Perspectives in Plant Ecology, Evolution and Systematics 44 (2020) 125520

Contents lists available at ScienceDirect

Perspectives in Plant Ecology, Evolution and Systematics

journal homepage: www.elsevier.com/locate/ppees

Review

Biological flora of Central Europe: *Utricularia intermedia* Hayne, *U. ochroleuca* R.W. Hartm., *U. stygia* Thor and *U. bremii* Heer *ex* Kölliker

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ARTICLE INFO

Keywords:
Aquatic carnivorous plants
European distribution
Critically endangered species
Ecophysiological traits
Ecological requirements
Overwintering
Conservation

ABSTRACT

Utricularia intermedia Hayne, *U. ochroleuca* R.W. Hartm., *U. stygia* Thor and *U. bremii* Heer *ex* Kölliker (Lentibulariaceae, Lamiales) are the four rarest and critically endangered European *Utricularia* (bladderwort) species from the generic section *Utricularia*. They are aquatic, submerged or amphibious carnivorous plants with suction traps which grow in very shallow, standing dystrophic (humic) waters such as pools in peat bogs and fens (also pools after peat or fen extraction), shores of peaty lakes and fishponds; *U. bremii* also grows in pools in old shallow sand-pits. These *Utricularia* species with boreal circumpolar distribution (except for *U. bremii*) are still commonly growing in northern parts of Europe (Scandinavia, Karelia) but their recent distribution in Central Europe is scarce to very rare following a marked population decline over the last 120 years. All species have very thin linear shoots with short narrow to filamentous leaves bearing carnivorous traps (bladders, utricles) 1 − 5 mm large. The first three species form distinctly dimorphic shoots differentiated into pale carnivorous ones bearing most or all traps, and green photosynthetic shoots with only a few (or without) traps, while the last species usually forms non-differentiated (monomorphic) or slightly differentiated shoots. The plants exhibit a marked physiological polarity along their linear shoots with rapid apical shoot growth. Their very high relative growth rate is in harmony with the record-high net photosynthetic rate of their photosynthetic shoots. Flowering of these species is common under favourable conditions and is stimulated by high temperatures but only *U. intermedia* sets seeds; the other species are sterile due to pollen malformation. Some molecular-taxonomic studies indicate that *U. ochroleuca* and *U. stygia* might be hybrids between *U. intermedia* and *U. minor*. All species propagate mainly vegetatively by regular branching and reach high relative growth rates under favourable conditions. All species form spherical dormant winter buds (turions). Suction traps actively form negative pressures of ca. -0.22 to -0.25 bar. The traps are physiologically very active organs with intensive metabolism: as a result of the presence of abundant glands inside the traps, which secrete digestive enzymes and absorb nutrients from captured prey carcasses (quadrifid glands) or take part in pumping water out of the traps and producing negative pressure (bifid glands), their aerobic respiration rate is ca. 2–3 times higher (per unit biomass) than that of leaves. Although oxygen concentrations inside reset traps are (almost) zero, traps are inhabited by many microscopic organisms (bacteria, euglens, algae, ciliates, rotifers, fungi). These commensal communities create a functional food web and in traps with captured macroscopic prey, they act as digestive mutualists and facilite prey digestion. Traps secrete a great amount of organic substances (sugars, organic acids, aminoacids) to support these commensals (‘gardening’). Yet the nutritional role of commensals in prey-free traps is still unclear. Quadrifid glands can also serve in the reliable determination of three species. Ecological requirements of *U. intermedia*, *U. ochroleuca* and *U. stygia* are very similar and include very shallow dystrophic waters (0 − 30 cm deep) with highly variable levels of dystrophy, common mild water level fluctuations, oligo-mesotrophic to slighly eutrophic waters, optimal pH values from 5.5 to 7.0 but always high free-CO_2 concentrations of 0.8–1.5 mM. Limited data indicate that *U. bremii* is partly a stenotopic species preferring only slightly acidic to neutral (pH 6–7), very soft to slightly hard, oligo-mesotrophic waters. Yet it can grow well both in strongly dystrophic and clear waters, in peat bogs as well as sand-pits over peaty soil and clayish sand. Long-term, very low water levels in combination with habitat eutrophication, whatever the reason, leading to peat bog and fen infilling, are the most common and unfavourable ecological threads at the most sites of the four rare *Utricularia* species. However, ecological consequences of high-water level at the sites can be ambiguous for the populations: it reduces the strongly competitive cyperoid and graminoid species but can speed up site eutrophication. All four species are considered (critically) threatened in European countries and are usually under official species protection or their sites are protected. Regeneration of infilled fens or peat bogs and creation of

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https://doi.org/10.1016/j.ppees.2020.125520
Received 24 June 2019; Received in revised form 31 January 2020; Accepted 5 February 2020

shallow fen pools and canals in these mires, combined with (re)-introductions of these species have shown to be a very successful and efficient measure to protect the natural populations for many decades. Old shallow sand-pit pools have become outstanding substitution habitats for the protection of *U. bremii*.

1. Introduction

Utricularia intermedia Hayne, *U. ochroleuca* R.W. Hartm., *U. stygia* Thor and *U. bremii* Heer *ex* Kölliker (Lentibulariaceae, Lamiales) are the four rarest and most critically endangered European *Utricularia* (bladderwort) species (Casper, 1974; Thor, 1988; Taylor, 1989; Kleinsteuber, 1996; Wildermuth, 2010; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018a, Astuti and Peruzzi, 2018b, 2019). They are rootless aquatic or amphibious (subterrestrial) carnivorous plants freely floating just below the water surface or attached to the bottom sediments in very shallow, standing dystrophic (humic) waters. They all can also grow permanently on wet substrates in the terrestrial ecophase. They grow in pools or depressions in peat bogs and fens (also pools after peat or fen extraction), shores (littorals) of peaty lakes and fishponds, and *U. bremii* also grows in pools in old shallow sand-pits. All four species grow in the temperate to subarctic zone of the northern hemisphere (Taylor, 1989; Kleinsteuber, 1996): *Utricularia intermedia* (UI), *U. ochroleuca* (UO) and *U. stygia* (US) cover a vast territory of Europe, Asia and North America, but *U. bremii* (UB) is strictly a European species.

All species have very thin linear shoots with short filamentous leaves bearing carnivorous traps (bladders, utricles) 1 − 5 mm large (Thor, 1988; Taylor, 1989; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018a). The first three species strongly resemble each other and form distinctly dimorphic shoots, differentiated into pale carnivorous ones bearing most or all traps, and green photosynthetic shoots with only a few (or without) traps (Figs. 1–3). The last species usually forms non-differentiated (monomorphic) or slightly differentiated shoots (Fig. 4). Due to the great similarity between UI, UO and US, these species have commonly been misidentified and the same applies for distinguishing of UB from the very similar *U. minor* (Thor, 1988; Taylor, 1989; Kleinsteuber, 1996). Moreover, US was constituted and distinguished from *U. ochroleuca s. lato* (UOs.l.) as a separate species as late as in 1988 (Thor, 1988). However, the differentiation of UOs.l. in UO and US became common in many studies only after the next 10–20 years (e.g., Adamec and Lev, 2002). All four species exhibit a marked physiological polarity along their linear shoots with rapid apical shoot growth (Adamec, 2007a, Adamec, 2010a). All species propagate mainly vegetatively by branching and reach high relative growth rates under favourable conditions (Adamec, 2010a, Adamec, 2011a, Adamec, 2018a). Flowering of these species is common and is stimulated by high temperatures but only *U. intermedia* sets seeds; the other species are sterile due to pollen malformation (Casper and Manitz, 1975; Thor, 1988; Taylor, 1989; Kleinsteuber, 1996; Wildermuth, 2010; Beretta et al., 2014; Fleischmann and Schlauer, 2014). In autumn, all species form spherical dormant winter buds (turions) as overwintering storage organs, which are dragged down to the bottom by decaying shoots (Diels, 1906; Sculthorpe, 1967; Casper, 1974; Adamec, 2008a; Adamec, 2018a; Adamec, 2018c).

Suction traps of all four (and all European) species are hollow bladders 1 − 5 mm long, they actively form a negative pressure of ca. -0.22 to -0.25 bar and their opening and closing ('firing'), like in other *Utricularia* species, takes only 3 − 5 ms, which represents the most rapid vital movement in the plant kingdom (Sasago and Sibaoka, 1985; Adamec, 2011b, Adamec, 2011c, 2018; Vincent et al., 2011; Adamec and Poppinga, 2016; Poppinga et al., 2016, 2018; Westermeier et al., 2017). The prey consists of small aquatic organisms - mostly zooplankton (Harms, 1999; Peroutka et al., 2008). Generally, *Utricularia* traps are physiologically very active organs with intensive metabolism. Thanks to the presence of abundant glands inside the traps, which secrete digestive enzymes and absorb nutrients from captured prey carcasses (quadrifid glands) or take part in pumping water out of the traps and producing the negative pressure (bifid glands), their aerobic respiration rate is ca. 2–3 times higher (per unit biomass) than that of the leaves (Sasago and Sibaoka, 1985; Adamec, 2006, Adamec, 2007b, Adamec, 2018a, Adamec, 2018b). Although oxygen concentration in the fluid inside reset (resting) *Utricularia* traps is (almost) zero (Adamec, 2007b) traps are permanently inhabited by many microscopic organisms (bacteria, euglens, algae, ciliates, rotifers, fungi) which propagate in the fluid (e.g., Peroutka et al., 2008; Sirová et al., 2018a, Sirová et al., 2018b). These facultatively anaerobic commensal communities create a functional food web (Sirová et al., 2009) and in traps with captured macroscopic prey, they act as digestive mutualists and facilite prey digestion (Adamec, 2018a, Adamec, 2018b; Sirová et al., 2018a, Sirová et al., 2018b). In addition, traps secrete a significant quantity of organic substances (sugars, organic acids, aminoacids) to support these commensals ('gardening'; Sirová et al., 2010, 2011; Borovec et al., 2012). Yet the nutritional role of commensals in prey-free traps is still ambiguous and unclear (cf. Adamec, 2018a, Adamec, 2018b; Sirová et al., 2018a, Sirová et al., 2018b).

Out of the four *Utricularia* species, ecological habitat factors including water and/or sediment chemistry, phytosociological characteristics and ecological requirements have been described more or less thoroughly at dozens of Central European sites (Poland, Czech Republic, Germany) only for UI, UO and US (or UOs.l.), while these data have been almost lacking for UB due to its rarity. From these numerous studies, UI, UO and US usually grow in very shallow and strongly dystrophic, brownish waters with organic sediment in peat bogs and fens at low pH values ranging between 4.1–7.5 (median ca. 5.5–6) and with low to medium concentrations of mineral N (NH_4^+) and P (soluble phosphate). Oxygen concentration in these waters is usually reduced while that of free CO_2 is very high (Melzer, 1976; Pietsch, 1977; Dierssen and Dierssen, 1984; Schäfer-Guignier, 1994; Hofmann, 2001; Adamec and Lev, 2002; Kosiba, 2004; Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b; Adamec, 2007a, Adamec, 2010a, Adamec, 2010b).

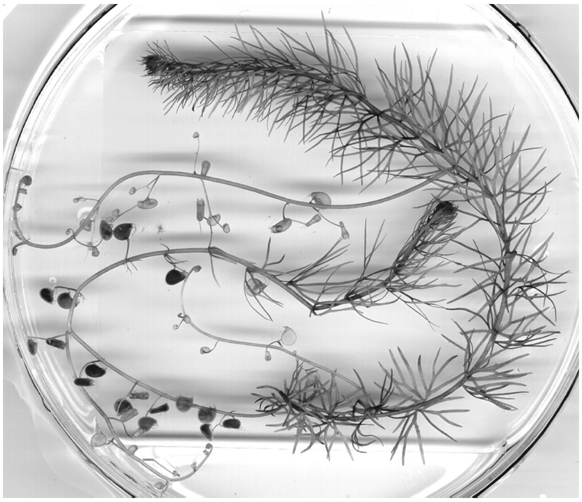

Fig. 1. Branched submerged photosynthetic shoot with three carnivorous shoots with traps of *Utricularia intermedia* raised in outdoor culture. The plants originated from the Třeboň Basin, South Bohemia, Czech Rep. In the middle of the image, the carnivorous shoot passes to a young photosynthetic one. Dark humic acids were aspirated in several traps. Diameter of the Petri dish 12 cm.

Fig. 2. Branched submerged shoots of *Utricularia ochroleuca* raised in outdoor culture; length of the dish 10.5 cm. The plants originated from the Třeboň Basin, South Bohemia, Czech Rep.

Fig. 3. Robust submerged shoots of introduced *Utricularia stygia* population from a fen pool at Karštejn, Třeboň Basin, S Bohemia, Czech Republic, 1 July 2016. Shoot bases and several traps are covered by precipitated humic acids with iron; length of the dish 10.5 cm.

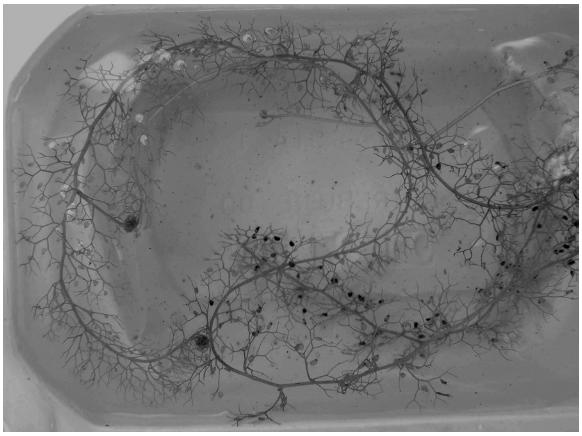

Fig. 4. Robust, strongly branched submerged shoots of introduced *Utricularia bremii* population from a shallow pool in a sand-pit near Suchdol nad Lužnicí, Třeboň Basin, S Bohemia, Czech Republic, 2 July 2016. The plants originated from a sand-pit at Munice, South Bohemia, Czech Rep. Dark traps were pigmented; width of the dish 6.5 cm.

About 240 species of the *Utricularia* L. genus have recently been recognized worldwide and around 60 species are aquatic or distinctly amphibious; others are terrestrial or epiphytic (Guisande et al., 2007; Adamec, 2018a; Jobson et al., 2018; Silva et al., 2018). The boundary between aquatic and terrestrial or epiphytic species is rather unclear as the majority of *Utricularia* species worldwide could be considered at least partly amphibious (see Taylor, 1989). Out of the 60 aquatic or distinctly amphibious species, the majority (ca. 39) are from the subgenus *Utricularia* L. and the generic section *Utricularia* L. (Jobson et al., 2018), to which the four rarest European species – UI, UO, US and UB – also belong. Although the special literature on the various branches of *Utricularia* biology (also including aquatic species) is very numerous (for the review, see Lloyd, 1942; Juniper et al., 1989; Taylor, 1989; Hofmann, 2001; Adamec, 2018a, Adamec, 2018b; Jobson et al., 2018), at least one of the four species has been infrequently studied or mentioned. Therefore, the literature including at least some of these four species is rather scarce and very scattered and fragmented in terms of subjects, geography, journals and languages. Very commonly, these publications have been published in national languages in local journals or issues and are not commonly available. Moreover, the older literature did not differentiate between UO and US.

During the last ca. 15 years, the strongly-elevated interest in studying all aspects of the biology of *Utricularia* species – from functional ecology, ecophysiology, trap physiology and biophysics to molecular taxonomy, evolution, genomics and transcriptomics – has resulted in the publishing of many original studies that have revolutionarily changed the classic views on these aspects. These aspects have recently been reviewed in several papers (Poppinga et al., 2016, 2018; Westermeier et al., 2017; Adamec, 2018a, Adamec, 2018b, Adamec, 2018c; Jobson et al., 2018; Silva et al., 2018; Sirová et al., 2018a, Sirová et al., 2018b), in which also some of the four rare species are included.

In this review, due to the scarcity of data focused only on some of the four rare species, I shall also cite the more general literature to characterize the more general ecophysiological traits (e.g., trap or turion ecophysiology, photosynthetic traits) for *all* aquatic *Utricularia* species, while species-specific traits related to the four species (e.g., distribution, ecology, phylogeny) shall be characterized only using exact literature items on these species. The aim of the present paper is to review all biological characteristics of the four rarest European *Utricularia* species – UI, UO, US and UB – with an emphasis on Central European populations, species determination, ecophysiological characteristics and ecological requirements. For this review, I have also utilized many unpublished pieces of information on the four species based on their cultivation in the collection of aquatic carnivorous plants in the Institute of Botany CAS at Třeboň for 20–30 years and on regularly visiting many sites of them in the Třeboň Basin Biosphere Reserve, South Bohemia, Czech Republic, over 30 years. Unpublished data are thus also included.

2. Morphology and taxonomy

2.1. Vegetative and flower morphology

The four rare *Utricularia* species are perennial, rootless, free-floating or weakly affixed (attached, anchored) submerged or amphibious, subterrestrial aquatic plants with thin linear shoots (Thor, 1988; Taylor, 1989; Kleinsteuber, 1996; Adamec, 2007a; Wildermuth, 2010; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018b). The poorly branched, thin stems with a highly modular structure bear regular successive leaf nodes with short filamentous or narrow leaves, which can bear carnivorous traps. Astuti and Peruzzi, 2018a have subdivided all seven Central European *Utricularia* species into three morphological aggregates: the *U. intermedia* aggregate comprises UI, UO and US, while the *U. minor* one includes also UB. The three species of the *U. intermedia* aggregate produce distinctly dimorphic (heterogenous) shoots differentiated in pale, whitish or greenish and fragile carnivorous ones bearing most or all of the traps, and green to dark red and firmer photosynthetic shoots with only a minor fraction of (or without) traps (Figs. 1–3). For simplicity, this functional terminology (“carnivorous “and “photosynthetic“) shall be used throughout this paper. In contrast, UB usually forms non-differentiated (monomorphic) or slightly differentiated shoots (Fig. 4).

2.1.1. *U. intermedia*

Adult submerged plants growing in deeper water are up to 30–40 (50) cm long, while adult terrestrial ones growing on drying soils can be only 5 – 10 cm long (Fig. 5). The photosynthetic shoots of adult plants are usually 6 – 24 cm long (Fig. 1; Table 1; Thor, 1988; Taylor, 1989; Adamec, 2007a, Adamec, 2010a) and grow mostly horizontally either in shallow water or terrestrially on the surface of the wet substrate. On average, 48 leaf nodes (range 37–53) occur on one photosynthetic shoot (Adamec, 2010a). Both photosynthetic and carnivorous shoots were found to initiate branches regularly (Table 1; Adamec, 2007a, Adamec, 2010a, Adamec, 2018a): the mean number of internodes between two successive branches (as 'branching rate') on the main photosynthetic shoots was 16.8 ± 0.4 and 17.7 ± 0.4 in two different studies and differed markedly from that of carnivorous shoots (5.9 ± 0.1). Carnivorous shoots of adult plants are usually 5 – 12 cm long (range 0.3–17.6 cm; Table 1). They grow mainly in the oblique position at an angle of around 70–75 degrees downwards to the sediment and, thus, similar to UO and US, they could penetrate about 7.5–13.5 cm into loose anoxic sediments (Adamec, 2007a). At three natural sites in the Czech Republic at the peak of the growing season, adult plants comprised on average 3.2 ± 0.2 (range 2–6) photosynthetic and 3.5 ± 0.2 (range 2–6) carnivorous shoots (Adamec, 2010a). The boundary between both types of shoots is usually distinct and is mostly separated by a branch. Carnivorous shoots can rise both on photosynthetic and carnivorous shoots, whereas photosynthetic shoots sprout directly from turions and can be initiated as branches only on carnivorous shoots (Adamec, 2007a). Therefore, underground shoots in adult plants consist of alternating carnivorous shoots growing downwards and successive photosynthetic ones growing upwards so that the shoots show a zig-zag pattern from a lateral view (Adamec, 2007a).

Leaves are numerous, ca. 3 – 20 mm long and distinctly polymorphic: those on terrestrial photosynthetic shoots are shorter, leathery, imbricate, palmato-dichotomously dissected into up to 15 segments, which are narrowly linear, markedly flattened and relatively obtuse in the apex (Fig. 5; Thor, 1988; Taylor, 1989; Astuti and Peruzzi, 2018b). Leaf segments contained 4–12 small teeth, each furnished with 1–2 small bristles (setulae, trichomes), on each side of leaf margin. Leaves on submerged photosynthetic shoots are longer, narrower, thinner and more acute. The mean leaf apex angle in three European UI populations was 75° but the angle varied from 39° to 111° (Astuti and Peruzzi, 2018b). It is evident (cf. Figs. 1 and 5) that the leaf morphology and, particularly, the leaf apex angle are greatly ecologically variable and depend much on submerged or terrestrial shoot growth: terrestrial leaves are much wider and more obtuse than submerged ones so that the difference could even be statistically significant (as found for US; Astuti and Peruzzi, 2018b). The colour of terrestrial photosynthetic shoots is green to light green, while submerged shoots growing at high irradiance can be yellow-green to slightly reddish or rose (unlike dark red UO and US; Thor, 1988; Fleischmann and Schlauer, 2014; L. Adamec, unpubl. observ.). Usually chlorophyll-free, below-ground carnivorous shoots have strongly reduced, filamentous and poorly branched leaves which bear 1–3 traps each. The largest majority of traps in UI occur on carnivorous shoots but 0–2 % of all traps can also occur on photosynthetic shoots (Adamec and Lev, 2002; Adamec, 2007a, Adamec, 2010a; Table 1). However, the traps found arbitrarily on photosynthetic shoots occurred rather near the boundary with carnivorous shoots (Adamec, 2007a).

The mean proportion of dry weight (DW) of all carnivorous shoots with traps to the total plant biomass, as an expression of the structural investment in carnivory, was 42 and 51 % (range 35–54 %) in two experiments on UI at several natural sites in S Bohemia, Czech Republic (Table 1), while the mean proportion of DW of all traps to the whole plant DW was 23–28 % (range 17–30 %) and significantly correlated with the number of traps per plant (Adamec, 2007a, Adamec, 2010a). These data indicate that the quantitative production of carnivorous shoots and also of traps are under ecological regulation (Adamec, 2007a; cf. Adamec, 2018a, Adamec, 2018b).

Traps of UI of foliar origin are hollow ovoid bladders, 1.5 – 5 mm long, provided with a mobile trap door, two long dorsal, branched setiform antennae (Fig. 1; Thor, 1988; Taylor, 1989; Adamec, 2010a; Fleischmann and Schlauer, 2014) and trap walls consisting of two cell layers. Suction traps of *Utricularia* function on the basis of actively formed negative pressure (e.g., Sasago and Sibaoka, 1985; Poppinga et al., 2016, 2018). As with all other (aquatic) *Utricularia* species, the traps contain five types of glands (hairs) the function of which is still partly unresolved (Lloyd, 1942; Juniper et al., 1989; Taylor, 1989; Poppinga et al., 2016, 2018; Westermeier et al., 2017; Adamec, 2018a; Jobson et al., 2018; Płachno et al., 2018). The numerous and large quadrifid and bifid glands are crucial for trap physiology. The former glands secrete digestive enzymes serving prey digestion and, probably, also absorb released nutrients, while the latter glands pump the water out of the traps and form the negative pressure essential for prey capture (Sasago and Sibaoka, 1985; Adamec, 2018a; Poppinga et al., 2016, 2018; Płachno et al., 2018). Regardless of the crucial role of the traps for prey capture and, thus, for plant ecophysiology, they can be used for reliable and quick determination of the three *Utricularia* species within the UI aggregate (Thor, 1988; Taylor, 1989; Kleinsteuber, 1996; Schlosser, 2003; Płachno and Adamec, 2007; Fleischmann and Schlauer, 2014). In UI, UO and US, quadrifid glands are X-shaped (see Fig. 6) and their exact shape (not the length of arms but the angles between them) is species specific. In UI,both pairs of longer and shorter arms are typically nearly parallel (Thor, 1988; Taylor, 1989; Fleischmann and Schlauer, 2014): the mean angle between the longer arms is 8° (range 3-18°) and that between the shorter arms is 13° (range 2–37°).

UI flowers from early June to early September with the peak from the beginning of July to mid-August (Thor, 1988; L. Adamec, unpubl. observ.). Like in UO, US and UB, prolific flowering requires a warm and rather dry summer season as submerged individuals growing in deeper water do not flower. The inflorescence is an erect raceme, 7 – 20 cm high, with 2–5 flowers (Thor, 1988; Taylor, 1989; Fleischmann and Schlauer, 2014). Rhizoids ("metamorphosed shoots at the base of the flowering stem") 10 – 40 mm long and growing down to the substrate can rarely occur at the base of the flower stem (Thor, 1988). They

Fig. 5. Terrestrial flowering stand of *Utricularia intermedia* in a peat bog close to Příbrazský fishpond, Třeboň Basin, S Bohemia, Czech Republic, 6 July 2015. The plants grew on wet organic litter in depressions among *Carex acuta* tussocks.

Table 1
Morphometric characteristics of UI and US estimated at natural sites or in field-growth experiments in the Třeboň Basin Biosphere Reserve, South Bohemia, Czech Republic. PS, photosynthetic shoots; CA, carnivorous shoots; means ± SE intervals are shown where possible, the values in italics denote the range of all values, the numbers in parentheses denote the number of parallel samples at each site. References: 1, Adamec, 2007a; 2, Adamec, 2010a; 3, Adamec and Lev (2002).

Species, No. of sites	Mean shoot length (cm)		Internodes between branches		No. of traps in shoots per plant		% of total plant biomass in		Ref.
	PS	CA	PS	CA	PS	CA	CA shoots	all traps	
UI	18.8 ± 0.9	11.0 ± 0.3	16.8 ± 0.4	5.9 ± 0.1	0.28 ± 0.16	114 ± 9	50.8 (4)	27.5 (4)	1
3 sites	*8.8-30.0*	*7.4-13.8*	*11.0-23.0*	*4.5–7.8*	*0-5*	*40-245*	*45.3-57.8*	*25.8–28.9*	
UI	12.1 ± 0.3	6.7 ± 0.6	17.7 ± 0.4	–	0	36.2 ± 4.1	41.8 ± 1.0	23.3 ± 1.4	2
1 site	*10.5-13.0*	*0.3-10.6*	*15-21*			*12–56*	*32.4-52.5*	*16.7-29.8*	
UI	–	6.7 ± 1.0	–	–	–	–	–	–	3
3 sites		*2.0-17.6*							
US	19.3 ± 1.4	10.8 ± 0.5	12.2 ± 0.4	6.7 ± 0.2	4.8 ± 0.8	89.5 ± 11.6	48.5 (3)	23.8 (3)	1
3 sites	*8.2–38.4*	*6.6-19.4*	*6.0-15.0*	*5.0-11.0*	*0-16*	*19-284*	*39.7-54.0*	*18.0–27.5*	
US	15.6 ± 0.5	6.7 ± 0.3	12.2 ± 0.2	–	7.9 ± 0.7	46.6 ± 3.1	42.8 ± 1.3	19.7 ± 1.1	2
1 site	*13.5–19.7*	*0.6-10.3*	*9-16*		*3-13*	*30-70*	*34.5-53.2*	*13.9-28.2*	
US	–	6.1 ± 0.3	–	–	–	–	–	–	3
3 sites		*2.0–14.1*							

probably stabilize flowering plants. Zygomorphic flowers are 10 − 16 mm long (Fig. 7). The dark yellow corolla has red-brown veins in the central part and the upper lip; the lower lip is flat. The spur is 8 − 10 mm long, nearly cylindric to subulate with the acute apex, and a little shorter that the lower lip. Only a small fraction of open flowers set ripe seeds (L. Adamec, unpubl. observ.). The ripe capsule is globose to broadly ovoid, 2.5 − 3 mm in diameter, circumscissile and contains only 2–8 seeds. Seeds of a polygonal shape (diameter 0.6-0.8 mm) are black and their mean weight is 0.172 mg (L. Adamec, unpubl. data). Pollen grains are suboblate, radially symmetric, subisopolar and zonocolporate with (11)-12-15-(16) colpori, 35 − 46 × 31 − 39 μm large (Casper and Manitz, 1975; Taylor, 1989; Beretta et al., 2014). No specific information is available on the pollination mode in UI. However, on the basis of anatomical similarity of UI flowers with those of UO, US and *U. vulgaris* including the presence of nectar glands inside the flower spur and, particularly, of the finding of a pollinator fly and bee in *U. vulgaris* (Thor, 1988; Płachno et al., 2018), it is possible to consider that UI flowers are entomophilous and self-pollinating (autogamy). The pale green turions are hairy, spherical to ovoid and are 3 − 8 mm long.

2.1.2. *U. ochroleuca*

Generally, the biology incl. morphology of UO (i.e., *U. ochroleuca s.str.*) has been described very little as while this species was distinguished from UOs.l. as late as in 1988, it only became commonly

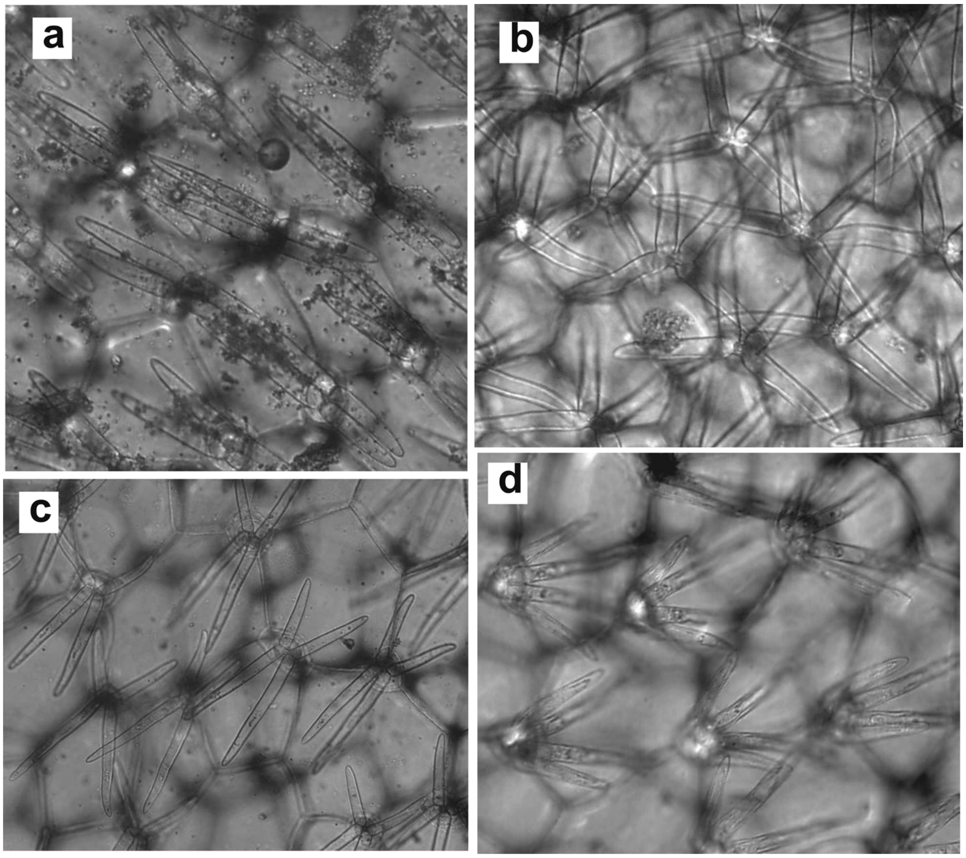

Fig. 6. Quadrifid glands in traps of *Utricularia intermedia* (a), *U. ochroleuca* (b), *U. stygia* (c) and *U. bremii* (d) under microscope at 200× magnification. The length of the glands is ca. 80 − 120 μm. The plants originated from the Třeboň Basin, Czech Rep.

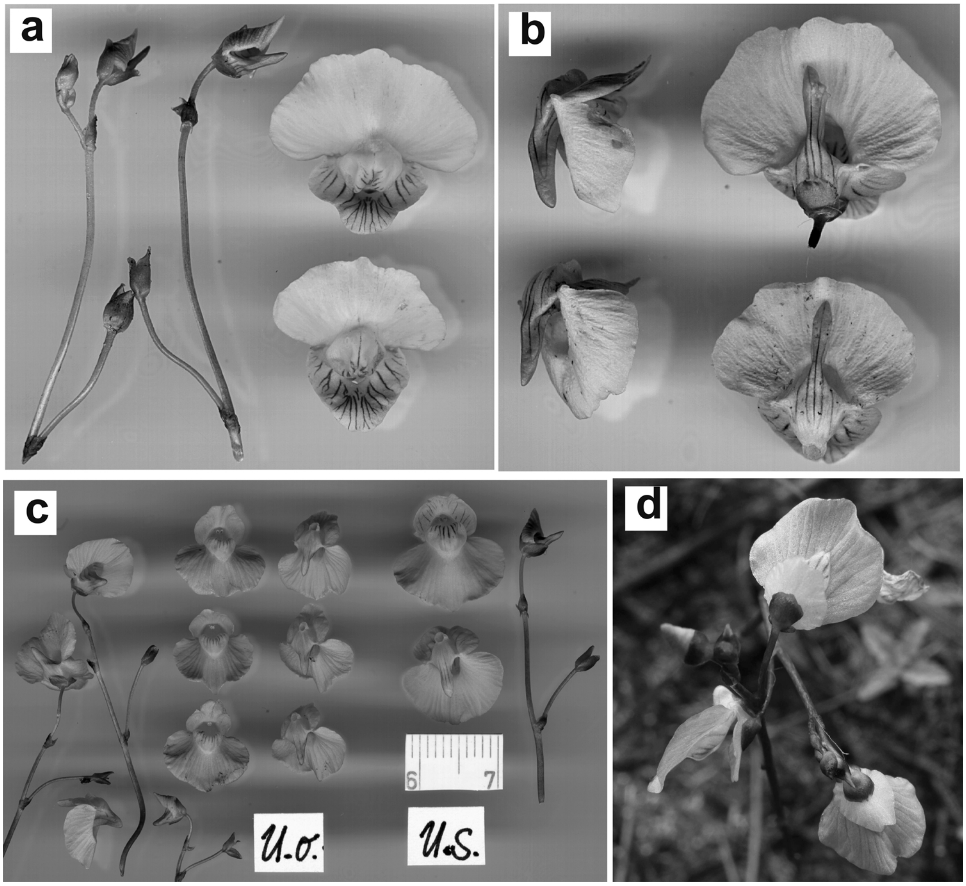

Fig. 7. Inflorescences and flowers of *Utricularia intermedia* (a, b), *U. ochroleuca* and *U. stygia* (c) and *U. bremii* (d). The plants originated from the Třeboň Basin, Czech Rep.

accepted by botanists much later. Moreover, it was recognized later that UO is much rarer than US in Europe (e.g., Płachno and Adamec, 2007; Fleischmann and Schlauer, 2014). It is obvious that dimorphic shoots of UO (Fig. 2) are morphologically and morphometrically (shoot length and branching rate) very similar to those of US (Thor, 1988; Kleinsteuber, 1996; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018b; Table 1). Adult submerged plants are up to 30–40 (60) cm long, while terrestrial ones can be only 10 – 20 cm long.

Leaves are numerous, ca. 4 – 18 mm long and distinctly polymorphic: those on terrestrial photosynthetic shoots are shorter, leathery, imbricate, palmato-dichotomously dissected into up to 20 segments, which are narrowly linear to subulate, markedly flattened and relatively acute in the apex (Fig. 2; Thor, 1988; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018b). On each side of the margin, leaf segments contain 1–6 (mean 3) distinct, papillose teeth each furnished with 1–2 small bristles. The teeth are more distinct and larger on submerged leaves. Leaves on submerged photosynthetic shoots are longer, narrower, thinner and more acute. In three European UO populations, the mean leaf apex angle was 29° with the range from 17–54° (Astuti and Peruzzi, 2018b). In general, leaves are morphologically very variable. Photosynthetic shoots usually also bear several traps. The colour of photosynthetic shoots is green to dark red depending on water depth and irradiance (Thor, 1988; Fleischmann and Schlauer, 2014). Usually chlorophyll-free, pale below-ground carnivorous shoots have strongly reduced, filamentous and poorly branched leaves bearing 1–3 traps each. The largest majority of the traps occur on carnivorous shoots but several traps regularly occur on photosynthetic shoots.

Traps of UO are 1.5–4.5 mm long (Fig. 2; Thor, 1988; Fleischmann and Schlauer, 2014; L. Adamec, unpubl. data). The quadrifid glands are markedly asymmetric (Fig. 6): the mean angle between the longer arms is 35° (range 19–52°) after Thor (1988) and 34° (range 26–45°) after Płachno and Adamec (2007), while that between the shorter arms is 171° (range 117–228°) after Thor (1988), but only 126° (range 107–161°) after Płachno and Adamec (2007) and 120–130° after Fleischmann and Schlauer (2014). The mean angle for North American populations of UO from Oregon and Colorado was only 104 ± 20° and 140 ± 26°, respectively (Schlosser, 2003). Thus, as regards to the angle between the shorter arms, UO is very variable in this trait and Scandinavian populations have much higher values than the Central European or American ones.

UO flowers from late May to late August with the peak from mid-June to early August (Thor, 1988; L. Adamec, pers. observ.). The inflorescence is an erect raceme 5 – 20 cm high with 2–4 flowers (Thor, 1988; Fleischmann and Schlauer, 2014). Rhizoids 20 – 40 mm long rarely occur at its base. Zygomorphic flowers are 10 – 15 mm long and 10 – 12 mm wide (Fig. 7). The dark yellow corolla has red-brown lines only in the central part. The lower lip is flat or (especially in young flowers) the margins may be partly bent downwards (C-shaped). The lower part of the peduncle (inflorescence stalk) and also pedicels, bracts and calyx are distinctly reddish or red. The spur is 3 – 5 mm long, distinctly conic with an obtuse apex, much shorter that the lower lip, and its position to the lower corolla lip is nearly perpendicular. The plants are always sterile due to pollen malformation and do not set seeds (Casper and Manitz, 1975; Taylor, 1989; Beretta et al., 2014). Pollen grains are oblate spheroidal, radially symmetric, subisopolar and zonocolporate with (11)-12–14-(15) colpori, 21 – 40 × 18 – 39 μm large (Beretta et al., 2014). Hairy, spherical to ovoid turions 2 – 7 mm long are dark green to dark pink.

2.1.3. *U. stygia*

Adult submerged plants are up to 20–40 (60) cm long, while terrestrial ones can be only 10 – 20 cm long (Kleinsteuber, 1996; Wildermuth, 2010; Fleischmann and Schlauer, 2014). Photosynthetic shoots of adult plants are usually 8 – 38 cm long (Fig. 3; Table 1; Adamec, 2007a, Adamec, 2010a) and grow mostly horizontally either in shallow water or terrestrially on the surface of the wet substrate. On average 51 leaf nodes (range 45–61) occurred on one photosynthetic shoot (Adamec, 2010a). Both photosynthetic and carnivorous shoots were found to initiate branches regularly (Table 1; Adamec, 2007a, Adamec, 2010a, Adamec, 2018a): the mean number of internodes between two successive branches on the main photosynthetic shoots was 12.2 ± 0.4 and 12.2 ± 0.2 in two different studies and differed markedly from that on carnivorous shoots (6.7 ± 0.2). Carnivorous shoots of adult plants are usually 7 – 11 cm long (range 0.6–19.4 cm; Table 1).

Leaves are numerous, ca. 4 – 18 mm long and distinctly polymorphic: those on terrestrial photosynthetic shoots are shorter, leathery, imbricate, palmato-dichotomously dissected into up to 20–30 segments, which are narrowly linear to subulate, markedly flattened and relatively acute in the apex (Fig. 3 and 8; Fleischmann and Schlauer, 2014; Astuti and Peruzzi, 2018b). On each side of leaf margin, leaf segments contain 5–10 (mean 7) distinct, papillose teeth each furnished with 1–2 small bristles. The teeth are more distinct and larger on submerged leaves. Leaves on submerged photosynthetic shoots are longer, narrower, thinner and more acute. In two European US populations, the mean leaf apex angle was 50° (range 17–54°; Astuti and Peruzzi, 2018b). Thus, both the number of teeth and the leaf apex angle overlap between UO and US and cannot be used for plant determination. In general, leaves are morphologically very variable (Fig. 8; see also Wildermuth, 2010). Photosynthetic shoots usually bear several traps (1–5 each) but the number of traps on carnivorous shoots can be 5.9–18.6 times higher (Table 1; Adamec, 2007a, Adamec, 2010a). The colour of photosynthetic shoots is green to dark red depending on water depth and irradiance (Wildermuth, 2010; Fleischmann and Schlauer, 2014). Usually chlorophyll-free, pale below-ground carnivorous shoots have strongly reduced, filamentous and poorly branched leaves bearing 1–3 traps each. Old traps on carnivorous shoots growing on the substrate can also be pigmented (green to red; L. Adamec, pers. observ.).

The mean proportion of DW of all carnivorous shoots with traps to the total plant biomass was 43 and 49 % (range 35–54 %) in two studies on US at several natural sites in S Bohemia, Czech Republic (Table 1), while the mean DW proportion of all traps to the whole plant DW was 20 and 24 % (range 14–28 %) and significantly correlated with the number of traps per plant (Adamec, 2007a, Adamec, 2010a). The great variation of the data indicates that the production of carnivorous shoots and also of traps are under ecological regulation (Adamec, 2007a; cf. Adamec, 2018a, Adamec, 2018b): low water level was found as a regulatory factor reducing the investment in carnivory in US.

Traps of US are 1.5 – 5 mm long (Fig. 3; Fleischmann and Schlauer, 2014; Adamec, 2016a; L. Adamec, unpubl. data). The quadrifid glands have comparatively (with UO or UI) long and narrow arms and are slightly asymmetric (Fig. 6): the mean angle between the longer arms is 41° (range 16–90°) after Thor (1988), 35° (range 12–53°) after Płachno and Adamec (2007) and 34° (range 3–54°) after Adamec, 2016a, while that between the shorter arms is 74° (range 30–140°) after Thor (1988), 62° (range 34–84°) after Płachno and Adamec (2007), 66° (range 28–113°) after Adamec, 2016a and 40–120° after Fleischmann and Schlauer (2014). Schlosser (2003) reported on average 45-85° between the shorter arms for four US populations from Europe or America. The angle measured between the shorter arms, which is used for reliable determination of UI, UO and US, is thus very variable in US. In this species, the great variability in this trait could partly be caused by the trap-size effect. Adamec, 2016a found a statistically significant and positive dependence of the short arm angle on the trap size: short arm angle (in deg.) = 12.1 + 15.7 trap length (in mm), which was neither found in *U. vulgaris* nor *U. australis*. Longer traps thus exhibit greater angles.

US flowers similarly as UO: from late May to late August with the peak from mid-June to early August (Thor, 1988; Fleischmann and Schlauer, 2014; L. Adamec, pers. observ.). Unlike the data on its very rare flowering in Bavaria, Germany (Fleischmann and Schlauer, 2014) and in Scandinavian countries (Thor, 1988), US flowers prolifically nearly at all sites in the Czech Republic possessing optimal ecological conditions (L. Adamec, pers. observ.). The inflorescence is an erect raceme 5 – 20 cm high with 1–5 flowers (Thor, 1988; Fleischmann and Schlauer, 2014). Rhizoids 10 – 40 mm long rarely occur at its base. Zygomorphic flowers are 10 – 16 mm long and 11 – 14 mm wide (Fig. 7; cf. Thor, 1988; Fleischmann and Schlauer, 2014). The lower lip is flat. The dark yellow corolla has a red-brown tinge in the central part and the upper lip contains distinct red-brown veins. Thus, typical US flowers look larger, wider and slightly darker than those of UO (Fig. 7). Unlike UO, the upper part of the inflorescence stalks and also pedicels, bracts and calyx are usually pale green, not red (Fleischmann and Schlauer, 2014; L. Adamec, pers. observ.). The spur is 4 – 7 mm long, narrowly conic with an obtuse apex, much shorter that the lower lip, and directed along the lower corolla lip at an acute angle (Thor, 1988; Fleischmann and Schlauer, 2014). US plants are always sterile due to pollen malformation and do not set seeds (Casper and Manitz, 1975; Taylor, 1989; Beretta et al., 2014). Pollen grains are ellipsoidal to spheroidal, asymmetric, heteropolar and often malformed with many gigapollen grains observed. The rare normal grains are zonocolporate with (10–11)-12–14-(15) colpori, 26 – 36 × 26 – 35 μm large (Beretta et al., 2014). Hairy, spherical to ovoid turions 3 – 8 mm long are dark green to dark pink.

2.1.4. *U. bremii*

The plant (Fig. 4) is very similar to the much more common species *U. minor*. Adult submerged plants growing in shallow water are up to 30–50 (60) cm long, while adult terrestrial ones with reduced foliage growing on drying soils can be only 10 cm long (Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014; L. Adamec, pers. observ.). The shoots are very plastic. They are usually monomorphic, pale green with many traps (Fig. 4), with only slight implications of differentiated pale carnivorous shoots in the form of branches. Markedly differentiated shoots occur very rarely and probably only in the terrestrial ecophase on wet peat (L. Adamec, pers. observ.). The shoot apex is positioned markedly asymmetrically on the stem (Fig. 4). Shoot apices forming turions may be slightly rose (Fig. 9).

Leaves are numerous, 4 – 20 mm long and distinctly polymorphic: those on submerged (photosynthetic) shoots are longer, filamentous or pinnate, pinnato-dichotomously dissected into up to 50 segments,

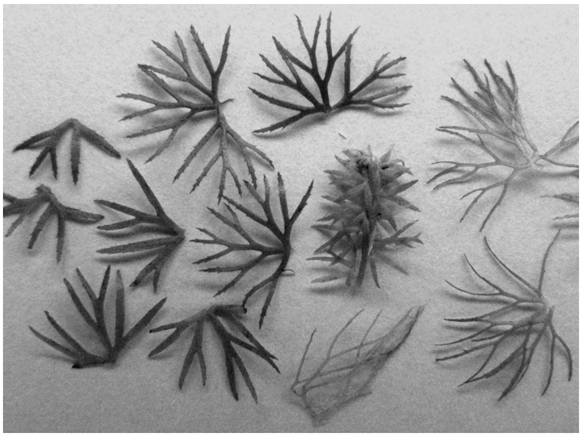

Fig. 8. Variability of foliar morphology of *Utricularia stygia*: wider terrestrial leaves collected from fen lake at Karštejn, Třeboň Basin, S Bohemia, Czech Republic, 15 September 2015 (on the left side) and narrower submerged leaves collected from outdoor culture (on the right side).

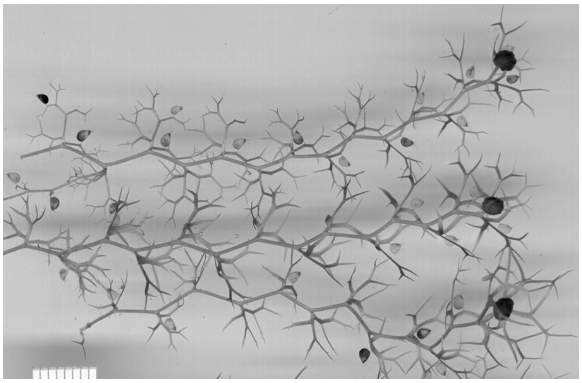

Fig. 9. Apical shoot segments of *Utricularia bremii* with nearly mature turions collected from a shallow pool in a sand-pit near Suchdol nad Lužnicí, Třeboň Basin, S Bohemia, Czech Republic, 16 September 2018; ticks indicate 1 mm.

which are narrowly linear to subulate (Fig. 4), or can be imbricate, palmato-dichotomously dissected, markedly flattened and acute in the apex (Fig. 9; Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014). Leaf segments are always without lateral teeth. Leaves on underground carnivorous shoots are greatly reduced and filamentous.

Traps of UB are ovoid bladders 1–2.8 mm long provided with two long dorsal, branched setiform antennae (Fig. 4, 9; Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014). They are usually greenish or pale but those on old shoots can be light rose to dark pink. The quadrifid glands (Fig. 6d) are very similar to those in *U. minor* but dissimilar to either in UI, UO or US (Taylor, 1989; Astuti and Peruzzi, 2018b). Long and short arms lie within one plane (like fingers within the palm): the angle between the longer arms is ca. 25–40°, while the angle between shorter arms forms an included angle of ca. 260-310° (Fig. 6d) or ca. 220° (Fleischmann and Schlauer, 2014).

UB flowers from early June to early September with the peak from early July to late August (Fleischmann and Schlauer, 2014; L. Adamec, pers. observ.; but cf. Casper, 1974). Its flowering is not scarce under optimal ecological conditions including mainly very shallow water (0 − 5 cm) without oscillations, high temperatures and full irradiance (L. Adamec, pers. observ.). The inflorescence is an erect raceme 5 − 60 cm high with 2–14 flowers (Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014). However, inflorescences only ca. 10 − 25 cm high were observed repeatedly at several Czech sites where the plants prolifically flower (L. Adamec, pers. observ.). Zygomorphic flowers are 8 − 12 mm long and 9 − 11 mm wide (Fig. 7d; Casper, 1974; Taylor, 1989; Macák, 2006; Fleischmann and Schlauer, 2014; Christians, 2016). The lower lip is flat and nearly circular. Thus, in a lateral view, the flower is nearly as long as wide or slightly wider: Macák (2006) determined the mean width:length ratio 1.17 (range 1.10–1.25) in a North Bohemian UB population. The light yellow corolla has a red-brown tinge in the central part. The inflorescences and also pedicels and calyx are usually red and it applies also for *U. minor* (Fleischmann and Schlauer, 2014; L. Adamec, pers. observ.). The spur is 2 − 3 mm long, shortly conic with an obtuse apex, and directed perpendicularly to the lower corolla lip (Casper, 1974; Taylor, 1989; Macák, 2006; Fleischmann and Schlauer, 2014). The basal part of the corolla lip ('palate') is densely covered by shortly stalked glandular trichomes (Płachno et al., 2017).

UB plants are usually sterile due to pollen malformation and do not set seeds (Casper and Manitz, 1975; Taylor, 1989; Beretta et al., 2014; Christians, 2016). Nevertheless, Casper (1974) states that "small, circular capsules are very rare". In line with this, Adamec (2002) described seed set and germination for cultivated UB plants originating from Lake On'ega in NW Russia. However, a suspicion exists that these plants were confounded for *Utricularia gibba*. Pollen grains are ellipsoidal to spheroidal, asymmetric, heteropolar and often malformed. A few normal grains were zonocolporate with 10-13(-14) colpori, 28 − 36 × 26 − 32 μm large (Beretta et al., 2014). Glabrous, spherical turions 1 − 5 mm long are dark green to reddish (Fig. 9).

2.2. Species determination

The three species within the UI aggregate (UI, UO, US) can easily be distinguished from other *Utricularia* species of the European flora (e.g., *U. minor*, *U. bremii*, *U. australis*) by distinctly dimorphic shoots (Figs. 1–3). However, small individuals of the three species with narrow shoots resemble *U. minor* or UB and the reliable determination into the aggregates is based on the presence (UI, UO, US) or absence (*U. minor*, UB; Fig. 9) of teeth on leaf margins (Casper, 1974; Thor, 1988; Kleinsteuber, 1996; Taylor, 1989; Fleischmann and Schlauer, 2014).

Within the aggregate, UI can be best determined by its flower: the spur is 8 − 10 mm long, nearly cylindric to subulate with an acute apex, and is only a little shorter that the lower lip (Fig. 7a, b). While the spur in UO and US is shorter and distinctly conic with an obtuse apex (Fig. 7c). Unlike UO and US, UI has only small lateral teeth on leaf margins which are not papillose and the leaf apices are comparatively obtuse (in UO and US, leaf apices are more acute (Fig. 8). Shoots of UI are usually not so dark red like UO and US can be. The presence of ripe capsules reliably determines UI but seed set is rather rare. Finally, trap quadrifid glands have almost parallel arms with very acute angles of < 37° (Fig. 6a, cf. 6b, c). Other reported differences (number of foliar teeth, absence of traps on photosynthetic shoots) are not reliable (see Adamec, 2007a; Astuti and Peruzzi, 2018b) and should not be used for plant determination.

Of all the different signs, UO can only be reliably distinguished from US by the shape of the quadrifid glands (cf. Thor, 1988; Schlosser, 2003; Płachno and Adamec, 2007; Adamec, 2016a) as the other differences described (see *2.1.*; number of foliar teeth, leaf apex angle, corolla size, spur length) more or less overlap or can be ecologically variable (Fig. 7c, 9; Astuti and Peruzzi, 2018b). Płachno and Adamec (2007) summarized the differences for world populations: for UO, "the mean angle between the shorter arms is always > 100°, the minimum angle can also be only 70° but there are always maximum angles (at least in 10 % of glands) > 120° and usually > 130°". They concluded for US: "the mean angle between the shorter arms is always < 85° but the maximum angle below 115°". It should be noted that measured angles can be considerably distorted during trap preparation when the arms are not sufficiently parallel to the cover slip (Fig. 6). Moreover, as found by Adamec, 2016a the angle between the shorter arms in US depends positively on the trap size. The same relationship might also be expected in UI and UO. To minimize this trap-size effect, traps of a homogenous size should be inspected.

Only flowering individuals of UB can be reliably determined. Unlike the very similar *U. minor*, UB has a flat and wide lower lip, while in *U. minor*, the lateral margins are markedly curved downwards so that the corolla appears much narrower (Taylor, 1989; Fleischmann and Schlauer, 2014; Christians, 2016; see Fig. 10). In UB, the lower lip is on average wider than longer (ratio ca. 1.17), whereas the ratio of the flattened lower lip in *U. minor* is on average only 0.92 (range 0.83–1.07; Macák, 2006). Yet in flowering UB populations in the Třeboň Basin, Czech Republic, ca. 10–30 % flowers have relatively narrow flowers with the width:length ratio < 1 (L. Adamec, unpubl. data). Thus, at least a half of the UB flowers should have typically wide flowers. The longer corolla spur in UB cannot be used reliably for plant determination.

2.3. Growth traits

All four rare *Utricularia* species are typical clonal plants which produce a dense, web-shaped arrangement of shoots at their microsites and propagate rapidly vegetatively (Adamec, 2007a, Adamec, 2010a, Adamec, 2011a). Unlike the free-floating species of *U. australis* or *U.*

Fig. 10. Inflorescences and mature capsules with seeds of *Utricularia minor* collected from the Třeboň Basin, Czech Rep. Note the typically curved margins of the lower lip.

vulgaris, which maintain more or less constant shoot length during a great deal of the growing season ('conveyer-belt' system of shoot growth; see Adamec, 2018a, Adamec, 2018b and the literature therein), the four rare *Utricularia* species rather increase gradually their mother shoot (photosynthetic in UI, UO and US) length up to the initial stage of autumnal turion formation (L. Adamec, pers. observ.). Afterwards, the decay of old, senescent shoot segments begins and the mother shoots are gradually shortened up to the turion length. The rapid vegetative propagation of the four species includes both rapid apical shoot growth (i.e., formation of new leaf nodes in the apex per unit time) of mother shoots and high branching rate (Table 1; Adamec, 2007a, Adamec, 2010a, Adamec, 2011a, Adamec, 2018b). In a field-growth experiment with shortened photosynthetic shoots, the mean apical shoot growth rate was 1.91 ± 0.06 leaf nodes day^{-1} in UI and 2.13 ± 0.06 leaf nodes day^{-1} in US (Adamec, 2010a). A similar value of 2.40 ± 0.14 leaf nodes day^{-1} was found in a greenhouse-growth experiment in UB shoot segments fed on prey (Adamec, 2011a). These rates are comparable with those found in some *Utricularia* species with monomorphic shoots (cf. Adamec, 2018a, Adamec, 2018b). Combining these data for UI, US and UB with those for branching rates in Table 1 (or with total number of branches in UB), the following mean values of 'branching frequency' (i.e., branching rate/apical shoot growth rate) can be calculated: 9.3 days per branch in UI, 5.7 in US and 5.0 days per branch in UB. Such a high branching frequency led to high relative growth rates (RGR). In UI and US, the doubling time of biomass (i.e., ln 2 / RGR) was 6.64 and 9.21 days, respectively (Adamec, 2010a), which is comparable with values found for other aquatic carnivorous plant species with monomorphic shoots (cf. Adamec, 2018a, Adamec, 2018b). Due to the rarity of the four species, other growth characteristics are unknown.

2.4. Taxonomy and evolution

The genus *Utricularia* is considered an immediate sister to *Genlisea*, and *Pinguicula* is sister to both. The phylogenetic age of the genus *Utricularia* is estimated to be 31 million years (Fleischmann et al., 2018; Jobson et al., 2018). The four rare European *Utricularia* species belong to the numerous generic section *Utricularia* comprising recently ca. 40 species, which are all strictly submerged aquatic or amphibious (semiaquatic, subterrestrial) species (Jobson et al., 2018; Silva et al., 2018). It is generally considered on the basis of molecular studies of more authors that terrestrial lineages (and/or generic sections comprising terrestrial species) within the genus *Utricularia* are evolutionary ancestral, whereas the aquatic lineage within the section *Utricularia* is relatively young and advanced (Jobson et al., 2018; Silva et al., 2018). The latter authors have recently presented a multilocus phylogeny for 78 *Utricularia* species based on five plastid and one nuclear DNA sequences. Using a molecular clock approach, they have proposed that the section *Utricularia* is only ca. 2–12 millions of years old and UI, UO, US and UB are young Pleistocene species ca. < 2.5 million years old.

While sexually reproducing UI and *U. minor* have always been considered taxonomically 'pure' species (e.g., Casper, 1974; Thor, 1988; Taylor, 1989; Fleischmann and Schlauer, 2014; Jobson et al., 2018; Silva et al., 2018), UO and US (and/or UOs.l.) have been considered polymorphic hybrids between the parental species UI and *U. minor* (Thor, 1988; Fleischmann and Schlauer, 2014). Moreover, Taylor (1989) suggested that both UOs.l. and UB are "morphologically slightly different vegetative apomicts, each with a different chromosome complement." As follows from the recentmost published study on species relationships within the section *Utricularia* (Silva et al., 2018; see above), UI and US are sister species and their clade is sister to UO, UB and *U. minor*. In a preliminary unpublished study using the AFLP method on the four rare species, A. Fleischmann (unpubl. res.) confirmed the same relationships among the four species: the sequences were extremely variable even among related populations and UO and US were indicated as hybrids, but of repeated hybridization events. Moreover, for US, UI has been found the mother and *U. minor* the pollen donor; in UO, it has been the opposite case. Some UO populations even underwent backcrosses with one of the parental species as pollen donor. In another DNA sequencing study (Astuti et al., 2019), the hybrid origin has been supported at least for US and UO. However, data on genome size (Veleba et al., 2014; see also 5) showed that none assumed hybridogenic species (UO, US, UB) had values intermediate between the putative parental species (UI and *U. minor*). Fleischmann and Schlauer (2014) claim that UO and US originate at many sites *de novo* when parental species (UI and *U. minor*) occur. A new origin of a US micropopulation at a site of UI and *U. minor* in the Třeboň Basin, Czech Republic, was observed in 2010 (L. Adamec, unpubl. data).

3. Life cycle and biology

3.1. Flowering and reproduction

All four rare European *Utricularia* species can prolifically flower but only UI set seeds (see *2.1*; Casper, 1974; Thor, 1988; Kleinsteuber, 1996; Taylor, 1989; Fleischmann and Schlauer, 2014). Consistently in all four species, flowering is promoted by high water temperatures, very shallow water (ca. 0 – 5 cm) without sudden oscillations and high irradiance at the level of the plants (L. Adamec, pers. observ.), which is in a deep discrepancy with a very low minimum irradiance requirement for growth in UI and UOs.l. (cf. Adamec and Lev, 2002). As in such shallow water a good deal of plant biomass is growing as amphibious and is in a direct contact with the atmosphere, a high free-CO_2 concentration in the ambient water may not be important (see Adamec, 2018a, Adamec, 2018b). Obviously, a population or ecological flowering study has never been conducted in the four species. Although seed germination was observed in UI in laboratory (L. Adamec, unpubl. data), no data are available on the longevity of UI seeds in the field or whether they form a seed bank or which habitat factors promote seed germination (cf. Cross et al., 2018). Thus, all four species propagate rapidly by vegetative growth (see *2.3*). In analogy with a rapidly growing rootless aquatic carnivorous plant *Aldrovanda vesiculosa* (Adamec, 1999), all four species could be able to propagate the number of turions at least 40 times under favourable conditions in Central Europe over one season. Spreading to new sites can occur by transferring their turions by water birds or big animals and flooded water ways are also possible.

3.2. Overwintering and turion biology

All four rare European *Utricularia* species regularly form turions at the end of the growing season (Fig. 9; Adamec, 2018a, Adamec, 2018c). Generally, *Utricularia* turions or winter buds are vegetative, dormant storage organs and protect fragile summer shoots from freezing and decay (Adamec, 2018a, Adamec, 2018c). They are formed by extreme condensation of short, modified trap-free leaves in shoot apices, are green and detachable from decaying mother shoots and function also as propagules. Various aspects of turion morphology and ecophysiology have been described also for all four rare *Utricularia* species (Glück, 1906; Sculthorpe, 1967; Casper, 1974; Adamec, 2008a, Adamec, 2008b, Adamec, 2010b, Adamec, 2011d; Adamec and Kučerová, 2013a; Płachno et al., 2014; see also Adamec, 2018a, Adamec, 2018c). Mature turions of all four rare species are usually less dense than water, are dragged down to the bottom by decaying shoots and usually overwinter in darkness or deep shade, under hypoxia or anoxia, while slightly covered by sediments. They usually germinate and sprout at the surface in warmer water (Adamec, 2018c). However, a part of them can lie in very shallow waters or on wet substrate or float at the surface over winter and thus be exposed to frosts or drought.

Turions of the four rare species are partly frost resistant. In a freezing experiment, turions of the four species, which overwintered in a refrigerator at 2.5 ± 1 °C for ca. three months, exhibited freezing of extracellular water from −7.9 to −10.2 °C but the freezing mostly killed all turions (Adamec and Kučerová, 2013a). However, the turions were hardened by weak frosts over winter and their frost hardiness was based on the shift from frost avoidance in non-hardened autumnal turions to frost tolerance. Hardened turions of the four species exhibited the freezing at only −2.9 to −3.3 °C, but nearly all turions survived the freezing exposure between −9 to −10 °C. Turion hardening leading to obtain the frost tolerance can be ecologically very important for successful overwintering of all four species, as their turions could be damaged by strong frosts. Under terrestrial conditions, they could also be damaged by drought. Turions of UI (and *U. vulgaris, U. australis, U. minor*) were able to withstand drying out at 24 ± 3 °C and 33 % relative humidity for 5–19 days and the drying markedly shortened innate turion dormancy (Maier, 1973). In another comparative study, US and partly UB turions were able to survive for only a five-day, but not a 375-day drought period (unlike *U. australis*) at 3 ± 1 °C; dried UB turions could even survive a 5-day period of freezing exposure to −11 °C (Adamec, 2008b). Great species-specific differences thus exist in the drying tolerance of turions of the four rare species and only a short drought period can be withstood. In a similar study (Adamec, 2015), UI turions could not survive a drought period for 17 months neither at 3 nor -12 °C, while UB and US turions could partly survive (at 15–25 %) the freezing treatment. Yet neither drying nor freezing of dried turions can be recommended for a long-term storage of *Utricularia* turions.

Two dormancy states were described in detail for turions of Canadian *U. macrorhiza* (Winston and Gorham, 1979) and were confirmed also for turions of US and UB (Adamec, 2011d). The states are innate dormancy starting at the end of summer (ca. late August to late January), when turion germination is inhibited by endogenous factors, and imposed dormancy when the turions can germinate and sprout at sufficient temperature and in light.

Utricularia turions as storage organs accumulate starch, free sugars, reserve proteins and lipids and, therefore, their dry matter content (DMC; i.e., % DW in fresh weight, FW) is ca. 2.5–4 times higher than that in their leafy shoots (Adamec, 2018c): in UI, 27.0 %; in UO, 31.1 %; in US 23.5–33.7 %; in UB, 27.1–31.6 % (Adamec, 2008a, Adamec, 2010b, Adamec, 2011d; L. Adamec, unpubl. data). In mature autumnal turions, the following content of starch was estimated (% DW, means ± SE, range, n = 4; L. Adamec, unpubl. data): UI, 13.9 ± 0.2 (13.5–14.3); UO, 13.9 ± 0.3 (13.0–14.4); US, 15.2 ± 0.9 (12.9–17.2); UB, 9.1 ± 0.5 (8.5–10.6). Thus, different batches of turions and also different individuals can have a variable starch content and, thus, DMC. In US turions kept in a refrigerator over winter, the cytoplasm of turion cells was also filled by protein storage vacuoles at a state of partial degradation and the nuclei contained para-crystalline inclusions of a proteinaceous nature (Płachno et al., 2014). Moreover, numerous lipid bodies occurred in the cells of epidermal glands. The content of the polyamines cadaverine, putrescin and spermidine in UI turions was too low (0.01-1.3 mmol $\mathrm{kg}_{\mathrm{DW}}^{-1}$) to act as N-storage but the polyamines could rather act as growth substances (Villanueva et al., 1985).

Turions of *Utricularia* also represent storage organs for mineral nutrients (at least for N, P, S and Mg) to support the growth of new organs though storing mineral nutrients is presumably less distinct than storing carbohydrates (Adamec, 2010b, Adamec, 2011d, Adamec, 2018c). In mature turions of UI, the tissue content of N (% DW) was 2.18 ± 0.17 and of P 0.31 ± 0.03, in UO turions, N 2.78 ± 0.02 and P 0.41 ± 0.03, in US, N 1.96 ± 0.14 and P 0.30 ± 0.02 and in UB, N 1.57 ± 0.04 and P 0.22 ± 0.02 (Adamec, 2010b; L. Adamec, unpubl. data). Although these values are comparable with those found in growing shoots of aquatic plants, due to the high accumulation of carbohydrates (and thus high DMC) in turions, Adamec, 2010b estimated that theoretically about 30 % of the total turion's N and about 50 % of the total P amount could be used as storage nutrients for supporting newly sprouting organs, without a decrease in their growth rate.

The aerobic dark respiration rate (RD) of turions of aquatic plants (mainly per unit DW) as typical storage organs with low intensity of metabolism is very low (Adamec, 2018a, Adamec, 2018c) and the same applies for turions of the four rare *Utricularia* species (Adamec, 2008a, Adamec, 2011d. FW-based mean RD values of US and UB turions at the state of innate dormancy measured at 20 °C (1.54–2.24 mmol O_2 kg^{-1} h^{-1}) were usually lower that those for the turions at the imposed dormancy (2.17-4.31 mmol O_2 kg^{-1} h^{-1}) and were similar to or even higher that those in trap-free summer leaves of these species (Adamec, 2008a, Adamec, 2011d cf. Adamec, 2006). However, per unit DW, the mean RD values in US and UB turions were 2.6–7.3 times lower that those in the leaves. The temperature quotient (Q_{10}, measured between 4 and 20 °C) of autumnal US and UB turions was 2.30–2.55 and rose slightly (2.59–2.93) in spring turions (Adamec, 2008a). The proportion of cyanide-resistant respiration as an estimate of the alternative oxidase pathway in turions was very high: 81 % in US and 90 % in UB, which is typical for storage organs with a low metabolism intensity (Adamec, 2008a). In sprouting US and UB turions both in old and new segments, the FW-based mean RD values increased about 2.5 times and those DW-based even ca. 4.4 times as compared to dormant turions (Adamec, 2011d).

4. Distribution and habitat requirements

4.1. Geographical distribution: natural and artificial distribution

4.1.1. U. intermedia

UI has a natural circumboreal distribution in Europe, Asia and North America (Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014). As stated by the last authors UI is spread southwards in Europe to ca. 42 °N in S France, in Asia to ca. 40 °N in Armenia and in America to ca. 38 °N in California. According to Casper (1974); Thor (1988) and Taylor (1989), UI has the centre of its European distribution in N Europe – in Fennoscandinavia. In Europe, it is distributed in SW Greenland, Ireland, Great Britain (mainly Scotland), Norway, Sweden and Finland (here very common, up to 70 °N), Denmark, NW part of Russia (Karelian Republic and Murmansk county; Fedorov, 1981), Estonia, NW Ukraine (W Carpathians; Fedorov, 1981), Caucasus (up to Armenia), Romania, Serbia (in former Yugoslavia, but here extinct; Fleischmann and Schlauer, 2014), N Italy, Switzerland, France, Belgium, The Netherlands, Germany, Austria, Czech Republic, Slovakia and Poland.

More detailed distribution of UI in European countries: three sites are in SW Greenland near the coast (Hennekens, 2018); two sites are in

W Ireland; within Great Britain, > 100 sites are in Scotland, dozens of sites are on the Inner and Outer Hebrides and seven sites on the Shetland islands, scattered records are in N, S, W and SW England (Hennekens, 2018) (however, after 2010, only one record is stated in N Scotland, one on the Colonsay island, one on the Shetlands, four in Northern Ireland and seven in Ireland; https://bsbi.org/maps); several sites in S and NE Belgium; several dozen sites in The Netherlands; ca. 20 sites are reported from France with the focus in coastal SW France S of Bordeaux; ca. 15 sites are in NE Switzerland (between the Lakes Zurich and Constance; e.g., Wildermuth, 2010) and ca. 15 sites in NW Switzerland (near Lake Neuchâtel; Hennekens, 2018; https://www.infoflora.ch); some dozens of sites are reported from the W part of Austria with the focus near the Bavarian border (Hennekens, 2018; www.flora-austriaca.at). In Germany, > 100 historical sites existed but UI is extinct in some German states. After 1990, UI is spread mainly in SE Baden-Württemberg, S Bavaria and in E Germany between the Elbe and Oder rivers with the reach over to SW Poland; some sites are also in N Bavaria and Lower Saxony (Kleinsteuber, 1996; Hofmann, 2001; Fleischmann and Schlauer, 2014; Hennekens, 2018; www.floraweb.de/pflanzenarten/register). Around 20 sites are in S and W Denmark (Hennekens, 2018); after 2000, three records are from the Province of South Tyrol in N Italy (http://www.florafauna.it/index) but they are considered a misidentification (for US) and UI does not occur in Italy (M. Beretta, unpubl. data). In the Czech Republic, UI recently (2018) occurs only at five sites in the Třeboň Basin, South Bohemia, Czech Republic (L. Adamec, unpubl. data; see Fig. 5): the older records in the Pladias database from W Bohemia include misidentification for UOs.l. Since 2011, two UI sites in the Třeboň Basin have been extinct due to drought (L. Adamec, unpubl. data). After the Flora of Slovakia (Goliašová, 1997), UI is considered extinct for ca. 60 years and has a recent status of a Regionally Extinct species (Eliáš et al., 2015). In Poland in 2001, UI had 326 historical records from all parts of the country with the focus in N Poland, E, SW and S Poland (https://atlas-roslin.pl/htm/wystepowanie-4491.htm). In Estonia, ca. 15 records are from W Estonia and the Saaremaa island (Hennekens, 2018); in Russia, records are from NW Russia from the watershed of the Pechenga river near the Norvegian border, from the floodplain of the Ponoi river in the E part of the Kola peninsula, from E Carpathians and from the watershed of the Dnieper river (i.e., probably W and N Ukraine, Belarus, E Russia; Fedorov, 1981). Localised records of UI exist also from shore regions of Lakes Ladoga and On'ega in Karelia in NE Russia from 1989 (the latter plants are cultured in the Institute of Botany at Třeboň, Czech Republic; L. Adamec, unpubl. data).

In Asia, the historical distribution of UI reaches Armenia on the west and extends from the Urals Mts. to the extreme east of Russia in the Far East (Casper, 1974; Fedorov, 1981; Taylor, 1989; Baikov, 2012; Hennekens, 2018): W and E Siberia, here in the watershed of the big rivers Ob', Jenisej, Angara (Lake Baikal region), Nizhnaya Tunguska and Lena. On the south, in the Tian-Shan Mts. in Kyrgyzstan and NW China, also in S China (Tibet, watershed of the Jinsha Jiang river) and E Nepal. In the Far East, UI extends in the watershed of the Amur river and in Kamtchatka peninsula, in N China (Province Nei Mongol), NE China (Province Heilongjiang, formerly Manchuria), North Korea, in Sakhalin island, Kurilen islands and in Japan (widespread in Hokkaido, scattered in Honshu, a single record in Kyushu). In America, it extends from the eastern coast of the USA (Pennsylvania, New Jersey) to the western coast southwards to N California and from Alaska throughout Canada to Labrador and Newfoundland. The single doubtful record from tropical Africa (Lake Rukwa in Tanzania; Hennekens, 2018) probably represents a misidentification for another *Utricularia* species.

4.1.2. *U. ochroleuca s.l. (U. ochroleuca and U. stygia)*

The older world and European distribution of UO published before ca. 1995–2005 (e.g., Casper, 1974; Taylor, 1989) usually includes both UO and US (i.e., UOs.l.). It also follows from the literature that many (older) records may represent misidentification for UI. UOs.l. has a circumboreal distribution in Europe, Asia and North America similar to UI (Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014). UOs.l. is spread southwards in Europe to ca. 45 °N in SW France, in Asia to ca. 35 °N in Iran and in America to ca. 40 °N in California (Fleischmann and Schlauer, 2014). According to Casper (1974); Thor (1988); Taylor (1989) and Kleinsteuber (1996), UOs.l. has the centre of its European distribution in N and NW Europe – in Fennoscandinavia. In Europe, UOs.l. is distributed in SW Greenland, Ireland, Great Britain (mainly Scotland), Norway, Sweden and Finland (in these three countries, very common with hundreds of records up to 69 °N), Denmark, NW part of Russia, Latvia, N Italy, Switzerland, France, Belgium, The Netherlands, Germany, Austria, Czech Republic and Poland.

More detailed distribution of UO or US in European countries: four records (UOs.l. but misidentification for UI?) are in SW Greenland near the coast (Hennekens, 2018); after 2010, six UO records are in N and NW Scotland, while dozens of US records are in NW Scotland, from the Inner and Outer Hebrides and other adjacent islands, but only three records in N and S England and one in W Ireland (https://bsbi.org/maps); several sites of UOs.l. are in SE Belgium (Hennekens, 2018) but Noé (2011) reports only some sites of UO in central and SE Belgium without any US site; a dozen of UOs.l. sites from the SE of The Netherlands; ca. 30 UOs.l. sites are in France with the focus in coastal SW France S of Bordeaux near the estuary of the Garonne river and in E France (Franche-Comté region; Schäfer-Guignier, 1994) with two sites in NW France (Hennekens, 2018). Around 15 sites of UOs.l. are reported in NW (near the Lake Neuchâtel) and NE Switzerland (near Lake Zurich; Hennekens, 2018; https://www.infoflora.ch). Yet between 2005–2008, Wildermuth (2010) verified only three US sites between the Lakes Zurich and Pfäffikon and has suggested that UO does not occur in Switzerland and that, probably, it has never occurred in this country. However, he has recently confirmed the three last US sites in Switzerland, two of them in the Nature Reserve Drumlinlandschaft Zürcher Oberland in SE part of the Canton of Zurich (Wildermuth, 2016 and pers. comm., 2019).

Several UO sites are reported from the W and S part of Austria between 2006–2016 (states Vorarlberg, Tirol, Kärnten; www.flora-austriaca.at) but the only US site at Seefeld W of Innsbruck in Tirol; Zidorn, 1996). Dozens of historical sites of UOs.l. are known from Germany (Casper, 1974; Kleinsteuber, 1996; Hofmann, 2001; Fleischmann and Schlauer, 2014; Hennekens, 2018; www.floraweb.de/pflanzenarten/register). As follows from records after 1990 or even more recently (Kleinsteuber, 1996; Hofmann, 2001; Fleischmann and Schlauer, 2014; www.floraweb.de/pflanzenarten/register), UO is distributed in Germany only in S and NE part of Bavaria, at a few sites in the SE tip of Baden-Württemberg near the Bavarian border and more sites are in E Germany between the Elbe and Oder rivers in states Brandenburg and Saxony (in SE tip of Saxony with the reach over to SW Poland; cf. Kosiba, 2004; https://atlas-roslin.pl/htm/wystepowanie). The spread of US in Germany after 1990 is similar to but more numerous than that of UO: several sites in SW part of Baden-Württemberg in the Black Forest Mts. and three sites in the SE tip of this state close to the Bavarian border, ca. 15 sites are in S and two in NE Bavaria, one is near Paderborn in the E part of Nordrhein-Westfalen and ca. a dozen sites are mainly in the SE tip of Saxony (Lusitia; Kleinsteuber, 1996; Hofmann, 2001; Fleischmann and Schlauer, 2014; www.floraweb.de/pflanzenarten/register). Around 10 historical sites of UOs.l. are reported in Denmark (Hennekens, 2018). In N Italy, all three extant sites of UOs.l. have been ascribed to US, while UO does not occur (Tassara, 2002; Beretta and Tassara, 2010a). US occurs in Lakes Monticolo and Caldaro in Trentino Alto Adige region in Bolzano county in South Tyrol Province, and at a montane site near Cortina d'Ampezzo in Belluno county in Veneto Province.

In the Czech Republic, UO and US have been distinguished since 2003 (Płachno and Adamec, 2007). UO has only three extant (2018) smaller sites in peat bogs adjacent to eutrophic fishponds in the Třeboň Basin in S Bohemia (all micropopulations are cultured in the Institute of

Botany at Třeboň; L. Adamec, unpubl. data). Over the last ca. five years, one UO site was extinct due to drought in the region. The extant natural spread of US in the Czech Republic includes six natural sites in the Třeboň Basin in S Bohemia, probably two sites (peaty fishponds) in the W tip of the country near Františkovy Lázně and another two sites in the foothills of the Bohemian Forest Mts. in the watershed of the Vltava river in SW Bohemia (both groups of sites misidentified as UO in Pladias, 2020; L. Adamec, unpubl. data). In the last ca. 20 years, two US sites were extinct in the Třeboň Basin. On the other hand, US has been successfully introduced to a dystrophic wetland in the Třeboň Basin (Adamec and Kučerová, 2013b). Another artificial site in the Česká Lípa district in N Bohemia (misidentified as UI in Pladias, 2020) was extinct due to drought in 2018 (M. Studnička, unpubl. observ.). In Poland, 24 sites of UOs.l. were reported mainly in S, SW and NW part of the country in 2001 (https://atlas-roslin.pl/htm/wystepowanie). However, a reliable occurrence of US has not yet been verified in Poland (Ł. Krajewski, unpubl. data) and thus, all data may refer to UO.

Two UOs.l. records are in NE Estonia (Hennekens, 2018). UOs.l. is recorded from Latvia and from Karelia and Murmansk county in NE Russia; Fedorov, 1981). In 2018, UO was found in Leningrad county near the E shore of Lake Ladoga (P.A. Volkova and L.A. Abramova, unpubl. data). The previous record (from 2001) of UOs.l. from the Tolvojarvi Nature Reserve NE of Lake Ladoga in the Suojarvi district in Karelia has been re-determined as US (Kravchenko et al., 2014). According to Kravchenko and Kuznetsov (2010), US was recorded at two sites in Karelia and at several in Murmansk county.

In Asia, there are UOs.l. records from N Afghanistan, E Siberia (Yakutsk and Magadan counties), E and W Chukotka, Kamtchatka peninsula, the Russian Far East (Baikov, 2012); according to recent unpublished data by O.A. Mochalova and A.A. Bobrov (see also Kravchenko and Kuznetsov, 2010), most of the newly revised records from Chukotka, Kamtchatka and the Russian Far East belong to US but UO is also distributed in the Russian Far East and several records are from Japan. In North America, UOs.l. extends from the NE part of the USA and E Canada (Labrador, Nova Scotia) to the western coast southwards to Oregon, N California and Colorado, and on the north from NW Canada to Alaska (Casper, 1974; Taylor, 1989; Schlosser, 2003; Hennekens, 2018).

4.1.3. *U. bremii*

UB has a West-Central European boreo-temperate distribution with its centre in Central Europe (Casper, 1974; Taylor, 1989; Fleischmann and Schlauer, 2014) though the last authors state also one isolated site in Japan (see Goliašová, 1997), but the Japanese plants are not identical with the European plants.

However, literature sources commonly admit that many UB records may represent a confusion with *U. minor*. Historical records of UB are from Ireland, Great Britain, France, Belgium, Germany, Denmark, Switzerland, Italy, Austria, Hungary, Czech Republic, Slovakia, Poland, Romania, Ukraine and NW Russia (Casper, 1974; Taylor, 1989; Kleinsteuber, 1996; Fleischmann and Schlauer, 2014).

More detailed distribution of UB in European countries: after 2010, there is no record in Ireland; in Great Britain, only one site is reported from S England near Southampton (https://bsbi.org/maps); no recent record in Belgium (Noé, 2011) and The Netherlands (Hennekens, 2018). In Germany, the three former sites in the basin of the Rhine river in the W part of Baden-Württemberg close to the French border are extinct (Kleinsteuber, 1996) and after 1990, UB is distributed only at four sites in N Bavaria (in the watershed of the Main river close to Nurenberg), one site in S Bavaria (Fleischmann and Schlauer, 2014) and one site in Hessen (www.floraweb.de/pflanzenarten/register). Several sites have recently been verified near Lyon in NE France (Christians, 2016). In Switzerland after 2010, ca. 10 sites were verified, mainly N of Lake Zurich (https://www.infoflora.ch.en; Wildermuth, 2016). Five recent sites of UB were reported from N Italy in 2010 (Beretta and Tassara, 2010b; Beretta et al., 2011): Lakes Caldaro and Monticolo near Bolzano, a shallow wetland (infilled lake) in the suburb Porto Mantovano of Mantova, a peat bog at Pian del Tivano near Como close to the Swiss border and lagoons near Mercurago N of Novara. In Austria after 2006, several UB records are from the Kärnten and Tyrol states on the S and W of the country (www.flora-austriaca.at).

In the Czech Republic, UB was considered extinct for 20 years till 1999 when a new site was found in S Bohemia, and several sites were found then (Kaplan et al., 2011). UB had ca. ten natural sites in three regions in 2010 (Macák, 2006; Vydrová et al., 2009; Kaplan et al., 2011) and, moreover, UB has been introduced to another region after 2008 (Adamec and Kučerová, 2013b; Kučerová et al., 2016). Three recent sites exist in the fens Dlouhá louka and Hůrky NW of Pilsen, four sites are in peat bogs near Hamr na Jezeře (Černý fishpond) and Doksy (Máchovo jezero fishpond) in the Česká Lípa district in the Liberec county in N Bohemia, and two natural sites are in the Budějovická Basin NW of České Budějovice in S Bohemia: an old shallow, partly forested sand-pit near Munice and forest pools after kaolin mining near Zahájí (a complex of adjacent ca. 10 pools inhabited by UB; Macák, 2006; Vydrová et al., 2009; Kaplan et al., 2011; Pladias, 2020). Moreover, between 2008–2012, UB was introduced to small shallow pools in four sand-pits in the Třeboň Basin in S Bohemia where numerous micro-populations have arisen: at Cep I near Suchdol nad Lužnicí, Rozvodí Lužnice, Branná and at Hluboká u Borovan (Kaplan et al., 2011; Adamec and Kučerová, 2013b; Kučerová et al., 2016). In Slovakia after about 60 years of being considered extinct, UB was rediscovered in fen pools at Hanšpilje near Plavecký Peter in Záhorská lowland in Senica district in W Slovakia (Dítě et al., 2013; Eliáš et al., 2015). In Poland in 2009, an abundant population of UB was found in shallow pools and ditches in a large excavated sand-pit complex at Kuźnica Warężyńska near Dąbrowa Górnicza in Katowice county in Upper Silesia in S Poland (Krajewski and Płachno, 2015). According to the authors, this may be the only recent Polish UB site as the other historical sites were misidentifications. Four UB sites were recorded from Hungary after 1990 (Bartha et al., 2015): two sites are N of Lake Balaton in W Hungary and two were near the Danube river in central Hungary.

Fedorov (1981) states historical sites from the former Soviet Union only from the East Carpathians, which agrees with Casper (1974) who states the area of the upper reaches of the Dniester river – i.e., W Ukraine. However, UB is now extinct in Ukraine, where it was known only from a single site in Transcarpathia (Kish and Danilik, 2009). A UB site was found on Kizhi island in the N part of Lake On‘ega in Karelia in NW Russia in 1989 and the plants have been cultured in the Institute of Botany at Třeboň, Czech Republic, since (L. Adamec, unpubl. data). It is thus highly probable that UB is distributed more frequently in NW Russia and is misidentified as *U. minor*.

4.2. Habitats and plant communities

The habitats of UI, UO and US (UOs.l.) are very similar to each other and, also due to the similarity of ecological requirements of these species, they can grow together: four cases are known in the Třeboň Basin, Czech Republic (L. Adamec, unpubl. data). The habitats of UB are partly different and a co-occurrence of UB with the other three rare *Utricularia* species is very rare (e.g., UI and UB on Kizhi island in Lake On‘ega in Karelia, NW Russia; L. Adamec, unpubl. data).

UI, UO and US can grow in a variety of habitats in shallow standing, strongly dystrophic, more or less acidic waters. In Europe, they usually grow on margins of fens or peaty lakes, peaty fishponds, mainly in shallow depressions (pools) in peat bogs and fens, in mineral-poor wet meadows and also in anthropogenic areas formed after peat or fen extraction and adjacent drainage ditches or canals (Casper, 1974; Melzer, 1976; Pietsch, 1977; Taylor, 1989; Schäfer-Guignier, 1994; Kleinsteuber, 1996; Hofmann, 2001; Adamec and Lev, 2002; Kosiba, 2004; Adamec, 2007a, 2010a; Fleischmann and Schlauer, 2014; Wildermuth, 2016).

In temperate Europe, UI can grow from lowlands to highlands and its altitudinal limit may be 900 − 1450 m a.s.l. (Casper, 1974). UI usually grows in free water depths of 0 − 30 cm (up to 1 m; Melzer, 1976) but may also grow terrestrially, above > 5 cm of an organic, loose sediment (peat; see Fig. 5). Seasonal water level fluctuations of 10 − 30 cm are common at the sites (e.g., Schäfer-Guignier, 1994; Navrátilová and Navrátil, 2005a). However, greater fluctuations might be deleterious for the plants affixed to the bottom growing in dark water due to shortage of light. According to the dominant vegetation from various studies, typical habitats of UI represent *Sphagnum* or loose sedge stands (co)dominated mostly by *Sphagnum* spp., *Carex rostrata, C. lasiocarpa, C. elata, Eriophorum angustifolium, Juncus bulbosus, Sparganium natans, Utricularia minor, U. australis* and *Drepanocladus fluitans* (Casper, 1974; Pietsch, 1977; Hofmann, 2001; Navrátilová and Navrátil, 2005a, 2005b; Adamec, 2007a, Adamec, 2010a; Fleischmann and Schlauer, 2014). Although sites of UI in Central Europe commonly extend to one hectare of total area, the UI stands are often limited to only dozens or hundreds of m^2 and the same may also apply for UO and US (Pietsch, 1977; L. Adamec, unpubl. data). As summarised by Pietsch (1977) and Hofmann (2001), UI occurs most often within the plant associations of the order *Utricularietalia intermedio-minoris*, for which the following accompanying species are typical: *Utricularia minor, U. ochroleuca* s.l.*, U. australis, Sparganium natans* and *Drepanocladus fluitans*, and form the association without mosses *Utricularietum intermedio-minoris*. Within the alliance *Sphagno-Utricularion*, it is most commonly found in the association *Sphagno-Utricularietum intermediae*, but also in associations *Sparganietum minimi, Scorpidio-Utricularietum* and those belonging to units *Eriophorion latifolii* or *Scheuchzerietalia* (Fleischmann and Schlauer, 2014).

From the literature, the habitats and phytosociological classification of UO and US are either the same or were not differentiated previously (e.g., Casper, 1974; Adamec, 2007a; Fleischmann and Schlauer, 2014). In temperate Europe, UO and US can grow from lowlands to highlands and their altitudinal limit may be up to 1300 − 1600 m a.s.l. (Austria, N Italy; Zidorn, 1996; Beretta and Tassara, 2010a). UO and US usually grow in shallow water 0 − 10 cm deep above an organic, peaty sediment and their terrestrial growth on wet substrate is also common (e.g., Thor, 1988; Kleinsteuber, 1996; Adamec, 2007a; Fleischmann and Schlauer, 2014). However, unlike UI, they also grow at 1–3 (5!) m depth (Melzer, 1976). Typical habitats of UO and US are usually dominated by *Sphagnum* spp., *Utricularia minor*, *U. australis*, *Juncus bulbosus, Lemna minor, Drosera intermedia, Carex rostrata, Rhynchospora alba* and *Drepanocladus fluitans* (Casper, 1974; Pietsch, 1977; Kleinsteuber, 1996; Hofmann, 2001; Navrátilová and Navrátil, 2005a; Adamec, 2007a; Fleischmann and Schlauer, 2014). UO and US occur most often as a diagnostic species within the plant association *Sphagno-Utricularietum ochroleuci* (or *Sphagno-Utricularietum stygiae*) of the alliance *Sphagno-Utricularion* and also within the *Rhynchosporion albae*.

Due to its rarity, the published data on the habitats and vegetation preferences of UB are much more sparse than those of the other rare *Utricularia* species. UB grows in shallow standing dystrophic, more or less acidic, soft waters in pools (depressions) in peat bogs and fens, in pools and canals after peat or fen extraction, on peaty shores of lakes and fishponds, but also in clear, non-dystrophic soft waters on the shallow shores of (usually old) sand-pits above clayish sand. It usually grows at 1 − 20 cm water depths, rarely much deeper, in lowlands or rarely in highlands to ca. 950 m a.s.l. (Casper, 1974; Kleinsteuber, 1996; Vydrová et al., 2009; Beretta et al., 2011; Kaplan et al., 2011; Adamec and Kučerová, 2013b; Dítě et al., 2013; Fleischmann and Schlauer, 2014; Krajewski and Płachno, 2015). In Czech sand-pits, it often grows in the terrestrial ecophase (Adamec and Kučerová, 2013b). UB usually co-occurs with *Sphagnum* spp., *Juncus bulbosus, J. articulatus, Eleocharis acicularis, Carex* spp. and *Utricularia australis*. Dítě et al. (2013) characterised UB as a member of species-poor vegetation of shallow mire pools and also as a diagnostic species of the alliance *Sphagno-Utricularion* (see also Kleinsteuber, 1996; Fleischmann and Schlauer, 2014). Vydrová et al. (2009) recorded several types of aquatic

Table 2

Summary of important water chemistry factors at European sites in stands of the four rare *Utricularia* species from the literature. TA, total alkalinity (approx. HCO$_3^-$ concentration); GH*, carbonate hardness as German Hardness (values of GH labelled by asterisk; GH = [Ca^{2+} + Mg^{2+}]; theoretically 1 meq/l TA ≈ 2.8 deg. GH); conduct., electrical conductivity. Range of values or mean (median) value ± SD interval is shown for groups of microsites, Ref., references; 1, Adamec and Lev, 2002; 2, Adamec, 2007a; 3, Adamec, 2010a; 4, Navrátilová and Navrátil, 2005a; 5, Kosiba and Sarosiek, 1989; 6, Kosiba, 2004; 7, Schäfer-Guignier, 1994; 8, Pietsch, 1977; 9, Hofmann, 2001; 10, Adamec, 1999; 11, Kosiba, 1993; 12, Melzer, 1976; 13, Dierssen and Dierssen, 1984; 14, Adamec, 2009; 15, Cross et al., 2016; 16, L. Adamec, unpubl. data; 17, Dítě et al., 2013; 18, Peroutka et al., 2008.

Spec.	Country, region	Habitat	pH	TA or GH* meq/l; deg.*	Conduct. mS/m	NO$_3$-N µg/l	NH$_4$-N	PO$_4$-P	Ca^{2+} mg/l	Ref.
UI	Czech R., Třeboň Bas.	5 bogs	4.85-6.62	0.27-1.89	–	–	2-237	–	8.1–19.4	1
UI	-“”-	3 bogs	5.63-7.10	0.18-1.16	12.7-22.7	0	37-121		5.7–19.9	2
UI	-“”-	peat bog	6.03-6.12	0.62-1.04	11.3-18.9	–	0-9.3	18-47	–	3
UI	-“”-	5 bogs	3.5–6.3	–	3.6-25.5	28	222	14	12.9	4
UI	Poland, Lower Silesia	pond	5.16-6.21	4.5-8.4*	–	2310-2730	3200-7380	130-210	12.4–19.4	5
UI	-“”-	5 sites	5.22 ± 0.62	2.82 ± 1.21*	–	1160 ± 360	1080 ± 410	620 ± 120	28.0 ± 8.6	6
UI	E France, Jura Mts.	fens	7.4	4.2-6.6*	14-20	–	–	–	–	7
UI	Europe, 176–238 sites	various	4.1–8.5	–	< 2.0- > 12.0	–	–	–	< 1- > 30	8
UI	Germany, Niedersach.	2 bogs	5.1–5.2	–	10.1–10.4	480-550	10-100	34-61	16.2–17.8	9
UO	Czech R., Třeboň Bas.	fen pools	6.46-6.87	1.02-1.79	–	0-2	25	14-18	32.0–37.8	10
UO	Poland, Lower Silesia	ditch	5.73-6.89	4.3-10.0*	–	1730-6110	5090-9430	60-710	10.7–37.1	11
UO	-“”-	5 sites	6.05 ± 0.73	2.92 ± 1.41*	–	1900 ± 850	610 ± 290	440 ± 290	35.5 ± 12.1	6
US	Czech R., Třeboň Bas.	8 bogs	5.48-8.77	0.15-2.55	–	–	0-225	–	4.8–31.8	1
US	-“”-	4 bogs	5.80-6.72	0.16-2.21	11.6-30.2	0-20	0-49	18-53	10.8–29.9	2
US	-“”-	peat bog	6.12-6.28	0.82-0.94	15.8-19.2	–	0	12-21	–	3
US	-“”-	6 bogs	3.4–6.2	–	0.90-38.1	34	198	18	5.6	4
US	Germany, Bavaria	2 lakes	7.8-8.3	4.45-4.95	33.0-41.5	1110-1830	6-98	2-6	62.6–81.5	12
US	Germany, Bad.-Würt.	peat bog	5.5–7.5	–	13.3 ± 2.7	–	–	–	–	13
US	Germany, Nordrh.-W.	pond	7.1	–	38.1	1050	340	20	55.3	9
UOs.l.	E France, Vosges	3 ponds	5.2-6.1	0.1-0.2*	1.2-1.5	–	–	–	–	7
UB	Czech R., Třeboň Bas.	3 sand-pits	6.13-7.01	0.11-0.46	3.0-10.8	–	0.2-19	11-16	–	14
UB	-“”-	2 sand-pits	6.18-6.98	0.05-0.17	3.3-35.8	0	0.9-41	1.9-25	–	15
UB	Czech R., S Bohem.	2 pools	5.90-6.60	–	7.0–9.0	–	–	–	–	16
UB	Czech R., S Bohem.	sand-pit	5.38	–	1.2	–	–	–	–	16
UB	W Slovakia, Záhorie	fen pool	7.0	–	27.2	–	–	–	–	17
UB	Austria, Vorarlberg	fen pool	6.8	–	42.4	–	–	–	–	18

plant communities at the largest Czech UB site near Zahájí. It was found in communities of floating (*Lemno-Utricularietum*, *Utricularietum australis*) or rooting aquatic plants (*Potametum natantis*) and in the vegetation of stoneworts (*Nitelletum flexilis, Charetum globularis*).

4.3. Habitat ecology and ecological requirements

The summarised values of important parameters of water chemistry (pH, total alkalinity/carbonate hardness, electrical conductivity and concentrations of ammonium, phosphate and Ca^{2+}) show that the four rare European *Utricularia* species (Table 2), can surprisingly grow within very broad ranges of all these water chemistry factors. UI, UO and US and could thus be considered at least moderately eurytopic, while UB, in spite of great shortage of data, should be considered stenotopic. The ecological plasticity of the three species from the UI aggr. is further supported by their ability to grow terrestrially on wet substrates which renders them independent of water chemistry in relation to photosynthetic CO_2 uptake.

All three species are able to tolerate great ranges of pH (Table 2; UI, 3.5–8.5; UO, 5.7–6.9 /but only three studies/; US, 3.4–8.8), total alkalinity (i.e., approx. concentration of HCO_3^-) and/or carbonate (German) hardness (i.e., sum of concentrations of Ca^{2+} and Mg^{2+}), concentration of Ca^{2+} (in all three species ca. 4–30 times) and electrical conductivity (in UI and US more than 30–40 times). The surprisingly low pH values of 3.4–3.5 at UI and US microsites (Navrátilová and Navrátil, 2005a), which were repeatedly measured only in mid-April before the growing season, did not relate to pH values occurring during the growing season, which were much higher (> 4.5-5.0; cf. Pietsch, 1977). Such great ranges of crucial parameters of water chemistry, which determine basic differentiation of fresh waters, clearly confirm that UI, UO and US can grow as favourably in very acidic, soft, Ca-poor and strongly dystrophic waters (peat bogs, e.g., Třeboň Basin, Czech Republic) as well as in neutral or moderately basic, very hard, Ca- and HCO_3^--rich and weakly dystrophic waters (fens, lakes, ponds, e.g., Bavaria, Germany). It follows therefore from the data for all three species that pH or total alkalinity (and/or carbonate hardness) in itself are not important for plant occurrence. However, these species are photosynthetic strict CO_2 users (Adamec and Pásek, 2009; see Adamec, 2018a, Adamec, 2018b and *4.5.*) and require a relatively high CO_2 concentration in the water: $free-CO_2$ concentrations from 1.0 to 6.5 mM were estimated in the ambient water at several sites of UI and from 0.02 to 4.9 mM at sites of US in the Třeboň Basin, Czech Republic; the medians for both species were ca. 1.1 mM (Adamec and Lev, 2002; Adamec, 2007a, 2010a). Surprisingly high CO_2 concentrations from 0.05-0.19 mM also result from the water chemistry data at US sites in two alkaline (pH 7.8–8.3), hard water Bavarian lakes in Germany (Melzer, 1976); similarly high CO_2 concentrations or even higher can also be deduced from many other water chemistry data shown in Table 2. High CO_2 concentrations originate from the decomposition of organic, peaty sediments, to which carnivorous shoots of these species penetrate. The intersticial water in these sediments usually contains higher CO_2 concentrations than those in the ambient water (Adamec, 2007a). In analogy with ecologically similar *A. vesiculosa* (cf. Adamec, 2018d), it may be concluded that a high CO_2 concentration (minimum ca. 0.05-0.1 mM; optimum ca. 0.8–1.5 mM) should occur in the water in the stands of these *Utricularia* species to support rapid plant growth and propagation.

Decomposition of peaty sediments at microsites of UI, UO and US and oversaturation by CO_2 are associated with marked undersaturation by O_2 in the ambient water. At UI and US microsites in S Bohemia, Czech Republic, and in NW Germany, O_2 saturation reached 23–116 % in the open water (on average ca. 48 %; Hofmann, 2001; Adamec and Lev, 2002; Adamec, 2007a, 2010a), but in loose sediments at 10 cm depth only ca. 0.3–2 % (Adamec, 2007a). Carnivorous shoots with traps thus may suffer from an O_2 shortage. It is suggested that O_2 diffuses from photosynthetic to carnivorous shoots via gas spaces in analogy with roots of submerged aquatic plants (Adamec, 2007a). Moreover, both UI and US tolerate a wide range of dystrophy of the stand water: from clear, slightly brownish to dark brown waters and the concentration of humic acids + tannins (as a criterion of dystrophy and water colour) ranged from 10.5 to 58.7 mg/l in UI and from 4.3 to 63.9 in US with optima between $15-25$ mg/l for both species (Adamec and Lev, 2002; Adamec, 2007a, 2010a). Similar data for UO are lacking but they could be similar to those for US.

At seven sites of UI or US in S Bohemia, the concentration of humic acids + tannins in the intersticial sediment water was on average by 40 % higher than that in the ambient stand water (Adamec, 2007a) indicating which zone is the source of these substances. According to concentrations of NO_3^-, NH_4^+ and PO_4, the most waters at UI, UO and US sites could be characterised as oligo-mesotrophic up to slightly eutrophic (Table 2). Extreme concentrations of all these nutrients (extending the usual ones by one to two orders of magnitude) were only recorded in industrial and agricultural regions (Lower Silesia, Poland, or Bavaria and Nordrhein-Westfalen, Germany) and could be caused by agricultural or municipal pollution. Generally, the concentration of NH_4^+-N, which is the main mineral form of N taken up by aquatic *Utricularia* species (Adamec, 2016b, Adamec, 2018a, 2018b), were usually within the range from $2-200$ μg/l and around the same ($10-120$ μg/l) for PO_4-P. At seven UI or US sites in S Bohemia, a highly significant linear correlation was confirmed between the total nitrogen (N_t) concentration pooled for the ambient water and sediment, and the concentration of humic acids + tannins (Adamec, 2007a). It shows that the main N_t pool (ca. 80–90 %) at the sites consisted of organic nitrogen contained in humic acids. At some Polish, German and Czech sites of the three species, surprisingly low K^+ concentrations between 0.01–1.1 mg/l were found in stand waters (Melzer, 1976; Kosiba and Sarosiek, 1989; Kosiba, 1993, 2004; Hofmann, 2001; Adamec and Lev, 2002; Navrátilová and Navrátil, 2005a), some of which were rich in Ca^{2+}. In these hard waters, the molar Ca/K ratio even extended to 100-1000. In UI and UO shoots growing in such waters in Silesia, Poland, shoot K content was only 1.34 and 1.08 % DW, respectively (Kosiba and Sarosiek, 1989; Kosiba, 1993; cf. Adamec, 2010c: 1.81–2.05 % DW).

What are differences in ecological requirements between UI, UO and US? Due to a shortage of available data (see Table 2), an ecological difference between UO and US cannot be ascertained. Judging from the fact that much more US sites than UO ones have recently remained in Europe (see *4.1.*), one could assume that US either has a broader amplitude of some habitat factors than UO or is competitively stronger or less vulnerable. Ecological differences between UI and UO/US are also ambiguous. Firstly, UI and UO/US can grow together at the same microsite and, also, most of habitat factors greatly overlap (Table 2). Adamec and Lev (2002) and Adamec (2007a) studied habitat factors at several similar UI and US microsites in the Třeboň Basin, Czech Republic. Out of all factors investigated which could differentiate between the species, only the level of shading on the water surface in plant stands (i.e., % of incident PAR irradiance at the level of photosynthetic shoots; Adamec and Lev, 2002) was weakly ($P < 0.05$) statistically different: UI grew in shadier spots (on average only 10 % incident irradiance, range 2–29 %), while US grew in much lighter spots (average 25 %, range 2–100 %). Thus, US/UO is highly tolerant of PAR irradiance level and can grow both in deep shade of ca. 2 % of incident irradiance as well as in full sunlight, with an optimum of about 15–30 (50)% irradiance. While UI prefers more shaded microhabitats with an optimum of only about 8–15 % irradiance; i.e., it is a facultative sciophyte which grows in full sunlight only on rare occasions (Adamec and Lev, 2002). Therefore, the main difference in light requirements between US/UO and UI is that US/UO often grows over wet peaty soils or *Sphagnum* spp. in a terrestrial ecophase in full sunlight and the plants are then reddish to dark red (see *2.1.*). While UI can only grow in full sunlight as submerged plants and its shoots are then only yellow-green or rose. Light conditions at sites could thus at least partly account for the segregation of sites by these species.

Relatively low total dry biomass of UI and US was estimated even in their very dense stands (cover 80–100 %) in the Třeboň Basin, Czech Republic. Mean DW of UI was 40.2 (range 14.7–97.2) g/m^2 and somewhat lower (mean 17.1, range 2.4–35.9 g/m^2) for US stands (Adamec and Lev, 2002; Adamec, 2007a). The mean dry biomass in the densest stands of UI and US is thus one to two orders of magnitude lower than that of other submerged or emergent aquatic plants (cf. Pokorný and Ondok, 1991).

In conclusion, the ecological requirements of UI, UO and US are fairly similar to those which have recently been listed for the ecologically very similar aquatic carnivorous plant *Aldrovanda vesiculosa* (Adamec, 2018d). If UI, UO and US are able to tolerate very broad amplitudes of important water chemistry factors themselves, but they are all very rare in Central Europe, it indicates that a shift from the optima of these factors may not be the primary reason for their decline or extinction at natural sites. It is rather a consequence of extensive vegetational, successional habitat changes (shift of dominant vegetation, overgrowing by tall dominants) primarily caused by other general unfavourable factors such as seasonal drought and/or water eutrophication leading to overgrowing of shallow, small-sized microhabitats by competitively strong vegetation and finally to their infilling (cf. Hofmann, 2001; Navrátilová and Navrátil, 2005a; Wildermuth, 2016; Adamec, 2018d for *A. vesiculosa*). Therefore, marked seasonal fluctuations of the water level at UI, UO and US microsites and temporary high water levels have been recognized as essential to prevent the development of dense stands of highly competitive wetland cyperoids and graminoids (Navrátilová and Navrátil, 2005a). Nevertheless, very high and sudden water level rises ($>$ 40 cm) at strongly dystrophic sites could also be harmful for the *Utricularia* species due to extreme shading. A disturbation of overgrowing and very shallow microsites of the rare *Utricularia* species by big animals (roe deer, wild pigs) leading to deeper depressions could also be favourable for a long-term sustainable state of the sites.

Limited data on water chemistry at UB sites (Table 2) suggest that UB is partly a stenotopic species preferring only slightly acidic to neutral, very soft to slightly hard, oligo-mesotrophic waters (see also Christians, 2016). Yet it can grow well both in strongly dystrophic and clear waters, in peat bogs as well as sand-pits over peaty soil and clayish sand (see *4.1.3.*). At three Czech UB sites in sand-pits, CO$_2$ concentration in the ambient water was only moderately increased (0.11-0.34 mM; Adamec, 2009). Unlike the very similar *U. minor*, which commonly also grows in hard and alkaline waters (e.g., Melzer, 1976; Adamec, 1999), UB probably avoids hard waters but both species can grow together (Kaplan et al., 2011). Light conditions in UB stands have never been measured, but UB tolerates a great range of irradiances: deep shading in forest pools (Vydrová et al., 2009) as well as full sunlight on the shores of shallow sand-pit pools where it commonly grows in the terrestrial ecophase on moist sand (Adamec and Kučerová, 2013b). Species-poor, very shallow (0.5 − 5 cm) microhabitats in a shallow sand-pit pool without water level fluctuations and in full sunlight may represent an ecological optimum for this species, which is characterized by high cover and stand biomass and prolific flowering (see Fig. 11).

4.4. Prey spectrum

Harms (1999) gave a detailed description of the prey spectrum and prey selection characteristics for UI and US, in addition to *U. minor* and *U. vulgaris,* at 10 sites in N Sweden. As she was not able to reliably differentiate between UI and US, she pooled all data for both species together. The mean trap size of UI/US plants was 2.96 ± 0.60 mm (range 1.33–4.73 mm). On average 76 % of all traps contained animal prey. The traps totally captured most of all the following taxa: Cyclopoida (of Copepoda), Ostracoda, Acari, genera *Acroperus, Alona, Alonella* and *Chydorus* of the family Chydoridae and Dipteran larvae. When compared with the potential prey availability at the microhabitats, the traps markedly selectively captured Ostracoda, Cyclopoida, Coleopteran larvae and *Alonella*. Thus, the traps of UI/US poorly captured planktonic or sediment-based prey items, but selectively captured those climbing on plants (i.e., phytophilous organisms) with an intermediate mobility; highly as well as poorly mobile prey items were not preferred. Around 40 % of the prey items fell into the 1 − 4 mm size category of, 35 % were $<$ 1 mm and 25 % were $>$ 4 mm. Medium-sized (2.2–3.2 mm) and large (3.3–4.7 mm) traps captured $>$ 95 % of all prey items. The prey spectrum characteristics of UI/US markedly overlapped with those of *U. vulgaris* due to similar trap size, although the latter species grew in deeper waters. Peroutka et al. (2008) investigated the content in mature traps in UB plants growing in a highland fen in Vorarlberg in S Austria. Out of all traps, 66.1 % traps caught any animal or algal prey, 15.7 % traps caught only animals, 19.1 % traps caught only algae, 31.3 % traps caught both animals and algae, and 16.5 % traps contained only detritus. Dead algae dominated in the traps. In total, seven caught algal genera were determined in the traps. The authors concluded that algal prey might have a great importance for the nutrition of aquatic *Utricularia* species (‘vegetarian plants‘). When traps of UI, UO and US grow in peaty sediments they often contain a lot of aspirated brown humic acids (L. Adamec, pers. observ.).

4.5. Ecophysiological characteristics and carnivorous traits

The four rare *Utricularia* species were used in a variety of ecophysiological studies dealing mainly with photosynthesis, dark respiration, mineral nutrition and trap characteristics. All four species are typical aquatic photosynthetic C3 plants and strict CO$_2$ users, like all other aquatic *Utricularia* species (Adamec, 2006, Adamec, 2011d, Adamec, 2018a, Adamec, 2018b; Adamec and Pásek, 2009). The latter authors compared photosynthetic compensation points of CO$_2$, as a measure of photosynthetic CO$_2$ affinity, in photosynthetic shoots of UI, US and UB plants raised under nearly-natural conditions in outdoor containers, with CO$_2$ compensation points of the same species grown *in vitro* in a half-strength Gamborg B5 liquid medium with 2.5 % sucrose. The CO$_2$ compensation points of UI, US and two distant UB populations grown outdoors (at pH of 7.5–8.1) ranged from 2.45 to 4.38 μM CO$_2$, whereas those of *in-vitro* grown (at pH of only 3.2) US and UB plants were 5.72 and 8.49 μM CO$_2$, respectively. All these values fall within the usual range of CO$_2$ compensation points in other *Utricularia* species and other aquatic plants (cf. Adamec and Pásek, 2009; Adamec, 2009, Adamec, 2018a, Adamec, 2018b).

In a comparative study (Adamec, 2006), aerobic RD in cut-off traps of UI, UO and UB ranged from 5.2-7.0 mmol $\mathrm{kg_{FW}^{-1}\ h^{-1}}$ or 126 − 153 mmol $\mathrm{kg_{DW}^{-1}\ h^{-1}}$ and exceeded RD in the shoots bearing the traps ca.

Fig. 11. Dense flowering stand of *Utricularia bremii* in a very shallow pool (2 − 5 cm) in a sand-pit near Suchdol nad Lužnicí, Třeboň Basin, S Bohemia, Czech Republic, 15 August 2015. The microsite represents an optimal habitat for this species. All photos by L. Adamec.

2–3 times (both on FW- or DW-basis). Such high RD values of traps are associated with their demanding physiological functions (water pumping, digestion of prey, absorption of prey-derived nutrients; Adamec, 2006, Adamec, 2018a, Adamec, 2018b). On the other hand, the oxygen-based net photosynthetic rate of greenish UB traps measured under favourable conditions was only 75 % of the RD (Adamec, 2006). These relations illustrate high maintenance and photosynthetic costs of traps: in UI and US with dimorphic shoots, the trap RD could cover 34–44 % of the total plant RD but their photosynthetic efficiency is minimal (Adamec, 2006, Adamec, 2007a, Adamec, 2018a, Adamec, 2018b). Unlike the traps, the O_2-based net photosynthetic rate of photosynthetic shoots of UI, UO and UB was very high ($40.0-117$ mmol $kg_{FW}^{-1}\,h^{-1}$ or $645-1860$ mmol $kg_{DW}^{-1}\,h^{-1}$) and exceeded the RD in traps by 5.7–28 times (Adamec, 2006). Such high values of the photosynthetic rate are comparable with those in leaves/shoots of *U. australis* or *U. vulgaris* with monomorphic shoots and are similar to or even higher than the highest values measured in submerged non-carnivorous plants (Adamec, 2006, 2018a). A high photosynthetic rate (30.2-76.6 mmol $kg_{FW}^{-1}\,h^{-1}$ or $148-1049$ mmol $kg_{DW}^{-1}\,h^{-1}$) was also found in old and new segments of sprouting US and UB turions (Adamec, 2011d; see *3.2.*). In summary, the very high photosynthetic rates found in photosynthetic shoots of UI and UO are a prerequisite for the rapid plant growth in these species (associated with the permanent loss of carbohydrates from decaying senescent shoots) and for covering the high maintenance costs of traps (high RD, secretion of many organic substances into the trap fluid; Sirová et al., 2011).

To estimate the mineral cost of carnivory, Adamec (2010c) analysed the tissue nutrient content in photosynthetic and carnivorous shoots (without traps) and traps in UI and US plants raised in an outdoor container. In both species in photosynthetic shoots, the mean N content ranged from 1.16 to 2.66% (DW), P content from 0.21-0.31 %, and K content from 1.81 to 2.05%; in carnivorous shoots (without traps), N content ranged from 0.43-0.58 %, P from 0.085-0.14 %, and K from 1.22 to 1.98%; in traps, N content ranged from 0.67-0.86 %, P from 0.17-0.21 %, and K from 4.82 to 4.87%. Combined with the data on the structural investment in carnivory in these species (Adamec, 2007a), Adamec (2010c) estimated the proportion of the amount of a given mineral element in traps or in carnivorous shoots with traps to the total plant amount, as mineral cost of carnivory. In UI and US, the mineral cost in whole carnivorous shoots was 18.7–33.3 % for N, 32.7–39.6 % for P, 58.7–64.5 % for K, 42.1–45.9 % for Ca, and 40.4–45.9 % for Mg. The values for traps were 11.5–21.5 % for N, 20.3–28.1 % for P, 42.6–53.2 % for K, 13.0–15.2 % for Ca, and 14.9–23.0 % for Mg. Surprisingly, these species with differentiated shoots invest most of the total plant K, Ca and Mg into their carnivorous shoots. Kosiba and Sarosiek (1989) stated a very high P content (ca. 0.92 % DW) in field-grown UI shoots in Lower Silesia, Poland, which suggests that captured prey in traps were also included in the analyses (cf. Kosiba, 1993). A marked polarity of N and P content was found in grown UB shoots between shoot apices and mature shoot segments (Adamec, 2011d). Only isolated photosynthetic shoots of US were able to take up K^+ from a solution of 80 μM in light, whereas carnivorous shoots were not (Adamec, 2016b).

Due to the rarity of the four species, only one experiment on prey feeding was conducted on UB (Adamec, 2011a). After 12 days of the greenhouse-growth experiment, zooplankton-fed plants were markedly and significantly longer with more leaf nodes, their apical shoot growth rate increased from 1.30 ± 0.15 nodes/day in unfed control plants to 2.40 ± 0.14 nodes/day and 3.3 times more branched, but the maximal trap size was the same. Feeding on prey in UB is thus just as important for supporting the growth as in other aquatic carnivorous plants (cf. Adamec, 2018a, Adamec, 2018b). However, in spite of the marked growth increase in fed UB plants, RD in shoot apices stayed unchanged, which has refuted the hypothesis on stimulation of cell divisions in shoot apices as a result of carnivory (Adamec, 2011a).

Due to demanding physiological functions and intensive energy metabolism of the internal structures of *Utricularia* traps (mainly quadrifid and bifid glands; e.g., Juniper et al., 1989), the RD of the traps is very high (see above). As a result of this, the steady-state O_2 concentration inside the prey-free traps of six aquatic *Utricularia* species always approached zero (Adamec, 2007b). In the fluid from excised traps or traps on intact shoots of UI and UO, the mean steady-state O_2 concentration was 0.3–1.4 μM (i.e., 0.01-0.045 mg/l) although the O_2 concentration in adjacent carnivorous shoots was 191–249 μM. Permanent trap anoxia is only interrupted after trap firing for $10-40$ min. Adamec, 2018a has suggested that the extremely low O_2 concentration inside the traps is due to a functional compromise. It should be very low (< 15–30 μM) to reliably kill all caught prey but higher that the threshold for effective aerobic respiration (ca. 0.4 μM) of the trap glands. Trap anoxia thus causes caught prey to die of suffocation, while all living trap commensals are adapted to facultative anoxia (Adamec, 2007b).

Traps of aquatic *Utricularia* species can fire after a mechanical stimulation but also spontaneously (Adamec, 2011b, Adamec, 2011c, 2018; Vincent et al., 2011; Poppinga et al., 2016, 2018; Westermeier et al., 2017) and this was observed also for UI, US and UB traps (L. Adamec, unpubl. data). Adamec, 2011c compared firing and resetting rates of separated traps of 13 aquatic *Utricularia* species. Of these species, UB traps belonged to the markedly above average species in terms of firing and resetting rates, which characterise trap efficiency to fire and reset, while UI and mainly US traps were markedly below the average, both on the absolute scale and per unit trap length or thickness. Adamec and Poppinga (2016) determined the critical negative pressure at which the traps located in air fire and aspirate an air bubble. In 13 species or populations in the generic section *Utricularia*, the mean value of this parameter was -17 ± 2 kPa, while the mean values for UI, UO and US traps fell within a very narrow range from -22 to -25 kPa (Adamec and Poppinga, 2016) and represented the lowest negative pressure of all species within this generic section.

Commensal microorganisms (mainly bacteria, algae, ciliates and rotifers) occur and propagate in the traps of all aquatic *Utricularia* species studied so far (Peroutka et al., 2008; Sirová et al., 2009, 2011, Sirová et al., 2018a, Adamec, 2018b). In some *Utricularia* species, a functional food web of commensal communities was revealed. In traps with captured prey, the communities act as digestive mutualists and facilite prey digestion (Adamec, 2018a, Adamec, 2018b; Sirová et al., 2018a, Sirová et al., 2018b). However, traps secrete a great quantity of organic substances to support these commensals ('gardening'; Sirová et al., 2010, 2011; Borovec et al., 2012). Out of the four rare European species, bacterial counts in the trap fluid and its composition were studied only in US (Sirová et al., 2011; Borovec et al., 2012). Alpha and beta Proteobacteria represented the dominant proportion in the US trap-associated communities both in the trap fluid and in the shoot periphyton in a growth experiment (Sirová et al., 2011). Total bacterial counts in the trap fluid increased three times in the variant with added phosphate to the ambient water but only 1.5 times with added NH_4^+. The concentration of organic carbon in the filtered trap fluid was $25-29$ mM (as C), of N ca. 2 mM and of P 0.055-0.11 mM (cf. Sirová et al., 2009). Within the total C content of 46 analysed organic compounds, the trap fluid of US contained 44 % sugars (mainly glucose, fructose, galactose), 24 % organic acids (mainly lactic acid), 21 % sugar alcohols (mainly mannitol) and 10 % amino acids. Around 24 % of all dissolved organic carbon in the US trap fluid was formed by easily biodegradable compounds. The concentrations of organic substances, N and P in the trap fluid in US were similar to those found in *U. australis* or *U. reflexa*. Nevertheless, as shown by Borovec et al. (2012) in a similar study, the total concentrations of the four main organic substances in the trap fluid were strongly dependent on irradiance and exhibited partly species-specific patterns. In summary, the nutritional role of commensals in prey-free traps is still ambiguous and unclear (cf. Adamec, 2018a, Adamec, 2018b; Sirová et al., 2018a, Sirová et al., 2018b).

5. Genetic data

Chromosome numbers were counted in UI, UOs.l. and UB. UI has 44 (2*n*) chromosomes (Casper and Manitz, 1975), UOs.l. 44 [46, 48] (2*n*) ones (Casper and Manitz, 1975) and UB (from Lake On'ega, NW Russia) 36 (2*n*) ones (Rahman et al., 2001). As found by the latter authors, the UB chromosomes are rather small in size (ca. $1-2$ μm). Rahman et al. (2001) reviewed chromosome numbers in 15 aquatic *Utricularia* species of the generic section *Utricularia* and the numbers found in UI, UOs.l. and UB are the same or very similar to those found in other (European) members (*U. australis*, *U. vulgaris*, *U. minor*). Veleba et al. (2014) has recently compared genome size and genomic DNA base composition (i.e., GC content) in 71 *Utricularia* species across all available genomic sections. UI had 203 Mbp (1C) with the GC content of 39.2 % and exactly the same values were found in UO, while US had 315 Mbp with the GC content of 40.6 %. UB had 299 Mbp with the GC content of 40.1 % (similar *U. minor* had 190 Mbp and the GC 38.8 %). In conclusion, the genome size in all four rare European *Utricularia* species is rather small, distinctly undersized within higher plants, and is comparable to or double that of the model species *Arabidopsis thaliana* (157 Mbp; Veleba et al., 2014). In a recent DNA sequencing study (Astuti et al., 2019), incongruences found between plastid and nuclear networks for the sterile species UO and US support the hypothesis of their hybrid origin (see also *2.4.*). Nevertheless, the DNA mutation rate in (aquatic) *Utricularia* species, even among neighbouring populations, is very high (see e.g., Veleba et al., 2014; Jobson et al., 2018; Astuti et al., 2019; A. Fleischmann, unpubl. res.). This impedes the performance of reliable molecular comparisons of highly related species using DNA sequencing. Hybridization between any of the four species is not known.

6. Threads and conservation

It follows from the many studies on European distribution, habitat factors and ecological requirements of UI, UO, US and UB conducted or compiled during the last 20–30 years (e.g., Kosiba and Sarosiek, 1989; Kosiba, 1993, 2004; Schäfer-Guignier, 1994; Kleinsteuber, 1996; Hofmann, 2001; Adamec and Lev, 2002; Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b; Adamec, 2007a; Beretta and Tassara, 2010a, Beretta and Tassara, 2010b; Wildermuth, 2010, 2016; Kaplan et al., 2011; Adamec and Kučerová, 2013b; Dítě et al., 2013; Fleischmann and Schlauer, 2014; Bartha et al., 2015; Krajewski and Płachno, 2015; Hennekens, 2018; see also 4), that the dominant majority of their historically known European sites (except Fennoscandinavia) have vanished over the last 80–120 years. This trend is especially conspicuous in Central and Western European countries (Germany, Poland, Czech Rep., Slovakia, Hungary, Austria, Switzerland, Belgium, France, Great Britain) with intensive agriculture. On the other hand, the number of recent UB sites known in some countries (Italy, Czech Rep., Slovakia, Poland) has increased since 2006–2012 when European botanists have learnt to reliably distinguish UB from the locally-common *U. minor* (e.g., Macák, 2006; Beretta and Tassara, 2010b; Dítě et al., 2013).

Based on literature data (Dierssen and Dierssen, 1984; Kleinsteuber, 1996; Hofmann, 2001; Adamec and Lev, 2002; Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b; Adamec, 2007a; Wildermuth, 2010, 2016; Fleischmann and Schlauer, 2014), the reasons for the decline of the competitively weak four rare *Utricularia* species are similar to those for *Aldrovanda vesiculosa* (cf. Adamec, 2018d) and can be freely subdivided into two groups. The first group of reasons includes evident and anthropogenic direct destruction of a site by any means: drying out and drainage, peat extraction, direct eutrophication of habitats from local agriculture, fishery or municipal pollution and more general land-use changes such as intensive agriculture and afforestation. High input of NO_3^-, NH_4^+ and SO_4^{2-} from acid precipitates can invisibly speed up habitat eutrophication in large wetland areas. The other group of reasons is mostly independent of man and usually occurs in strongly protected areas (nature reserves) without any obvious human impact: marked water level fluctuations leading to water level decline or floods may directly result in population weakening, and spontaneous habitat succession and deterioration may lead ultimately to marked vegetational changes or even afforestation (see also *4.3.*). As many (Central) European sites of the four rare *Utricularia* species are subject to frequent and long-term water level decline or drought, global climate change can markedly accelerate this unfavourable water regime in habitats. In line with this, Kleinsteuber (1996) explained the decline of a variety of German UI and UOs.l. sites by enormous droughts in the 1980s. Although all four species (unlike *A. vesiculosa*, cf. Adamec, 2018d) can satisfactorily grow in the terrestrial ecophase on wet substrates (organic or sandy-clayish) without being submerged (see Fig. 5), under otherwise favourable conditions, for the whole vegetation season, this ecological state may support faster overgrowing and stronger competition by wetland cyperoids or graminoids (e.g., *Eriophorum angustifolium, Carex* spp., *Phragmites australis, Calamagrostis canescens, Agrostis* spp.; Navrátilová and Navrátil, 2005a; L. Adamec, unpubl. data). Wildermuth (2010) reported the threatening of UI, UO and US sites in peat bog depressions due to succession, infilling and dry seasons in the Canton of Zurich. The depressions originated after peat extraction as peat cutting holes ('Torfstiche') in the 1950s.

In summary, long-term, very low water level in combination with habitat eutrophication, for whatever reason, are the most common and unfavourable ecological threads at most sites of the four rare *Utricularia* species. On the other hand, ecological consequences of high-water level at the sites for the populations can be ambiguous (Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b). For example, in the Czech Republic, extant sites of UI, UO and US are usually situated in peat bogs adjacent to strongly eutrophicated fishponds (Adamec and Lev, 2002; Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b; Adamec, 2007a). Thus, any marked increase in water level in these fishponds leads to an inflow of nutrient-rich fishpond water to these nutrient-poor dystrophic sites rendering them more eutrophic; they can then be easily overgrown either by filamentous algae or by tall wetland vegetation. However, seasonal water-level fluctuations and high water levels were simultaneously recognized as crucial in preventing the unfavourable succession of the microsites by dense stands of tall wetland vegetation (Navrátilová and Navrátil, 2005a, Navrátilová and Navrátil, 2005b). Very little is known on the reasons for the decline of UB sites but they are probably the same as for the other species. Non-dystrophic UB sites in shallow sand-pits (Adamec and Kučerová, 2013b; Krajewski and Płachno, 2015) can be endangered by spontaneous succession and eutrophication of these originally oligo-mesotrophic habitats. No data are available on the threatening of UI, UO and US sites in North America. Generally, the above ecological reasons for habitat threatening are incomparably greater that a casual collection of some plant specimens by botanists to herbaria.

Due to the marked population decline of UI, UO, US (UOs.l.) and UB over the last few decades, extant rarity and small fragmented populations in Europe, UI, UO and UB have been officially declared within The IUCN (2019) as Endangered under the following criteria: UI: B2b (iii) c (iv); UO: B2b (iii) c(iv); UB: B2ab (iii)); US has not been listed. None of the four species has been listed in the CITES appendices or included in the Bern Convention. These four species have also been included in the European Red List by IUCN within the category Data Deficient (Bilz et al., 2011). In most European countries of the distribution of any of the four rare *Utricularia* species, these species are declared as Critically Threatened (e.g., Austria, Germany, Switzerland, Czech Republic, Slovakia, Hungary, Poland; e.g., Wildermuth, 2010; Grulich, 2012; Eliáš et al., 2015) either at the whole-country (federal) level or at the level of single federal states (Austria, Germany) and protected. However, in some other countries (Italy, Switzerland), the species are not officially protected as such at the country level, but their sites are under state protection.

In Central Europe, the most natural sites of the four rare *Utricularia* species occur in small-sized protected areas (nature reserves or natural parks) and are thus without any obvious and direct negative human impact (Wildermuth, 2010, 2016). However, as in the case of *A. vesiculosa* (see Adamec, 2018d), this passive protection does not help much to protect the sites and populations as the main reasons of threat (eutrophication and water-level decline) come both from the watershed, the precipitates and also as a result of water level fluctuations and seasonal drought. Generally, an extinction of a micropopulation is usually preceded by a long-term, spontaneous botanical succession and infilling of free water areas (depressions) in peat bogs and fen pools (Wildermuth, 2010, 2016). Therefore, a regeneration of infilled fens or peat bogs and a man-made creation of shallow pools and canals in these mires have proven to be a very successful and efficient measure of nature conservation for the protection of the natural populations of these species for many decades. In line with this, Wildermuth (2016) described the recovery of fen pools and canals and, subsequently, of US and UB populations in a fen complex in the Drumlin area in the Canton of Zurich in NE Switzerland, where peat extraction finished in the middle of the 18th century. Similarly, Babbi and Krüsi (2013) have described the regeneration of a fen complex Hänsiried with the recovery of shallow fen pools and canals in the surroundings of Zurich, to which UI and *A. vesiculosa* were introduced from nearby sites. US from a local population was introduced to an extracted fen complex in Karštejn in the Třeboň Basin, Czech Republic, in 2001 where a stable abundant population counting ca. 10,000 induviduals has arisen (Adamec and Kučerová, 2013b; see also Adamec, 2018d). During 2004–2009, UB plants from a local population were introduced to four old, shallow, extracted oligo- to mesotrophic sand-pits with very soft water in the Třeboň Basin, Czech Republic, in which stable flowering micropopulations counting ca. 100-10,000 individuals have arisen (Adamec and Kučerová, 2013b; Kučerová et al., 2016). These successful introductions have helped to specify the ecological requirements of this rare species with partly unknown ecology (Fig. 11).

In conclusion, the four rare *Utricularia* species often inhabited shallow dystrophic pools or canals arising after peat or fen extraction in many European countries in the previous centuries. Therefore, a purposeful regeneration of infilled peat bogs or fens, creating of shallow pools or depressions and combined with (re)-introductions as an up-to-date measure of active nature protection, can efficiently conserve the biodiversity of rare *Utricularia* species and other endangered wetland plants (e.g., *A. vesiculosa*) as well as many animals (e.g., dragonflies – Odonata; Wildermuth, 2010, 2016).

7. Inspirations for further research

Due to rarity and protection of the four *Utricularia* species, the study of their biology has been so far neglected. Evidently, a good deal of research on these species (see *3.2.* and *4.5.*; Adamec, 2018a, Adamec, 2018b) has been done on plants raised in outdoor cultures. To gain further insight into the biology of these four *Utricularia* species, the following topics and questions should be studied. It follows from some studies that all four species are genetically closely related. However, what is the genetic relatedness between UB and UO or US? Some questions are related to ecological properties of the plants. It is well known that all four species can grow in the terrestrial ecophase but to what extent are they able to grow vigorously in the terrestrial ecophase on a wet substrate for the whole season? UO, US and UB are sterile species. In which form (turions or shoot fragments) are they spread to new sites and what are the dominant vectors – water birds or large animals? How do seeds of UI contribute to spreading this species? Some literature sources (e.g., Fleischmann and Schlauer, 2014) state that UO and US flower rather rarely in Germany though these species flower prolifically in South Bohemian populations in the Czech Republic. What ecological factors besides high temperature are responsible for their flowering when the plants grow at an optimal water level?

Further questions relate to the ecophysiology of plant nutrition and trap-commensal interactions. Carnivorous shoots of UI, UO and US commonly grow down to loose peaty sediments and their traps frequently contain sedimented dark humic substances instead of prey. Are these substances used for nitrogen or organic carbon uptake and what is the efficiency of this N or C uptake? How and why do humic acids and tannins dissolved in the water optimise growth and development of the four species? On the model basis, Adamec, 2011c suggested that microorganisms living inside prey-free traps of aquatic *Utricularia* species represent rather parasites than commensals. Is this suggestion valid for the four species, too? The following questions are the same for all aquatic carnivorous plants: Does catching of prey stimulate mineral nutrient uptake from the water by shoots like in terrestrial carnivorous plants does by roots? What is the seasonal (daily) N, P and K gain (consumption) from prey in natural habitats? Which proportion of the total C uptake can be covered by carnivory? Does the structural investment in carnivory (trap proportion) in UI, UO and US with dimorphic shoots depend on the same external and internal factors as in other *Utricularia* species with monomorphic shoots?

Acknowledgements

The paper is dedicated to Miloslav Studnička, Botanical Garden in Liberec, Czech Republic, on his 70th birthday and for his great merits in studying, conservation and popularization of carnivorous plants in the Czech Republic. This study was partly supported by a long-term research development project of the Czech Academy of Sciences (No.RVO 67985939). Thanks are due to all who have provided any item of literature or unpublished information for this review. Sincere thanks are due to Andrea Kučerová (Institute of Botany, Třeboň, Czech Rep.) for critically reading the manuscript and valuable comments and to Brian McMillan (Glasgow, Scotland, U.K.) for language correction.

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