5	3	4	4	2	6	3	3	4						
Relevé number by author	Ор38_23	Я40_22	НМ6_22	БН7_20	L39_20	L56_20	ОР6	НГ1А_21	ОР7	ОР16	7a	84 ГТ	406	БН21_20	КУМ81	КУМ88	НГ51_21	Кум24_23	L54_20	L53_20	Т24-060	Т12-284	Т20-245a	Т10-208	К-23-53/2	Т13-029	Т12-281	К-18-34	Т05-027	Т05-024	К-21-65	К-23-79	Т15-Х15	Кум26_23	Т15-151	Т18-178	Т08-190	Т07-030	Т15-139	К-18-41	К-23-123	К-у23-8	К-у23-16	К-20-67	К-18-39	К-20-66/2	К-23-127						
Table number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38***	**39**	**40**	**41**	**42***	**43**	**44**	**45***	**46**	**47**	**a**	**b**	**c**	**d**	**e**	**f**
Diagnostic species of the ass. Sarmentypnetum trichophylli																																																					
Sarmentypnum trichophyllum	5	5	5	5	5	5	5	5	5	5	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V^{5}	.	I^{1}	.	.	.
Diagnostic species of the ass. Drepanocladetum adunci																																																					
Drepanocladus aduncus	.	.	.	.	.	.	.	.	.	.	5	5	4	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	$3^{4,5}$	$II^{+,1}$	.	.	.
Diagnostic species of the ass. Calliergonetum megalophylli																																																					
Calliergon megalophyllum	.	.	.	.	.	.	.	.	.	.	.	.	.	5	5	5	5	5	5	5	5	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	V^{5}	$I^{1,2}$	.	.
Constant species of the ass. Calliergonetum megalophylli																																																					
Hippuris lanceolata	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	+	+	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	IV^{r-1}	.	.	.
Diagnostic species of the ass. Myriophyllo sibirici–Sarmentypnetum exannulati																																																					
Sarmentypnum exannulatum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2	3	5	5	5	5	5	4	4	5	5	5	5	5	5	5	5	5	5	2	2	.	.	2	.	.	.	.	.	II^{2}	V^{3-5}	2^{2}	1^{2}
Constant species of the ass. Myriophyllo sibirici–Sarmentypnetum exannulati																																																						
Myriophyllum sibiricum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	+	+	1	1	1	1	+	+	+	.	+	+	.	.	.	.	I^{r}	$III^{+,1}$	3^{+}	2^{+}
Diagnostic species of the ass. Charo globularis–Calliergonetum gigantei																																																					
Calliergon giganteum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	5	5	.	.	.	.	.	.	.	.	$4^{4,5}$	.
Diagnostic species of the ass. Charo strigosae–Scorpidietum scorpioidis																																																					
Scorpidium scorpioides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	5	4	5	.	.	.	.	.	$4^{4,5}$
Diagnostic species of the class Charetea intermediae																																																					
Chara strigosa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	2	.	.	.	.	.	.	3^{+-2}
Chara globularis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1^{1}	.
Nitella flexilis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	1	.	.	.	.	.	.	.	1^{+}	1^{1}
Diagnostic species of the class Platyhypnidio–Fontinalietea antipyreticae																																																					
Fontinalis antipyretica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{1}	.	.
Fontinalis hypnoides	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{+}	I^{+}	.	.
Diagnostic species of the class Potamogetonetea																																																					
Potamogeton alpinus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{2}	.	.
Potamogeton berchtoldii	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1^{+}	.	I^{1}	.	.
Potamogeton gramineus	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1^{1}	.	.	.	.
Potamogeton natans	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{1}	.	.	.
Potamogeton obtusifolius	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1^{+}	.	.	.	.
Potamogeton perfoliatus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	$I^{+,1}$	.	.
Potamogeton pusillus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{+}	.	.
Potamogeton sibiricus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{+}	.	.	.
Potamogeton × salicifolius	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	1^{+}
Stuckenia pectinata	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1^{+}	.	.	.	.
Myriophyllum verticillatum	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{2}	I^{+}	.	.
Ranunculus kauffmannii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	r	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	I^{r}	.	.

Table 2. Continued.

Table number	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38*	39	40	41	42*	43	44	45*	46	47	a	b	c	d	e	f
Ranunculus trichophyllus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Callitriche hamulata	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1[2]	·	·	·	·
Callitriche palustris	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	I[1]	·	·
Callitriche hermaphroditica	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Nuphar lutea	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Diagnostic species of the alliance Sparganion hyperborei and the class Littorelletea uniflorae																																																					
Sparganium hyperboreum	·	·	·	·	·	·	·	+	1	2	·	·	·	r	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	II+2	·	II[r]	I+	·	·
Sparganium angustifolium	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Diagnostic species of the class Lemnetea																																																				
Lemna trisulca	·	·	·	·	·	·	·	·	·	·	·	·	3	·	·	1	·	·	·	2	1	·	·	·	·	·	·	·	·	2	·	·	+	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1[3]	II[1,2]	I+,2	·	·
Lemna minor	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1[2]	·	·	·	·
Utricularia minor	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I[1]	I+	·	·
Utricularia vulgaris	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	1	·	·	·	·	·	·	·	·	·	·	I[1]	I[1]	·	·
Utricularia sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	+	+	·	·	·	·	·	3+
Ceratophyllum demersum	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	I+,1	·	·
Stratiotes aloides	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	I[1]	·	·
Hydrocharis morsus-ranae	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	I+	I+	·	·
Diagnostic species of the class Phragmito–Magnocaricetea																																																				
Naumburgia thyrsiflora	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Alisma plantago-aquatica	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	1	·	·	·	·	·	·	·	·	·	1+	I+,1	·	·
Cicuta virosa	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Comarum palustre	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I2	·	·
Equisetum fluviatile	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	I[1]	·	·
Hippuris vulgaris	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	2	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	I+	·	I+–2	·	·
Sparganium emersum	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	+	1	1	1	·	·	·	·	·	·	·	·	·	1+	·	II+,1	·	·
Agrostis stolonifera	·	·	·	·	·	·	·	·	·	·	+	+	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	2+	I[r]	·	·	·
Bolboschoenus maritimus	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Butomus umbellatus	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Carex acuta (juv.)	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Rorippa amphibia	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Eleocharis palustris	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Other species																																																				
Carex sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Polygonum amphibium var. *natans*	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1+	·	·	·	·
Ranunculus gmelinii	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·
Ranunculus subrigidus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	1+	·
Ranunculus sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	1+
Salix sp. (juv.)	·	·	·	·	·	·	·	·	·	·	·	r	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1[r]	·	·	·	·
Drepanocladus sordidus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	·	·	·	·	I[1]	·	·
Hamatocaulis lapponicus	·	·	·	·	·	·	·	·	·	·	·	·	·	·	+	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	I+	·	·	·
Nostoc sp.	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	·	1	·	·	·	·	·	·	·	·	1[1]	·

Location of communities (GPS coordinates WGS 84, N, E), authors and date of relevés:

Nenets Autonomus Area. *Western part of the Bolshezemelskaya tundra*: **1** – Ortina River in the middle stream, floodplain lake (67.94014, 54.03397), O.V. Lavrinenko, 29.07.2023; **7** – ibid, floodplain lake (67.93510, 54.04239), N.V. Tsyvkunova, 20.07.2023; **9** – ibid, floodplain lake (67.93533, 54.04245), N.V. Tsyvkunova, 20.07.2023; **10** – ibid, floodplain lake, heavily overgrown with vegetation (67.93983, 54.0343), N.V. Tsyvkunova, 23.07.2023; **2** – Yachey River in the lower stream, Nenetskii Nature Reserve cardon, shallow water at the edge of a small lake (68.08614, 54.78286), O.V. Lavrinenko, 12.08.2022; **3** – Severnaya River near the bridge, roadside waterlogged ditch (67.64397, 53.99883), O.V. Lavrinenko, 26.07.2022; **4** – Cape Bolvanskii Nos, a system of interconnected small lakes between hills (68.28411, 54.50092), O.V. Lavrinenko, T.V. D'yachkova, 27.07.2020; **14** – ibid, a system of small floodplain lakes along the right bank of the Pechora River (68.26889, 54.43081), O.V. Lavrinenko, T.V. D'yachkova, 28.07.2020. *Lovetskii Island in the Pechora Bay*: **5** – southern part, widening of the channel connected to the shallow lake (68.324, 53.90675), O.V. Lavrinenko, T.V. D'yachkova, 10.08.2020; **6** – northern part, thermokarst lake 30 m in diameter (68.35222, 53.9625), O.V. Lavrinenko, T.V. D'yachkova, 13.08.2020; **19** – northern part, floodplain lake of the size 5 × 15 m (68.35961, 53.95756), O.V. Lavrinenko, 13.08.2020; **20** – northern part, elongated lake along the sandy terrace (68.35883, 53.96278), O.V. Lavrinenko, T.V. D'yachkova, 13.08.2020. *Eastern part of the Malozemelskaya tundra*: **8** – Nenets Ridge, lake in a runoff hollow (68.349, 53.10506), O.V. Lavrinenko, 27.07.2021; **17** – wet shore of a dried-up lake (68.35311, 53.1731), O.V. Lavrinenko, 07.07.2021. *Pechora River delta (territory of the Kumzha gas condensate field)*: **15** – low lacustrine and marshy terrace, shallow, heavily vegetated lake (68.19809, 53.76902), N.V. Tsyvkunova, 01.08.2023; **18** – ibid (68.19817, 53.76947), O.V. Lavrinenko, 01.08.2023; **34** – ibid (68.19811, 53.76956), O.V. Lavrinenko, 01.08.2023. *Kashin Island in the Korovinskaya Bay*: **16** – a large lake in the south-western part (68.24681, 53.86417), N.V. Tsyvkunova, 02.08.2023. *Eastern part of the Bolshezemelskaya Tundra*: **33** – Vatyarty Lake, surroundings of Khasyrei settlement (67.64643, 60.46980), B.Yu. Teteryuk, 26.06.2015.

Komi Republic, relevés by B.Yu. Teteryuk. *Sysolskii district*: **21** – surroundings of the Vizinga village, old overgrown clay quarry (61.04528, 50.06255), 22.06.2024; *Intinskii district*: **22** – Zhelannoye base, valley lake (65.21770, 60.2858), 30.07.2012; **27** – ibid, floodplain lake (65.22268, 60.2786), 30.07.2012; **36** – surroundings of the Inta, floodplain lake (66.02917, 60.1633), 07.08.2018; *Troitsko-Pechorskii district*: **23** – surroundings of the Znamenka-Mamyl village, floodplain lake (61.97031, 56.8278), 13.08.2020; *Vorkutinskii district*: **24** – vicinity of the Niya-Yu River canyon, thermokarst tundra lake (67.4367, 65.09339), 13.08.2010; *Koigorodskii district*: **26** – surroundings of the Kazhim village, water reservoir (60.36177, 51.5956), 09.07.2013; *Ukhtinskii district*: **29** – 60 km west of thr Kedvavom village, floodplain

Table 2. Continued.

lake (64.25642, 52.7429), 04.07.2005; **30** – ibid, floodplain lake (64.23996, 52.7068), 04.07.2005; **35** – surroundings of the Yarega NSH-1settlement, water reservoir (63.40114, 53.4894), 04.08.2015; **39** – ibid (63.43693, 53.5827), 04.08.2015; *Kyuzhpogostskii district*: **37** – surroundings of the Meshchura settlement, floodplain lake (63.33853, 50.9067), 10.07.2008; *Korkerovskii district*: **38** – surroundings of the Mordino village, floodplain lake (61.34563, 51.8832), 27.06.2007.

Altai Mountains, releves by L.M. Kipriyanova. *Altai Territory*: **25** – Kuryinskii district, Mokhovoye Lake (51.25271, 82.56112), 23.07.2023. *Republic of Altai*: **28** – Ulaganskii district, Balyktukel Lake (50.54084, 87.69443), 08.07.2018; **41** – ibid, (50.54138, 87.69500), 12.08.2023; **31** – ibid, vicinity of the Tashtukel Lake, water body on marshy meadow (50.46392, 87.61654), 18.07.2021, **32** – ibid, Uzunkel Lake (50.47669, 87.61850), 09.08.2023; 18.07.2021; **40** – ibid, (50.50218, 87.62352), 09.07.2018; **42** – ibid, (50.47914, 87.62286), 09.08.2023, **43** – ibid, Kidelyu Lake (50.4988, 87.6508), 10.08.2023; **44** – ibid, nameless lake above the lake at the Forel fishing base (50.47392, 87.55690), 25.07.2020; **46** – ibid, (50.46852, 87.55688), 25.07.2020; **45** – ibid, Sarulukel Lake (50.45978, 87.51718), 09.07.2018; **47** – ibid (50.45304, 87.51578), 15.08.2023.

Tomsk Region. **11** – Alexandrovskii district, vicinity of the Topolevka village, temporary reservoir on the Ob river terrace, Taran G.S., 11.07.1987 (Taran, 1997).

Khanty-Mansi Autonomous Area – Yugra. **12** – Surgutskii District, Nizhny Zubatinskii Island, Ob River floodplain (between 72°30' and 73°50' E), 14.09.1999 (Taran & Tyurin 2006).

Poland, vicinity of the Warsaw. **13** – overgrowth of drainage ditches on peatlands, 06.10.1962 (Podbielkowski, 1967).

Substrate: c – clay, p – peaty, s – stony, sa – sandy, si – silty.

Syntaxa: **D. a. – Drepanocladetum adunci, C. s.–S. s. – Charo strigosae–Scorpidietum scorpioidis, C. g.–C. g. – Charo globularis–Calliergonetum gigantei.**

* – nomenclature types (holotypus) are indicated by a gray fill and an asterisk; bold type indicates high abundance.

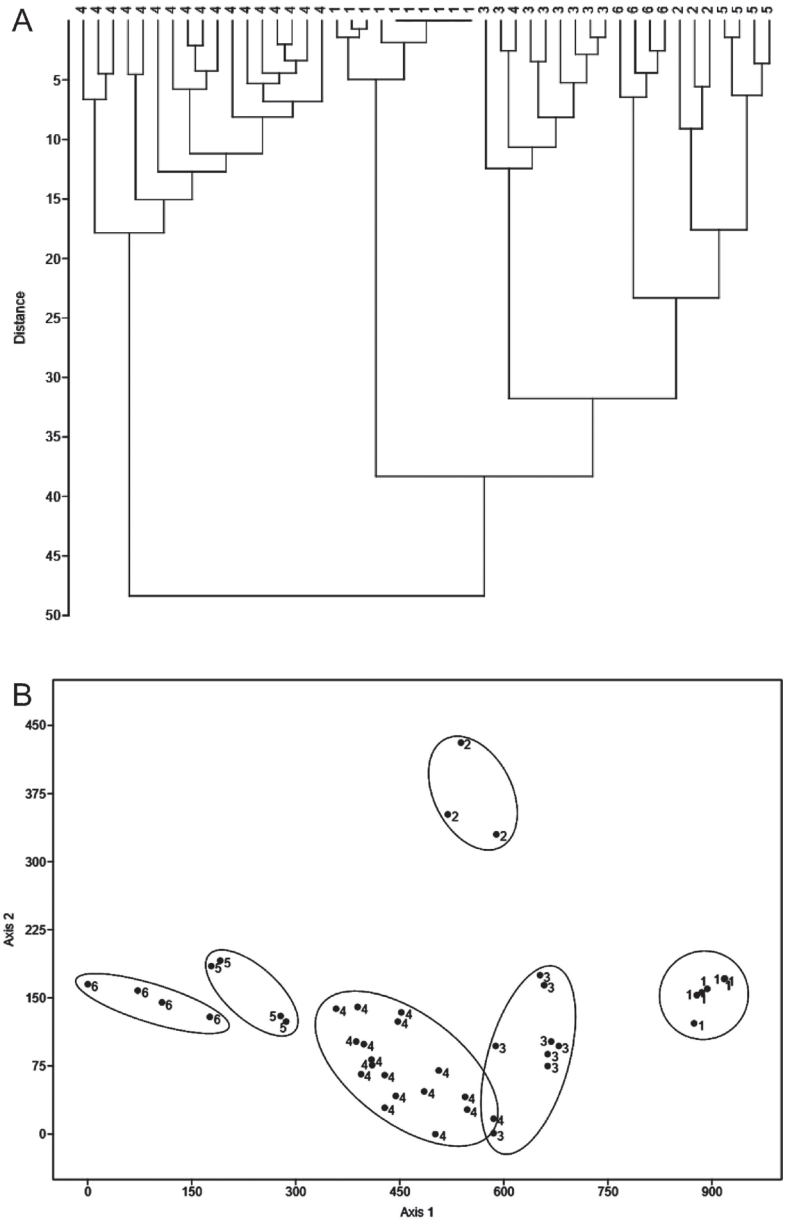

Figure 2 The similarity of relevés of submerged and amphibious bryophyte communities of the class Calliergonetea megalophylli, established by the cluster analysis (Ward's method) (A) and the DCA-ordination (B). Associations: 1 – Sarmentypnetum trichophylli; 2 – Drepanocladetum adunci; 3 – Calliergonetum megalophylli; 4 – Myriophyllo sibirici–Sarmentypnetum exannulati; 5 – Charo globularis–Calliergonetum gigantei; 6 – Charo strigosae–Scorpidietum scorpioidis

Structure. Submerged dense cover of *Sarmentypnum trichophyllum* on the bottom, less frequently floating mats near water surface (up to 10 m across).

Habitats. Shallow (up to 1 m deep), well-warmed in the summer meso- and eutrophic lakes, river-formed lakes and artificial water bodies (drainage ditch) with water pH from slightly acidic to neutral (5.4–7.0), with silty sandy and muddy bottoms.

Distribution. Communities of the association have been described in the tundra zone of European Russia: in water bodies of the eastern part of the Malozemelskaya tundra (Nenets Ridge), the western part of the Bolshezemelskaya tundra (Bolvanskii Nose Cape, Ortina, Severnaya and Yachey River basins), and Lovetskii Isl. in the Pechora Bay of the Barents Sea. *Sarmentypnum trichophyllum* – a circumpolar northern species described from Finland. In the Asian part of Russia it is found in Siberia (up to Transbaikalia) and in the Far East (Sakhalin), while in European Russia it is found only in

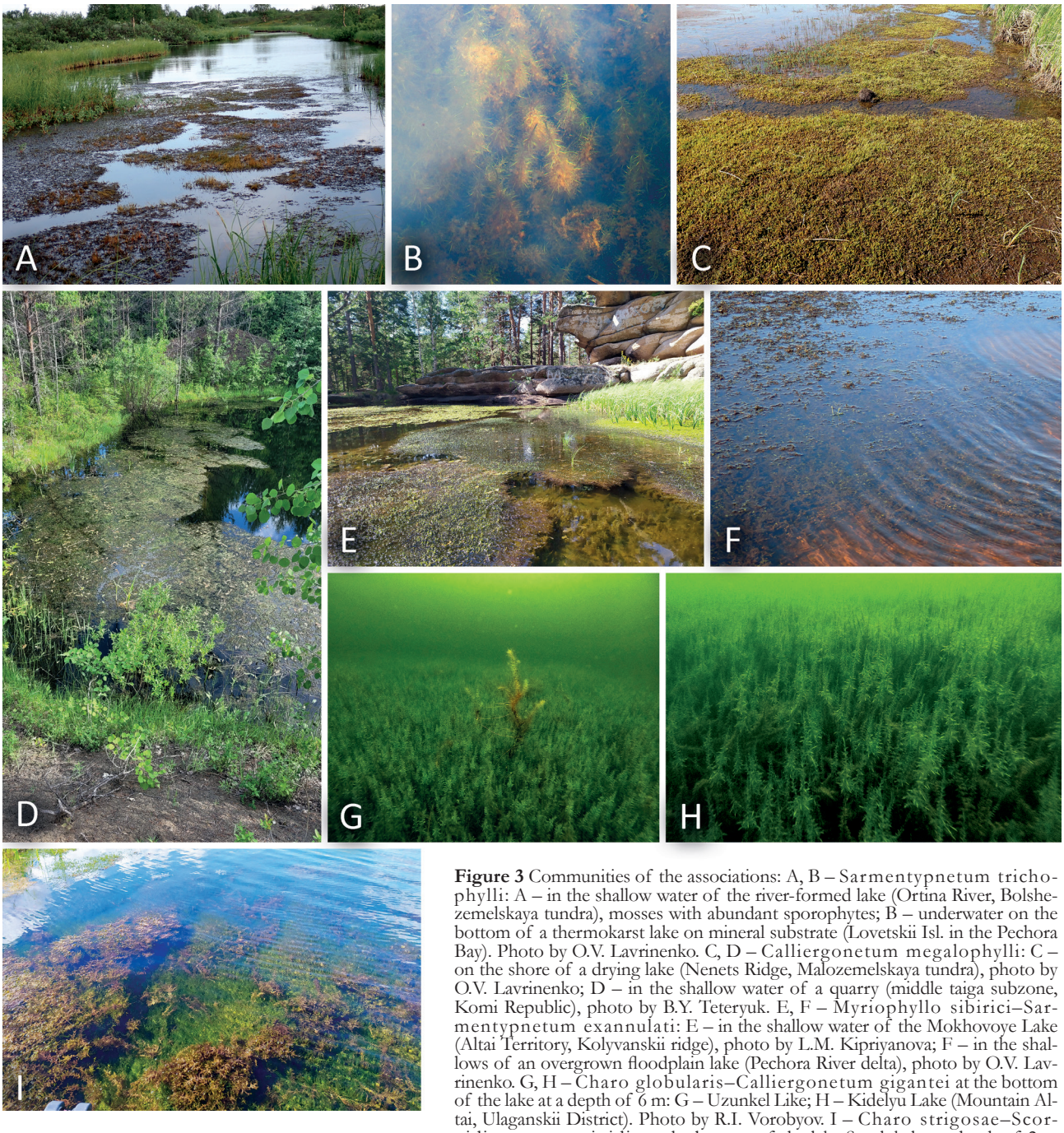

Figure 3 Communities of the associations: A, B – Sarmentypnetum trichophylli: A – in the shallow water of the river-formed lake (Ortina River, Bolshezemelskaya tundra), mosses with abundant sporophytes; B – underwater on the bottom of a thermokarst lake on mineral substrate (Lovetskii Isl. in the Pechora Bay). Photo by O.V. Lavrinenko. C, D – Calliergonetum megalophylli: C – on the shore of a drying lake (Nenets Ridge, Malozemelskaya tundra), photo by O.V. Lavrinenko; D – in the shallow water of a quarry (middle taiga subzone, Komi Republic), photo by B.Y. Teteryuk. E, F – Myriophyllo sibirici–Sarmentypnetum exannulati: E – in the shallow water of the Mokhovoye Lake (Altai Territory, Kolyvanskii ridge), photo by L.M. Kipriyanova; F – in the shallows of an overgrown floodplain lake (Pechora River delta), photo by O.V. Lavrinenko. G, H – Charo globularis–Calliergonetum gigantei at the bottom of the lake at a depth of 6 m: G – Uzunkel Like; H – Kidelyu Lake (Mountain Altai, Ulaganskii District). Photo by R.I. Vorobyov. I – Charo strigosae–Scorpidietum scorpioidis at the bottom of the lake Sarulukel at a depth of 2 m (Mountain Altai, Ulaganskii district), photo by L.M. Kipriyanova

more northern areas and in the Southern Urals (Hedenäs & Ignatov 2022). On this basis, the range of the association can be extended to the north of the European part of Russia, Siberia and the Far East.

Note. According to Hedenäs & Ignatov (2022), sporophytes are not known in *S. trichophyllum* specimens from Russia. Mats of this moss with mass development of sporophytes were found in floodplain lakes in the west of the Bolshezemelskaya tundra (Fig. 3A).

Ass. Calliergonetum megalophylli Lavrinenko et D'yachkova 2021 (Table 2, rel. 14–20; Fig. 3C, D).

Name-giving taxon: *Calliergon megalophyllum* Mikut. (Bryoth. Balt. No. 141. 1908).

Description. Submerged (up to 1 m deep) and amphibious bryophyte communities of *Calliergon megalophyllum* in the lakes and other water bodies with slow water exchange.

Composition. Diagnostic species – *Calliergon megalophyllum* (dominant). Very large mosses (10–20, up to 40 cm long) often form almost single-species stands. Littoral *Hippuris lanceolata* is the constant species with low in abundance, which is explained by the location of the studied communities in coastal areas. Other aquatic bryophytes are also found in the moss mats (*Drepanocladus aduncus*, *Fontinalis hypnoides*, *Hamatocaulis lapponicus*, *Sarmentypnum exannulatum*, *S. trichophyllum*). Macrophytes are occasionally found in the moss mats, among which there are diagnostic species of classes Potamogetonetea Klika in Klika et Novák 1941

(*Myriophyllum verticillatum*, *Potamogeton natans*, *P. sibiricus*), Lemnetea (*Lemna trisulca*, *Utricularia minor*, *U. vulgaris*) and alliance Sparganion hyperborei Teteryuk, Lavrinenko et Kipriyanova 2022 (*Sparganium hyperboreum*). All companion species have low abundance (r–2) and total cover less than 5 % (20 % in 2 communities only). Total number of taxa registered in association is 16: 10 herbs and 6 moss; 1–7 species in communities.

Structure. The communities of the association have a single layer. Moss *Calliergon megalophyllum* grows underwater, in the entire water column at a depth of about 40 cm (only shoot tips protrude above the surface) and in mats floating in the near-surface water layer, as well as in mats on over-watered shores of drying lakes.

Habitats. Shallow waters of well-warmed, overgrown eutrophic lakes and river-formed lakes and artificial reservoirs (old overgrown quarry) with water pH close to neutral (pH = 7.5 in rel. 21 (T24-060)), with silted sandy, silted clay and mud bottoms, as well as over-watered shores of lakes.

Distribution. Communities have been described in the north of European Russia. Most communities are studied in the tundra zone: in lakes in the eastern part of the Malozemelskaya tundra (Nenets Ridge), western part of the Bolshezemelskaya tundra (Bolvanskii Nose Cape), on Lovetskii Isl. in Pechora Bay and in the Pechora River delta. One community was described in the shallow water of a quarry in the middle taiga subzone of the Komi Republic. The species with circumpolar range inhabits the northern parts of Russia, but does not occur in the high-latitude Arctic, and finds in the boreal zone are sporadic (Czernyadjeva & Ignatova 2022). Based on the distribution of the species, the range of the association can be extended to the entire tundra zone and the northern part of the taiga zone of Russia.

Ass. Myriophyllo sibirici–Sarmentypnetum exannulati Teteryuk in Teteryuk, Lavrinenko et Kipriyanova ass. nov.

(Table 2, rel. 21–38; Fig. 3E, F)

Holotypus: Relevé 38 in Table 2 (author's no. – T07-030). 27.06.2007; Komi Republic, Kortkerosskii district, vicinity of Mordino village, floodplain lake (N 61.3456, E 51.8832). Author – B.Yu. Teteryuk.

Name-giving taxa: *Myriophyllum sibiricum* Kom. Repert. (Spec. Nov. Regni Veg. 13: 168 (1914)), *Sarmentypnum exannulatum* (Schimp.) Hedenäs (J. Hattori Bot. Lab. No. 100: 132. 2006).

Synonym: Warnstorfietum exannulati Szańkowski 1998 nom. inval. (ICPN Art. 1).

Description. Aquatic dense "carpet" communities of *Sarmentypnum exannulatum* with submerged and free-floating hydrophytes in lakes and reservoirs with slow water exchange.

Composition. Diagnostic species – *Sarmentypnum exannulatum* (dominant). Moss is dark or brownish green, often with wine-red pigmentation, with a floating or erect stem 5–10(20) cm long. Total number of taxa registered in association is 33: 5 moss and 28 herbs; average number of species in the community – 4. Hydrophytes, most of which belong to diagnostic species of the classes Potamogetonetea and Lemnetea, account for more than half of the species composition (Table 2). Their general cover in communities does not exceed 10 %.

Structure. The communities are fully submerged moss "carpets" with sparse submerged and floating near the water surface hydrophytic plants (*Lemna trisulca*, *Myriophyllum sibiricum*, *Utricularia vulgaris*). The submerged rooting hydrophyte *Myriophyllum sibiricum* is present in communities quite often (III1). Aquatic forms of helophytes (*Sparganium emersum* var. *fluitans*) are found along the periphery of the phytocoenoses on the shore side. Some helophytes are occasionally found in shallow areas near the shoreline.

Habitats. The communities of the association are formed on wind-protected areas of shallow waters with silty, sandy-silty, peaty-silty soils, less often clay and stony soils, but with silt deposits. The water has a slightly acidic (pH = 6.27) to slightly alkaline (pH = 8.52) reaction and low (0.04–0.16 g/dm^3) mineralization. No desiccation of habitat occupied by communities was observed. Assessment of ecological conditions of habitats according to the Ellenberg scales showed (Fig. 4) that they are characterized by good light and belong to meso- and meso-eutrophic.

Distribution. Communities of the association have been described in the European North of Russia and the Altai Mountains. A little earlier they were described in Poland under the of Warnstorfietum exannulati (Szańkowski 1998, Szańkowski & Klosowski 2004). *Sarmentypnum exannulatum* – widespread and massive species in the Arctic and in the boreal zone (Ignatov & Ignatova 2003, Hedenäs & Ignatov 2022). The range of the association appears to coincide with the distribution of this phytocoenosis-forming species and covers all sectors of the Holarctic.

Note. In 1933, V. Krajina described ass. Drepanocladetum exannulati Krajina 1933 within the class Scheuchzerio palustris–Caricetea nigrae, which unites moss–sedge mires. He noted that the association's community habitats are only moderately moistened by water and can dry out significantly during extended periods of drought. Even communities of facies typicum do not grow in highly watered habitats («…Allerdings wächst nicht einmal die Fazies typicum in größeren Wassermengen, nur von leicht fließendem Wasser ist diese Assoziation mäßig befeuchtet» (Krajina 1933:138). The differential taxa of the association V. Krajina designated *Caltha palustris* subsp. *laeta*, *Deschampsia caespitosa*, *Ligusticum mutelliana* (= *Mutellina adonidifolia*). Hydrophytes are completely absent in its composition (Krajina 1933: 136–137, table 59). This radically distinguishes the mire communities of the ass. Drepanocladetum exannulati from those of the association we have described.

We also include the ass. Drepanocladetum adunci Taran 1997 (Taran 1997, Taran et al. 2005, Taran & Tyurin 2006) to the alliance Calliergonion megalophylli.

Ass. Drepanocladetum adunci Taran 1997

(Table 2, rel. 11–13)

Name-giving taxon: *Drepanocladus aduncus* (Hedw.) Warnst. (Beih. Bot. Centralbl. No 13: 400. 1903).

Diagnostic species: *Drepanocladus aduncus* (dominant).

Description. According to the author's definition (Taran 1997) the association unites communities dominated by hypnum moss *Drepanocladus aduncus* that occupy temporary water bodies in temporarily flowing hollows of the Ob River floodplain.

Note. "During flooding, the communities are moss mats attached to the ground or suspended in the water column ... about 15 cm high. By late summer, dried moss carpet up to 2–4 cm thick are colonized by explerents [R strategy] (*Rorippa palustris*, *Agrostis stolonifera*) as well as juvenile and immature individuals of helophytes (*Comarum palustre*, *Cicuta virosa*, *Ranunculus gmelinii*, *Stellaria palustris*, *Cardamine pratensis*, *Pedicularis karoi*, *Rumex aquaticus*), the general cover of which is very small" (Taran 1997:76).

All. Charo strigosae–Scorpidion scorpioidis Kipriyanova et Baisheva all. nov.

Holotypus: ass. Charo strigosae–Scorpidietum scorpioidis Kipriyanova et Baisheva **ass. nov.** (described bellow).

Name-giving taxa: *Scorpidium scorpioides* (Hedw.) Limpr. (Laubm. Deutschl. 3: 571. 1899), *Chara strigosa* A. Braun

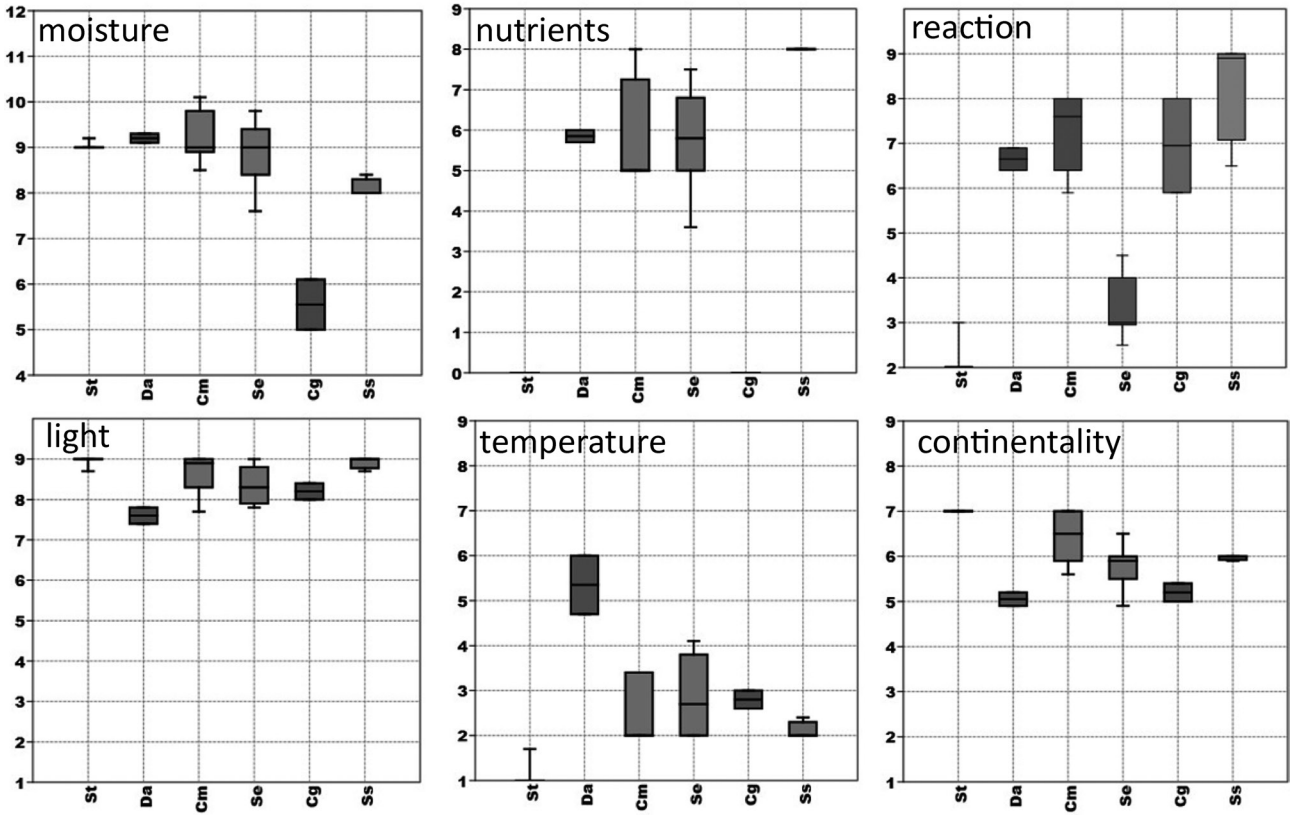

Figure 4 A comparison of aquatic bryophyte associations by means of Ellenberg indicator values. Associations: St – Sarmentypnetum trichophylli, Da – Drepanocladetum adunci, Cm – Calliergonetum megalophylli, Se – Myriophyllo sibirici–Sarmentypnetum exannulati, Cg – Charo globularis–Calliergonetum gigantei, Ss – Charo strigosae–Scorpidietum scorpioidis

(Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften. No. 10(3): 16. 1849).

Diagnostic species: *Calliergon giganteum*, *Chara strigosa*, *Nitella flexilis*, *Scorpidium scorpioides*.

Description. Communities of aquatic bryophytes in deep, transparent lakes and water bodies with similar hydrological regimes in the forest and forest-tundra belts of the mountains and the boreal and tundra zones of the Holarctic.

Note. Deep water prevents the helophytes and hydrophytes characteristic of shallow littoral depths from penetrating the communities of this alliance. Thus, if in the communities of the alliance Calliergonion megalophylli species of the genus *Hippuris* and *Sparganium* and other diagnostic species of the class Phragmito–Magnocaricetea Klika in Klika et Novák 1941 are found with good consistency, then in the communities of the alliance Charo strigosae–Scorpidion scorpioidis, carried out at depths of up to 6 m, only real hydrophytes were noted – vascular plants and charophytes.

Ass. Charo globularis–Calliergonetum gigantei Kipriyanova et Baisheva ass. nov. (Table 2, rel. 40–43; Fig. 3G, H)

Holotypus: Relevé 42 in Table 2 (author's no. – K-y23-8), 09.08.2023; Republic of Altai, Ulaganskii District, Uzunkel Lake (50.47914N 87.62286E). Author – L.M. Kipriyanova.

Name-giving taxa: *Calliergon giganteum* (Shimp.) Kindb. (Canad. Rec. Sci. No. 6(2): 72 1894), *Chara globularis* Thuiller (Flore des environs de Paris, Ann VII [éd. 2]. p. 472. 1799).

Description. Aquatic "carpet" communities of *Calliergon giganteum* with submerged hydrophytes in the lakes and other water bodies with slow water exchange.

Composition. Diagnostic species – *Calliergon giganteum* (dominant). The mosses are large, green, golden or brownish-green, stem 5–20 cm long. Total number of taxa registered in the association is 7: 2 – bryophytes, 2 – vascular plants, 2 – charophytes, 1 – other macroalgae; 2–4 species per community. Some diagnostic species of the Potamogetonetea (*Myriophyllum sibiricum*) and Charetea intermediae F. Fukarek 1961 (*Nitella flexilis*, *Chara globularis*) classes are present in the composition of the association communities.

Structure. The communities are moss "carpets" completely submerged in water, with rare inclusions of hydrophytes submerged. The height of moss shoots in the studied communities reaches 44 cm.

Habitats. Communities of *Calliergon giganteum* are formed in the littoral zone of the lakes up to 6 m depth with a predominance of rocky soils silted on top. The lakes are ultra-fresh (mineralization from 0.03 to 0.06 g/dm^3), hydrocarbonate-calcium. The waters range from slightly acidic (pH = 6.7) to slightly alkaline (pH = 8.0). The trophic status changes from oligo-mesotrophic lakes Uzunkel and Kidelyu to mesotrophic Balyktukel.

Distribution. Communities were observed in the lakes of the forest and forest-tundra belts of the Altai Mountains (Uzunkel, Kidelyu (Fig. 3G, H), Balyktukel), and most likely of the other mountain regions of the Holarctic. Given the widespread distribution of mass moss *Calliergon giganteum* in the boreal regions of the Holarctic, communities of the association will be discovered during a detailed examination of lakes in the boreal and tundra zones.

Notes. T. Lipmaa (1933) does not provide relevés, but indicates that its association *Drepanocladus lycopodioi–Calliergon giganteum*-Ass. is characteristic of bogs – "This bog association is typical of calcareous bogs." Therefore, it was

necessary to describe a new association with *Calliergon giganteum* as a dominant – which, in conditions of deep transparent reservoirs, can successfully grow at depths of up to 6 m, which includes species of true hydrophytes, both vascular and cryptogamous.

Ass. Charo strigosae–Scorpidietum scorpioidis Kipriyanova et Baisheva ass. nov.
(Table 2, rel. 44–47; Fig. 3I)

Holotypus: Relevé 45 in Table 2 (author's number – K-18-39. 09.08.2023; Republic of Altai, Ulaganskii District, Lake Sarylukel, 09.07.2018, (N50.45978, E 87.51718). Author – L.M. Kipriyanova.

Description. Aquatic "carpet" communities of *Scorpidium scorpioides* with submerged hydrophytes in the lakes and other water bodies with slow water exchange.

Name-giving taxa: *Chara strigosa* A. Braun (Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften. No. 10(3): 16. 1849), *Scorpidium scorpioides* (Hedw.) Limpr. (Laubm. Deutschl. 3: 571. 1899).

Composition. Diagnostic species – *Chara strigosa*, *Scorpidium scorpioides* (dominant). Moss large, black or dark purple, stem 5–15 cm long. Total number of taxa registered in association is 8: 2 – bryophytes, 4 – vascular plants, 2 – charophytes; 3–6 species in communities. Charophytes are the diagnostic species of the class Charetea intermediae.

Structure. The communities are moss "carpets" completely submerged in water, with rare inclusions of hydrophytes submerged.

Habitats. Communities of *Scorpidium scorpioides* are formed in the littoral zone of the lakes up to 3.6 m depth with a predominance of rocky soils silted on top. The lakes are ultra-fresh (mineralization from 0.09 to 0.11 g/dm^3), hydrocarbonate-calcium. The waters range from slightly acidic (pH = 6.7) to slightly alkaline (pH = 8.1). The trophic water status is mesotrophic.

Distribution. Communities have been described in the lakes of the forest and forest-tundra belts of the Altai Mountains (Sarulukel, unnamed lake above the Forel fishing base), and most likely of the other mountain regions of the Holarctic. Moss is widespread in the Arctic and northern boreal zone; penetrates southward into the mountains of Eurasia. Apparently, communities of the association will be discovered during a detailed examination of lakes in the boreal and possibly tundra zones of the Holarctic.

Notes. Lipmaa (1933) indicates that his association *Scorpidium scorpioides*-Ass. is characteristic of mires, so, as in the case of *Calliergon giganteum* communities, we described a new association characteristic of deep clear lakes, including other species of true hydrophytes, both vascular and cryptogamous.

We propose to combine the two alliances described above into a new order and class of bryophyte vegetation of the same name.

Cl. Calliergonetea megalophylli Teteryuk, Lavrinenko et Kipriyanova cl. nov.

Holotypus: ord. Calliergonetalia megalophylli Teteryuk, Lavrinenko et Kipriyanova **ord. nov.** (described below).

Name-giving taxon: *Calliergon megalophyllum* Mikut. (Bryoth. Balt. No. 141. 1908).

Diagnostic species: *Calliergon giganteum*, *C. megalophyllum*, *Drepanocladus aduncus*, *Sarmentypnum exannulatum*, *S. trichophyllum*, *Scorpidium scorpioides*.

Description. Submerged and amphibious bryophyte vegetation in lakes of various origins, enclosed water bodies and permanently watered depressions of relief in tundra and boreal zones and southward in the mountainous regions of the Holarctic.

Ord. Calliergonetalia megalophylli Teteryuk, Lavrinenko et Kipriyanova ord. nov.

Holotypus: all. Calliergonion megalophylli Lavrinenko ex Teteryuk, Lavrinenko et Kipriyanova **all. nov.** (described in this paper).

Description, Name-giving taxon and Diagnostic species. Same as class.

Syntaxonomic structure of the class Calliergonetea megalophylli

Class
Order
Alliance
Association

Calliergonetea megalophylli Teteryuk, Lavrinenko et Kipriyanova **cl. nov.**

Calliergonetalia megalophylli Teteryuk, Lavrinenko et Kipriyanova **ord. nov.**

Calliergonion megalophylli Lavrinenko ex Teteryuk, Lavrinenko et Kipriyanova **all. nov.**

Calliergonetum megalophylli Lavrinenko et D'yachkova 2021

Sarmentypnetum trichophylli Lavrinenko et D'yachkova 2021 mut. Lavrinenko, Lavrinenko, Tsyvkunova et D'yachkova 2024

Myriophyllo sibirici–Sarmentypnetum exannulati Teteryuk in Teteryuk, Lavrinenko et Kipriyanova **ass. nov.**

Drepanocladetum aduncі Taran 1997

Charo strigosae–Scorpidion scorpioidis Kipriyanova et Baisheva in Teteryuk, Lavrinenko et Kipriyanova **all. nov.**

Charo globularis–Calliergonetum gigantei Kipriyanova et Baisheva in Teteryuk, Lavrinenko et Kipriyanova **ass. nov.**

Charo strigosae–Scorpidietum scorpioidis Kipriyanova et Baisheva in Teteryuk, Lavrinenko et Kipriyanova **ass. nov.**

DISCUSSION

The class Calliergonetea megalophylli is described on the basis of the authors' own data from the European North of Russia and the mountains of South Siberia, as well as on published data for Western Siberia (Taran 1997, Taran & Tyurin 2006) and Central Europe (Podbielkowski 1967). The core of the coenoflora of the class is composed of broad-areal species with predominantly Holarctic (60 % of the coenoflora of the class) and hemocosmopolitan (17 %) distribution. These groups include all the phytocoenosis-forming species of the class. In latitudinal respect, distinct arcto-boreal features characterize the geographical structure of the class coenoflora. It is dominated by species of temperate latitudes (41 %), with about a third of species (36 %) distributed in the Arctic. The remaining species (23 %), among which mosses *Drepanocladus aduncus* and *Sarmentypnum exannulatum*, have an almost ubiquitous (plurizonal) distribution.

The ecotopes occupied by communities of the class (shallow waters of floodplain, thermokarst, mountain-valley and mountain lakes, watered depressions in river floodplains, shallow waters of overgrown bays of reservoirs, roadside ditches, overgrown quarries, reclamation ditches) determined the ecological spectrum of its coenoflora. Hydrophytes make up more than half of the coenoflora composition (57 %). Aquatic-mire species (hygrohelophytes and helophytes) account for 24 % and 17 %, respectively.

Communities of the class, forming in water bodies with slow water exchange, consist of species with a wide ecological amplitude (60 %), indifferent to the presence of water current according to the factor "mobility of water masses" (59 %). The remaining species (41 %) prefer ecotopes with standing water (lentibionts). Two species (*Calliergon giganteum* and *Drepanocladus aduncus*) from among phytocoenosis-forming species are indifferent to the mobility of water masses, but their communities were not found in rivers on the stream.

Ecological analysis of the class coenoflora using Ellenberg scales demonstrates confinement to mesotrophic, well-lit habitats with pH from slightly acidic to slightly alkaline (Fig. 4). The coenoflora of the class is composed of cold-tolerant species whose areal tends to regions with suboceanic and subcontinental climate. The above characterization of the coenoflora gives a basis to consider that communities of the class Calliergonetea megalophylli have a predominant distribution in the Arctic and temperate latitudes of the Holarctic.

The main difference between alliances in this class is the characterization of habitats: communities of the alliance Calliergonion megalophylli are distributed mainly in shallow mesotrophic and meso-eutrophic plain water bodies, while communities of the alliance Charo strigosae–Scorpidion scorpioidis are formed in relatively deep oligo-mesotrophic lakes. An additional distinctive feature of the second alliance is the significant participation of char algae in its communities (Table 2).

The class Calliergonetea megalophylli (CAL) has characteristic features that distinguish it from other aquatic and mire classes where bryophytes are important – Platyhypnidio–Fontinalietea antipyreticae (PLA) and Scheuchzerio palustris–Caricetea nigrae (SCH) (Table 3). These differences in composition, leading ecobiomorphs, and habitats emphasize the distinctive features of the class Calliergonetea megalophylli and constrain it well in syntaxonomic space.

CONCLUSIONS

The new class Calliergonetea megalophylli is proposed for bryophytic vegetation of lakes and other enclosed water bodies with slow water exchange, with organic and organic-mineral substrates (clay, peat, sandy, muddy). Mosses (families Amblystegiaceae, Calliergonaceae, Scorpidiaceae etc.) form mats or carpets of several tens and hundreds of square meters in different ecotopes – underwater at the bottom of lakes, in the entire water column, floating in the near-surface water layer, as well as on waterlogged shores of drying lakes. Bryophytes form complete communities in which the participation of vascular plants is insignificant. These are mainly low abundant hygro- and hydrophytes, characteristic of other classes of aquatic vegetation, which do not influence the structure of bryophyte communities (in particular, they are not a supporting framework for mosses and do not form an independent layer). The class Calliergonetea megalophylli is clearly distinguished from other aquatic and mire classes where bryophytes are important – Platyhypnidio–Fontinalietea antipyreticae (epilithic bryophyte vegetation in running water courses and cascades growing submerged inwater and splashzones) and Scheuchzerio palustris–Caricetea nigrae (sedge-moss vegetation of fens, transitional mires and bog hollows).

The order Calliergonetalia megalophylli and the alliances Calliergonion megalophylli (submerged and amphibious bryophyte vegetation in the shallow, well-warmed meso- and eutrophic lakes and other enclosed water bodies) and Charo strigosae–Scorpidion scorpioidis (communities of aquatic bryophytes in deep, clear oligo-mesotrophic lakes) are described in the new class. There are currently 6 associations included in the class, but the number may increase significantly as research progresses.

The newly described syntaxa expand the understanding of the syntaxonomic structure of the vegetation cover of hydromorphic habitats. Its further study will make it possible to judge with greater objectivity the functioning and successional processes of overgrowth of aquatic ecotopes.

Table 3. Comparative characterization of the communities of the classes Calliergonetea megalophylli (CAL), Platyhypnidio–Fontinalietea antipyreticae (PLA) and Scheuchzerio palustris–Caricetea nigrae (SCH)

Indicator	Class		
	PLA	**CAL**	**SCH**
*** Constancy and abundance of the same diagnostic species (for alliances)**			
Fontinalis antipyretica	**VI^{4}–V^{5}**	I^{1}	–
Fontinalis hypnoides	**VI^{4}–V^{5}**	I^{+}	–
Sarmentypnum exannulatum	–	**V^{5}**	**V^{+-5}**
Habitats	watercourses (rivers, streams)	enclosed water bodies (lakes, ponds, reservoirs)	mires, wet waterlogged banks of water bodies
Substrate	mineral (stones, gravel, pebbles)	organic / organic-mineral (clay, peaty, sandy, silty)	organic / mineral-organic (peaty), overwatered mineral
Leading ecobiomorphs	hydro- and hygrohelophytic mosses	submerged hydrophytic mosses	Helophytic graminoids and bog and mire mosses

Note. * – calculated from published data (Taran 1997, Baisheva et al. 2004, Chemeris 2004, Bobrov & Chemeris 2005, 2006, Taran & Tyurin 2006, Baisheva 2010, Chepinoga 2015, Lavrinenko et al. 2016, Kipriyanova 2019, Kipriyanova & Kleshchev 2019, Ermolaeva et al. 2022, Sokolova et al. 2023).

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