Hybridization of *Potamogeton* species in the Czech Republic: diversity, distribution, temporal trends and habitat preferences

Hybridizace druhů rodu *Potamogeton* v České republice z pohledu diverzity, rozšíření, změn v čase a preference biotopů

Zdeněk K a p l a n

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A revision of the diversity and distribution of *Potamogeton* hybrids in the Czech Republic is presented. Thorough examination of herbarium material and recent extensive field studies revealed the present and/or past occurrence of eight *Potamogeton* hybrids in the Czech Republic. In addition to morphological characters, stem anatomy and/or molecular analysis were used to identify some of the hybrids. All the hybrids detected are between broad-leaved species of the genus, suggesting that hybrids between linear-leaved species may be overlooked because of the overall morphological similarity of taxa within this group. Four of the hybrids identified, *P.* ×*nitens*, *P.* ×*olivaceus*, *P.* ×*sparganiifolius* and *P.* ×*undulatus*, are recorded for the first time from the Czech Republic. Four of the hybrids are now extinct in the Czech Republic and the extant hybrids are rare. The occurrence of *P.* ×*lintonii* was not confirmed; the previous record was based on extreme forms of *P. gramineus*. The name *P.* ×*concinnitus*, proposed for a putative hybrid combination "*P. pusillus* × *P. crispus*", was lectotypified and reduced to a synonym of *P. crispus*. Although the absolute number of finds of specimens of *Potamogeton* hybrids per decade is increasing, this is not a result of more frequent hybridization but of an increase in recording activity. Most records for recent decades are associated with targeted research by a few experts. The typical habitat of *Potamogeton* hybrids in the Czech Republic are ponds that were previously drained in summer and allowed to dry out. Many historical localities disappeared when the traditional fishpond management was largely abandoned and fish farming become more intensive. In the 19th century in particular some hybrids were recorded also in rivers but these occurrences generally disappeared after the extensive channelling of rivers at the beginning of the 20th century. Many hybrids occur at the same localities as their parents but it is documented that hybrids can persist vegetatively in the absence of the parental species, presumably as relics of the previous presence of the parent plants. Although almost all *Potamogeton* hybrids are consistently sterile, a cultivation experiment showed that *P.* ×*angustifolius* set seeds that were fertile and successfully produced adult plants.

K e y w o r d s: *Potamogeton*, hybridization, taxonomy, revision, distribution, herbarium, morphology, nomenclature, typification, temporal changes, new records

Introduction

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

Although the great majority of *Potamogetonaceae* hybrids are consistently sterile (e.g. Hagström 1916, Dandy 1975, Preston 1995a, Wiegleb & Kaplan 1998, Kaplan & Fehrer 2007, Kaplan et al. 2009) many of the hybrid clones survive for long periods as they possess very efficient mechanisms of vegetative propagation. The perennial structures, such as rhizomes or turions, enable hybrid colonies to persist at a locality for a considerable period, even hundreds or thousands of years (Hollingsworth et al. 1996, Preston et al. 1998b, King et al. 2001, Kaplan & Wolff 2004, Kaplan & Fehrer 2007), providing the ecological conditions remain suitable. In addition, some hybrid clones can spread vegetatively and subsequently produce dominant stands or even occupy considerable areas. The hybrids can be also further dispersed by fragmentation of stems. Whereas in standing waters the dispersal occurs only locally within the pond or the lake in which they evolved, in rivers they may be transported downstream quite easily, particularly during spring floods with rapid water flow (e.g. Kaplan et al. 2002, Kaplan & Wolff 2004). The long-term survival of hybrid clones sometimes results in them occurring at localities after their parents have disappeared. The relic occurrence of *Potamogetonaceae* hybrids in the absence of one or both parents is documented for many hybrids (e.g. Dandy & Taylor 1946, Hollingsworth et al. 1996, Preston et al. 1998a, b, 1999, King et al. 2001, Kaplan & Fehrer 2004, 2009, Kaplan & Wolff 2004, Kaplan et al. 2009).

All these factors make *Potamogetonaceae* hybrids at some sites an important component of aquatic communities. Wiegleb & Kaplan (1998) point out that more attention should be given to the study, description and recognition of hybrids because of their ecological importance. Hybridization is one of the most important sources of taxonomy-relevant diversity. The neglect or exclusion of hybrids from taxonomic treatments may lead to erroneous determinations of many specimens, and fragments our understanding of variation within the genus (Wiegleb & Kaplan 1998, Preston 2001, Alix & Scribailo 2006, Kaplan et al. 2009).

Identification of *Potamogetonaceae* hybrids is often difficult and requires detailed expert inspection of a large set of key features. For a long time, identification of hybrids depended on traditional methods that included mainly morphological investigation and field observations. Starting with Raunkiær's pilot studies (Raunkiær 1896, 1903), some authors also used anatomical features, which helped to resolve some intricate taxonomic problems and contributed to the detection of hybrids between species with different types of stem anatomy (e.g. Fischer 1904, 1905, 1907, Hagström 1916, Ogden 1943, Symoens et al. 1979, Wiegleb 1990a, b, Kaplan 2001, 2005a, b, Kaplan & Wolff 2004, Kaplan & Symoens 2004, 2005, Zalewska-Gałosz et al. 2009, 2010).

Recently research on hybridization in *Potamogetonaceae* has made considerable progress and a lot of new facts have accumulated. 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 (e.g. Hollingsworth et al. 1995, 1996, Preston et al. 1998b, Fant et al. 2001a, b, Iida & Kadono 2002, Kaplan et al. 2002, Fant & Preston 2004, Kaplan & Wolff 2004, Kaplan 2007) or DNA-based analyses (King et al. 2001, Fant et al. 2003, 2005, Kaplan & Fehrer 2004, 2006, 2009, Ito et al. 2007, Wang et al. 2007, Du et al. 2009, Kaplan et al. 2009, Zalewska-Gałosz et al. 2009). Direct DNA sequencing and RFLPs have contributed to the discovery and/or exact identification of several entirely new hybrid combinations (Kaplan et al. 2009, 2010, Zalewska-Gałosz et al. 2010) and even confirmed the existence of a triple hybrid in *Potamogeton* (Kaplan & Fehrer 2007).

On a worldwide scale, Wiegleb & Kaplan (1998) recognized 50 sufficiently documented hybrids in the *Potamogetonaceae*, some of which are locally frequent and represent clearly circumscribed biological entities. These hybrids are reported from various countries in Europe (e.g. Fischer 1907, Hagström 1916, Dandy & Taylor 1957, Dandy 1975, Wiegleb & Herr 1984, Ploeg 1987, 1990, Wolf et al. 1997, Preston et al. 1998, Kaplan & Zalewska-Gałosz 2004, Kaplan 2005a, Bobrov & Chemeris 2006), North America (e.g. Ogden 1943, Haynes & Williams 1975, Brayshaw 2000, Alix & Scribailo 2006, Kaplan et al. 2009), Siberia (Kashina 1988, Chepinoga et al. 2008), China (Wiegleb 1990a, Wang et al. 2007, Du et al. 2009) and Japan (Miki 1937, Kadono 1983, Kadono & Wiegleb 1987, Ito et al. 2007, Iida & Kadono 2002). Only recently a *Potamogeton* hybrid was identified also in the Southern Hemisphere, in Australia (Kaplan et al. 2010). The number of identified and now recognized *Potamogetonaceae* hybrids has increased to 86 (Z. Kaplan, unpubl.).

In spite of this recent progress, the precise knowledge of the diversity and distribution of *Potamogetonaceae* hybrids is highly uneven. A modern detailed revision, based on careful identification of large sets of specimens and listing herbarium vouchers and/or providing maps of distribution, is available only for three European countries: the British Isles (Preston 1995a), Poland (Zalewska-Gałosz 2002, 2008) and Germany (Wiegleb et al. 2008).

This paper summarizes the results of long-term taxonomic research on hybridization in *Potamogetonaceae* in the Czech Republic. Many of the herbarium records presented here are those accumulated during a revision of the family for the Flora of the Czech Republic (Kaplan 2010).

Materials and methods

The main source of distribution records came from herbarium collections. All major Czech institutional herbaria (acronyms according to Holmgren et al. 1990, with updates according to Thiers 2010) were consulted: BRNM, BRNU, CB, CHOM, FMM, HR, LIM, LIT, MJ, MMI, MP, NJM, OL, OLM, OMJ, OP, PL, PR, PRA, PRC, ROZ, SOKO and VM, as well as other central-European herbaria known to host important sets of mainly historical collections from the Czech Republic: B, BP, BRA, M, SAV, SLO, W and WU. Some *Potamogeton* collections of Czech origin were detected in other major European herbaria including BM, C, CGE, E, FR, G, GOET, K, KRAM, L, LD, LE, LY, OLD, P, POLL, S, UPS, Z and ZT. A few hybrids were identified in private herbaria, particularly that of F. Krahulec, Průhonice. In addition, many records came from my field investigation in 1990–2009. Because of the frequent misidentification of pondweeds, literature records not supported by a herbarium voucher are generally omitted. Only three such literature records for *P.* ×*angustifolius* by S. Hejný were accepted. *Potamogeton* hybrids are rarely recorded in the Czech literature and some of them proved to be erroneous when their herbarium vouchers were located.

Temporal changes in recording hybrids were analysed and calculated per decade for the period 1810–2010. The assignment of the few undated pre-1860 collections to particular decades was facilitated by the existence of other dated collections made on the same occasions or using various literature sources (such as Presl & Presl 1819, Berchtold & Presl 1821, Opiz 1822, 1823, 1824, 1826, Berchtold & Fieber 1838, Fieber 1838, and the analysis

of the contribution of early Bohemian botanists to *Potamogeton* taxonomy in Kaplan 1997). Duplicate records (records of the same hybrid from the same site and year) were reduced to single records.

In the following text, records of localities given on herbarium labels are presented in their more or less original form for rare hybrids and with abridged locality information for *P.* ×*angustifolius* and *P.* ×*fluitans*. Specifications of the sites or updates of historical topographic names are occasionally supplemented in square brackets.

In the following account, only the most important diagnostic morphological characters of hybrids are given. Detailed descriptions of parental species are available elsewhere (e.g., Preston 1995a, Kaplan 2010). Besides the records collected directly for the Flora of the Czech Republic, abundant morphological data compiled for previous studies (e.g., Wiegleb & Kaplan 1998, Kaplan 2001, 2002b, 2002c, 2005b, 2007, Kaplan & Wolff 2004, Kaplan & Fehrer 2004, 2006, 2007, 2009) and available in modern taxonomic revisions (mainly Preston 1995a) were also included in this study in order to cover the morphological variation of the respective taxa as completely as possible.

A list of papers that provide molecular evidence for the existence of particular hybrids is given. Many of the cited studies helped to refine the understanding of the morphological variation of the hybrids. Descriptions of habitats are confined to the occurrences in the Czech Republic. Only herbarium specimens seen are listed and arranged first according to units of the phytogeographical division of the Czech Republic (Skalický 1988) and then according to grid numbers of the Mapping the Flora of Central Europe scheme (Niklfeld 1971).

Results

Account of hybrids

Potamogeton ×*angustifolius* J. Presl in Bercht. et J. Presl, Rostlinář 1, fasc. Žábnjkowité: 19, 1821.

Syn.: *P.* ×*zizii* W. D. J. Koch ex Roth, Enum. Pl. Phaen. Germ. 1/1: 531, 1827.
= *P. gramineus* × *P. lucens*

Diagnostic characters: Although variable, it is always intermediate between the parental species, particularly in terms of quantitative characters such as leaf width, stipule length and fruit size. The main stem leaves tend to be more robust and similar to those of *P. lucens*, whereas the leaves on the terminal parts of branches are more slender and reminiscent of *P. gramineus*. Besides their intermediate appearance, the best diagnostic character is the length of petioles: all true submerged leaves (uppermost transitional leaves excluded) of *P. gramineus* are sessile whereas those of *P. lucens* with unreduced lamina are always shortly (2–7 mm long) petiolate, with this length being almost constant along the stem; in the hybrid there is mostly a combination of these characters with the lower submerged leaves usually sessile and the uppermost leaves of adult (flowering) plants markedly petiolate, with petioles up to 27 mm long. It is necessary to become familiar with the range of variation in both parental species before one can reliably identify their hybrids because most quantitative characters show some overlap.

Molecular evidence: Identity of plants from the Czech Republic and Montenegro were confirmed by DNA sequencing (Z. Kaplan & J. Fehrer, unpubl.).

H a b i t a t s: Typically (85% of records) this hybrid occurs in less intensively managed fishponds, particularly those that are regularly drained in summer. The other habitats include side pools of lowland rivers and flooded pits (from the time of the construction of railways) with one record from a mill-race.

D i s t r i b u t i o n i n t h e C z e c h R e p u b l i c: Recorded at 39 localities, mainly in the Eastern Labe River and South Bohemian basins, only exceptionally found elsewhere (Fig. 1).

H e r b a r i u m s p e c i m e n s s e e n: **11b. Poděbradské Polabí:** 5855b: V tůních blíže dráhy u Kostomlat [nad Labem] směrem k Nymburku (1879 Polák, PRC; 1879 Velenovský, PRC; 18 VII 1880 K. Polák, PR). – Kostomlaty: tůň při pravém okraji silnice k převozu před lesem (3 VII 1947 S. Kaufman, herb. Vlastiv. Muz. Nymburk). – **13a. Rožďalovická tabule:** 5656c: Rybník Vrbičkový u Chudíře (1 VIII 1948 S. Kaufman, PR). – 5756a: Okr. Nymburk: rybník Lutovník v oboře u Loučeně (30 VII 1947 S. Kaufman, PRC; 20 VII 1952 S. Kaufman, BRNM, MP, PR; 20 VII 1952 Šourek et Kaufman, PR; 20 VIII 1952 S. Kaufman, BRNM, PR; 20 VIII 1952 F. Černoch, PR; 3 VII 1953 F. Černoch, BRNM, CB; 1953 David, OP). – 5857b: Distr. Kolín, pag. Dlouhopolsko, pars Na Kopičáku: in piscina Kopičák (6 X 1978 V. Skalický, PRC, p. p.). – 5858a: okr. Nymburk: Kněžičky: rybník u severního okraje východní části Žehuňské obory 1,3 km JV od J okraje obce, 237 m n. m. (1 VII 2002 J. Rydlo, ROZ; 3 VII 2002 Z. Kaplan no. 02/175, PRA; 15 VI 2004 J. Rydlo, I. Hodálová & M. Molíková, ROZ). – **15b. Hradecké Polabí:** 5662a: Přehrada Rozkoš u České Skalice: horní nádrž (11 IX 1974 H. Nováková, MP; 1977 & 1978 F. Krahulec, herb. F. Krahulec). – Přehrada Rozkoš u České Skalice: dolní nádrž (1978 F. Krahulec, herb. F. Krahulec). – 5761b: Smiřice: v přítoku rybníka Lhoťáku [= Závěšťák] u silnice vých. Libřic, 250 m (2 VIII 1941 J. Šourek no. 2121, PR). – 5761c: Náhon u Malšovic (VIII 1918 K. Prokeš, PRC). – **15c. Pardubické Polabí:** 5858d: Okr. Hradec Králové: Štít: rybník Horní Flajšar 0,5 km JZ od obce, 50°06'43,5"N, 15°28'20,6"E, 218 m n. m. (8 VI 2009 Z. Kaplan no. 09/149, PR, PRA). – 5860d/5960b: Čeperka Teich (s. d. Čeněk, PR). – 5959b: Bohdaneč: r. Nadýmač I. (4 VIII 1941 E. Hadač, MP). – 5960a: A. Teichen b. Bohdanetz [= Lázně Bohdaneč] (s. d. Tausch, PRC, p. p.); Teich Rozkož bei Bohdanetsch (s. d. Opiz, C, PR; 1860 Čeněk, PR). – 5960b: Okr. Pardubice: Hrobice: severní mělký okraj rybníka Baroch 0,8 km JZ od obce, 224 m n. m. (31 VIII 1994 Z. Kaplan no. 94/441, PRA). – 5961a: Rybník Labská u Sezemic (VII 1887 J. Jahn & J. Košťál, PR; 1887 J. Jahn, PR; VIII 1888 J. Košťál, W; VIII 1889 J. Košťál, MP). – 5961b: Holice: při JV břehu rybníka Smílek (10 VIII 1975 F. Černohous, MP; 14 VIII 1975 F. Černohous, MP; 4 IX 1976 H. Nováková, MP, PRC; 4 IX 1976 Š. Husák, PRA). – **18a. Dyjsko-svratecký úval:** 7166d: Mähren: in dem Flußarm der Thaya [= Dyje] b. Prittlach [= Přítluky] (25 VI 1898 Teuber, BRNM). – 7267c: Břeclav: příkopy dle dráhy (1901 J. Podpěra, BRNU); Tůně u Břeclavi (29 V 1921 I. Klášterský, PR; 1921 Viniklář, PRC). – **36a. Blatensko:** 6548d: Kadov: rybník Paseka, při cestě do Bezděkova (8 VIII 1946 J. Vaněček). – Distr. Blatná: in piscina Starý Pálenec apud vicum Vrbno (12 IX 1954 V. Skalický & A. Klásková, PR; 10 VI 1958 V. Skalický & A. Češka, PRC). – 6649a: V rybníku u Bratronic (1882 Velenovský, PRC). – 6649d: V malém rybníčku nad Milavou u Sedlice (29 VIII 1882 Velenovský, BM, PR, PRC). – **37f. Strakonické vápence:** 6749a: V rybníčku u Domanic (25 VII 1882 Velenovský, PR). – **38. Budějovická pánev:** 6750b: Ražice: Ražický rybník asi 1,5 km severovýchodně obce (Vondrák 1999, Hejný 2000). – 6751d: Distr. Písek: in piscina Nový u Krče dicta prope Zelendarky non procul Krč apud Protivín (VI 1963 S. Hejný, PRA). – 6851b: Distr. Týn n. Vlt.: in aqua piscinae Čekal prope Chvalešovice, ca. 420 m s. m. (1947 S. Hejný, PRC). – 6851c: Distr. Vodňany: in marginibus meridionalibus piscinae Velký Černoháj prope Radomilice, ca 400 m s. m. (1947 S. Hejný, PRC). – 6851c: Distr. Vodňany: in piscina Malý Černoháj prope Strpí apud Radomilice (3 VIII 1964 S. Hejný, PRA). – 6851c: Rybník Horní Pilant u Černohájů (obec Čičenice blíže Vodňan) (Hejný 2000). – 6851d: Radomilický rybník u Radomilic (Hejný 2000). – **39. Třeboňská pánev:** 6954b: Kolence: rybník Karel I. pod hrází Zadního Paseckého rybníka (8 VI 1979 Š. Husák, PRA). – Kolence: rybník Prostřední Pasecký (11 VII 1984 R. Kurka, CB). – Kolence: rybník Okřínek (18 VII 1980 Š. Husák, PRA). – **52. Ralsko-bezdězská tabule:** 5354c: Okr. Česká Lípa: Hradčany u Mimoně: lesní rybník Držník 1,1 km VJV od Hradčan (5 VIII 1996 Š. Husák, PRA; 18 VI 1997 Š. Husák, ROZ; 18 IX 1996 Z. Kaplan no. 96/640, PRA; 3 VIII 2003 Z. Kaplan no. 03/164, IBIW, IRKU, KRA, PRA; 24 VI 2006 M. Ducháček no. 5032, PR; 8 VI 2007 V. Grulich no. VG07/638, BRNU, p. p.). – 5453b: Distr. Česká Lípa: Máchovo jezero Fishpond near Doksy, Zmijí palouk (3 VIII 1996 Š. Husák, PRA); Okr. Česká Lípa: Staré Splavy: tůňky v zazemněné části V zátoky na S okraji Máchova jezera 1,5 km VSV od železniční stanice (17 VII 2009 G. Leugnerová, Jan Rydlo & Jar. Rydlo, ROZ; 1 IX 2009 Z. Kaplan, G. Leugnerová & Jar. Rydlo nos 09/389 & 09/390, PRA). – 5454a: Doksy: NPR Břehyňský rybník (4 VII 1994 D. Stančík no. 6082, PRC). – **52. Ralsko-bezdězská tabule or 53a. Českolipská kotlina:** Nimes [= Mimoň] (s. d. Lorinser, WU) [most likely collected from one of the fishponds near Hradčany, which are located 3.5 km S of Mimoň]. – **63j. Lanškrounská kotlina:**

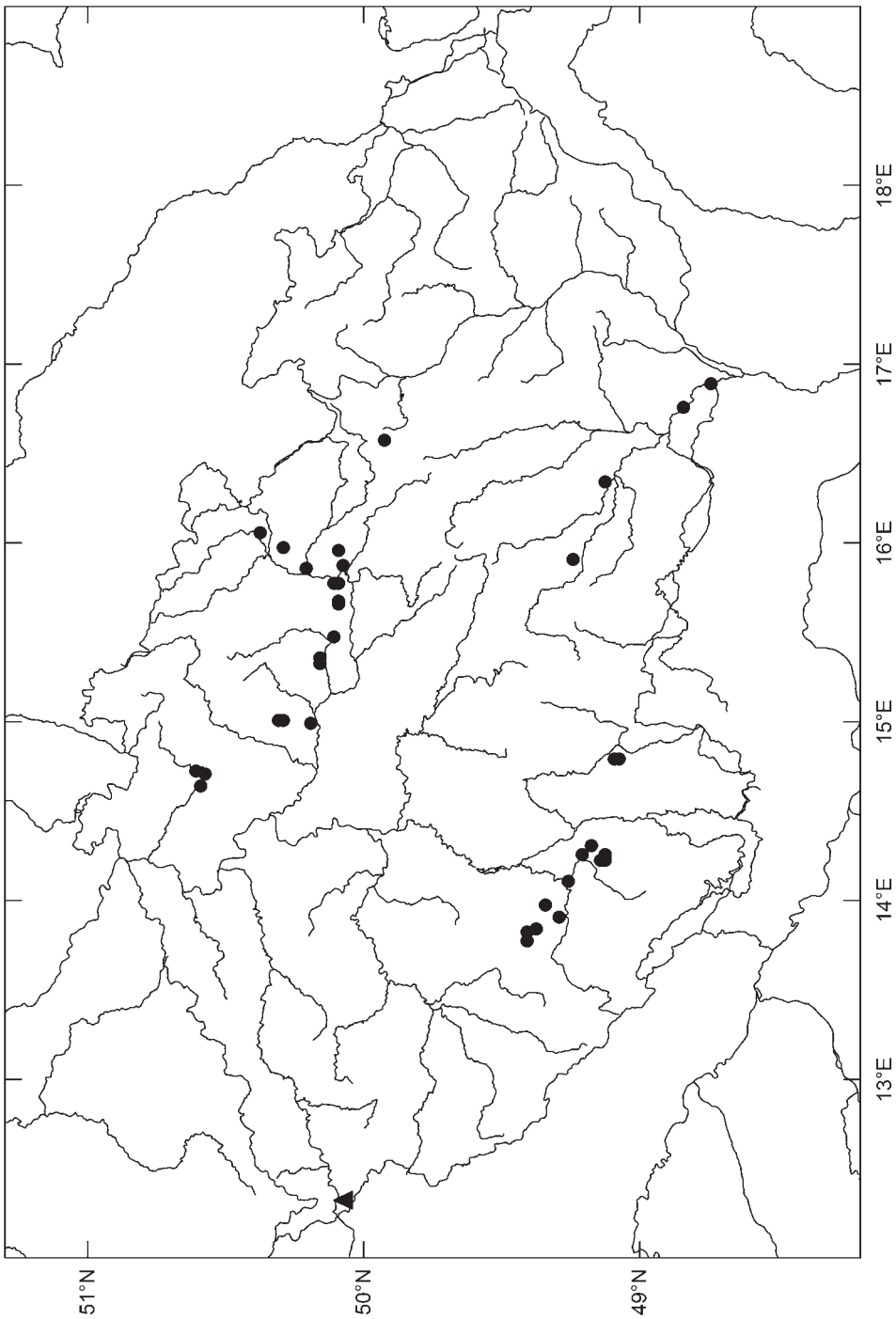

Fig. 1. – Distribution of *P.* ×*angustifolius* (circles) and *P.* ×*olivaceus* (triangle) in the Czech Republic.

6065c: Landskron [= Lanškroun] (1819 Steinmann, PR) [probably collected in Olšový fishpond, where *P. gramineus* was recorded at that time]. – 6065d: Okr. Ústí nad Orlicí: Lanškroun: Dlouhý rybník 2,3 km ZSZ od středu obce (29 VII 2008 L. Bureš & D. Ciprová in herb. Z. Kaplan no. 08/637, PRA; 18 VI 2009 Z. Kaplan no. 09/216, PR, PRA, PRC, ROZ). – **68. Moravské podhůří Vysočiny:** 6761c: Ptáčov: rybník Židloch (27 VII 1878 F. Zavřel, PRC, p. p.; 5 VIII 1907 R. Dvořák, BRNM; 7 VIII 1907 R. Dvořák, BRNM). – 6864c: Flusstümpel bei Oslavan (VIII 1889 A. Schwöder, LD).

Notes: This hybrid was first recorded at the beginning of the 19th century, although at that time its hybrid origin was not recognized. It is one of the very few *Potamogetonaceae* hybrids that are capable of producing well developed fruit and the only one that sets fruit regularly. However, it is unknown whether the seed is viable (Wiegleb & Kaplan 1998). Plants of this hybrid (presumably F1 generation) from the Držník fishpond near Hradčany were cultivated (under no. 333) in the Experimental garden at Průhonice. These plants produced almost a full set of fruit on each spike. The seeds were sown the following season and most of them germinated (96%). Eight of the seedlings were selected and successfully developed into adult plants. The individuals of this F2 generation (cultivated under no. 899) were morphologically very variable, more so than the maternal clone. Whereas the F1 plants were rather uniform and clearly intermediate between the parental species, the F2 plants segregated into several phenotypes, which were intermediate or more similar to one of the parents, namely *P. gramineus*. The F2 plants also flowered and produced well formed fruit. In contrast, of the 113 clones of 32 other hybrid combinations involving broad-leaved *Potamogeton* species cultivated in 1995–2009, none produced fruit. This observation is also supported by the study of herbarium material.

Potamogeton ×*cooperi* (Fryer) Fryer, J. Bot. 35: 311, 1897.

Syn.: *P.* ×*cymatodes* Aschers. et Graebn., Synops. Mitteleur. Fl. 1: 337, 1897, nom. illeg. [Vienna ICBN Art. 52.1; McNeill et al. 2006]
= *P. crispus* × *P. perfoliatus*

Diagnostic characters: The parental species are quite distinct morphologically and are only rarely confused with one another. Their hybrid combines the characters of both parents. In contrast to *P. perfoliatus* with a terete stem, the stem of the hybrid is compressed and grooved but less markedly than is usual in *P. crispus*. The leaves are intermediate in shape and width (Fig. 2) as well as in the number of longitudinal veins. The leaf base is semi-amplexicaul in the hybrid, in contrast to the markedly amplexicaul bases in *P. perfoliatus* and broadly cuneate to auriculate but never amplexicaul in *P. crispus*. Specimens collected early in the season are often more *P. crispus*-like in general appearance and shape of leaves, whereas adult flowering plants may resemble *P. perfoliatus*. Flower spikes of the hybrid are generally shorter than in both parents, the flowers do not open and have abortive carpels. The entire spikes rot after flowering instead of setting fruit. For detailed comparison of the diagnostic characters see Kaplan & Fehrer (2004).

Molecular evidence: Identity of plants from the United Kingdom and the Czech Republic were confirmed by DNA sequencing and RFLP (Kaplan & Fehrer 2004).

Habitats: This hybrid was once found in a river and once in a recently constructed small and shallow water reservoir.

Distribution in the Czech Republic: Recorded only at two localities, one in northern Bohemia and the other in southern Moravia (Fig. 3). It has not been recollected and is almost certainly an extinct taxon of the Czech flora.

Fig. 2. – *Potamogeton ×cooperi* from the Ploučnice River in northern Bohemia (18 VIII 1851 Malinský, PR).

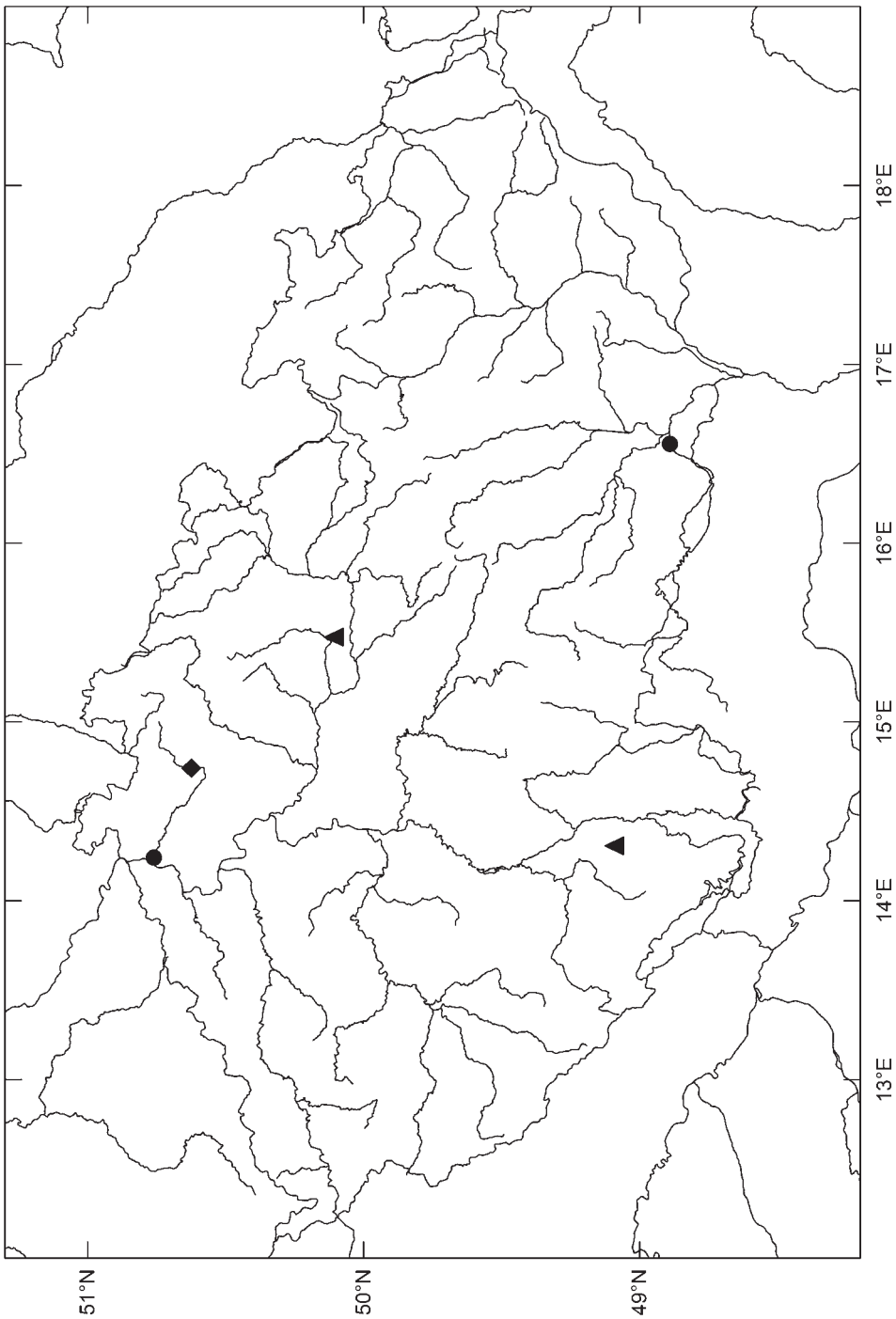

Fig. 3. – Distribution of *P.* ×*cooperi* (circles), *P.* ×*sparganiifolius* (triangles) and *P.* ×*undulatus* (diamond) in the Czech Republic.

Herbarium specimens seen: **18a. Dyjsko-svratecký úval:** 7165a: Okr. Břeclav: Pasohlávky, Malá laguna 2 km VJV od vsi (21 VI 2002 J. Rydlo, ROZ); Okr. Břeclav: Pasohlávky: nádrž Malá laguna na severním břehu Horní nádrže vodního díla Nové Mlýny 1,4 km VJV od obce (21 VI 2002 J. Rydlo; cult. as Z. Kaplan no. 1420, pressed 9 IX 2002 Z. Kaplan, PRA, ROZ, 2003–2009 Z. Kaplan, PRA). – **45a. Lovečkovické středohoří:** 5251a: Zwischen *P. crispus* & *perfoliatus* im Bolzenflusse [= Ploučnice] im n[ördlichen]. Böhmen (18 VIII 1851 Malinský, B, BRNU, PR, W) [The collection presumably originates from the lowermost section of the Ploučnice River near the town of Děčín, where Malinský lived].

Notes: Only recently confirmed for the Czech Republic (Kaplan & Fehrer 2004). The previous records were erroneous. Petrak (1910) reported the occurrence of *P.* ×*cymatodes* = *P. perfoliatus* × *P. crispus* "im Mühlbache der Bečura [sic!, misprint, correctly: Bečva] bei Mähr.-Weisskirchen und zwar zwischen der Tuchwalke und seiner Mündung". This record was adopted also by Hejný (1950). The voucher specimens are in BRNU and PR. All plants have 13–17-veined leaves with amplexicaul bases and are a narrow-leaved form of *P. perfoliatus*, not the hybrid.

Potamogeton ×*fluitans* Roth, Tent. Fl. Germ. 1: 72, 1788.

= *P. lucens* × *P. natans*

Diagnostic characters: This hybrid is easily distinguished from its parents. The submerged leaves are clearly intermediate between those of *P. lucens*, with an oblong to broadly elliptical lamina on a short petiole, and those of *P. natans*, which are always reduced to linear phyllodes. The hybrid is in general appearance and shape of floating leaves more similar to *P. natans* but differs from this species in that most of its submerged leaves have a well developed lamina and the petioles of floating leaves lack a flexible junction between the petiole and the lamina, which is mostly present in *P. natans*. The best characters for separating *P.* ×*fluitans* from *P. lucens* are the shape of the lamina of submerged leaves, longer petioles and the capacity to produce floating leaves. For detailed comparison of diagnostic characters see Kaplan (2001). *Potamogeton* ×*fluitans* is more difficult to separate from the unrelated species *P. nodosus* than from its parents. However, in this species the lowest leaves are never reduced to phyllodes, there is on average a greater number of veins in lamina of submerged leaves and the petioles are longer. Fragmentary material or extreme phenotypes are often difficult to distinguish morphologically, but stem anatomy provides additional characters that are highly reliable (see Kaplan 2001). For distinguishing *P.* ×*fluitans* from other similar *P. natans* hybrids see Preston (1995a, b), Preston et al. (1998a) and Kaplan & Wolff (2004).

Molecular evidence: Isozyme electrophoresis confirmed identity of plants from the United Kingdom (Fant et al. 2001) and the Czech Republic (Kaplan et al. 2002). DNA sequencing was used to check the hybrid origin of plants from the United Kingdom (Fant et al. 2005) and the Czech Republic (Z. Kaplan & J. Fehrer, unpubl.).

Habitats: Almost all recent collections are from fishponds with one historic record from a stream.

Distribution in the Czech Republic: Found at 13 localities in northern, eastern and central Bohemia, with most records from the past 15 years (Fig. 4).

Herbarium specimens seen: **11b. Poděbradské Polabí:** 5856d: Okr. Nymburk: Libický luh, nová mělká nádrž na zdevastované louce na pravém břehu Labe mezi dálnicí a ústím Cidliny (7 IX 1991 J. Rydlo, ROZ; 9 IX 1991 J. Rydlo, ROZ). – **13a. Rožďalovická tabule:** 5656c: Mladá Boleslav: Jabkenice: dolní rybníček na kraji lesa 300 m Z od samoty Ovčárny 1,8 km SSV od obce (11 VI 1999 Z. Kaplan; cult. as Z. Kaplan no. 1137,

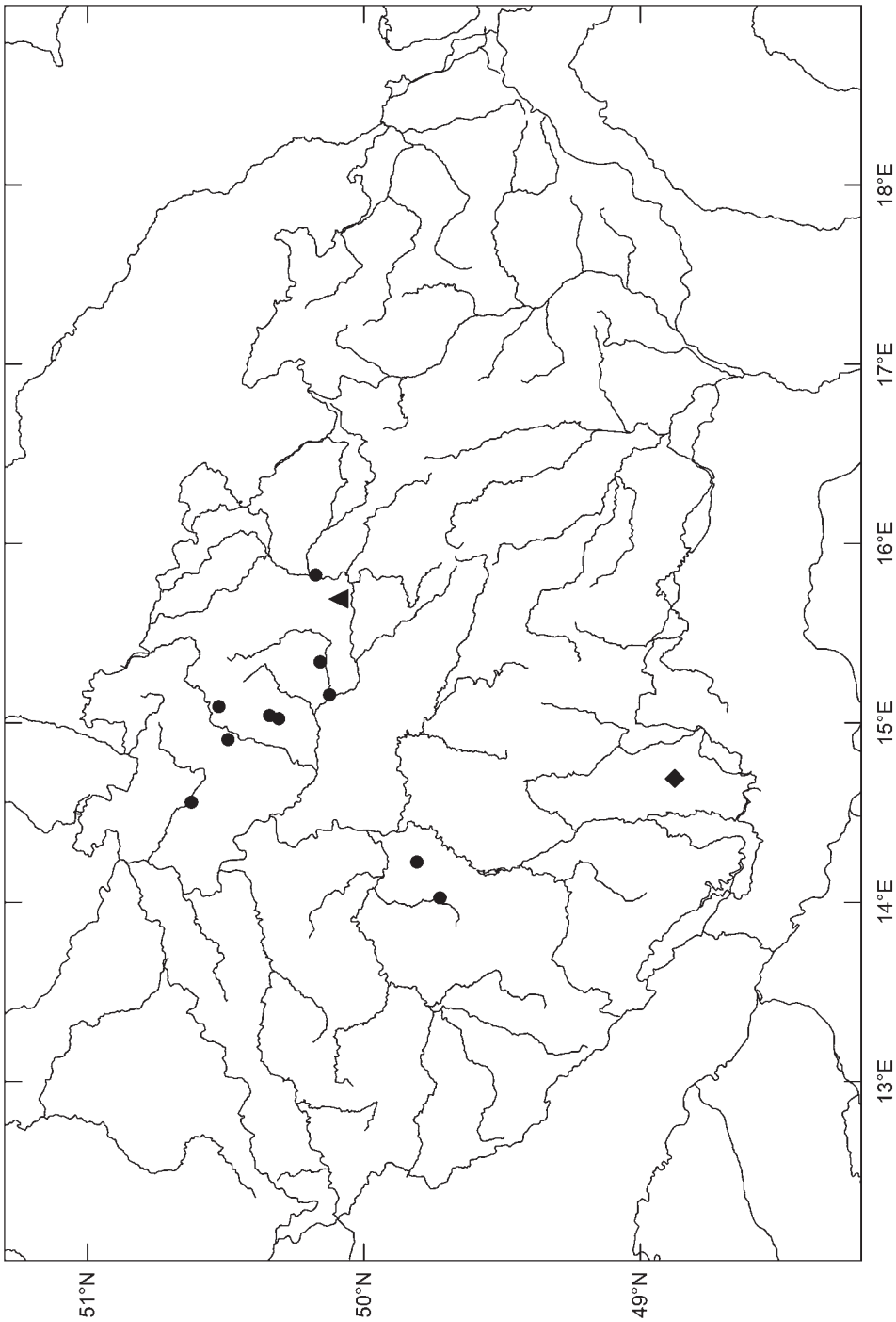

Fig. 4. – Distribution of *P.* ×*fluitans* (circles), *P.* ×*nitens* (triangle) and *P.* ×*schreberi* (diamond) in the Czech Republic.

pressed 12 VII 2002 Z. Kaplan, PRA). – 5656c: Okr. Nymburk: Loučeň: rybník Sladovník v lese Helma 400 m SSV od hájovny Loučeňka, 1,5 km S od obce (1 VII 2002 Z. Kaplan no. 02/140, PRA; 25 VIII 2002 J. Rydlo, ROZ). – 5756a: Okr. Nymburk: Loučeň: obnovený lesní rybníček 450 m SZ od hájovny Loučeňka, 1,35 km S(–SSZ) od křižovatky silnic na S okraji obce (11 IX 2004 Z. Kaplan no. 04/319, PRA; 26 VI 2005 Z. Kaplan no. 05/248, PRA). – 5858a: Okr. Nymburk: Kněžičky: Dolní Čihadelský rybník v Žehuňské oboře 1,8 km J–JJV od J okraje obce (3 VII 2002 Z. Kaplan no. 02/182, PRA; 1 VII 2002 J. Rydlo, ROZ). – **35c. Příbramské Podbrdsko:** 6250c: Okr. Příbram: Kardavec, rybník 600 m JJV od vsi (23 VII 2004 J. Rydlo, ROZ). – **41. Střední Povltaví:** 6151c: Okr. Příbram: Voznice: lesní rybník Prostřední Tušimy (= Prostřední rybník) 1 km JJV od obce (29 VI 2006 J. Rydlo, ROZ; 9 VII 2006 Z. Kaplan no. 06/235, PRA). – **52. Ralsko-bezdězská tabule:** 5353c: Okr. Česká Lípa: Zahrádky: Novozámecký rybník (24 VIII 2002 D. Turoňová in herb. Z. Kaplan no. 02/268, PRA). – 5555a: In rivo Bělá prope Rečkov versus urbem Bělá [= Bělá pod Bezdězem] (22 VII 1897 J. Podpěra, BRNU, PR; 28 VII 1897 J. Podpěra, PR; 1897 J. Vilhelm, PRC). – **55b. Střední Pojizeří:** 5456d: Český ráj: Žehrov, rybníček pod oborou u ZJZ okraje osady Arnoštice, 247 m n. m. (29 VII 1997 J. Rydlo & D. Vacková, ROZ; 29 VII 1997 D. Vacková, HR; 18 IX 1997 Z. Kaplan no. 97/915, PRA; 29 VII 1999 Z. Kaplan no. 99/144, PRA). – 5456d: Český ráj: Žehrov, rybník v oboře 300 m ZJZ od samoty Arnoštice (17 V 2007 J. Rydlo & D. Vacková, ROZ). – **61c. Chvojenská plošina:** 5860b: Hradec Králové: rybník Roudnička (6 VIII 1975 F. Černohous, MP; 5 IX 2006 R. Prausová, HR).

Notes: Although *P.* ×*fluitans* was recorded as a new taxon for the Czech Republic only recently (Kaplan 2001), due to targeted field research it is now recorded from nine other localities. This hybrid is typically found in recently filled fishponds that were previously drained and the bottom mud exposed and dried out during summer (Kaplan et al. 2002, Kaplan & Fehrer 2004). However, *P.* ×*fluitans* does not persist long in this habitat but soon disappears as a consequence of intensive fish farming (Kaplan & Fehrer 2004). It is usually associated with much more abundant stands of its parental species and of other macrophytes and is therefore not easily found. All this implies that it is likely to be more frequent but is unrecorded because of its temporary occurrence.

Potamogeton ×*nitens* Weber, Suppl. Fl. Holsat. 5, 1787.

= *P. gramineus* × *P. perfoliatus*

Diagnostic characters: This hybrid is generally intermediate between its parents, showing a combination of parental characters. Many phenotypes are more similar to *P. gramineus*, resembling this species in its general appearance and shape of leaves. These are relatively easy to distinguish from *P. perfoliatus* as the submerged leaves of the hybrid are narrower with fewer longitudinal veins, more acute and sometimes with an apiculate apex, more persistent stipules and some clones produce floating leaves. Unlike *P. gramineus*, the hybrid has a more sparingly branched stem, broader submerged leaves with semi-amplexicaul bases, a more obtuse apex and more numerous longitudinal veins. Both parental species differ from *P.* ×*nitens* in their capacity to produce well-formed fruits; in contrast, the hybrid is sterile. The most important diagnostic characters of all three taxa are summarized in Kaplan & Fehrer (2006).

Molecular evidence: DNA sequencing and/or RFLP confirmed the hybrid origin of plants from Sweden (Kaplan & Fehrer 2006), Finland (Z. Kaplan & J. Fehrer, unpubl.), Germany (Kaplan & Fehrer 2006), Russia (Z. Kaplan & J. Fehrer, unpubl.) and the U. S. A. (Kaplan et al. 2009).

Habitats: The only Czech record is for a pond.

Distribution in the Czech Republic: Recorded only in the vicinity of Lázně Bohdaneč in eastern Bohemia (Fig. 4). All available collections almost certainly originate from the same site, which was the former fishpond Rozkoš, drained and dried-out in the 1860s.

Herbarium specimens seen: **15c. Pardubické Polabí:** 5960a: Rozkoš bei Bohdaneč [= Lázně Bohdaneč: zaniklý rybník Rozkoš 0,5 km V města] (s. d. Opiz, PRC, ut *P. heterophyllus*); In piscinis, fossis (s. d. Opiz, PRC, ut *P. heterophyllus*); Bohdaneč (1818 Opiz, PR, ut *P. Zizii* β *elongatus*); Bohdannez (1818 Opiz, PR, ut *P. Zizii* β *elongatus*, p. p., *P.* ×*angustifolius* admixt.); Bohdanetsch (s. d. [possibly in 1860] Čeněk, BRNM, PRC).

Notes: This hybrid is recorded here from the Czech Republic for the first time.

Potamogeton ×*olivaceus* Baagöe ex G. Fisch., Ber. Bayer. Bot. Ges. 11: 33, 1907.

= *P. alpinus* × *P. crispus*

Diagnostic characters: This hybrid is similar to *P. alpinus* in general appearance, shape and colour of leaves but can be distinguished by its compressed stem (usually apparent only on fresh plants), leaves with fewer longitudinal veins (5–7) and often by the stem being branched rather than unbranched as in *P. alpinus* (Fig. 5). The lateral veins in the leaves are often slightly shifted towards margins, with the outermost pair being faint and running close along the margins (character inherited from *P. crispus*) rather than of more or less identical strength and evenly distributed as in *P. alpinus*.

Molecular evidence: No fresh material for molecular analyses was available.

Habitats: The collector of the only herbarium specimen from the Czech Republic indicated that the habitat was a pool. Most probably it was a side pool of the Ohře River. Both parental species are recorded from the river in this area.

Distribution in the Czech Republic: Recorded only once in the vicinity of Cheb in western Bohemia (Fig. 1). It is now extinct.

Herbarium specimen seen: **24a. Chebská pánev:** 5939b: V tůni u Kreuzensteinu [= osada Podhoří] blíž Chebu (22 VII 1887 L. Čelakovský fil., PR, ut *P. rufescens*).

Notes: *Potamogeton* ×*olivaceus* is recorded here for the first time from the Czech Republic. Although this hybrid is not particularly difficult to identify it is recorded only for Great Britain (Dandy 1975, Preston 1995a), Denmark (Hagström 1916), Germany (Wiegleb et al. 2008), Poland (Zalewska-Gałosz 2002, 2008) and European Russia (Bobrov & Chemeris 2009). In none of these countries is it widespread, in Poland it is known only from two localities and in each of the Czech Republic and Russia only from a single site. Its rarity indicates that it is produced only exceptionally.

Potamogeton ×*schreberi* G. Fisch., Mitt. Bayer. Bot. Ges. 1/37: 471, 1905.

= *P. natans* × *P. nodosus*

Diagnostic characters: This hybrid combines some characteristic features of both parental species. The specimens with well preserved submerged leaves show some characters of *P. natans*, such as the presence of phyllodes near the base of the stem. However, upper submerged leaves have a slightly expanded linear-elliptical lamina distally, which have up to 9 lateral veins and the base tapers very gradually into the petiole. Floating leaves resemble those of *P. nodosus* but on some plants petiole adjacent to the lamina may be slightly browner, which is a vestige of the flexible discoloured junction present in *P. natans*. Well developed adult plants sometimes produce transitional leaves, which are intermediate in shape and size between submerged phyllodes and floating laminar leaves. The hybrid is easiest to identify in late spring and early summer when the submerged

Fig. 5. – *Potamogeton ×olivaceus* from the vicinity of Cheb in western Bohemia (22 VII 1887 L. Čelakovský fil., PR).

leaves are still extant and summer floating leaves are present. Such plants reveal most features showing the composite ("hybrid") pattern of their morphology. As the season advances, the typical phyllodes and phyllode-like submerged leaves of *P.* ×*schreberi* decay and disappear. Thus, one of the key diagnostic features of the hybrid is lost and at this stage the hybrid plants can be easily misidentified as *P. nodosus*. The most important diagnostic characters are summarized in Kaplan & Wolff (2004), for photographs of *P.* ×*schreberi* at different ontogenetic stages see Kaplan & Wolff (2004) and Kaplan & Fehrer (2009). As the stem anatomy differs markedly between the species it is a very efficient means of distinguishing this hybrid from extreme forms of the parental species (Kaplan & Wolff 2004). Because of the overall similarity of *P.* ×*schreberi* to its parents and other *P. natans* hybrids, it is advisable to have molecular proof of the identity of questionable plants (Kaplan & Fehrer 2009).

Molecular evidence: Isozyme electrophoresis confirmed identity of plants from the United Kingdom (Hollingsworth et al. 1995), France and Germany (Kaplan & Wolff 2004). DNA sequencing and/or RFLP provided identification of plants from the Czech Republic (Kaplan & Fehrer 2009) and the U. S. A. (Z. Kaplan & J. Fehrer, unpubl.).

Habitats: Discovered in an upper section of a meandering stream in a relatively well-preserved and unpolluted landscape.

Distribution in the Czech Republic: Recorded only along a 550 m long stretch of the stream Stropnice in southern Bohemia (Fig. 4).

Herbarium specimens seen: **39. Třeboňská pánev:** 7154a: Okr. České Budějovice: Třebeč: říčka Stropnice 0,9 km VSV od obce, 48°52'39"N, 14°41'32"E, 450 m n. m. (3 IX 2006 Z. Kaplan no. 06/417, PRA; 29 VI 2007 Z. Kaplan no. 07/214, PRA; 14 VI 2008 Z. Kaplan & J. Zalewska-Gałosz no. 08/395, PRA; 8 VIII 2008 A. Vydrová & V. Hans no. VG08/1213–1223, BRNU).

Notes: A rare hybrid, often occurring in running water in the absence of the parental species (Hollingsworth et al. 1995, Kaplan & Wolff 2004, Kaplan & Fehrer 2007). It was only recently detected as a new taxon for the Czech Republic (Kaplan & Fehrer 2007).

Potamogeton ×*sparganiifolius* Laest. ex Fr., Novit. Fl. Suec. Mant. 1: 9, 1832.

= *P. gramineus* × *P. natans*

Diagnostic characters: Particularly conspicuous are the phenotypes of this hybrid from fast running water, which have long and ribbon-like submerged leaves, dissimilar to that of any other *Potamogeton* taxon. These plants can be recognized as a separate entity like one would recognize a distinct species. The plants from standing water are more difficult to identify as they often resemble one of their parental species. The hybrid is intermediate particularly in its submerged leaves, which are strongly reminiscent of the phyllodes of *P. natans* but expand into a narrow lamina. It also differs from *P. natans* in often having a markedly branched stem and floating leaves without a flexible junction between the petiole and the lamina (sometimes only obscure traces of a discoloured section are visible). In contrast to the submerged leaves of *P. gramineus* they are longer and narrower in the hybrid (Fig. 6), with only 1–5 longitudinal veins. Like many other hybrids of *P. natans* (Kaplan & Wolff 2004) and those of similar and related North American *P. oakesianus* (Kaplan et al. 2009), *P.* ×*sparganiifolius* also sometimes produces transitional leaves that are intermediate between submerged and floating leaves in their shape, size, structure and petiolation.

Molecular evidence: The Czech plants cited below were confirmed as this hybrid by DNA sequencing (Z. Kaplan & J. Fehrer, unpubl.).

Habitats: Large colonies discovered in two adjacent shallow ponds not currently used for intensive fish breeding. A third locality was a shallow pool in wetland at the edge of a fishpond.

Distribution in the Czech Republic: Three localities are know, two of them close to each other in eastern Bohemia, the third in southern Bohemia (Fig. 3).

Herbarium specimens seen: **15c. Pardubické Polabí:** 5858d: Okr. Hradec Králové: Štít: rybník Dolní Flajšar 0,6 km ZJZ od obce, 50°06'50,6"N, 15°28'02,5"E, 216 m n. m. (23 V 2009 Z. Kaplan no. 09/56, PRA, PRC; 23 V 2009 Z. Kaplan, Jan Rydlo & Jar. Rydlo, ROZ). – Okr. Hradec Králové: Štít: rybník Horní Flajšar 0,5 km JZ od obce, 50°06'43,5"N, 15°28'20,6"E, 218 m n. m. (8 VI 2009 Z. Kaplan no. 09/148, PR, PRA). – **38. Budějovická pánev:** 6951b: Bohemia, okr. České Budějovice, Dívčice: Zbudovská výtopa, tůňka V od trati (26 VI 1994 A. Vydrová no. VG94/008, BRNU, ut *P.* cf. *gramineus*).

Notes: This hybrid is recorded here for the first time for the Czech Republic.

Potamogeton ×*undulatus* Wolfg. in Schult. et Schult. fil., Mant. 3: 360, 1827.

= *P. crispus* × *P. praelongus*

Diagnostic characters: This hybrid resembles *P. praelongus* in general appearance, particularly the small-leaved forms of this species. However, it differs in having a compressed stem with shallow grooves along the broader sides (which can usually be observed only on fresh plants), leaves with fewer longitudinal veins (5–9) and sometimes also by the terminal parts of the stem being characteristically richly branched (Fig. 7).

Molecular evidence: Identity of plants from Denmark was confirmed by DNA sequencing (Z. Kaplan & J. Fehrer, unpubl.).

Habitats: Recorded from the middle section of a small river with rich macrophyte vegetation.

Distribution in the Czech Republic: Collected at the end of the 19th century at a single site or small area in northern Bohemia (Fig. 3). Never re-collected and now extinct in the Czech Republic.

Herbarium specimens seen: **53a. Českolipská kotlina:** 5354c: Flumen Ploučnice (1879 R. Faustus, W); Mimoň (VIII 1887 R. Faustus, BRA, p. p.); Mimoň: v Ploučnici (IX 1887 R. Faustus, PR); Flumen Ploučnice apud Mimoň (IX 1887 R. Faustus, PR); Mimoň (VII 1898 J. Židlický, ROZ); U Habšteina [= Jestřebí] (1887 Attkesz [?], PR).

Notes: About a dozen collections originating from the vicinity of Mimoň and identified as *P. praelongus* were found in herbaria. However, some of these specimens show characters inherited from *P. crispus* in addition to the features typical of *P. praelongus* (see diagnostic characters above). These plants are morphologically consistent with the collections of *P.* ×*undulatus* from Lithuania, Denmark, Poland and other countries. In addition, the collection preserved in BRA is a mixture that contains one shoot of each *P. praelongus* and *P.* ×*undulatus* mounted together on a single sheet. This indicates that both of them grew together in the Ploučnice River where they were repeatedly collected but not distinguished. The other parental species, *P. crispus*, is also recorded from this river.

Attkesz did not indicate the exact origin of his collection, as he wrote just "u Habšteina", i. e. "near Jestřebí". This specimen was possibly not collected close to Jestřebí but more likely from the Ploučnice River 5–6 km NE of Jestřebí, halfway to

Fig. 6. – *Potamogeton* ×*sparganiifolius* from one of two localities in the Labe River Basin in eastern Bohemia (23 V 2009 Z. Kaplan no. 09/56, PRA).

Fig. 7. – *Potamogeton* ×*undulatus* from the surroundings of Jestřebí in northern Bohemia, most likely the Ploučnice River close to the town of Mimoň (1887 Attkesz [?], PR).

Mimoň, where all other Czech specimens of *P.* ×*undulatus* were collected. Attkesz's specimen is dated 1887, as is one of Faustus' specimens. The identical origin of these collections is also supported by the fact that these plants are very similar in many ways: the same morphotype, similar size and shape of leaves and stipules, the same colour of leaves and stem, etc. These facts indicate that these collections were probably collected simultaneously during a joint field trip by both botanists.

Excluded records

Bennett (1908) described *P.* ×*concinnitus* as a putative new hybrid combination "*P. pusillus* × *P. crispus*" based on material from the Czech Republic. A duplicate annotated by Bennett is preserved in the Kew herbarium. The authentic sheet bears two small underdeveloped shoots of the phenotype of *P. crispus* with narrow and plane leaves (called *P. serrulatus* or *P. crispus* var. *serrulatus* in the past, see Kaplan 1997), which contrasts with the characteristically undulate leaves in the common form. The proposed taxon is therefore excluded from the list of hybrids and the name *P. concinnitus* is reduced to the synonymy of *P. crispus*.

Potamogeton concinnitus A. Benn., J. Bot. 46: 162, 1908.

(= *Potamogeton crispus*)
Type: [original label written by Bennett:] "Bečva bei Lásky, Moravia, 7/6/[18]82, leg. J. Bubela, ex herb. Polák", [later annotation by Bennett:] "× *P. concinnitus* Ar. Benn. … , *crispus* × *pusillus* ?" (**lectotype designated here**: K).

The record of *P.* ×*lintonii* (= *P. crispus* × *P. lintonii*) in the Rozkoš Reservoir in eastern Bohemia (Nevečeřal & Krahulec 1994) was erroneous. The voucher specimens were of submerged forms of *P. gramineus* with extremely narrow and spirally twisted leaves that superficially resemble the hybrid (Kaplan 2002b, 2010).

Dostál (1989) lists in his Flora many other hybrid combinations based on names proposed in the European literature but in no way is this an overview of hybrids reported or confirmed for the Czech Republic (see also Kaplan 2001).

Discussion

Changes in frequency of Potamogeton hybrids in time

More than 8600 herbarium specimens of *Potamogeton* collected from the Czech Republic were investigated and 84 of them (i.e. 0.97%) proved to be hybrids. These hybrids originated from 59 localities. Considering the fact that hybrids recognized in the field by experts and experienced field botanists attract more attention and thus are much more likely to be collected for herbaria than common species, such as *P. natans* or *P. crispus*, the actual proportion of plants that are hybrids in the field is likely to be considerably lower.

The earliest herbarium specimens of *Potamogeton* hybrids were collected in 1810s. These included a plant that became a nomenclatural type of *P.* ×*angustifolius* (see Kaplan 1997). Three of the eight hybrids detected in the Czech Republic (*P.* ×*nitens*, *P.* ×*olivaceus* and *P.* ×*undulatus*) are known only from historical collections, the fourth (*P.* ×*cooperi*) was last observed in the field in 2002. The extinction of these hybrid clones is associated with the general decline in the diversity of macrophyte vegetation in the Czech Republic. *Potamogeton*

×*undulatus* disappeared together with one of its parents, *P. praelongus*, which currently occurs at only two localities (Kaplan 2010). Similarly, the parental species of *P.* ×*nitens*, namely *P. gramineus* and *P. perfoliatus*, became extremely rare and currently there is no site in the Czech Republic hosting both these species that could potentially produce the hybrid. The rarity of *P.* ×*cooperi*, *P.* ×*schreberi* and *P.* ×*sparganiifolius* are also associated with the rarity of one of their parental species (*P. perfoliatus*, *P. nodosus* and *P. gramineus*, respectively).

In contrast, *P.* ×*fluitans* was recorded as a new taxon for the Czech Republic only recently (Kaplan 2001) and since than found at a further nine localities. The total number of finds of specimens of *Potamogeton* hybrids is also increasing (Fig. 8). This provokes one to ask does this increase indicate a more frequent hybridization of the parental species. It should be noted that the absolute numbers of records are not corrected for the temporal changes in floristic activity. If records of all *Potamogetonaceae* herbarium collections from the same region (Z. Kaplan, unpubl.) are plotted on same time scale, similar relative values and trends are revealed (Fig. 9). Identical peaks (in 1880s, 1940s, 1970s and the last two decades), which are associated with the recording activity of a few experts or exceptionally active field botanists, occur on both graphs. Although the absolute number of collections of hybrids has markedly increased during the last decades, their relative percentage, when compared to all *Potamogetonaceae* collected, remains more or less constant (mean = 0.98%, standard deviation = 0.55; data prior to 1830s not considered due to the very low number). This clearly shows that the most variable parameter is the recording activity. The high numbers collected over the last few decades is associated with the increase in research activity on the diversity of macrophytes and not the result of more frequent hybridization of parental species. Similar fluctuations associated with differences in research activity and political changes rather than with the actual occurrence of plants in the field are identified for several other groups of plants (e.g. Bureš et al. 2008, Danihelka et al. 2009, J. Danihelka, unpubl., Z. Kaplan, unpubl.).

Relation between habitats and the occurrence of hybrids

The same hybrid combinations sometimes occupy very different habitats in different regions. In many countries, *Potamogeton* hybrids occur mainly in natural lakes or in lowland rivers. This is particularly true for previously glaciated landscapes (Kaplan 2007, Kaplan et al. 2009). The few natural lakes in the Czech Republic are confined to the Šumava Mts. These lakes are oligotrophic and host macrophyte vegetation very poor in species, which does not include any *Potamogeton* taxa. Six hybrids were recorded in Czech rivers and their side pools (*P.* ×*olivaceus*, *P.* ×*schreberi*, *P.* ×*undulatus*, *P.* ×*cooperi*, and exceptionally also *P.* ×*angustifolius* and *P.* ×*fluitans*), mostly in the 19th century. However, almost all disappeared as a result of rivers in the lowlands being extensively channelled, mainly in the late 19th and 20th centuries, which dramatically affected the distribution and diversity of river vegetation. The only exception is a clone of *P.* ×*schreberi*, which survived in one stream situated in a relatively well-preserved and unpolluted landscape (Kaplan & Fehrer 2009). As natural lakes and lowland rivers are not really suitable for *Potamogeton* hybrids in the Czech Republic, most of the records for the 20th century came from fishponds.

Ponds were even more frequent in the territory of the Czech Republic in 15th–18th centuries (Andreska 1997, Čítek et al. 1998). At that time fishponds were not managed as intensively as today. As shown previously (Kaplan 2001, Kaplan et al. 2002, Kaplan &

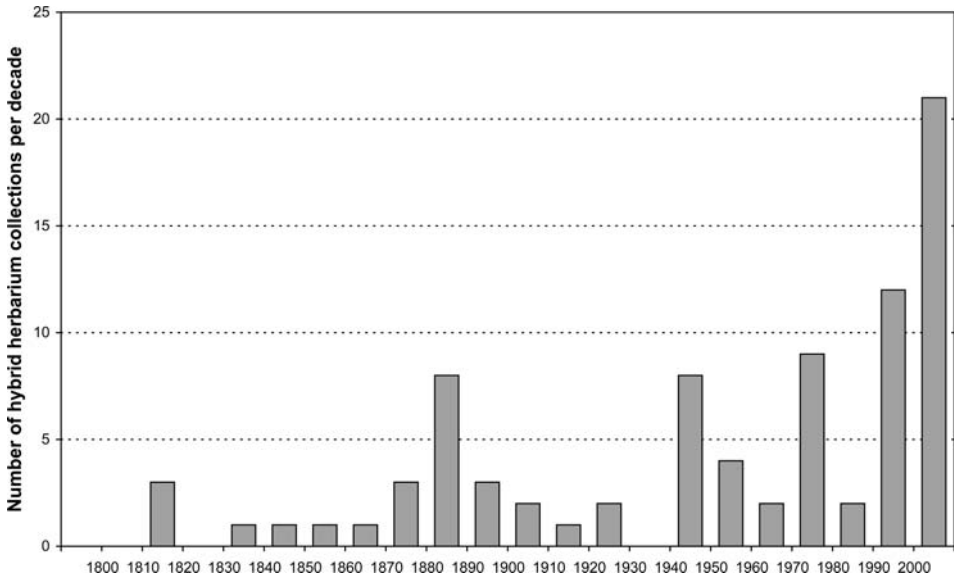

Fig. 8. – Numbers of herbarium specimens of *Potamogeton* hybrids collected in each decade. The four most apparent peaks (in 1880s, 1940s, 1970s and last two decades) are associated with the activity of a few experts or exceptionally active field botanists who collected aquatic plants.

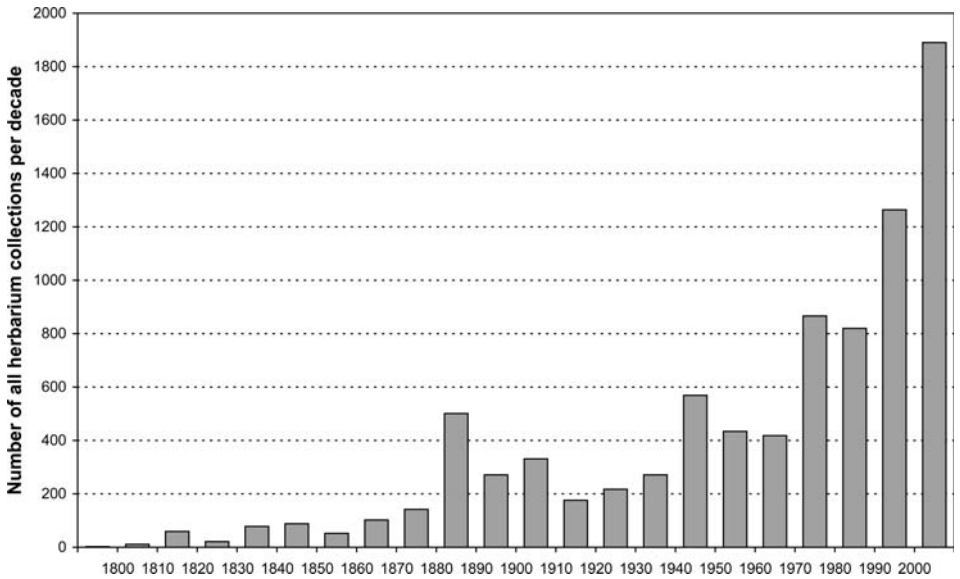

Fig. 9. – Numbers of herbarium specimens of all *Potamogetonaceae* collected in each decade, which reflect the increase in floristic activity. The same general trend and identical peaks occur also in Fig. 8, which indicates that the number of hybrids as a proportion of all the *Potamogetonaceae* collected remains more or less constant.

Fehrer 2004), the occurrence of *Potamogeton* hybrids in Central European fishponds is supported by the exposure and drying out of the bottom of the ponds that occurs when they are occasionally drained. Fishponds that have not been drained for many years become eutrophic, with cloudy water and bottoms covered with thick organic-rich sediment (sapropel), which is often toxic because of anaerobic conditions. Such conditions inhibit germination of seeds. In contrast, the sediment in the fishponds that are drained at intervals is oxidized and mineralized when it is exposed and dries out. After the fishpond is filled again, a high concentration of nutrients is released from the sediment while the water is clear. Sufficient nutrients, weak competition and clear water provide ideal conditions for the germination of seeds, including hybrid seed (Kaplan & Fehrer 2004, Kaplan et al. 2009). This is supported by the recent discoveries of *P.* ×*fluitans*: 8–9 of 10 finds were from fishponds that were drained in summer (and some also de-silted) in previous years. Unfortunately, the traditional cycle of fishpond management, which included regular summer draining, is now rare (Šumberová et al. 2006). This indicates that the frequency of *Potamogeton* hybrids might have been markedly higher when fishponds were managed traditionally than it is today. This change may account for the strong decline in *P.* ×*angustifolius*, which may have been relatively common in the past, as the proportion of historical vs. recent collections suggests.

Co-occurrence of parental species and hybrids

It is not possible to assess the exact incidence of co-occurrence of hybrids with their parents because for many records the presence of the parental species at the locality is unknown. However, recent field investigations have provided many records and some can also be deduced from historical collections.

All recently discovered plants of *P.* ×*fluitans* came from ponds where both parental species occurred. This is associated with the occurrence of this hybrid in occasionally summer drained fishponds and repeated hybridization events. The South-Moravian locality of *P.* ×*cooperi* also hosted both parental species (Kaplan & Fehrer 2004). This is also true for the North-Bohemian historical site: Malinský noted "zwischen *P. crispus* & *perfoliatus*" on the herbarium label of the *P.* ×*cooperi* he collected. Similarly, the collections of *P.* ×*sparganiifolius* and *P.* ×*undulatus* came from sites where both parental species were present. *Potamogeton* ×*olivaceus* was found in a side pool of a river, with both parental species present in the main channel of the river at that time. In contrast, the clone of *P.* ×*schreberi* growing in a South-Bohemian stream in the absence of the parental species is likely to be a relic, which has persisted vegetatively after its parents disappeared (Kaplan & Fehrer 2009).

The situation is more complicated in *P.* ×*angustifolius*. Both occurrences with one or both parental species and without them are recorded for Czech fishponds. As this hybrid is fertile and produces viable seed, it can potentially spread to other sites and establish new populations. When growing on its own at a locality then its origin (whether a local relic or hybrid seed from elsewhere) may remain unclear because detailed knowledge of the previous composition of the macrophyte vegetation is rarely available.

Diversity of Potamogeton hybrids and limitations of morphological identification

The *Potamogeton* hybrids detected include eight different parental combinations. In this respect, the Czech Republic occupies middle position among European countries in the

diversity of *Potamogeton* hybrids. This corresponds to previous observations on the general pattern of the occurrence of *Potamogetonaceae* hybrids in Europe: both hybrid diversity and the number of localities with hybrids increases with latitude (Kaplan 2007, Kaplan & Fehrer 2007). The Czech Republic, positioned in the centre of Europe, is predetermined to occupy an intermediate position between Mediterranean countries with only a few records and northern regions with the highest diversity of about 25–30 hybrids.

The reliability of morphological identifications of *Potamogetonaceae* hybrids varies greatly between hybrid combinations. These range from easily recognizable hybrids to those that cannot be identified morphologically with certainty (Kaplan et al. 2009). Previous studies demonstrate that due to extensive phenotypic plasticity, some hybrids can imitate species and remain unrecognized (Kaplan 2002b, Kaplan & 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 & Wolff 2004, Kaplan & Fehrer 2007).

All the hybrids identified for the Czech Republic so far are those between the broad-leaved species of the genus. The majority of them are between species that can be reliably identified morphologically, although in some cases the identification process requires substantial experience. It is highly likely that several other hybrids occur in the Czech Republic and remain to be identified. Four of the eight identified hybrids (*P.* ×*nitens*, *P.* ×*olivaceus*, *P.* ×*schreberi* and *P.* ×*undulatus*) were recorded at only one locality. The rarity of some hybrid combinations may therefore be another reason why their existence escaped attention. The hybrids between linear-leaved species are particularly likely to be overlooked because of the morphological similarity of the parental species and low number of distinguishing features. Large-scale molecular screening, particularly of plants from localities with high species diversity and ecological conditions favouring hybridization, is therefore needed in future studies.

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Souhrn

Práce přináší výsledky studia výskytu kříženců rdestů (rod *Potamogeton*) v České republice. Podrobná revize všech dostupných herbářových dokladů (více než 8600) a cílený terénní výzkum odhalily současný nebo historický výskyt celkem osmi hybridů. K jejich identifikaci byly kromě morfologických znaků použity i anatomické znaky ve stavbě lodyhy a analýzy isozymů a DNA. Všechny zjištění kříženci patří do skupiny širokolistých druhů. Podobná míra hybridizace je předpokládána také u úzkolistých rdestů, jejich kříženec je však velmi obtížné odhalit kvůli malé morfologické diferenciaci mezi taxony této skupiny. Čtyři kříženci (*P.* ×*nitens*, *P.* ×*olivaceus*, *P.* ×*sparganiifolius* a *P.* ×*undulatus*) jsou zde uvedeni jako nové taxony pro květenu České republiky. Čtyři z osmi zjištěných kříženců jsou již vyhynulí, zbývající čtyři jsou velmi vzácní. Údaj o výskytu vzácného hybrida *P.* ×*lintonii* byl založen na extrémním morfotypu druhu *P. gramineus* s neobyčejně úzkými a krátkými ponořenými

listy. Podobně rostlina popsaná z České republiky pod jménem *P. concinnitus* není kříženec, jak se domníval jeho původní autor, ale pouze mladý exemplář druhu *P. crispus* s úzkými a plochými listy. Přestože se celkový počet zjištěných výskytů kříženců v průběhu času zvyšuje, nelze tento nárůst interpretovat jako důsledek větší frekvence hybridizace v přírodě. Korekce dat ukázala, že podíl kříženců na celkovém počtu zaznamenaných výskytů všech druhů čeledi *Potamogetonaceae* zůstává více méně stejný. Nejvíce nálezů pochází z posledních dvou desetiletí, což je však projevem cíleného výzkumu několika specialistů a výjimečně aktivních floristů. Nejčastějším biotopem kříženců rdestů v České republice jsou druhově bohaté, ekologicky vyvážené, alespoň občas letněné rybníky bez neúměrně vysoké rybí obsádky a bez nadměrného přihnojování. Naprostá většina historických lokalit cenné vodní vegetace s výskytem kříženců zanikla v důsledku upuštění od tradičního pravidelného letnění a intenzifikace hospodaření na rybnících. Zvláště v 19. století byli někteří kříženci nalézáni také v řekách. Tyto výskyty však vymizely po masivních regulacích řek na začátku 20. století. Kříženci jsou obvykle nalézáni na lokalitách spolu se svými rodiči. Občas jsou však schopni na lokalitě přežívat i poté, co rodičovské druhy vymizely. Naprostá většina kříženců je sterilní; kultivační experimenty však prokázaly, že *P.* ×*angustifolius* je plodný, vytváří klíčivá semena, která dávají vznik životaschopným rostlinám, jež jsou rovněž fertilní.

References

Andreska J. (1997): Lesk a sláva českého rybářství [Glitter and glory of the Czech fishery]. – Nuga, Pacov.

Alix M. S. & Scribailo R. W. (2006): First report of *Potamogeton* × *undulatus* (*P. crispus* × *P. praelongus*, *Potamogetonaceae*) in North America, with notes on morphology and stem anatomy. – Rhodora 108: 329–346.

Bennett A. (1908): Notes on *Potamogeton*. – J. Bot. 46: 160–163.

Berchtold B. W. et Presl J. S. (1821): O přirozenosti rostlin aneb rostlinář [On the natural properties of plants, alias Plant book] … Sect. III, vol. 1, fasc. 2: Rostliny žábnjkowité [*Alismatales*]. – Praha.

Berchtold F. G. & Fieber F. X. (1838): Die Potamogeta Böhmens. – Prag.

Bobrov A. A. & Reshetnikova N. M. (2002): Novyi dlya flory Rossii rdest – *Potamogeton* × *schreberi* G. Fisch. (*Potamogetonaceae*) iz Smolenskoi oblasti [*Potamogeton* × *schreberi* G. Fisch. (*Potamogetonaceae*) – a new species for the flora of Russia, from the Smolensk region]. – Novosti Sist. Vyssh. Rast. 34: 7–11.

Bobrov A. A. & Chemeris E. V. (2009): Pondweeds (*Potamogeton*, *Potamogetonaceae*) in river ecosystems in the north of European Russia. – Dokl. Biol. Sci. 425: 167–170.

Brayshaw T. C. (2000): Pondweeds, bur-reeds and their relatives of British Columbia: Aquatic families of monocotyledons. Ed. 2. – Royal British Columbia Museum, Victoria.

Bureš P., Danihelka J., Husáková M. & Pařil P. (2008): Psárky *Alopecurus aequalis* a *A. geniculatus* v České republice: jejich určování a rozšíření [*Alopecurus aequalis* and *A. geniculatus* in the Czech Republic: their identification and distribution]. – Muz. a Souč., ser. natur., 23: 3–61.

Chepinoga V. V., Stepantsova N. V., Grebenyuk A. V., Verkhozina A. V., Vin'kovskaya O. P., Gnutikov A. A., Dulepova N. A., Enushchenko I. V., Zarubin A. M., Kazanovskii S. G., Konovalov A. S., Korobkov A. A., Luferov A. N. et Rosbakh S. A. (2008): Konspekt flory Irkutskoi oblasti (Sosudistye rasteniya) [Check-list of the vascular flora of the Irkutsk region] – Irkutskii gosudarstvennyi universitet, Irkutsk.

Čítek J., Krupauer V. & Kubů F. (1998): Rybníkářství [Fishpond management]. – Informatorium, Praha.

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

Dandy J. E. & Taylor G. (1946): An account of × *Potamogeton suecicus* Richt. in Yorkshire and the Tweed. – Trans. Proc. Bot. Soc. Edinb. 34: 348–360.

Dandy J. E. & Taylor G. (1957): Two new British hybrid pondweeds. – Kew Bull. 12: 332.

Danihelka J., Niklfeld H. & Šípošová H. (2009): *Viola elatior*, *V. pumila* and *V. stagnina* in Austria, Czechia and Slovakia: a story of decline. – Preslia 81: 151–171.

Dostál J. (1989): Nová květena ČSSR [New flora of Czechoslovakia]. – Academia, Praha.

Du Z.-Y., Yang C.-F., Chen J.-M. & Guo Y.-H. (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. – Aquatic Bot. 91: 47-50.

Fant J. B., Preston C. D. & Barrett J. A. (2001a): Isozyme evidence for the origin of *Potamogeton* × *sudermanicus* as a hybrid between *P. acutifolius* and *P. berchtoldii*. – Aquatic Bot. 71: 199–208.

Fant J. B., Preston C. D. & Barrett J. A. (2001b): Isozyme evidence of the parental origin and possible fertility of the hybrid *Potamogeton* × *fluitans* Roth. – Pl. Syst. Evol. 229: 45–57.

Fant J. B., Kamau E. A. & Preston C. D. (2003): Chloroplast evidence for the multiple origins of the hybrid *Potamogeton* × *sudermanicus* Hagstr. – Aquatic Bot. 75: 351–356.

Fant J. B., Kamau E. & Preston C. D. (2005): Chloroplast evidence for the multiple origins of the hybrid *Potamogeton* × *fluitans*. – Aquatic Bot. 83: 154–160.

Fieber F. X. (1838): *Potamogeton*. – In: Berchtold F. G. & Opiz P. M. (eds), Oekonomisch-technische Flora Böhmens 2(1): 242–287, Prag.

Fischer G. (1904): Beitrag zur Kenntnis der bayerischen Potamogetoneen IV. – Mitt. Bayer. Bot. Ges. 1: 356–366 & 375–388.

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.

Haynes R. R. & Williams D. C. (1975): Evidence for the hybrid origin of *Potamogeton longiligulatus* (*Potamogetonaceae*). – Michigan Bot. 14: 94–100.

Hejný S. (1950): *Potamogetonaceae*. Rdestovité – Rudavcovité. – In: Dostál J. (ed.), Květena ČSR [Flora of Czechoslovakia] 2: 1722–1737, Přírodovědecké nakladatelství, Praha.

Hejný S. (2000): Rdest *Potamogeton angustifolius* J. S. Presl v severní části Českobudějovické pánve [*Potamogeton angustifolius* J. S. Presl in the northern part of the Českobudějovická basin]. – Sborn. Jihočes. Muz. České Budějovice, Přír. Vědy, 40: 45–48.

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

Hollingsworth P. M., Preston C. D. & Gornall R. J. (1995): Isozyme evidence for hybridization between *Potamogeton natans* and *P. nodosus* (*Potamogetonaceae*) in Britain. – Bot. J. Linn. Soc. 117: 59–69.

Hollingsworth P. M., Preston C. D. & Gornall R. J. (1996): Isozyme evidence for the parentage and multiple origins of *Potamogeton* × *suecicus* (*P. pectinatus* × *P. filiformis*, *Potamogetonaceae*). – Pl. Syst. Evol. 202: 219–232.

Holmgren P. K., Holmgren N. H. & Barnett L. C. (1990): Index herbariorum. Part I: The herbaria of the world. Ed. 8. – Regnum Veg. 120: 1–693.

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

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

Kadono Y. (1983): [New hybrids of *Potamogeton* from Lake Inba-numa, Chiba prefecture.] – Acta Phytotax. Geobot. 34: 51–54. [in Chinese]

Kadono Y. & Wiegleb G. (1987): Two new *Potamogeton* hybrids from Japan. – J. Jap. Bot. 62: 73–77.

Kaplan Z. (1997): Names of *Potamogeton* (*Potamogetonaceae*) proposed by Bohemian botanists in the period 1819–1902. – Preslia 69: 193–239.

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*]. – Zpr. 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., Hrouda L., Chrtek jun. J., Kaplan Z., Kirschner J. et Štěpánek J. (eds), Klíč ke květeně České republiky [Key to the flora of the Czech Republic], p. 736–743, Academia, Praha.

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. – Pl. Biosystems 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. (2010): *Potamogetonaceae* Dumort. – rdestovité. – In: Štěpánková J., Chrtek J. jun. & Kaplan Z. (eds), Květena České republiky [Flora of the Czech Republic] 8: 329–384, Academia, Praha.

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

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

Kaplan Z., Fehrer J. & Hellquist C. B. (2009): New hybrid combinations revealed by molecular analysis: The unknown side of North American pondweed diversity (*Potamogeton*). – Syst. Bot. 34: 625–642.

Kaplan Z., Fehrer J. & Hellquist C. B. (2010): *Potamogeton* ×*jacobsii* (*Potamogetonaceae*) from New South Wales, Australia – the first *Potamogeton* hybrid from the Southern Hemisphere. – Telopea 13 (in press).

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

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

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

Kaplan Z., Plačková I. & Štěpánek J. (2002): *Potamogeton* ×*fluitans* (*P. natans* × *P. lucens*) in the Czech Republic. II. Isozyme analysis. – Preslia 74: 187–195.

Kashina L. I. (1988): *Potamogetonaceae* – Rdestovye. – In: Krasnoborov I. M. (ed.), Flora Sibiri [Flora of Siberia], [Vol. 1] *Lycopodiaceae – Hydrocharitaceae*, p. 93–105 & 165–176, Nauka, Novosibirsk.

King R. A., Gornall R. J., Preston C. D. & Croft J. M. (2001): Molecular confirmation of *Potamogeton* × *bottnicus* (*P. pectinatus* × *P. vaginatus*, *Potamogetonaceae*) in Britain. – Bot. J. Linn. Soc. 135: 67–70.

McNeill J., Barrie F. R., Burdet H. M., Demoulin V., Hawksworth D. L., Marhold K., Nicolson D. H., Prado J., Silva P. C., Skog J. E., Wiersema J. H. & Turland N. J. (eds) (2006): International code of botanical nomenclature (Vienna Code) adopted by the seventeenth International Botanical Congress Vienna, Austria, July 2005. – Regnum Veg. 146: 1–568.

Miki S. (1937): [The water phanerogams in Japan, with special reference to those of the province Yamashiro]. – Reports on the historical remains, scenic places and natural monuments in Kyoto Pref. 18: 1–127. [in Japanese]

Niklfeld H. (1971): Bericht über die Kartierung der Flora Mitteleuropas. – Taxon 20: 545–571.

Nevečeřal P. & Krahulec F. (1994): Dva noví zástupci rodu *Potamogeton* ve flóře České republiky: *P. polygonifolius* a *P.* × *lintonii* (*P. crispus* × *P. friesii*) [Two *Potamogeton* species new to the flora of the Czech Republic: *P. polygonifolius* and *P.* × *lintonii* (*P. crispus* × *P. friesii*)]. – Preslia 66: 151–158.

Ogden E. C. (1943): The broad-leaved species of *Potamogeton* of North America north of Mexico. – Rhodora 45: 57–105, 119–163 & 171–214.

Opiz P. M. (1822): Pflanzenverzeichnisse. Nachtrag zu Hrn. M. D. Presl's Flora cechica. – Flora (Regensburg) 5: 266–270.

Opiz P. M. (1823): Böheims phänerogamische und cryptogamische Gewächse. – Prag.

Opiz P. M. (1824): Vorräthige Pflanzen. – Naturalientausch 10: 214–278.

Opiz P. M. (1826): Authentisches Herbar. – Naturalientausch 11: 325–342.

Petrak F. (1910): Beiträge zur Flora von Mähren. – Allg. Bot. Z. 16: 4–6 & 20–23.

Ploeg D. T. E. van der (1987): *Potamogeton* x *sudermanicus* Hagstrom, de vermoedelijke bastaard van *P. acutifolius* Link en *P. berchtoldii* Fieber, in Nederland gevonden [*Potamogeton* x *sudermanicus* in the Netherlands]. – Gorteria 13: 173–176.

Ploeg D. T. E. van der (1990): De Nederlandse breedbladige Fonteinkruiden [Dutch broad-leaved taxa of *Potamogeton*]. – Wetensch. Meded. Kon. Ned. Natuurhist. Ver. 195: 1–98.

Presl J. S. & Presl C. B. (1819): Flora čechica. Kwětena česká [Flora of Bohemia]. – Pragae.

Preston C. D. (1995a): Pondweeds of Great Britain and Ireland. – Botanical Society of the British Isles, London.

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. (2001): [Review of] Flora of North America north of Mexico. Volume 22 Magnoliophyta: Alismatidae, Arecidae, Commelinidae (in part), and Zingiberaceae. – Watsonia 23: 458–459.

Preston C. D. & Croft J. M. (1997): Aquatic plants in Britain and Ireland. – Harley Books, Colchester.

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

Preston C. D., Hollingsworth P. M. & Gornall R. J. (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., Hollingsworth P. M. & Gornall R. J. (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. (1896): De danske Blomsterplanters Naturhistorie. I. Enkimbladede [Natural history of Danish flowering plants. I. Monocotyledons]. – Kjøbenhavn.

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

Skalický V. (1988): Regionálně fytogeografické členění [Phytogeographical divisions of the Czech Republic]. – In: Hejný S. & Slavík B. (eds), Květena České socialistické republiky [Flora of the Czech Socialist Republic] 1: 103–121, Academia, Praha.

Symoens J. J., van de Velden J. & Büscher P. (1979): Contribution a l'étude de la taxonomie et de la distribution de *Potamogeton nodosus* Poir. et *P. thunbergii* Cham. et Schlechtend. en Afrique. – Bull. Soc. Roy. Bot. Belgique 112: 79–95.

Šumberová K., Lososová Z., Fabšičová M. & Horáková V. (2006): Variability of vegetation of exposed pond bottoms in relation to management and environmental factors. – Preslia 78: 235–252.

Thiers B. (2000). Index Herbariorum: A global directory of public herbaria and associated staff. – New York Botanical Garden's Virtual Herbarium. URL: [http://sciweb.nybg.org/science2/IndexHerbariorum.asp, accessed February 2010]

Vondrák J. (1999): *Potamogeton* × *angustifolius* – nový taxon flóry Písecka [*Potamogeton* × *angustifolius* – a new taxon in the surrounding of the town of Písek]. – Zpr. Čes. Bot. Společ. 34: 49–50.

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

Wiegleb G. (1990a): A redescription of *Potamogeton wrightii* (*Potamogetonaceae*). – Pl. Syst. Evol. 170: 53–70.

Wiegleb G. (1990b): The importance of stem anatomical characters for the systematics of the genus *Potamogeton* L. – Flora (Jena) 184: 197–208.

Wiegleb G. & Herr W. (1984): Die *Potamogetonaceae* niedersächsischer Fliessgewässer, Teil 1. – Göttinger Florist. Rundbr. 18: 65–86.

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

Wiegleb G., van de Weyer K., Bolbrinker P. & Wolff P. (2008): *Potamogeton*-Hybriden in Deutschland. – Feddes Repert. 119: 433–448.

Wolff P., Ortscheit A. & Simon M. (1997): *Potamogeton* × *bennettii* Fryer (= *P. crispus* × *trichoides*), un nouvel hybride pour le continent européen en France, en Alsace, deuxième station dans le monde. [*Potamogeton* × *bennettii* Fryer (= *P. crispus* × *trichoides*), a new hybrid for the European continent in Alsace, second occurrence in the world.] – Acta Bot. Gall. 144: 269–283.

Zalewska-Gałosz J. (2002): Occurrence and distribution of *Potamogeton* hybrids (*Potamogetonaceae*) in Poland. – Feddes Repert. 113: 380–393.

Zalewska-Gałosz J. (2008): Rodzaj *Potamogeton* L. w Polsce – taksonomia i rozmieszczenie [The genus *Potamogeton* L. in Poland – taxonomy and distribution]. – Institute of Botany of the Jagiellonian University, Kraków.

Zalewska-Gałosz J., Ronikier M. & Kaplan Z. (2009): The first European record of *Potamogeton* ×*subobtusus* identified using ITS and cpDNA sequence data. – Preslia 81: 281–292.

Zalewska-Gałosz J., Ronikier M. & Kaplan Z. (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.

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