

## Pondweeds (*Potamogeton*, *Potamogetonaceae*) in River Ecosystems in the North of European Russia

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Pondweeds (*Potamogeton* L., *Potamogetonaceae* Dumort.) are a poorly studied group of macrophytes in river ecosystems in the north of European Russia (Karelia Republic, Arkhangel'sk oblast, Komi Republic, Vologda oblast, northern Yaroslavl oblast, and Kostroma and Kirov oblasts). To date, the "Florals" [1–3] remain the main sources of data on this genus for the given territory. However, many of these data have become outdated in the light of the latest taxonomic revisions [4–6] and numerous new herbarium materials. Regional surveys are largely based on the early studies cited above and require revision. Recent Russian publications on *Potamogeton* [7, 8] relevant to the region and object in question are not completely consistent with current views and need correction. No special studies on the composition, distribution, ecology, and role of pondweeds in river ecosystems have been carried out thus far.

Results of field surveys, as well as available published and herbarium data, show that 15 species and 13 hybrids of the genus *Potamogeton* have been identified to date in streams and rivers in the north of European Russia (table). The greatest species diversity of *Potamogeton* has been found in watercourses of Komi Republic, which has a large area and has been surveyed in sufficient detail, as well as in the best studied streams and rivers of Yaroslavl oblast. The number of identified hybrids is also the greatest in watercourses of Komi Republic and is slightly smaller in rivers of Arkhangel'sk and Kostroma oblasts. The total number of species and hybrids is the greatest in watercourses of Komi Republic and Arkhangel'sk and Yaroslavl oblasts. This tendency is quite explainable. Komi Republic, Arkhangel'sk oblast have large areas with a wide diversity of physical-geographic conditions, and Yaroslavl oblast is thus far the best studied with respect to aquatic vegeta-

tion, in particular river one. The most common species of pondweeds in streams and rivers of the study area were, first, species with wide ecological niches (*Potamogeton gramineus*, *P. lucens*, *P. natans*, *P. pectinatus*, and *P. perfoliatus*), i.e., the species generally nonspecific for the type of the water body; second, the species characteristic of streams and upper stretches of rivers (*P. alpinus* and *P. berchtoldii*), i.e., those predominantly found in river ecosystems. The species that are more typical of lakes but also grow in rivers (*P. crispus*, *P. friesii*, and *P. praelongus*) are slightly less spread. Predominantly lake and lake-oxbow species (*P. filiformis*, *P. obtusifolius*, *P. pusillus*, and *P. trichoides*) and species with a specific ecology (the Arctic *P. subretusus*) are rare in rivers. The most widespread hybrids are *P. × angustifolius*, *P. × nitens*, *P. × salicifolius*, and *P. × sparganiiifolius*, which is not unexpected considering earlier data on the Upper Volga basin [9]; *P. × fluitans* and *P. × suecicus* are slightly less spread; and *P. × bottnicus* and *P. × fennicus* are rare. The remaining hybrids (*P. × cognatus*, *P. × cooperi*, *P. × olivaceus*, *P. × prussicus*, and *P. × vepsicus*) are known from one locality each.

The boundary of the taiga zone has proved to be the northern limit of the distribution of almost all river *Potamogeton*. An almost entire diversity of the identified taxa is preserved up to 65° N. Most species with wide ranges (*P. lucens*, *P. natans*, *P. pectinatus*, *P. perfoliatus*, etc.) become rare and disappear towards this limit. The distribution of *P. friesii*, *P. obtusifolius*, and *P. praelongus* follow about the same pattern. The northern boundary of the *P. crispus* range is at approximately 60° N. Nonspecific for rivers and more thermophilic *P. pusillus* and *P. trichoides* are known from a few isolated findings in the southern and middle taiga subzones. *P. alpinus*, *P. berchtoldii*, *P. filiformis*, and *P. gramineus* are found up to the polar circle and northward, in rivers of the tundra zone. In watercourses of the middle taiga subzone, these species are the most common and active. The Arctic *P. subretusus*, whose range does not go beyond the polar circle, occurs in tundra rivers. Farther to the south, *P. filiformis* becomes

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The list of species and hybrids of *Potamogeton* in streams and rivers of northern European Russia

Nos.	Taxon	Karelia Repub- lic	Arkhan- gel'sk oblast	Komi Repub- lic	Vologda oblast	Yaro- slavl oblast	Kos- troma oblast	Kirov oblast	All regions
Species									
1	<i>P. alpinus</i> Balb.	+	+	+	+	+	+	+	7
2	<i>P. berchtoldii</i> Fieb.	+	+	+	+	+	+	+	7
3	<i>P. crispus</i> L.	-	-	+	+	+	+	+	5
4	<i>P. filiformis</i> Pers.	+	+	+	-	-	-	-	3
5	<i>P. friesii</i> Rupr.	-	+	+	+	+	-	+	5
6	<i>P. gramineus</i> L.	+	+	+	+	+	+	+	7
7	<i>P. lucens</i> L.	+	+	+	+	+	+	+	7
8	<i>P. natans</i> L.	+	+	+	+	+	+	+	7
9	<i>P. obtusifolius</i> Mert. et W. D. J. Koch	-	-	+	+	+	-	+	4
10	<i>P. pectinatus</i> L.	+	+	+	+	+	+	+	7
11	<i>P. perfoliatus</i> L.	+	+	+	+	+	+	+	7
12	<i>P. praelongus</i> Wulf.	-	+	+	+	+	-	+	5
13	<i>P. pusillus</i> L.	-	-	+	-	+	-	-	2
14	<i>P. subretusus</i> Hagstr.	-	+	+	-	-	-	-	2
15	<i>P. trichoides</i> Cham. et Schlecht.	-	-	-	-	+	-	-	1
All species		8	11	14	11	13	8	11	15
Hybrid									
16	<i>P. × angustifolius</i> J. Presl (6 × 7)	+	+	+	+	+	+	+	7
17	<i>P. × bottnicus</i> Hagstr. (10 × <i>P. vaginatus</i> Turcz.)	+	+	+	-	-	-	-	3
18	<i>P. × cognatus</i> Asch. et Graebn. (11 × 12)	-	-	-	-	+	-	-	1
19	<i>P. × cooperi</i> (Fryer Fryer (3 × 11)	-	-	-	-	-	+	-	1
20	<i>P. × fennicus</i> Hagstr. (4 × <i>P. vaginatus</i> )	-	+	+	-	-	+	-	3
21	<i>P. × fluitans</i> Roth (7 × 8)	+	+	+	-	+	+	-	5
22	<i>P. × nitens</i> Web. (6 × 11)	+	+	+	+	+	+	+	7
23	<i>P. × olivaceus</i> Baagöe ex G. Fisch. (1 × 3)	-	-	-	-	-	-	+	1
24	<i>P. × prussicus</i> Hagstr. (1 × 11)	-	-	+	-	-	-	-	1
25	<i>P. × salicifolius</i> Wolfg. (7 × 11)	+	+	+	+	+	+	+	7
26	<i>P. × sparganiifolius</i> Laest. ex Fries (6 × 8)	+	+	+	+	+	+	+	7
27	<i>P. × suecicus</i> K. Richt. (4 × 10)	+	+	+	+	-	+	+	6
28	<i>P. × vepsicus</i> A. A. Bobrov et Chemeris (1 × 8)	-	-	-	+	-	-	-	1
All hybrids		7	8	9	6	6	8	6	13
All pondweeds (species and hybrids)		15	19	23	17	19	16	17	28

Note: A dash means the absence of the species.

rare; it is absent in rivers farther to the south than 61° N. The contribution of *P. gramineus* to the vegetation cover decreases towards the south also. The hybrid *P. × angustifolius*, *P. × nitens*, *P. × salicifolius*, and *P. × sparganiifolius* are widespread in watercourses of the studied territory, reaching the polar circle. The occurrence of *P. × angustifolius* and *P. × sparganiifolius* increase towards the north, whereas *P. × nitens* and *P. × salicifolius* become more spread towards the south. The more south distribution is also found for *P. × flu-*

*itans*. The hybrids *P. × bottnicus*, *P. × fennicus*, and *P. × suecicus* are distinctly more common in rivers of outwash plains at the boundary of the latest glaciations, usually near outcrops of carbonate rocks, as well as in areas of karst development. *P. × bottnicus* and *P. × fennicus* are relicts, because they are hybrids with participation of *P. vaginatus*, which was extinct in this region after the last Valdai glaciation. In the south of the study area, *P. × suecicus* is also a relict, here it is found to the south of the current range of *P. filiformis*. The distribu-

tion of *P. × cognatus*, *P. × cooperi*, *P. × olivaceus*, *P. × prussicus*, and *P. × vepsicus* is difficult to analyze yet.

We have found characteristic distribution of different taxa along the longitudinal profile of watercourses (upper, middle, and lower stretches) and among the types of watercourses (streams, small, medium, and large rivers). So, *P. alpinus*, *P. berchtoldii*, *P. gramineus*, *P. natans*, and *P. obtusifolius* are characteristic of upper stretches of watercourses. They are more common in streams and small rivers. *P. crispus*, *P. filiformis*, *P. friesii*, *P. perfoliatus*, and almost all hybrids are more typical of middle stretches of rivers. These pondweeds predominantly grow in small and medium rivers. *P. lucens*, *P. pectinatus*, and *P. praelongus* are common for lower stretches of rivers. These species also prefer the largest watercourses. Thus, the watercourses combines in their vegetation cover the species and hybrids of *Potamogeton* that are characteristic of the given type of watercourses and watercourses of smaller orders. In addition, having significant length and considerable diversity of habitats they include pondweeds typical of other types of water bodies (bogs, lakes, oxbows, etc.) are found there. These are, e.g., *P. friesii*, *P. obtusifolius*, *P. praelongus*, *P. pusillus*, and *P. trichoides*.

The identified taxa occupy a wide range of river habitats. *P. lucens*, *P. natans*, *P. pectinatus*, *P. perfoliatus*, *P. praelongus*, *P. subretusus*, *P. × salicifolius* and other pondweeds (mainly large ones) have been found in reaches; *P. alpinus*, *P. crispus*, *P. filiformis*, *P. gramineus*, *P. pectinatus*, *P. perfoliatus*, *P. × angustifolius*, *P. × fennicus*, *P. × fluitans*, *P. × nitens*, *P. × salicifolius*, *P. × sparganiifolius*, *P. × suecicus*, *P. × vepsicus* and others (species and hybrids capable of forming narrow, ribbon-like leaves), in riffles and rapids; *P. alpinus*, *P. berchtoldii*, *P. friesii*, *P. gramineus*, *P. natans*, *P. obtusifolius*, *P. pusillus*, *P. subretusus*, *P. × angustifolius*, *P. × nitens*, and others (small species and pondweeds with floating leaves), in backwaters and macrophyte stands (*Nymphaeaceae* and helophyte communities); *P. alpinus*, *P. gramineus*, *P. natans*, *P. × angustifolius*, *P. × nitens*, *P. × sparganiifolius* (species and hybrids capable of forming, when out of water, rosettes of coriaceous leaves), in shallows.

This distribution of taxa in river ecotopes largely depends from relation pondweeds to current, the main factor of river ecosystems. Species and hybrids with linear and ribbon-like leaves are well adapted to fast current. *P. lucens* and *P. praelongus*, which generally prefer still waters, can also be tolerant to current, they form here narrower and longer leaves. In general, many pondweeds are represented by specific morphotypes in flowing water. Small species from the section *Graminifolii* Fries distinctly avoid currents. Predominantly lake *P. filiformis* and lake-oxbow *P. gramineus* in the southern part of the study area northward become common components of river vegetation, and in some places are abundant in riffles and rapids.

Regarding the ground, pondweeds also display specific tendencies. Pondweeds from the subgenus *Coleogeton* (Reichenb.) Raunk. distinctly prefer sandy grounds; but in places with outcrops of solid bed rocks (usually carbonate ones) they also grow fairly well. Most identified taxa successfully develop on various stony grounds (with sand, clay, or silt admixtures), because they are the stablest and provide strong attachment of the plants. Silty grounds rich in nutrients are characteristic of river ecotopes with still waters; the large *P. alpinus*, *P. lucens*, and *P. natans* and, especially, the small *P. berchtoldii*, *P. friesii*, *P. obtusifolius*, *P. pusillus*, and *P. trichoides* tend to grow there. There is also relationship with the chemical composition of the water. *P. alpinus*, *P. berchtoldii*, *P. gramineus*, *P. natans*, *P. obtusifolius*, *P. subretusus*, *P. × sparganiifolius*, and *P. × vepsicus* can grow in poorly mineralized, soft waters. In waters with a medium mineralization and hardness, most identified taxa grow. *P. filiformis*, *P. lucens*, *P. pectinatus*, *P. praelongus*, *P. × bottnicus*, *P. × fennicus*, *P. × fluitans*, and *P. × suecicus* have been found in highly mineralized, hard waters. The trophic characteristics and pollution level also affect the species composition of pondweeds in watercourses.

In many rivers, especially those with favorable conditions, including well-structured channels (reaches, riffles), solid stony or clayey grounds, and waters with medium mineralization, pondweeds are active primary producers. *P. gramineus*, *P. lucens*, *P. natans*, *P. perfoliatus*, *P. × fennicus*, *P. × nitens*, *P. × salicifolius*, *P. × sparganiifolius*, and *P. × suecicus* may be considered to be the most important producers. In addition, stands of pondweeds may considerably affect hydrological parameters (substantially decrease the current velocity, increase the accumulation of detritus and alluvium, and decrease the illumination of the bottom layer of water) and hydrochemical characteristics (increase the temperature and pH, cause the variation in oxygen content, etc.). They create the environment, serve as a substrate, food, and shelter for various organisms and play an important role in self-purification of river ecosystems.

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