Nordic Journal of Botany 29: 477–483, 2011
doi: 10.1111/j.1756-1051.2011.01240.x,

Subject Editor: Torbjörn Tyler. Accepted 9 June 2011

Potamogeton × *exilis* (*P. alpinus* × *P. natans*), a new hybrid pondweed from Finland

Zdenek Kaplan and Pertti Uotila

Z. Kaplan (kaplan@ibot.cas.cz), Inst. of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Průhonice, Czech Republic. – P. Uotila (pertti.uotila@helsinki.fi), Botanical Unit, Finnish Museum of Natural History, PO Box 7, FI-00014 University of Helsinki, Finland.

A *Potamogeton* hybrid recently discovered in Finland was proven to be a new taxon, which has a different parentage than the most similar *P.* × *vepsicus* (= *P. natans* × *praelongus*) described from Russia. Based on molecular and morphological investigation, the new hybrid was identified as *P. alpinus* × *natans* and is here described as *P.* × *exilis* nothosp. nov. The hybrid is known only from several nearby localities in a single river system. All discovered colonies almost certainly originate from a single hybridization event that occurred in the upper part of the river system. Other localities downstream have been established through fragmentation and dispersal of stems and rhizomes of this sterile hybrid. A detailed morphological comparison of the new hybrid with similar hybrids and species is provided.

The Potamogetonaceae is one of the most diverse and taxonomically difficult families of aquatic plants (Wiegleb and Kaplan 1998, Kaplan 2002a). The main sources of taxonomic complexity include the reduced morphology, which limits the number of taxonomic characters that can be used to separate species (Preston and Croft 1997, Kaplan and Štěpánek 2003, Kaplan et al. 2009), extensive phenotypic plasticity (Kaplan 2002b, Kaplan and Zalewska-Gałosz 2004, Kaplan 2008), partitioning of genetic variation between rather than within populations (Hettiarachchi and Triest 1991, Kaplan and Štěpánek 2003) and the occurrence of numerous hybrids (Preston 1995a, Wiegleb and Kaplan 1998, Kaplan and Fehrer 2007, Kaplan et al. 2009, Kaplan 2010a).

The occurrence of hybridization in Potamogetonaceae has been known for more than a century (reviewed by Wiegleb et al. 2008, Kaplan et al. 2009). With the advent of molecular methods over the last two decades, more convincing evidence became available and many taxonomic problems were solved. The existence of many hybrids were confirmed using isozyme electrophoresis (Hollingsworth et al. 1995, 1996, Preston et al. 1998b, Fant et al. 2001a, b, Iida and Kadono 2002, Kaplan et al. 2002, Kaplan and Wolff 2004, Kaplan 2007) and DNA-based analyses (King et al. 2001, Fant et al. 2003, 2005, Kaplan and Fehrer 2004, 2006, 2009, Ito et al. 2007, Wang et al. 2007, Du et al. 2009, 2010, Kaplan et al. 2009, Zalewska-Gałosz et al. 2009, Zalewska-Gałosz and Ronikier 2010). DNA sequencing and RFLPs have contributed to the discovery and/or exact identification of several entirely new hybrid combinations (Kaplan et al. 2009, 2011, Du et al. 2010, Zalewska-Gałosz et al. 2010, Kaplan and Fehrer 2011, Zalewska-Gałosz and Ronikier 2011) and even confirmed the existence of a triple hybrid in *Potamogeton* (Kaplan and Fehrer 2007). Erroneous identifications of two *Potamogeton* hybrids recollected from their type clones have been corrected by molecular analysis (Kaplan and Fehrer 2011). The total number of identified and now recognized *Potamogeton* hybrids has reached about the same number as the number of species (Kaplan 2010a).

The reliability of morphological identifications of Potamogetonaceae hybrids varies greatly depending on parentage. These range from easily recognizable hybrids to those that cannot be identified morphologically with certainty (Kaplan et al. 2009, Kaplan 2010a). Previous studies demonstrate that due to extensive phenotypic plasticity, some hybrids can imitate species and remain unrecognized (Kaplan 2002b, Kaplan and Wolff 2004, Kaplan et al. 2009). Other hybrids can be identified morphologically only when specific key structures are carefully examined (Preston 1995a, Preston et al. 1999, Kaplan 2008, Kaplan et al. 2009) or if the particular plant is fully developed and shows diagnostic features of the species involved in the hybridization (Kaplan and Wolff 2004, Kaplan and Fehrer 2007, Kaplan 2010a).

Sometimes it is easier to identify the particular plant as a hybrid than to establish its exact parentage. These hybrids often belong to one of several groups of highly similar *Potamogeton* taxa (species and other hybrids). An example is the group of *P. natans* hybrids (Kaplan and Wolff 2004, Kaplan and Fehrer 2009), which includes taxa that share the same general appearance and several taxonomically important morphological characters, such as linear to oblanceolate submerged leaves and the capacity to produce floating leaves with a coriaceous lamina, which is generally cuneate at the base and gradually tapering into the petiole. These hybrids often produce transitional leaves, which are intermediate in shape and size between the very narrow submerged leaves (reduced to phyllodes near the base of the stem) and broad floating leaves. The identification of the members of this complex is extremely difficult. Some of these sterile hybrids even resemble the unrelated fertile species *P. nodosus* (Raunkiær 1903, Hagström 1916, Kaplan 2001, 2005a, 2010a). In addition to detailed analysis of morphology, studies of stem anatomy (Raunkiær 1903, Fischer 1905, 1907, Kaplan 2001), cytological investigation (Preston et al. 1998a), isozyme analysis (Hollingsworth et al. 1995, Fant et al. 2001b, Kaplan et al. 2002, Kaplan and Wolff 2004) or DNA analysis (Kaplan and Fehrer 2009) are usually necessary for reliable identification.

A recent molecular study (Kaplan and Fehrer 2011) analyzed the identity of two similar hybrids, which apparently belonged to the group of *P. natans* hybrids. A plant described from Russia as *P.* × *vepsicus* and believed to be *P. alpinus* × *natans* (Bobrov and Chemeris 2006) was shown to be misunderstood and its correct identity was revealed as *P. natans* × *praelongus*. In contrast, a similar plant discovered in Finland proved to be the true hybrid *P. alpinus* × *natans*, which was unknown so far. The aim of this paper is to provide morphological analysis of these similar hybrids and to provide a binomial for the new Finnish hybrid.

Material and methods

Fresh material of the hybrid *P. alpinus* × *natans* was first encountered by P. U. in 1971 from the river Nuorittajoki and in 1977 by Tauno Ulvinen from a side brook of the river Olvasoja, which empties into the river Nuorittajoki (H, OULU). The latter place was revisited by Lasse Pihlajaniemi in 2005 (H), and studied during joint fieldwork of P. U. and Z. K. in 2009. Voucher specimens were deposited in PRA and H (herbarium acronyms according to Thiers 2011). Herbarium specimens of the parental species and of similar species and hybrids from around the world were investigated for comparison (for the complete list of studied herbaria see Kaplan 2008, 2010a, 2010c).

Morphological observations were made mainly on recently collected and carefully prepared herbarium material. Abundant morphological data compiled for previous studies (Wiegleb and Kaplan 1998, Kaplan 2001, 2002b, c, 2005b, 2010a, b, Kaplan and Wolff 2004, Kaplan and Symoens 2004, 2005, Kaplan and Fehrer 2009) and available in modern taxonomic revisions (Preston 1995a, b, Bobrov and Chemeris 2006) were also considered in order to cover the morphological variation of the respective species as completely as possible. Rare extremes were excluded from the quantitative data. Numbers of leaf veins include all longitudinal veins present in the lamina. As these are sometimes very faint, their number was scored under a stereomicroscope at a magnification of 20–75 ×. Only a brief description, mainly consisting of diagnostic characters, is given here for the new hybrid *P. alpinus* × *natans*. The most important diagnostic characters are summarized in Table 1 to facilitate comparison. The general morphology of the new hybrid is shown in scanned images of type specimens.

***Potamogeton* × *exilis* Z. Kaplan & Uotila nothosp. nov. (Fig. 1–3)**

(= *P. alpinus* Balb. × *P. natans* L.)

Planta hybrida, primo aspectu P. natantem revocans sed differt laminis foliorum submersorum superiorum bene evolutis et petiolo foliorum natantium ad apicem sub lamina absque articulo flexili discolori; P. × *vepsico maxime similis, a quo habito glaciliore, foliis submersis angustioribus, stipulis brevioribus, foliis natantibus rubescentioribus, cum lamina basi in petiolum subito contracta et petiolo vix alatiore differt.*

Type: Finland, Ostrobottnia ouluensis, Pudasjärvi: 26 km south of Pudasjärvi, 3.9 km southsouthwest of Keinäsperä village, small dystrophic river Olvasoja running through coniferous forests and peatland ca 100 m downstream of bridge on forest track from Keinäsperä–Olvasjärvi road to Hirsimaa, 65°07′55.0″N, 26°55′14.2″E (WGS 84), 112 m a.s.l., 16 Jul 2009, coll. Z. Kaplan 09/314 and P. Uotila (holotype: PRA, isotypes: H, OULU, PRA).

Etymology

Exilis = slender, meagre, weak; referring to the slender habit and markedly narrow submerged leaves.

Rhizome slender, creeping. Stem simple (unbranched), slender. Basal submerged leaves phyllodial, upper submerged leaves with very narrow lamina, linear to narrowly oblanceolate, 90–330 mm long, 1.5–6.0 mm wide, 24–165 times as long as wide, slightly concave on the upper side, acute at the apex or tapering to a very narrow but obtuse tip, 3–5-veined, with a narrow to broad band of lacunae, particularly towards the leaf base. Transitional leaves intermediate in shape and size between submerged and floating leaves almost always present. Floating leaves present on adult plants that reach the water surface, petiolate; lamina narrowly oblong to elliptical, 65–120 mm long, 8–26 mm wide, coriaceous, reddish brown or green, often with reddish to brownish tinge at least along veins, especially when dried, 5–17-veined, subobtuse at the apex, cuneate or sometimes narrowly cuneate at the base and rather shortly tapering into the petiole; petiole 28–120 mm long, 0.6–1.4 times as long as the lamina, unwinged or only shortly winged towards lamina, without a discoloured section at the junction with the lamina. Stipules axillary, convolute, 35–72 mm long. Generative organs extremely rare (only two inflorescences seen). Peduncle 80–85 mm long, 3.0–4.3 times as long as the spike, as thick as the stem, inserted in the axils of floating leaves. Spike cylindrical, 20–27 mm long in fruit, contiguous. Flowers numerous, with 4 abortive carpels. Fruits not observed and presumably not produced (plants sterile).

Habitat, ecology and distribution

The moderately sized river Nuorittajoki is the main tributary of the river Kiiminkijoki, which empties into the Gulf of Bothnia of the Baltic Sea. The 2–5 m broad river

Table 1. Comparison of the most important diagnostic characters of *Potamogeton* × *exilis* and *P.* × *vepsicus*, their parental species, and the most similar hybrid *P.* × *sparganiifolius*.

	P. alpinus	*P.* ×*exilis*	*P. natans*	*P.* ×*vepsicus*	*P. praelongus*	*P.* ×*sparganiifolius*
Stem						
Branching pattern	always unbranched but occasionally with horizontal leafless stolons	unbranched	unbranched or very sparingly branched	unbranched or sparingly branched	unbranched or sparingly, rarely to richly branched	sparingly to richly branched
Submerged leaves						
Presence of phyllodial leaves	absent	present near the base of the stem	present throughout the stem up to floating leaves	present near the base of the stem	absent	present near the base of the stem
Shape of upper submerged leaves	narrowly lanceolate to oblong	linear to narrowly oblanceolate	linear (phyllodial; laminar leaves absent)	linear-lanceolate to narrowly oblanceolate	lanceolate to ovate-oblong	linear-lanceolate to narrowly oblanceolate
Shape of apex	broadly obtuse or tapering to a narrow but obtuse tip	acute or tapering to a very narrow but obtuse tip	acuminate or tapering to a very narrow but obtuse tip	acute or tapering to a very narrow but obtuse tip	obtuse to rounded	acute to acuminate
Length:width ratio	4–10(–14)	24–165	70–240	(14–)20–70(–85)	(2.5–)3.3–7.5(–15)	16–90
Length (mm)	60–220	90–330	100–450(–600)	110–450	(45–)60–180(–220)	60–520
Width (mm)	(7–)10–25(–35)	1.5–6	0.8–3.5	3–9(–12)	14–40	1.5–7(–12)
Number of longitudinal veins	9–17	3–5	1–3	3–9(–11)	11–19(–23)	1–9(–13)
Presence of lacunae in lamina along midrib	broad band of lacunae, particularly towards base	narrow to broad band of lacunae, particularly towards base	–	narrow to broad band of lacunae, particularly towards base	narrow band of lacunae	narrow to broad band of lacunae
Transitional leaves						
Presence on adult flowering plants	sometimes present	almost always present	generally absent	mostly present	absent	mostly present
Floating leaves						
Presence on adult flowering plants	mostly present	always present	always present	mostly present	absent	mostly present
Colour of dry lamina	reddish brown or green with reddish to brownish tinge at least along veins	reddish brown or green with reddish to brownish tinge at least along veins	green, sometimes with yellowish or brownish tinge	green, sometimes with yellowish or brownish tinge	–	green, sometimes with brownish tinge
Shape of lamina	oblong or oblanceolate to obovate	narrowly oblong to elliptical	oblong to broadly elliptical or broadly ovate	oblong to elliptical	–	narrowly oblong to elliptical or ovate
Shape of base of lamina of floating and transitional leaves	narrowly cuneate and mostly gradually tapering into the petiole	cuneate or sometimes narrowly cuneate and rather shortly tapering into the petiole	rounded to subcordate, sometimes cuneate	cuneate to narrowly cuneate and often very gradually tapering into the petiole	–	cuneate to rounded or subcordate
Length of lamina of floating leaves (mm)	40–90	65–120	40–120	60–120(–150)	–	25–120
Width of lamina of floating leaves (mm)	8–27	8–26	(10–)20–45(–80)	10–25	–	7–35
Number of longitudinal veins in floating leaves	9–19	5–17	13–31(–35)	9–21	–	7–25
Length of petiole: length of lamina ratio	0.1–0.8	0.6–1.4	(1.0–)1.3–5.0(–6.2)	0.8–2.1	–	(0.4–)0.7–2.6
Winging of petioles of floating leaves	markedly winged towards lamina	unwinged or only shortly winged towards lamina	unwinged	often markedly winged towards lamina	–	mostly unwinged, sometimes shortly winged towards lamina
Length of petiole of floating leaves (mm)	10–35	28–120	50–180(–420)	(25–)60–100(–150)	–	(17–)30–100(–250)
Presence of discoloured section between petiole and lamina of floating leaves	absent	absent	almost always present	absent	–	sometimes present
Stipules						
Length (mm)	18–45	35–72	40–140(–170)	(35–)50–90(–120)	15–70(–80)	17–65(–95)

Figure 1. Holotype of *Potamogeton × exilis*.

Olvasoja gathers much of its water from extensive oligotrophic peatland areas and the small Lake Olvasjärvi, and empties into the river Nuorittajoki. The brook Syrjäoja, running to the river Olvasoja, is mostly about 1 m broad and gets its water from peatlands. Only more or less narrow mineral soil stripes with conifer forest (mostly spruce) separate the river Olvasoja from peatlands. Most of the peatlands in the catchment area of Olvasoja–Syrjäoja have been ditched already decades ago, which means that the water in the river is dystrophic, i.e. rather acid, humic and brown in colour. The river bed has quite steep but low shore banks, and the bottom is mostly fine sand. The water is shallow, slow to fairly fast running, and the variation of the water amount is considerable between seasons and years. The hybrid mostly produces almost mono-dominant dense colonies where sometimes only a few shoots of *Hippuris vulgaris*, *Lysimachia thyrsiflora* and *Sparganium emersum* were seen (Fig. 4). In the brook Syrjäoja, it grows not far from *P. alpinus* and *Sparganium natans*, downstream of them.

So far, *P. × exilis* is known only from sites in a single river system (Fig. 5). However, major part of the more than 8 km long river course from the uppermost finds in brook Syrjäoja to the lowermost ones at the mouth of river Olvasoja has not been studied, and probably the hybrid occurs in the whole river course. The three main localities examined in 2009 (together less than one km of the river course) hosted dozens of 5–10 m, sometimes to 20 m long, mostly rather narrow colonies along shore water and patches in the middle of the stream (Fig. 4). We did not calculate the exact number of shoots, but we estimate that in each of the localities there were a few hundred to many thousands of ramets of *P. × exilis*. All discovered colonies almost certainly originated from a single hybridization event that occurred in the upper part of the river system. The uppermost locality is in the brook Syrjäoja, where one of the parental species, *P. alpinus*, occurs. As for *P. natans*, at present Syrjäoja appears as a quite too small brook and otherwise unsuitable as a habitat for it. Although the great majority of *Potamogetonaceae* hybrids are consistently sterile (Hagström 1916, Dandy 1975, Preston 1995a, Wiegleb and Kaplan 1998, Kaplan and Fehrer 2007, Kaplan et al. 2009, Kaplan 2010a), they are able to persist vegetatively for long periods using their perennial structures (Hollingsworth et al. 1996, Preston et al. 1998b, King et al. 2001, Kaplan and Wolff 2004, Kaplan and Fehrer 2007). In rivers they can even spread downstream quite easily through fragmentation and dispersal of stems and rhizomes, particularly during spring floods with rapid water flow, and subsequently occupy new areas (Kaplan et al. 2002, Kaplan and Wolff 2004).

Figure 2. Floating leaves of *Potamogeton × exilis*.

Similar taxa

Potamogeton × exilis at the first sight resembles *P. natans*, particularly its running-water form, because they share the general appearance and basic superficial features such as shape and colour of leaves (Fig. 2). However, they differ in details of the leaves. Submerged leaves of *P. × exilis* are strongly reminiscent of linear phyllodes of *P. natans* but unlike those of the species, particularly the upper submerged leaves expand into a well-developed lamina (Fig. 1, 3). The floating leaves of *P. × exilis* lack a flexible junction between the petiole and the lamina, which is almost always present in *P. natans*. Some floating leaves of the hybrid are intensively reddish (Fig. 1, 3), which indicates that the other parent is *P. alpinus*, which has the same colour tinge, at least when dry. Otherwise, *P. alpinus* differs markedly from *P. × exilis*, in having all submerged leaves with expanded, narrowly lanceolate to oblong lamina

Figure 3. *Potamogeton* × *exilis* showing different sorts of leaves, ranging from basal phyllodium-like leaves over upper submerged leaves with slightly expanded lamina to floating leaves with a well developed narrowly oblong to elliptical lamina. Some floating leaves exhibit characteristic reddish pigment.

(never reduced to phyllodia), with more numerous longitudinal veins. In addition, the petioles of floating leaves of *P. alpinus* are substantially shorter than the lamina and markedly winged towards the lamina, whereas in *P.* × *exilis* they are approximately as long as or even slightly longer than the lamina and are unwinged or only shortly winged towards the lamina. Also the stipules are shorter in *P. alpinus* than in the hybrid. Values of the quantitative characters are given in Table 1.

Figure 4. A stretch of river Olvasoja with a colony of *Potamogeton* × *exilis*.

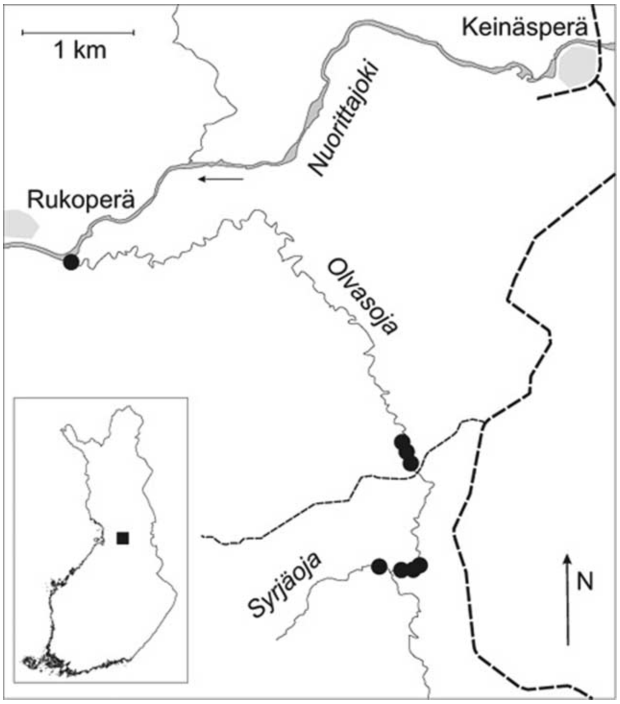

Figure 5. A map showing the distribution of *Potamogeton* × *exilis* in the catchment area of the river Olvasoja, and the position of the area in Finland.

Rather than to its parents, *P.* × *exilis* is most similar to another hybrid, *P.* × *vepsicus*, which was originally believed to be *P. alpinus* × *natans* (Bobrov and Chemeris 2006) but was recently identified as *P. natans* × *praelongus* (Kaplan and Fehrer 2011). These hybrids differ mainly in quantitative characters and most of them show some overlap. *Potamogeton* × *exilis* is on average smaller than *P.* × *vepsicus*, more slender, with narrower, phyllodium-like submerged leaves, with only slightly expanded lamina, and shorter stipules. Plants from the type collection of *P.* × *vepsicus* often show floating and transitional leaves with the lamina very gradually tapering to the base and forming prominent wings along the petiole. These were not observed in *P.* × *exilis*, which tends to have the lamina rather shortly tapering into the more or less unwinged petiole (Fig. 1). The floating leaves of *P.* × *exilis* turn reddish when dried, showing exactly the same tinge of the pigment known from *P. alpinus* and obviously inherited from this species, which were not observed in *P.* × *vepsicus.*

Some running-water forms of *P.* × *sparganiifolius* (= *P. gramineus* × *natans*) are also similar but they can be distinguished from *P.* × *exilis* by their mostly branched stem, slightly stiffer submerged leaves and the lack of the characteristic reddish pigment in floating leaves, sometimes also by obscure traces of a discoloured section between the petiole and the lamina of floating leaves.

The most important diagnostic characters of all these hybrids and of selected parental species are summarized in Table 1. Because of the overall similarity of these hybrids, it is advisable to have molecular proof of the identity of questionable plants.

Additional specimens examined (paratypes)

Finland, Ostrobottnia ouluensis, Pudasjärvi: 26 km south of Pudasjärvi, 4.8 km southsouthwest of Keinäsperä village, small dystrophic brook Syrjäoja running through coniferous forests and peatland ca 40 m upstream of its mouth to river Olvasoja, 65°07′24.1″N, 26°54′58.9″E (WGS 84), 113 m a.s.l., 16 Jul 2009, coll. Z. Kaplan 09/310 and P. Uotila (PRA, H); small dystrophic river Olvasoja running through coniferous forests and peatland ca 30 m downstream of mouth of brook Syrjäoja, 65°07′23.3″N, 26°55′03.1″E (WGS 84), 113 m a.s.l., 16 Jul 2009, coll. Z. Kaplan 09/311 and P. Uotila (PRA, H); Rukoperä, south shore of the river Nuorittajoki, at the mouth of the river Olvasoja, Grid 27°E: 72280: 4933, 22 Aug 1971, coll. P. Uotila 13205 (H); Keinäsperä–Viinivaara, in brook Olvasoja downstream of mouth of brook Syrjäoja, Grid 27°E: 7225:496, 113 m a.s.l., 9 Aug 1977, coll. T. Ulvinen (H, OULU); brook Syrjäoja ca 50 m before its entry into Olvasoja, Grid 27°E: 72252: 4961, 113 m a.s.l., 27 Aug 2005, coll. L. Pihlajaniemi (H, OULU, PRA, TUR).

Acknowledgements – We would like to thank the curators of the studied herbaria who allowed us to study the plant material in their collections. Mr Sampsa Lommi prepared the map in Fig. 5 and Mr Heino Vänskä checked the Latin diagnosis. The research was supported by grant no. 206/09/0291 from the Czech Science Foundation and by the long-term institutional research plan no. AV0Z60050516 of the Academy of Sciences of the Czech Republic.

References

Bobrov, A. A. and Chemeris, E. V. 2006. *Potamogeton* × *vepsicus* (Potamogetonaceae) – novyi gibridnyi rdest iz Verchnego Povolzhya [*Potamogeton* × *vepsicus* (Potamogetonaceae), a new hybrid pondweed from the Upper Volga region]. – Bot. Zhurn. 91: 71–84.

Dandy, J. E. 1975. *Potamogeton* L. – In: Stace, C. A. (ed.), Hybridization and the flora of the British Isles. Academic Press, pp. 444–459.

Du, Z.-Y. et al. 2009. Nuclear and chloroplast DNA sequences data support the origin of *Potamogeton intortusifolius* J. B. He in China as a hybrid between *P. perfoliatus* Linn. and *P. wrightii* Morong. – Aquat. Bot. 91: 47–50.

Du, Z.-Y. et al. 2010. Identification of hybrids in broad-leaved *Potamogeton* species (Potamogetonaceae) in China using nuclear and chloroplast DNA sequence data. – Plant Syst. Evol. 287: 57–63.

Fant, J. B. et al. 2001a. Isozyme evidence for the origin of *Potamogeton* × *sudermanicus* as a hybrid between *P. acutifolius* and *P. berchtoldii.* – Aquat. Bot. 71: 199–208.

Fant, J. B. et al. 2001b. Isozyme evidence of the parental origin and possible fertility of the hybrid *Potamogeton* × *fluitans* Roth. – Plant Syst. Evol. 229: 45–57.

Fant, J. B. et al. 2003. Chloroplast evidence for the multiple origins of the hybrid *Potamogeton* × *sudermanicus* Hagstr. – Aquat. Bot. 75: 351–356.

Fant, J. B. et al. 2005. Chloroplast evidence for the multiple origins of the hybrid *Potamogeton* × *fluitans.* – Aquat. Bot. 83: 154–160.

Fischer, G. 1905. Beitrag zur Kenntnis der bayerischen Potamogetoneen. V. – Mitt. Bayer. Bot. Ges. 1: 471–475.

Fischer, G. 1907. Die bayerischen Potamogetonen und Zannichellien. – Ber. Bayer. Bot. Ges. 11: 20–162.

Hagström, J. O. 1916. Critical researches on the Potamogetons. – Kungl. Svenska Vetenskapsakad. Handl. 55(5): 1–281.

Hettiarachchi, P. and Triest, L. 1991. Isozyme polymorphism in the genus *Potamogeton* (Potamogetonaceae). – Opera Bot. Belg. 4: 87–114.

Hollingsworth, P. M. et al. 1995. Isozyme evidence for hybridization between *Potamogeton natans* and *P. nodosus* (Potamogetonaceae) in Britain. – Bot. J. Linn. Soc. 117: 59–69.

Hollingsworth, P. M. et al. 1996. Isozyme evidence for the parentage and multiple origins of *Potamogeton* × *suecicus* (*P. pectinatus* × *P. filiformis*, Potamogetonaceae). – Plant Syst. Evol. 202: 219–232.

Iida, S. and Kadono, Y. 2002. Genetic diversity and origin of *Potamogeton anguillanus* (Potamogetonaceae) in Lake Biwa, Japan. – J. Plant Res. 115: 11–16.

Ito, Y. et al. 2007. Inferring the origin of *Potamogeton* × *inbaensis* (Potamogetonaceae) using nuclear and chloroplast DNA sequences. – J. Jap. Bot. 82: 20–28.

Kaplan, Z. 2001. *Potamogeton* × *fluitans* (*P. natans* × *P. lucens*) in the Czech Republic. I. Morphology and anatomy. – Preslia 73: 333–340.

Kaplan, Z. 2002a. Hlavní příčiny taxonomických obtíží v rodu *Potamogeton* [Main sources of taxonomic difficulties in *Potamogeton*]. – Zprávy Čes. Bot. Společ 37: 43–46.

Kaplan, Z. 2002b. Phenotypic plasticity in *Potamogeton* (Potamogetonaceae). – Folia Geobot. 37: 141–170.

Kaplan, Z. 2002c. Potamogetonaceae Dum. – rdestovité. – In: Kubát, K. et al. (eds), Klíč ke květeně České republiky [Key to the flora of the Czech Republic]. Academia, pp. 736–743.

Kaplan, Z. 2005a. Neotypification of *Potamogeton* × *fluitans* Roth and the distribution of this hybrid. – Taxon 54: 822–826.

Kaplan, Z. 2005b. *Potamogeton schweinfurthii* A. Benn., a new species for Europe. – Preslia 77: 419–431.

Kaplan, Z. 2007. First record of *Potamogeton* × *salicifolius* for Italy, with isozyme evidence for plants collected in Italy and Sweden. – Plant Biosyst. 141: 344–351.

Kaplan, Z. 2008. A taxonomic revision of *Stuckenia* (Potamogetonaceae) in Asia, with notes on the diversity and variation of the genus on a worldwide scale. – Folia Geobot. 43: 159–234.

Kaplan, Z. 2010a. Hybridization of *Potamogeton* species in the Czech Republic: diversity, distribution, temporal trends and habitat preferences. – Preslia 82: 261–287.

Kaplan, Z. 2010b. Potamogetonaceae Dumort. – rdestovité. – In: Štěpánková, J. et al. (eds), Květena České republiky [Flora of the Czech Republic]. Academia 8, pp. 329–384.

Kaplan, Z. 2010c. Tiselius' *Potamogeton* exsiccates: changes in taxonomy and nomenclature from one-century perspective. – Ann. Bot. Fenn. 47: 373–393.

Kaplan, Z. and Fehrer, J. 2004. Evidence for the hybrid origin of *Potamogeton* × *cooperi* (Potamogetonaceae): traditional morphology-based taxonomy and molecular techniques in concert. – Folia Geobot. 39: 431–453.

Kaplan, Z. and Fehrer, J. 2006. Comparison of natural and artificial hybridization in *Potamogeton*. – Preslia 78: 303–316.

Kaplan, Z. and Fehrer, J. 2007. Molecular evidence for a natural primary triple hybrid in plants revealed from direct sequencing. – Ann. Bot. Oxford 99: 1213–1222.

Kaplan, Z. and Fehrer, J. 2009. An orphaned clone of *Potamogeton* × *schreberi* in the Czech Republic. – Preslia 81: 387–397.

Kaplan, Z. and Fehrer, J. 2011. Erroneous identities of *Potamogeton* hybrids corrected by molecular analysis of plants from type clones. – Taxon 60: 758–766.

Kaplan, Z. and Symoens, J.-J. 2004. Proposal to conserve the name *Potamogeton schweinfurthii* A. Benn. (Potamogetonaceae) with a conserved type. – Taxon 53: 837–838.

Kaplan, Z. and Symoens, J.-J. 2005. Taxonomy, distribution and nomenclature of three confused broad-leaved *Potamogeton* species occurring in Africa and on surrounding islands. – Bot. J. Linn. Soc. 148: 329–357.

Kaplan, Z. and Štěpánek, J. 2003. Genetic variation within and between populations of *Potamogeton pusillus* agg. – Plant Syst. Evol. 239: 95–112.

Kaplan, Z. and Wolff, P. 2004. A morphological, anatomical and isozyme study of *Potamogeton* × *schreberi*: confirmation of its recent occurrence in Germany and first documented record in France. – Preslia 76: 141–161.

Kaplan, Z. and Zalewska-Gałosz, J. 2004. *Potamogeton* taxa proposed by J. F. Wolfgang and his collaborators. – Taxon 53: 1033–1041.

Kaplan, Z. et al. 2002. *Potamogeton* × *fluitans* (*P. natans* × *P. lucens*) in the Czech Republic. II. Isozyme analysis. – Preslia 74: 187–195.

Kaplan, Z. et al. 2009. New hybrid combinations revealed by molecular analysis: The unknown side of North American pondweed diversity (*Potamogeton*). – Syst. Bot. 34: 625–642.

Kaplan, Z. et al. 2011. *Potamogeton* × *jacobsii* from New South Wales, Australia – the first Potamogetonaceae hybrid from the Southern Hemisphere. – Telopea 13: 245–256.

King, R. A. et al. 2001. Molecular confirmation of *Potamogeton* × *bottnicus* (*P. pectinatus* × *P. vaginatus*, Potamogetonaceae) in Britain. – Bot. J. Linn. Soc. 135: 67–70.

Preston, C. D. 1995a. Pondweeds of Great Britain and Ireland. – Bot. Soc. British Isles Lond.

Preston, C. D. 1995b. *Potamogeton* × *schreberi* G. Fisch. (*P. natans* L. × *P. nodosus* Poir.) in Dorset, new to the British Isles. – Watsonia 20: 255–262.

Preston, C. D. and Croft, J. M. 1997. Aquatic plants in Britain and Ireland. – Harley Books.

Preston, C. D. et al. 1998a. A reassessment of the hybrid *Potamogeton* × *gessnacensis* G. Fisch. (*P. natans* × *P. polygonifolius*, Potamogetonaceae) in Britain. – Watsonia 22: 61–68.

Preston, C. D. et al. 1998b. *Potamogeton pectinatus* L. × *P. vaginatus* Turcz. (*P.* × *bottnicus* Hagstr.), a newly identified hybrid in the British Isles. – Watsonia 22: 69–82.

Preston, C. D. et al. 1999. The distribution and habitat of *Potamogeton* × *suecicus* K. Richt. (*P. filiformis* Pers. × *P. pectinatus* L.) in the British Isles. – Watsonia 22: 329–342.

Raunkiær, C. 1903. Anatomical *Potamogeton*-studies and *Potamogeton fluitans*. – Bot. Tidssk. 25: 253–280.

Thiers, B. 2011. Index Herbariorum: a global directory of public herbaria and associated staff. – New York Bot. Gard. Virt. Herb. <http://sciweb.nybg.org/science2/IndexHerbariorum.asp>, accessed Feb 2011.

Wang, Q. D. et al. 2007. Phylogenetic relationships and hybrid origin of *Potamogeton* species (Potamogetonaceae) distributed in China: Insights from the nuclear ribosomal internal transcribed spacer sequence (ITS). – Plant Syst. Evol. 267: 65–78.

Wiegleb, G. and Kaplan, Z. 1998. An account of the species of *Potamogeton* L. (Potamogetonaceae). – Folia Geobot. 33: 241–316.

Wiegleb, G. et al. 2008. *Potamogeton*-Hybriden in Deutschland. – Feddes Rep. 119: 433–448.

Zalewska-Gałosz, J. and Ronikier, M. 2010. Are linear-leaved *Potamogeton* hybrids really so rare? Molecular evidence for multiple hybridizations between *P. acutifolius* and *P. compressus* in central Europe. – Nord. J. Bot. 28: 257–261.

Zalewska-Gałosz, J. and Ronikier, M. 2011. *Potamogeton* × *maëmetsiae*: a new hybrid of linear-leaved pondweeds from central Europe. – Preslia 83: 265–279.

Zalewska-Gałosz, J. et al. 2009. The first European record of *Potamogeton* × *subobtusus* identified using ITS and cpDNA sequence data. – Preslia 81: 281–292.

Zalewska-Gałosz, J. et al. 2010. Discovery of a new, recurrently formed *Potamogeton* hybrid in Europe and Africa: Molecular evidence and morphological comparison of different clones. – Taxon 59: 559–566.