

## PHENOTYPIC PLASTICITY IN *POTAMOGETON* (*POTAMOGETONACEAE*)

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**Abstract:** Sources of the extensive morphological variation of the species and hybrids of *Potamogeton* were studied, especially from the viewpoint of the stability of the morphological characters used in *Potamogeton* taxonomy. Transplant experiments, the cultivation of clones under different values of environmental factors, and the cultivation of different clones under uniform conditions were performed to assess the proportion of phenotypic plasticity in the total morphological variation. Samples from 184 populations of 41 *Potamogeton* taxa were grown. The immense range of phenotypic plasticity, which is possible for a single clone, is documented in detail in 14 well-described examples. The differences among distinct populations of a single species observed in the field were mostly not maintained when grown together under the same environmental conditions. Clonal material cultivated under different values of environmental factors produced distinct phenotypes, and in a few cases a single genotype was able to demonstrate almost the entire range of morphological variation in an observed trait known for that species. Several characters by recent literature claimed to be suitable for distinguishing varieties or even species were proven to be dependent on environmental conditions and to be highly unreliable markers for the delimitation of taxa. The unsatisfactory taxonomy that results when such classification of phenotypes is adopted is illustrated by three examples from recent literature. Phenotypic plasticity was found to be the main source of morphological variation within the species of *Potamogeton*, having much more influence than morphological differences caused by different genotypes.

### INTRODUCTION

The extensive morphological variation of members of the genus *Potamogeton* (incl. *Stuckenia*) was known to botanists from at least as early as the 19th century. The first attempts to describe all particular morphotypes within a species and to give a formal name to them often produced a complicated system of infraspecific taxa. As early as 1828 FRIES distinguished 9 infraspecific taxa at two taxonomic levels within a single species, namely *P. gramineus*. All of them are still considered to belong to this species, but have recently only exceptionally been accepted taxonomically (e.g. by TOPA 1966, MÄEMETS 1984, MARKGRAF 1981, SERGIEVSKAYA 1966). Several other authors from this period (e.g. MERTENS & KOCH 1823, FIEBER 1838, REICHENBACH 1845) followed this practice in order to interpret the whole morphological variation range of individual species in terms of formal taxonomy. This activity culminated with the works of German botanists of the late 19th and early 20th centuries (ASCHERSON & GRAEBNER 1897, FISCHER 1907, GRAEBNER 1907). The enormous number of phenotypes led taxonomists to split species into a number of taxa of every rank between

species and forma and to arrange these taxa into a hierarchical system. Many species were subdivided into subspecies or varieties, which were often based on a single morphological character. The last author who recognized infraspecific taxa to such a large extent was probably HAGSTRÖM (1916) who attempted to treat this variation on a world-wide level. However, even recent authors have followed this approach in more restricted geographical areas: GALINIS (1969) distinguished approximately 90 infraspecific taxa, mostly based on a single plastic character, in an account of new *Potamogeton* taxa in Lithuania.

Since the first third of the 20th century, some taxonomists studying *Potamogeton* have become more aware of the inadequacies of such classification and have stopped distinguishing infraspecific taxa at all (e.g. DANDY 1937, 1958, MUENSCHER 1944) or, less conveniently, begun to reduce their rank (e.g. SOÓ 1934, 1936, 1938a,b, 1971 [Soó was the only botanist ever to use a taxonomic level of subforma in *Potamogeton*], SUESSENGUTH 1936, TZVELEV 1987, 2000a). On the other hand, taxa previously treated as varieties have been elevated to the subspecific rank as a reaction to the current trend (HAYNES & HELLQUIST 1996, LES & HAYNES 1996, VOLOBAEV 1991, formerly also HARA 1985, HULTÉN 1937, 1941, 1964, CALDER & TAYLOR 1965).

Surprisingly, the origin of the morphological variation observed by many authors has not been much studied systematically. Probably the first botanist to devote interest to an extensive sophisticated field study and transplant experiments was A. Fryer. He was familiar with plants of broad-leaved *Potamogeton* occurring in localities in the vicinity of his house and observed them repeatedly for several seasons. That is why he was later able to note “the difference between states of species and varieties of species, between forms that are only temporary and speedily revert to the type, and forms that are permanent, for the life of the individual at least” (FRYER 1890). He also grew dissimilar clones of selected taxa from several localities. He proved that while in certain cases (e.g. in *P. ×cooperi*) their differences were not maintained in cultivation (FRYER & BENNETT 1915), in others (e.g. in *P. polygonifolius* f. *cancellatus* FRYER) they remained distinct (FRYER 1900). Observation of cultivated plants led him to the conclusion that recognized varieties of some species (especially *P. natans* and *P. polygonifolius*) were “merely the natural changes of form, which take place according to the progressive growth of the plant” (FRYER 1898) and that these changes were not “permanent under cultivation” (FRYER 1894). A comprehensive review of Fryer’s work is given by PRESTON (1988).

Special studies devoted to phenotypic plasticity have only rarely discussed *Potamogeton* taxa. The effects of light conditions and water chemistry on the leaf shape of *P. perfoliatus* were revealed by PEARSALL & HANBY (1925). Only recently, several studies have appeared describing changes of character states in response to conditions of the environment. The influence of planting depth on *P. pectinatus* was studied by OGG et al. (1969) and by SPENCER (1987) and on *P. gramineus* by SPENCER & KSANDER (1990a). Plastic responses in the morphology of *P. pectinatus* to sediment and above-sediment conditions were observed by KAUTSKY (1987) and IDESTAM-ALMQUIST & KAUTSKY (1995). The influence of temperature, light and nutrient limitation on the reddish-brown color in *P. gramineus* was tested by SPENCER & KSANDER (1990b) and on the early growth of this species by SPENCER & KSANDER (1991). The relation between photoperiod and the initiation of winter bud production was studied by SPENCER et al. (1994). Differences in selected traits of biomass production of

*P. filiformis*, *P. pectinatus* and *P. perfoliatus* in relation to sediment type were also recorded by KAUTSKY (1991). The mean shoot length of *P. filiformis* is higher when the plants are protected from waves as noted by JUPP & SPENCE (1977). Specific leaf area of *P. obtusifolius* increased and leaf dry weight decreased with water depth according to observations of MABERLY (1993).

Variation due to seasonal development was also recognized. HAYNES (1974) reported variation in the development of lacunae and in the shape of the leaf apex between plants of *P. berchtoldii* collected in early summer and those collected later in the season. The length and length : breadth ratio of leaves of *P. richardsonii* increase from the first mature leaves near the base of the stem to the youngest leaves near the apex (SPENCE & DALE 1978). PRESTON (1995) enumerated other examples of both seasonal variability and variability due to the environment.

At present, the manifestation of phenotype variation not supported by genetic differences but induced solely by differences among habitats is still underestimated in some taxonomic classifications. The aim of the present paper is to stress the extensive capacity of *Potamogeton* plants to respond in their morphology to different habitat conditions.

## MATERIALS AND METHODS

### Study taxa

Cultivation experiments were carried out with 41 *Potamogeton* taxa. These are listed in Table 1. The species concept, delimitation of taxa and the nomenclature follow WIEGLEB & KAPLAN (1998) with an exception of *P. berchtoldii* and *P. groenlandicus* that are distinguished as separate species in this study. Samples from 184 populations were grown. Most of them originated from Europe, although additional material came from Africa, Siberia, Japan, New Zealand, and North and South America. Samples were grown in the experimental garden at the Institute of Botany, Průhonice, Czech Republic, from 1995 to 2000. The origin and reference numbers (corresponding to numbers of vouchers) of the plants treated in the text in detail are given in Table 2. Dried reference specimens from both the field and the cultivation experiments are kept in the herbarium of the Institute of Botany, Průhonice (PRA).

### Experimental treatments

Plants were grown in plastic tanks of two sizes (180 cm × 140 cm × 80 cm and 200 cm × 120 cm × 35 cm) filled with water and sunk in the ground in order to prevent overheating the water in the summer. Each sample was planted in a plastic pot submerged in a cultivation tank. Pond mud after desiccation treatment, peat and sand or their mixtures were used according to experimental conditions and species' requirements.

Three kinds of cultivation experiments have been carried out:

- (1) Transplant of clones from the field into different conditions in cultivation tanks.
- (2) Cultivation of clones under different values of environmental factors in order to show the effect of different environment on the same genotype.
- (3) Cultivation of different clones under uniform conditions in order to neutralize the effects of the different environments on the phenotype.

Table 1. A list of taxa used in the cultivation experiments.

Taxon	Total range	Origin of cultivated samples	No. of populations sampled
<i>P. acutifolius</i> LINK	Temperate regions of Europe	Czech Republic	6
<i>P. alpinus</i> BALB.	Circumboreal	Czech Republic	11
<i>P. berchtoldii</i> FIEBER	Europe, Asia, North America	Austria, Czech Republic, Russia, Switzerland	12
<i>P. cheesemani</i> A. BENN.	New Zealand, Australia, Tasmania	New Zealand	3
<i>P. coloratus</i> HORNEM.	W, C and S Europe, N Africa, SW Asia	Austria, Germany	2
<i>P. compressus</i> L.	Boreal and temperate regions of Europe and Asia	Denmark, Sweden	3
<i>P. crispus</i> L.	Europe, Africa, Asia, Australia, introduced in New Zealand, North America and S South America	Czech Republic	5
<i>P. distinctus</i> A. BENN.	E and SE Asia, Pacific islands	Japan	1
<i>P. ephedrus</i> RAF.	North America, British Isles	USA	4
<i>P. filiformis</i> PERS.	Europe, W, C and N Asia, North and South America	Sweden, Russia, Switzerland, USA	9
<i>P. foliosus</i> RAF.	North and Central America	USA	2
<i>P. friesii</i> RUPR.	Boreal and temperate regions throughout the Northern Hemisphere	Germany, Russia, Sweden	3
<i>P. fryeri</i> A. BENN.	E Asia	Japan	2
<i>P. gayi</i> A. BENN.	South America	garden plants, wild origin unknown	2
<i>P. gramineus</i> L.	Boreal and temperate regions throughout the Northern Hemisphere	Czech Republic, France, Germany, Sweden	11
<i>P. groenlandicus</i> HAGSTR.	Greenland	Greenland	2
<i>P. hillii</i> MORONG	E North America	USA	1
<i>P. illinoensis</i> MORONG	North and South America	Argentina, USA	2
<i>P. lucens</i> L.	Europe, N Africa, W, N and E Asia	Czech Republic, Netherlands, Switzerland	7
<i>P. natans</i> L.	Boreal and temperate regions of the Northern Hemisphere	Austria, Czech Republic, Denmark, Switzerland	8
<i>P. nodosus</i> POIR.	Subcosmopolitan	Czech Republic, France, Italy	5
<i>P. obtusifolius</i> MERT. et W.D.J. KOCH	Europe, W and N Asia, N North America	Canada, Czech Republic, Sweden	7
<i>P. ochreatus</i> RAOUL	SW, S, SE and E Australia, New Zealand	New Zealand	3
<i>P. pectinatus</i> L.	Cosmopolitan	Argentina, Austria, Canada, Czech Republic, Denmark, Italy, Sweden, Switzerland	19

<i>P. perfoliatus</i> L.	Europe, N and C Africa, Asia, Australia, E North and C America	Austria, Czech Republic, Sweden, Switzerland	7
<i>P. polygonifolius</i> POURR.	W, N, C and S Europe, the Azores, Madeira, N Africa, E North America	Czech Republic, Germany	3
<i>P. praelongus</i> WULFEN	Circumboreal	Czech Republic, Denmark, Germany	3
<i>P. pusillus</i> L.	Europe, Africa, Asia, North and South America	Austria, Czech Republic, Switzerland	10
<i>P. Robbinsii</i> OAKES	North America	USA	1
<i>P. schweinfurthii</i> A. BENN.	Africa, Madagascar, Mascarene Islands, the Azores, Mediterranean islands	Kenya, Tanzania	2
<i>P. tepperi</i> A. BENN.	Australia	Australia	1
<i>P. trichoides</i> CHAM. et SCHLTDL.	Temperate regions of Europe and W half of Asia, N, E and S Africa	Czech Republic, Germany, Slovakia	6
<i>P. vaginatus</i> TURCZ.	N Europe, N Asia, N North America	Canada	1
<i>P. wrightii</i> MORONG	C, E and SE Asia, Pacific islands	garden plants, wild origin unknown	2
<i>P. X angustifolius</i> J. PRESL (= <i>P. gramineus</i> × <i>P. lucens</i> )	-	Czech Republic	1
<i>P. X botanicus</i> HAGSTR.	-	Denmark	2
(= <i>P. pectinatus</i> × <i>P. vaginatus</i> )	-		
<i>P. X fluitans</i> ROTH (= <i>P. lucens</i> × <i>P. natans</i> )	-	Austria, Germany, Czech Republic	4
<i>P. X lanceolatifolius</i> (TISELIUS) C.D. PRESTON (= <i>P. gramineus</i> × <i>P. polygonifolius</i> )	-	Sweden	1
<i>P. X nitens</i> WEBER (= <i>P. gramineus</i> × <i>P. perfoliatus</i> )	-	Germany, Sweden	5
<i>P. X salicifolius</i> WOLFG. (= <i>P. lucens</i> × <i>P. perfoliatus</i> )	-	Sweden	4
<i>P. X undulatus</i> WOLFG. (= <i>P. crispus</i> × <i>P. praelongus</i> )	-	Denmark	1

For any final comparison of morphological differences only clones were used. Clonal material has been obtained by partitioning of branched vertical shoots, fragmenting the lower horizontal shoots (rhizomes) or from turions developed on a single plant. The factors studied were water depth (10–80 cm in cultivation, or up to 150 cm when compared with plants from the field), nutrient conditions of substrate (only the rough scale eu-, meso- and oligotrophic conditions has been used for three types of sediment: solely mud, 1 : 1 mixture of mud and sand, and 1 : 5 mixture of these, respectively), light intensity (0%, 30% and 60% shading with gratings of wooden bars), and water current (only standing water available in cultivation).

The morphological changes caused by different treatments were studied. Particular attention was paid to the characters that are considered in the respective recent literature (e.g. DANDY 1971, OGDEN 1974, HAYNES 1974, BUSIK 1979, SCOGGAN 1979, DANDY 1980, CASPER & KRAUSCH 1980, MARKGRAF 1981, TUR 1982, MÄEMETS 1984, TZVELEV 1987, KASHINA 1988, PRESTON 1995) to have diagnostic value for distinguishing closely related taxa and to those that are claimed to serve in the subdivision of species into infraspecific taxa.

### Terminological notes

Since the terms variation and variability are often interchanged in the literature, both expressions are defined here first in order to ensure precision in describing the observed phenomena.

The term “variation” here describes the differences actually present among the individuals in a population. Variation can be directly observed as a property of a collection of items. In contrast, “variability” is used as a term that refers to the potential to vary. Variability of a phenotypic trait describes the way it changes in response to environmental influences or during the seasonal development of an individual. Phenotypic plasticity is one of the sources of variability.

The description of phenotypic plasticity in the following text includes not only the results of the response of the plant to environmental factors, but also changes connected with the ontogenetic development of the individual. The reason why these two phenomena have not been distinguished is that the primary aim of this study was not to study which factor is responsible for which morphological change, but (1) to distinguish true genetic differences manifested morphologically from all other non-genetic variations, and (2) to reveal what range of morphological variation in a single clone is possible. The final purposes of these experiments were (1) to identify which characters remain  $\pm$  stable over a wide range of conditions and thus can be utilized in the taxonomy of *Potamogeton*, (2) to find out which species, as currently delimited, show morphological variation even when the effect of the environment is neutralized, and (3) to assess the proportion of phenotypic plasticity in the total morphological variation.

### RESULTS

The extensive number of taxa studied and the cultivation treatments led to large numbers of observations. All studied *Potamogeton* taxa showed a certain level of phenotypic plasticity. Differences among distinct populations of a single species observed in the field were mostly not maintained when samples of these were grown together under the same environmental conditions. Clonal material cultivated under different values of environmental factors

Table 2. The origin and reference numbers of the specimens discussed in the text. The abbreviation "coll. number" refers to the collector number of specimens collected in the field, "cult. number" to vouchers collected from the cultivated plants.

Taxon	coll. number	cult. number	origin
<i>P. acutifolius</i>	96/623	C 321	Czech Republic: Bohemia: Distr. Pardubice: in the Baroch fishpond 0.7 km SSW of the Hrobice village, 224 m a.s.l., 9.IX.1996, coll. Z. KAPLAN
<i>P. alpinus</i>	96/681	C 338	Czech Republic: Bohemia: Distr. Hradec Králové: in a backwater (detached river arm) of the Orlice River by Malšova Lhota village, 232 m a.s.l., 8.X.1996, coll. Z. KAPLAN
<i>P. ×fluitans</i>	98/129	C 983	Austria: Distr. Vorarlberg: Bregenz: in a ditch with running water at the NNE margin of the Fußach village (near Höchst), 397 m a.s.l., 23.VI.1998
<i>P. gramineus</i>	97/831	C 887	Czech Republic: Bohemia: Distr. Náchod: in the E margin of the Rozkoš Reservoir by the Šereč village, 280 m a.s.l., 22.VIII.1997, coll. Z. KAPLAN
<i>P. lucens</i>	97/833	C 884	Czech Republic: Bohemia: Distr. Náchod: in the SE margin of the Rozkoš Reservoir by the Doubravice village, 280 m a.s.l., 22.VIII.1997, coll. Z. KAPLAN
	99/115	C 1140	Czech Republic: Moravia: Distr. Nový Jičín: in the Nový rybník fishpond 1–1.5 km SSE of the Studénka town, 232 m a.s.l., 9.VII.1999, coll. Z. KAPLAN
<i>P. natans</i>	98/380	C 1028	Denmark: Distr. Sønderjylland: in the Uge Baek stream at the N margin of the Højstrup village (1 km SE of Bylderup-Bov), 19.VIII.1998, coll. Z. KAPLAN
	97/913	C 911	Czech Republic: Bohemia: Distr. Turnov: in a small fishpond at the WSW margin of Arnošovice settlement near the Žehrov village, 247 m a.s.l., 18.IX.1997, coll. Z. KAPLAN
<i>P. pectinatus</i>	96/21	C 133	Italy: Friuli-Venezia Giulia: Distr. Udine: in the Áusa River (and its tributaries) by Cervignano del Friuli, 17.IV.1996, coll. Z. KAPLAN
	98/127	C 981	Switzerland: Distr. St. Gallen: in a ditch with running water 200 m SSW of Altenrhein village (near Rorschach), 396 m a.s.l., 23.VI.1998, coll. Z. KAPLAN
<i>P. perfoliatus</i>	93/477	-	Russia: Siberia: Buryatia: Lake Baikal: in loose sedge stands in shallow SSW margins of the Chivyruiskii Gulf near E foot of the Svyatoi Nos Peninsula, 455 m a.s.l., 29.VII.1993, coll. Z. KAPLAN
	-	-	Russia: European part: Distr. Voronezh: in the Ul'yanovskoe Lake in Khoperskii Reserve 20 km NE of Novokhopersk, 23.IX.1982, coll. E. V. PECHENYUK (LE)
<i>P. bercholdii</i>	98/88	C 991	Switzerland: Distr. Bern: Interlaken: in a small pool on the E bank of the Thuner See (lake) W of the Unterseen town, 560 m a.s.l., 21.VI.1998, coll. Z. KAPLAN
	97/837	C 925	Czech Republic: Bohemia: Distr. Hradec Králové: forest ditch 2.8 km NE of the Vysoké Chvojno village, 269 m a.s.l., 4.IX.1997, coll. Z. KAPLAN

produced distinct phenotypes and in a few cases a single genotype was able to demonstrate almost the entire range of morphological variation in an observed trait known for that species. Several characters claimed in the literature to be suitable for distinguishing taxa were proven to be dependent on environmental conditions. The most striking and illustrative results of the cultivation experiments are described in detail.

### ***Potamogeton acutifolius***

An interesting population of a linear-leaved species of *Potamogeton* was found along a shore in heavily eutrophicated water of a forest fishpond near Hrobice, Czech Republic. Only vegetative material was available. The plants were morphologically uniform and showed vegetative characters often claimed in the literature (e.g. KAPP 1978, MARKGRAF 1981, CASPER & KRAUSCH 1980) for *P. compressus*: mucronate leaf tips and longer, wider (up to 4.1 mm) and darker leaves (Fig. 1a) than it is usual in *P. acutifolius*.

Samples from this population were collected for cultivation. In contrast to original conditions, the plants were planted in shallow water moderately supplied with nutrients and without any shading during the vegetation season. All samples came to flower and produced well-developed fertile fruits. The fertile material enabled unequivocal assignment of the plants to *P. acutifolius*: the leaves were acute at apex and comparatively short, extremely narrow (only 1.3–1.8 mm and with 10–12 additional sclerenchymatous strands when mature) and bright. Especially the 1-carpelled flowers in almost globose spikes on short peduncles are typical of this species (Fig. 1b). Plants cultivated in deeper mesotrophic water with low values of shading also corresponded to ordinary *P. acutifolius* in the width of their leaves.

Even though both *P. acutifolius* and *P. compressus* are well defined and distinct taxa and usually easily determinable when generative structures are available, a morphological overlap of vegetative characters may occur. Identification of such “intermediate” plants may be difficult. In any case, they cannot be simply considered to be a hybrid between the two species as was sometimes done in the past (e.g. FISCHER 1907, GRAEBNER 1907, HAGSTRÖM 1916, 1922, GLÜCK 1936).

### ***Potamogeton alpinus***

Obvious morphological variation of this species was noted by early taxonomists who distinguished varieties, subspecies or even separate species mainly on the development of submerged and/or floating leaves. Even OGDEN (1943, 1974), otherwise sceptical about the value of infraspecific units in most broad-leaved species, accepted three varieties within this species. Shape and size of submerged leaves and tendency to produce floating leaves served as main features for their identification.

A rich population of *P. alpinus* in an old detached river arm in Malšova Lhota, Czech Republic, was found growing in up to 1 m deep water above organic-rich sediment (sapropel) in the shade of alders and poplars on the backwater banks. All plants were  $\pm$  morphologically uniform. They had extremely well-developed submerged leaves (up to 21 cm  $\times$  22 mm) but did not produce floating leaves and inflorescences (Fig. 2a). Samples from this clone were cultivated in opposite environmental conditions: in shallow water and under full daylight. All plants changed their appearance. They formed relatively small submerged leaves (ca. 6 cm  $\times$  7 mm), and when the vertical shoots reached the water surface, floating leaves and peduncles



bearing spikes were produced freely (Fig. 2b). Plants cultivated in deeper water but still under full light conditions had leaves of intermediate size and produced both floating leaves and inflorescences when the upper part of shoots projected above the water.

### ***Potamogeton* × *fluitans* (= *P. lucens* × *P. natans*)**

A rich population of *P. nodosus*-like pondweed (Fig. 3a) was found in a shallow ditch with slowly running water in Fußach, Austria. These plants were accompanied by *P. natans* and *P. pectinatus*. However, the morphology of samples taken in cultivation changed considerably. It then became apparent that the grown plants cannot be *P. nodosus*, but are a *P. natans* hybrid. These originally broad- and coriaceous-leaved plants now had narrow membranous submerged leaves and the foliage of some vertical shoots was even confined to leaves almost reduced to phyllodes (Fig. 3b).

A study of stem anatomy confirmed that these plants are identical with *P. ×fluitans*. This hybrid between *P. natans* and *P. lucens* is morphologically often extremely similar to *P. nodosus* or other *P. natans* hybrids and sometimes even completely indistinguishable without additional anatomical data, especially when only fragmentary material (like e.g. incomplete herbarium specimens) is available (see also RAUNKIAER 1903, FISCHER 1904, 1905, 1907, HAGSTRÖM 1916, KAPLAN 2001).

### ***Potamogeton gramineus***

An amazingly rich macrophyte vegetation appeared in the newly constructed lowland water reservoir Rozkoš near Česká Skalice, Czech Republic, soon after its filling in 1973 (KRAHULEC et al. 1980, 1987, KRAHULEC & LEPŠ 1993, 1994). Besides the 11 taxa of *Potamogeton* identified there (KRAHULEC & KAPLAN 1995), several floating fragments of taxonomically unclear pondweed were collected. The plants were remarkable with narrow leaves and denticulate margins (Fig. 4a). Based on their morphological features, the plants were at first considered a hybrid between *P. crispus* and a linear-leaved species. After comparison with species diversity in the reservoir, the identification *P. ×lintonii* FRYER (= *P. crispus* × *P. friesii*) was proposed for this plant (NEVEČEŘAL & KRAHULEC 1994).

After 7 years during which the strange plant was missing there, it was refound and recollected by the present author in 1997. Besides herbarium specimens, enough material for cultivation was collected. The plentiful fresh material and especially the phenotypes developed in cultivation made new study and identification possible. The plants produced larger submerged leaves and then also floating coriaceous leaves like ordinary *P. gramineus* (Fig. 4b). Subsequent study of stem anatomy showed U-type endodermis and the presence of interlacunar bundles, which excluded the original hypothesis and confirmed the determination of the unusual plant as an extreme phenotype of *P. gramineus*.

### ***Potamogeton lucens***

This species is highly variable in the size and shape of its leaves. In particular two extreme morphotypes attract the attention of botanists (e.g. GALINIS 1963, SERGIEVSKAYA 1966, BUSIK 1979, MARKGRAF 1981, MÄEMETS 1984, KASHINA 1988): plants with remarkably elongated leaves (called “*longifolius*” or “*macrophyllus*”) and those with leaves reduced to phyllodes in

the upper part of vertical shoots (called “*cornutus*” or “*caudatus*”). Long-leaved plants were usually collected in running waters and the elongation may be a result of water current. This modification occurs in all pondweeds and one example in *P. natans* is also described below.

Plants of *P. lucens* with phyllodial leaves at the stem apices were studied in the original populations and collected for cultivation from water reservoirs near Česká Skalice and Studénka, Czech Republic. The samples originally growing in about 1 m deep mesotrophic water were cultivated under several environmental conditions, which differed in water depth, nutrient amount and light intensity, but none of the plants continued to form phyllodes in the upper part of the stem. This may explain why this morphotype is relatively scarce in nature. It is not clear whether all genotypes are able to produce this kind of reduced leaves, but it has been confirmed that a single genotype can develop either phenotypes with all upper leaves with broadly elliptical lamina, or with phyllodes mixed with fully developed leaves in the upper parts, or clonal colonies with some vertical shoots with laminar leaves only and other with mixed types of leaves.

### ***Potamogeton natans***

Some hybrids of *P. natans* may be sometimes difficult to distinguish from extreme phenotypes of this parental species. The extreme morphological variability of this species is one of the reasons. Interesting *P. natans*-like plants (Fig. 5a) were found in a fast-running stream near Hajstrup, Denmark. Leaves of these samples were extremely long in relation to their width and rather reminiscent of running-water forms of *P. nodosus* or *P. polygonifolius*. The discoloured section between the petiole and the lamina of floating leaves usually found in *P. natans* was indistinct in these plants. Some of the leaves were even intermediate in shape between floating leaves with developed lamina and submerged phyllodes, so that they resembled certain forms of *P. natans* hybrids, e.g. *P. ×schreberi* G. FISCH. (= *P. natans* × *P. nodosus*) or *P. ×gessnacensis* G. FISCH. (= *P. natans* × *P. polygonifolius*). However, in cultivation in standing water the plants easily reverted to the common shape of *P. natans* (Fig. 5b), and other typical features like the discoloured section at the junction of floating leaves were also apparent. No influence of other species has also been found in the study of the stem anatomy.

Typically, *P. natans* is found with abundant large, opaque, coriaceous floating leaves. One such plant from Žehrov, Czech Republic, is shown in Fig. 6a. However, plants with numerous submerged phyllodes rather than floating leaves are sometimes found. Even though these phenotypes with predominantly submerged phyllodial leaves are usually connected with early-season states or plants of rapidly flowing streams, they are not strictly confined to these conditions. On the contrary, they can be even obtained from the contrasting phenotypes as documented by the appearance of the plant from Žehrov that was collected in autumn from the clear mesotrophic water of a cultivation tank (Fig. 6b).

### ***Potamogeton pectinatus***

Many attempts to evaluate the extensive morphological variation and to distinguish infraspecific units in *P. pectinatus* have appeared in the literature. However, the relatively simple morphology of this species does not seem to provide enough features for an adequate morphology-based classification. Therefore most of these classifications rely on the length

and width of leaves, the shape of leaf apex, the length of internodes and the distance between whorls in a spike (e.g. GALINIS 1963, TOPA 1966, BUSIK 1979, CASPER & KRAUSCH 1980, MARKGRAF 1981, PIGNATTI 1982, MÄEMETS 1984, TZVELEV 1987, 1996, KASHINA 1988). Unfortunately, these characters have been proved to be dependent on environmental conditions as illustrated in the following examples.

An unbranched to only sparingly branched form of *P. pectinatus* with few but extremely broad linear leaves and expanded leaf sheaths was collected from fast-running water above a nutrient-rich bottom in Cervignano del Friuli, Italy (Fig. 7a). These plants entirely changed their appearance when they were cultivated in standing mesotrophic water as early as 2 months later (Fig. 7b). Then, new vertical shoots were heavily branched with the main foliage concentrated at the upper part of the shoots near the water surface and even at the base both the leaves and leaf sheaths were significantly narrower than in the original plants.

A similar conversion was observed in plants from a ditch with running water near Altenrhein, Switzerland (Fig. 8a). Among obvious changes in most of the vegetative traits (leaf shape, length, width and colour, branching pattern, etc.) in cultivation, important alterations in spike features were also noted (Fig. 8b). Plants with up to 6 whorls of fruits in a relatively contiguous spike produced in the new environment inflorescences with only 3–4 fruit whorls in a markedly remote spike.

### ***Potamogeton perfoliatus***

This species is described in all taxonomic treatments as a species with submerged membranous leaves that never produces floating thickened leaves. If the upper parts of vertical shoots reach the water surface they bend and form a canopy just below the surface. When in flower, the peduncles project above water while the leaves remain submerged.

During research at wetlands in Lake Baikal an extremely distinctive plant was found in a population of *P. perfoliatus* (Fig. 9a). This plant had small (10–15 × 3–5 mm), opaque, (sub)coriaceous leaves with a cuneate base, in contrast to the larger, translucent, membranous leaves of this species. However, no trace of influence of hybridization with other species or of disease was found. The short shoot of this plant grew or rather only survived lying on wet mosses in a loose sedge stand, stranded after the receding of the water level. The plant was very probably only an extremely strange ecomorphosis of one of the shoots of the ordinary plants of *P. perfoliatus* that grew in plenty in the area (Fig. 9b).

Evidence that this phenotype is only a modification of typical *P. perfoliatus* has been recently found in the herbarium LE. Another specimen with upper coriaceous floating upper leaves were collected in European Russia (Fig. 10a). According to the text on the herbarium label, the plants were again collected in unusually shallow water (0.1–0.2 m deep). In this case, submerged parts of shoots with many leaves are also preserved (Fig. 10b). The typical shape of leaves of *P. perfoliatus* with an amplexicaul base confirmed the previous observation from Lake Baikal that this species is, as an extremely rare event and perhaps only under specific conditions, able to produce such an anomalous ecomorphosis. This capacity may also be restricted to certain genotypes only.

The capacity of this species to produce terrestrial forms has not been recorded until now. The rare occurrence of terrestrial forms in otherwise strictly aquatic plants has also been noted for other species, e.g. *Callitriche truncata* subsp. *occidentalis* (ROUY) BRAUN-BLANQ.

(LANSDOWN 1999). It was also reported for *Myriophyllum alterniflorum* DC. (COX 1997) but the terrestrial forms of this species are not rare in Great Britain (PRESTON & CROFT 1997).

### ***Potamogeton pusillus* and *P. berchtoldii***

Samples from 22 populations of *P. pusillus* agg. have been subjected to study. In the field, the samples from different sites often differed considerably from each other in characters such as general appearance, branching pattern, width and colour of leaves, details of venation, shape of leaf apex, etc. However, most of this variation is environmentally induced. Most dissimilar clones from different localities did not maintain their differences when grown together under the same environmental conditions.

The plants are able to change their phenotypes significantly and often also very rapidly when transplanted into different environments. Broad-leaved and almost unbranched plants of *P. berchtoldii* (Fig. 11a) were collected in a small shady pool by Unterseen, Switzerland in June. These plants were taken for cultivation in a sunny shallow tank. The plants soon rooted and continued to grow. They produced many heavily branched renewal shoots with short internodes and narrow leaves as early as 6 weeks later (Fig. 11b). The resulting general appearance was totally different from the original one. This observation corresponds with the general tendency of plants to have usually fewer but longer branches in the shade than in the sun (SCHMID 1992).

Even though *P. berchtoldii* does not develop true floating leaves, it rarely has the uppermost leaves with the lamina floating on the water surface, sessile, linear-oblongate, almost subcoriaceous, with broad rows of lacunae bordering the midrib (WIEGLEB & KAPLAN 1998). Such plants are occasionally found in eutrophic or dystrophic waters and the floating leaves probably improve gas income. This phenotype was found also near Vysoké Chvojno, Czech Republic, where it grew in a eutrophic forest ditch (Fig. 12a). The plants failed to produce fruit there. When samples of this modification were cultivated in sunny mesotrophic water they stopped forming floating leaves and produced fruit freely, having the general appearance and all the characters of normal *P. berchtoldii* (Fig. 12b).

## **DISCUSSION**

The basic principle in contemporary taxonomy is that only genetically fixed variation should be used for formal classification. However, in the absence of experimental cultivation it is often impossible to distinguish between genetically fixed variations and environmental modifications. Much of the phenotypic variation encountered by the taxonomist is the result of the plastic response of the individual to factors of the environment. Such phenotypic plasticity has tended to be underestimated in taxonomic and evolutionary work on plants (DAVIS & HEYWOOD 1963). In many taxonomic works dealing with morphological variation in *Potamogeton* no distinction has been made between plastic and genetic variations.

Phenotypic plasticity in plants (and in water plants in particular) is a well-described phenomenon (e.g. ALLSOPP 1965, BRADSHAW 1965, SCHMID 1992) but its extent in *Potamogeton* was found to be surprising. In most samples studied, a high degree of phenotypic plasticity has been revealed. Morphological differences among distinct populations of a single species observed in the field mostly disappeared when these were grown together under the same environmental conditions. Sometimes they showed intergradations but only in a few

instances persisted. On the other hand, clonal material cultivated under different values of environmental factors often produced very distinct phenotypes. In a few cases a single genotype cultivated in two contrasting conditions produced almost the entire range of morphological variation in an observed trait known for that species. The range of leaf width of *P. acutifolius* in studied herbaria was found to be 1.8–3.8(–5.5) mm by WIEGLEB & KAPLAN (1998). The leaf width of this species from the locality Hrobice changed from up to 4.1 mm, when grown in eutrophic half-shaded water, to 1.3–1.8 mm, when cultivated in shallow, slightly mesotrophic water under full daylight conditions. Also the great range of change in the size of the floating leaves of *P. natans* from the locality Žehrov covers an important part of the species' variation range of this character. Thus even though genetic differences coding leaf size in these species may occur, they cannot be directly observed in the field because they are hidden behind plastic variation.

Extreme phenotypes of some *Potamogeton* taxa may morphologically be (almost) indistinguishable from their relatives or even totally unrelated species or hybrids. It has been shown that *P. natans* hybrids may be easily overlooked as *P. nodosus* while a bizarre extreme phenotype of *P. gramineus* may imitate *P. ×lintonii* (= *P. crispus* × *P. friesii*). This phenomenon was observed in a number of other taxa (SCHMID 1992). Thus phenocopies of high-altitude ecotypes can for example easily be produced in *Carex flava* L. If individuals of the typical lowland var. *flava* are transplanted to high altitude they acquire the same phenotype as individuals of the high-altitude var. *alpina* KNEUCKER (SCHMID 1983).

Several studies interpreting small morphological differences among specimens of *Potamogeton* in terms of formal taxonomy have appeared recently. CHEN (1987) described 6 new *P. pectinatus*-like species from material collected in a single Chinese lake during a 3-day excursion. He based these descriptions on minute or insignificant differences in vegetative and generative morphology, e.g. shape of leaf apex, branching pattern, size of whole plants, and length of peduncles. Each of these "species" is documented only by its type collection. TZVELEV (1996, 2000b) divided *P. pectinatus* in the territory of NW European Russia into 3 species (*P. marinus* L., *P. pectinatus* s. str. and *P. zosteraceus* FR.), corresponding to 3 varieties distinguished in the European literature in the past (*P. pectinatus* vars. *scoparius* WALLR., *pectinatus* and *zosteraceus* (FR.) CASP.). Essentially, these are based on a single character, leaf width (the measurements 0.2–0.4 mm, 0.4–0.8 mm, and 0.6–2.7 mm, respectively, are given), because other mentioned features (leaf length and vein number) are directly derived from or highly correlated with the leaf width. PAPCHENKOV (1997) split *P. gramineus* into 6 species, among which he included phenotypes described in the past under names *P. graminifolius* (FR.) FRYER or *P. heterophyllus* SCHREB. His "species" are based on the development of floating leaves, general shape and number of submerged leaves, shape of leaf apex, branching extent, internode length, and number, shape and length of peduncles. Intermediates between these (at least partly) ecomorphoses were also observed but they were described as hybrids. In fact, these ultimate forms grade so insensibly into each other that lines can scarcely be drawn. In many cases a specimen cannot be identified as belonging to one or the other. In my view, the holotype of *P. ×biformoides* PAPCH. studied at LE falls within variation range of *P. gramineus*. My investigation of stem anatomy of *P. ×mariensis* PAPCH. proposed with parentage *P. biformis* [= *P. gramineus*] × *P. nodosus* did not prove any influence of the latter species. Anatomical characters of type specimen (U-type endodermis,

interlacunar bundles present in 2 circles, subepidermal bundles present) are in conflict with those of *P. nodosus* (O-type endodermis, interlacunar bundles absent, only rarely a few individual ones present, subepidermal bundles absent).

Most if not all morphological characters used in these papers for distinguishing taxa were in the present study proved to be dependent on environmental conditions and thus are highly unreliable markers for the delimitation of taxa. None of these studies paid attention to the stability of morphological distinctness over a range of environmental conditions. The true distinctness of the claimed "species" was not confirmed by experimental work or study of biological characters. Plant taxonomy is vulnerable to errors when modifications of a species are erroneously named as distinct taxa (cf. MEYER 1987, PIGLIUCCI et al. 1991, SULTAN 1995). This would result in mere classification of phenotypes. And these observations are even more significant in water plants with their great proportion of phenotypic plasticity. In the British Isles, SIMPSON (1988) found that the wide range of morphological variation of two species of *Elodea*, a feature that has caused many problems of identification, is entirely due to phenotypic plasticity. The problem is more serious when morphological delimitation of such "new taxa" relies on herbarium observations only. In such cases it is often simply impossible to speak about any genetic differences between taxa.

Variability of vegetative structures of *P. pectinatus* was recently studied by van Wijk. First, he (VAN WIJK 1988) described and provided a photograph of a specimen collected in the Baltic by Byviken, SW Finland. It was shown that even within one single plant very different leaves may occur, representing both the *pectinatus*-form and the *zosteraceus*-form of leaves. Later (VAN WIJK 1989) he noted a rapid change of appearance of vegetative parts of newly developed shoots growing from detached apical parts. Densely branched brush-shaped shoots of the *scoparius*-form gave rise to new simply branched shoots of the *pectinatus*-form with prolonged internodes and wider leaves. Results of the present study are in agreement with the observations of van Wijk and clearly confirm that morphological characters alone are highly unsuitable for distinguishing taxa within this species.

It is possible that species like *P. gramineus* as currently understood comprise several distinct evolutionary lineages. *P. pectinatus* with its high variation of chromosome number on aneuploid levels (KALKMAN & VAN WIJK 1984) may be an example of this. However, their existence is highly unlikely to be revealed on a solely morphological basis since they are poorly or not at all distinguished by their morphology. In contrast, each species in the concept adopted e.g. by PRESTON (1995) or WIEGLEB & KAPLAN (1998) is definable by a specific variation pattern. And even if these evolutionary species were identified in studies of natural history of live plants, their acceptance in formal taxonomy is questionable since it is not advisable to distinguish evolutionary species that cannot be determined with morphological features in most of their phenotypes.

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Fig. 1. *Potamogeton acutifolius* from Hrobice, Czech Republic; a -- specimen KAPLAN 96/623 collected in the field, b -- specimen KAPLAN C 321, genetically identical material from cultivation; scale bars = 2 cm.



Fig. 2. *Potamogeton alpinus* from Malšova Lhota, Czech Republic; a – specimen KAPLAN 96/681 collected in the field, b – specimen KAPLAN C 338 from cultivation; scale bars = 5 cm.



Fig. 3. *Potamogeton xfluitans* from Fußsach, Austria; a – specimen KAPLAN 98/129 with submerged leaves from cultivation; scale bars = 5 cm. b – specimen KAPLAN C 983 with floating leaves collected in the field.



Fig. 4. *Potamogeton gramineus* from Česká Skalice, Czech Republic; a – specimen KAPLAN 97/831 collected in the field, b – specimen KAPLAN C 887 from cultivation; scale bars = 5 cm.

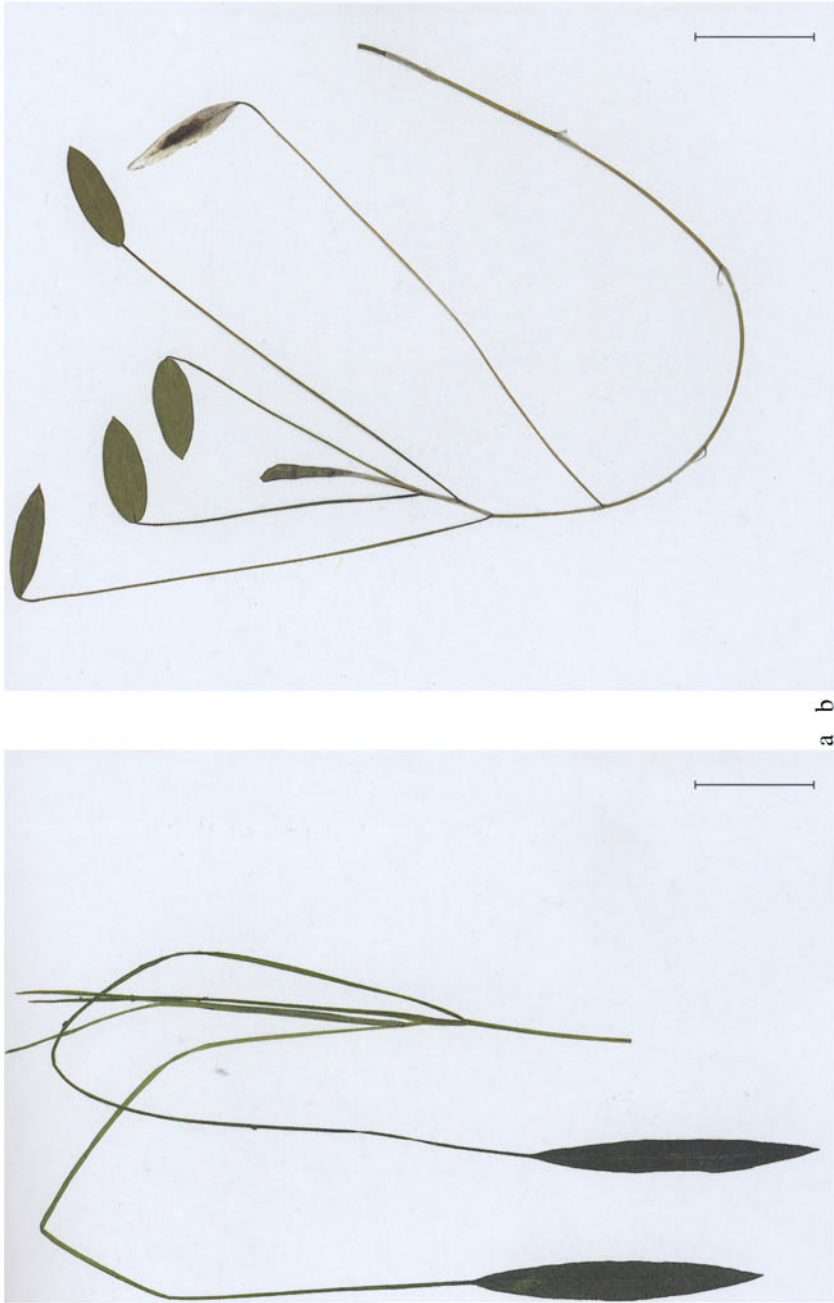


Fig. 5. *Potamogeton natans* from Hajstrup, Denmark; a – specimen KAPLAN 98/380 collected in the field, b – specimen KAPLAN C 1028 from cultivation; scale bars = 5 cm.



Fig. 6. *Potamogeton natans* from Žehrov, Czech Republic; a – specimen KAPLAN 97/913 collected in the field, b – specimen KAPLAN C 911 from cultivation; scale bars = 5 cm.





Fig. 7. *Potamogeton pectinatus* from Cervignano del Friuli, Italy; a – specimen KAPLAN 96/21 collected in the field, b – specimen KAPLAN C 133 from cultivation; scale bars = 5 cm.



Fig. 8. *Potamogeton pectinatus* from Altenrhein, Switzerland; a – specimen KAPLAN 98/127 collected in the field, b – specimen KAPLAN C 981 from cultivation; scale bars = 5 cm.



Fig. 9. *Potamogeton perfoliatus*; a, b – specimens KAPLAN 93/477 from Lake Baikal, Russia, collected in the field; scale bars = 2 cm.



Fig. 10. *Potamogeton perfoliatus*; a, b – specimens PECHENYUK s. n. from Khoperskii Reserve, Russia, collected in the field; scale bars = 2 cm.

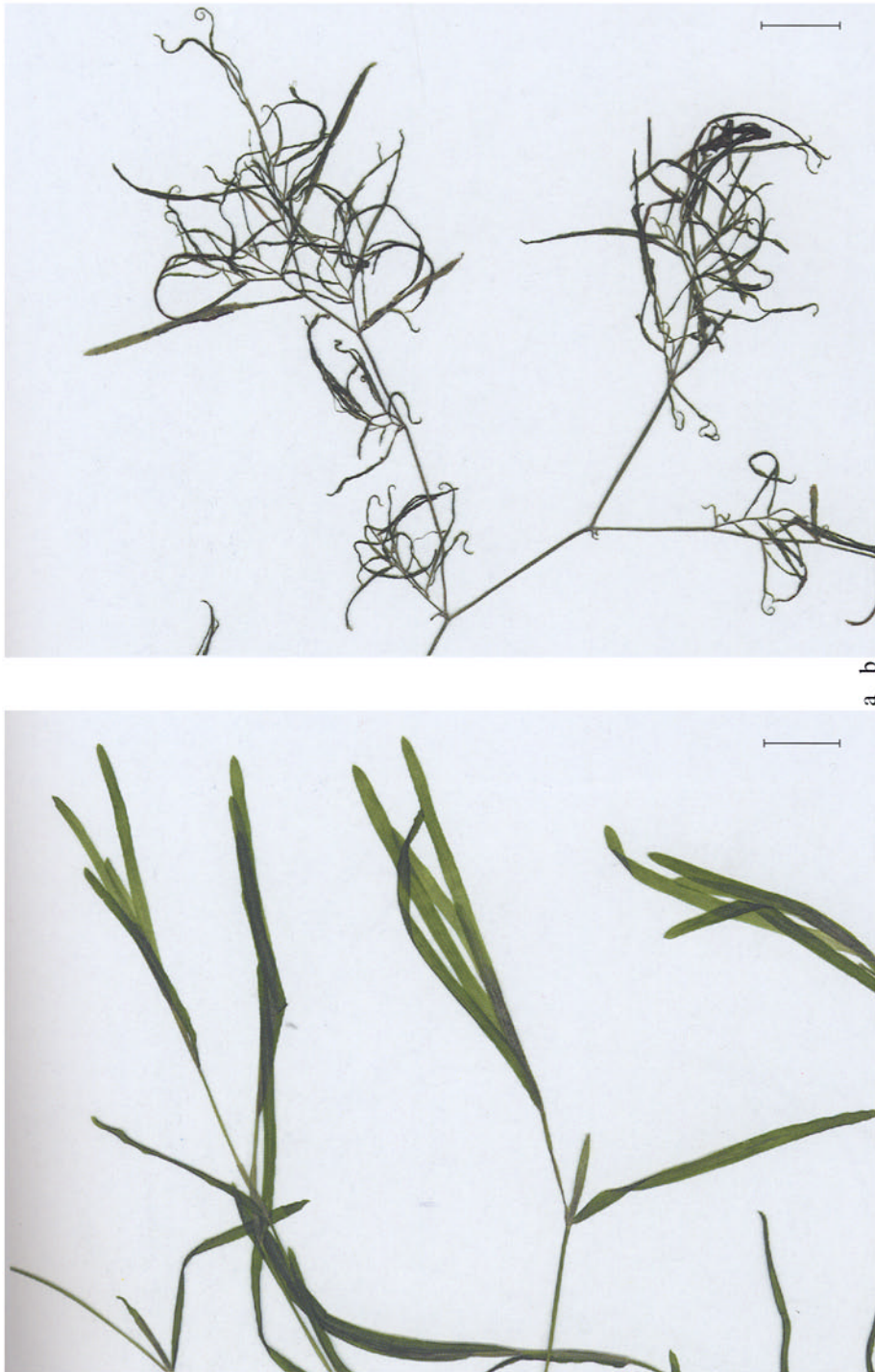


Fig. 11. *Potamogeton bertholdii* from Unterseen, Switzerland; a – specimen KAPLAN 98/88 collected in the field, b – specimen KAPLAN C 991 from cultivation, scale bars = 1 cm.

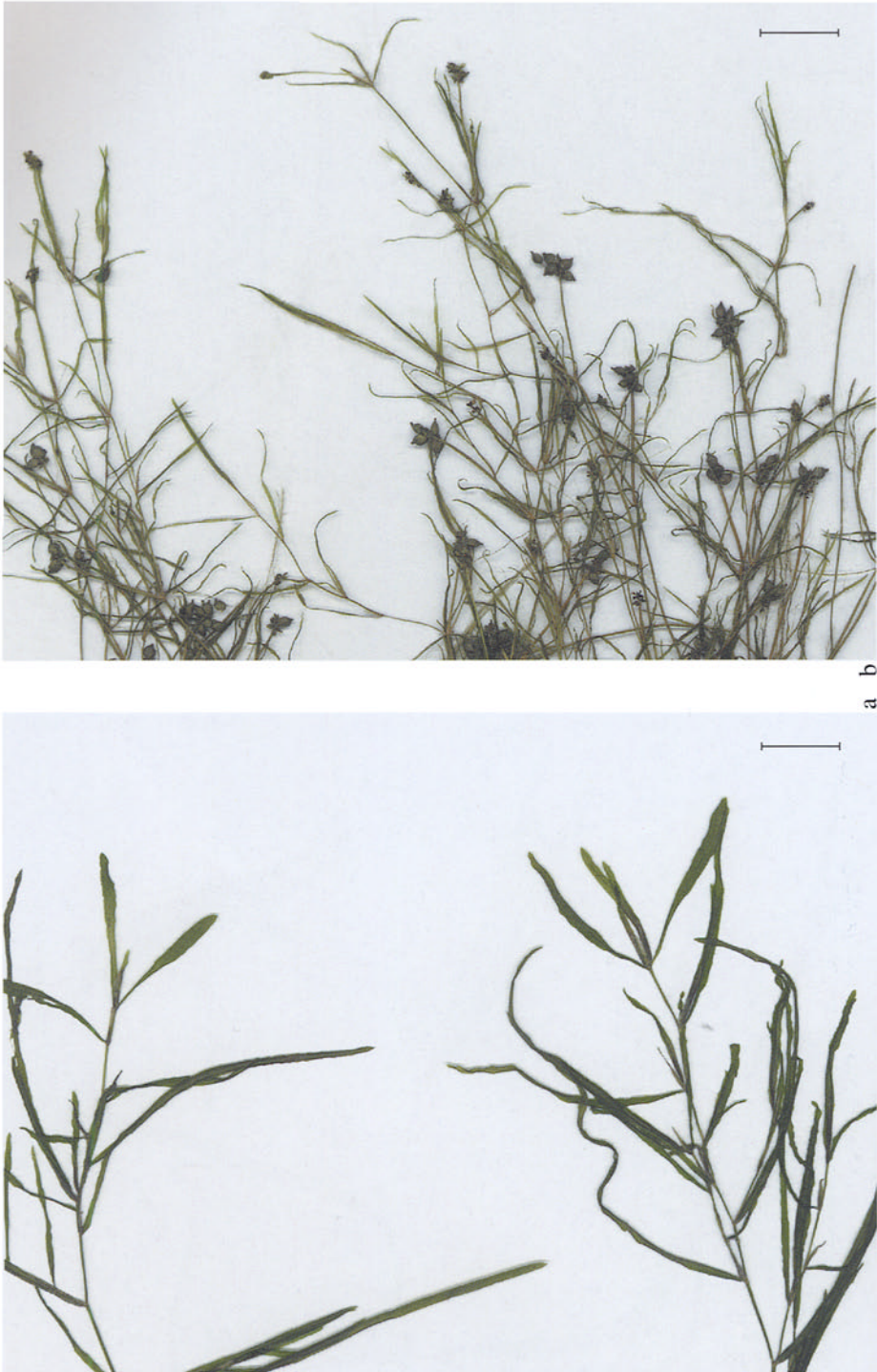


Fig. 12. *Potamogeton bertholdii* from Vysoké Chvojno, Czech Republic; a – specimen KAPLAN 97/837 collected in the field, b – specimen KAPLAN C 925 from cultivation; scale bars = 1 cm.