

Potamogeton × *subrufus* Hagstr.: a neglected *Potamogeton* hybrid

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The original material of *Potamogeton* × *subrufus* Hagstr. [= *P. lucens* L. × *P. nodosus* Poir.] and the herbarium material of the morphologically most similar hybrid, *P.* × *fluitans* Roth [= *P. lucens* L. × *P. natans* L.], were examined taxonomically. Approximately 45 characters were studied on 42 herbarium specimens of both taxa. The analysis shows that *P.* × *subrufus* displays several characters consistently different from those of *P.* × *fluitans*. Two new European localities of *P.* × *subrufus* found during the study are also provided and a morphological description of the hybrid, including distinguishing characters, is given.

Key words: anatomy, aquatic plants, clones, Denmark, distribution, hybridisation, morphology, taxonomy

Introduction

Hagström (1916) described *Potamogeton* × *subrufus* as a hybrid between *P. lucens* L. and *P. nodosus* Poir. based on herbarium specimens gathered from two separate locations in Europe and North America. The Gudenå River near Kongensbro, Jutland, Denmark, where the hybrid was collected by I. Baagöe in 1895, 1897, 1899 and 1900, is given in the protologue as the European locality. Baagöe identified these plants as “*P. fluitans* Roth (*P. lucens* + *P. natans*) f. *sublucens* Baagöe” while Hagström, when he examined the material in 1899, regarded the specimens as a hybrid between *P. alpinus* Balb. and *P. lucens* (Hagström 1916). Probably influenced by Hagström, Baagöe later labelled some specimens as “*P. alpinus* + *P. lucens* (*P. olivaceus* mihi non

O. F. Lang)”. In fact, plants from all the Danish gatherings are morphologically and anatomically very similar, and are likely to represent the same clone. The lectotype of *P.* × *subrufus* was designated by Kaplan (2005) and chosen from among Baagöe’s European collections preserved in UPS. The original view of Baagöe and Hagström, who finally described the plants as a hybrid between *P. lucens* and *P. nodosus*, was not adopted later by *Potamogeton* taxonomists and *P.* × *subrufus* was reduced to synonymy with *P.* × *fluitans* Roth, a hybrid between *P. lucens* and *P. natans* L. (Dandy & Taylor 1942, Wiegleb & Kaplan 1998, Kaplan 2005). *Potamogeton* × *fluitans* is fairly common with a very wide range of morphological variability. Plants collected in the Gudenå River near Kongensbro were thought to be part of this variation. The fact that one of

the proposed parental species, *P. nodosus*, had not been recorded either from the area or from other parts of entire Scandinavia was also cited against the existence of a hybrid between *P. lucens* and *P. nodosus* in Denmark (Pedersen 1976, Hultén & Fries 1986).

Potamogeton species abundantly involved in crossing are known to occur in most cases sympatrically in the place of hybrid creation or its vicinity. On the other hand, populations of established *Potamogeton* hybrids are long persistent and a hybrid population can exist despite the absence of one or both parental species. The case of *P. × bottnicus* Hagstr., a hybrid between *P. pectinatus* L. and *P. vaginatus* Turcz., provides an interesting example. This hybrid was identified in the British Isles, but one of the parents, *P. vaginatus* Turcz., had been missing from the area for some 30 000 years (Preston *et al.* 1998). It is highly probable that *P. × bottnicus* is a relic in Britain, owing its origin to ancient hybridisation involving indigenous *Potamogeton* species (King *et al.* 2001). This shows that the recognition of a *Potamogeton* hybrid should be based exclusively on taxonomical characters and the actual overlap of the ranges of parental species can only be treated as additional premise and not as decisive argument.

Another hybrid growing together with a plant described by Hagström as *P. × subrufus* was collected by Baagöe on 28 July 1895. It was morphologically different from *P. × subrufus* and was labelled “*P. fluitans* Roth f. *rivularis* Baagöe”. *Potamogeton* morphotypes within a population of the same taxon are very similar because of the predominance of vegetative propagation and due to the influence of habitat factors (Kaplan 2002). Therefore, it is difficult to explain why two distinct forms of the same (as nowadays regarded) taxonomical entity occurred in one habitat at the same time. Furthermore, stem anatomy characters of the two morphotypes differ markedly. The form “*rivularis* Baagöe” is a true *P. × fluitans* in the present author’s opinion while morphotypes described as *P. × subrufus* constitute another taxon. A hypothesis that it could be *P. × sparganiifolius* Laest. ex Fr., a third hybrid similar to *P. × fluitans* and *P. × subrufus*, was excluded based on the general morphological appearance of the plants.

The aim of the present study is to evaluate morphological and anatomical characters of *P. × subrufus* using the available original material collected in Denmark, to compare the characters with those of the most similar *P. × fluitans*, and to resolve unequivocally the taxonomical status of *P. × subrufus*.

Material and methods

The available original herbarium specimens of *P. × subrufus* collected by I. Baagöe in the Gudenå River near Kongensbro, Jutland, Denmark, and preserved in the Herbarium of the University of Copenhagen (C) were investigated taxonomically. Twenty herbarium specimens of *P. × fluitans* representing a range of distinct morphotypes of this taxon, also preserved in C, were examined for comparison. Morphological characters of the stem, submerged and floating leaves, stipules, inflorescence, peduncles and flowers were measured or described qualitatively. Anatomical characters of all specimens were also assessed. Short pieces of the stem (ca. 2 mm) were cut from the internode of the main stem. Pieces were embedded in water for a few minutes and transverse sections, ca. 0.05 mm thin, were next made. Slices were kept in an aquatic solution of toluidine blue for 1–3 minutes. Stained tissues were washed in distilled water. Stem anatomy was investigated under a transmitted light microscopy at magnification 50× (general anatomical pattern) and up to 400× (detailed view). Approximately 45 morphological and five anatomical characters were examined for each of 42 individuals of both taxa.

Results

Potamogeton × subrufus and *P. × fluitans* are morphologically very similar. Consequently, variation ranges of most of their features overlap. The analysis, however, reveals some characters that differentiate these two taxa (Table 1). The best distinguishing characters are those of stem anatomy. *Potamogeton × fluitans* is rich in sclerenchyma while the number of sclerenchymatous strands (subepidermal and cortical ones) is always reduced in *P. × subrufus*.

A detailed description of *P. × subrufus* is given below. Comparative descriptions of *P. × fluitans* are available in studies by Preston (1995), Kaplan (2001) and Zalewska-Gałosz (2002, 2008).

Description of *P. × subrufus*

Stem up to 1.5 m, robust, terete, unbranched; nodal glands absent. *Submerged leaves* with lamina (160–)170–250(–340) mm long, (15–)21–26(–29) mm wide, 6.4–11.3 times as long as wide, translucent, brownish green when dried, narrowly elliptical, gradually tapering to a petiolate base and semiacute or acute apex, minutely denticulate at margin, midrib bordered by a band of lacunae; lateral veins 4–6 on each side of the midrib, two stronger than others; secondary veins numerous, ascending; petioles 20–40(–50). *Floating leaves* with lamina 135–215 mm long, 21–34 mm wide, 4.82–10 times as long as wide, opaque, coriaceous, broadly elliptical, cuneate at base and obtuse or apiculate at apex; lateral veins 6–9 on each side of midrib, secondary veins numerous, obscure; petioles 34–83 mm. *Stipules* 52–120 mm, open, enfolding stem, translucent, pale brown when dry, fairly persistent, veins inconspicuous when dry, 2 more prominent than others, forming ridges or narrow wings along stipule. *Turions* absent. *Inflorescences* 20–31 mm long, 3–6 mm wide; peduncles 62–95 mm long, robust, terete, broader, spongy and wider than spike. *Flowers* numerous, contiguous with 4 carpels. *Fruits* not seen. *Stem anatomy*: stele or complex oblong type, endodermis of U(O)-type, interlacunar bundles present in 1(2) circles (inner

one not fully developed), subepidermal bundles absent or only few present, pseudohypodermis absent or only partly developed.

New localities of *P. × subrufus*

Two localities not published previously were found during the study in the herbarium C. One locality is situated in the Gudenå River, near Ans, not far away from the *locus classicus*. *Potamogeton* × *subrufus* was collected there by J. Grøntved and K. Jessen on 14 August 1918 and identified as *P. lucens* × *P. alpinus*. The other locality was originally indicated as Ostpreussen, Darkehmen, in Angerapp bei Dombrowken (nowadays the Węgorapa River near Dąbrówka Nowa, Węgorzewo district, north-eastern Poland), where H. Kuehn collected the plant on 6 July 1892. Kuehn identified the specimen as “*Potamogeton lucens* L. γ *longifolius* Gay”.

Discussion

An appropriate evaluation of variation limits of taxa is blurred by high levels of plasticity observed in *Potamogeton* individuals (Kaplan 2002). Formal descriptions of almost all morphotypes commonly applied in their systematics in the late 19th and the early 20th centuries resulted in a very complicated nomenclature. James E. Dandy and George Taylor were the first to elucidate the taxonomy of *Potamogeton*. In their studies of British pondweeds, they introduced a broader concept of *Potamogeton* species, under which many varieties and forms

Table 1. Diagnostic features distinguishing *Potamogeton* × *subrufus* and *P. × fluitans*.

	<i>P. × subrufus</i>	<i>P. × fluitans</i>
Morphological characters		
apex of submerged leaves	semiacute or acute, never mucronate	mucronate
lacunae along stronger lateral veins	broad band up to the apex	narrow band not reaching the apex
length of petiole	20–50 mm long	25–90 mm long
Stem anatomy characters		
number of subepidermal strands	up to 2 strands	more than 3 strands
cortical strands	1 or 2 circles (but inner one not fully developed)	2–3 fully developed circles

described previously were regarded as developmental stages only, unworthy of taxonomical recognition (Taylor 1949). As a consequence, many taxonomical names were reduced to synonyms (*see* Preston 1995 and literature cited therein). A broad concept of taxa was also adopted in a recent worldwide treatment of *Potamogeton* (Wiegleb & Kaplan 1998). While undoubtedly more appropriate in the case of morphologically plastic plants such as pondweeds, this approach can also be misleading. Aquatic habitats restrict potential morphology, thereby limiting the range of phenotypic differences between species (Niklas 1997). In specific ecological conditions, different taxa can produce morphotypes impossible to distinguish using morphological or even anatomical characters. Only a careful and thorough evaluation of the plant material, cultivation experiments, biochemical or molecular approaches can finally resolve taxonomical problems. Dandy and Taylor (1942) did not provide a detailed study of *P. × subrufus* and *P. × fluitans* characters, but simply indicated that the former is the riverine state of the latter. Their point of view was later adopted by Wiegleb and Kaplan (1998) and Kaplan (2005). The present study, however, shows that *P. × subrufus* should be placed among taxa worth recognising. It is currently known from three localities and appears to be one of the rarest *Potamogeton* hybrids, but individuals of this taxon may have been overlooked and identified as *P. × fluitans*.

The occurrence of *P. × subrufus* in Denmark could be an argument for the ancient presence of *P. nodosus* in the area although the latter was not identified in fossils (Jessen & Milthers 1928). A historical long-distance dispersal of hybrid seeds seems to be an equally probable scenario. The available evidence however is too scanty to support any of these hypotheses.

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