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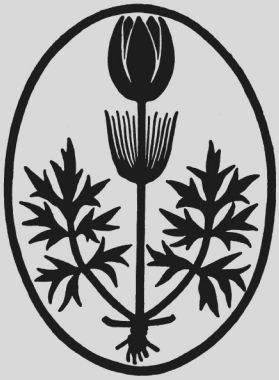

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The Morphometry of Quadrifid Digestive Glands in Traps of Three *Utricularia* Species: Does Gland Size Correlate with Trap Size?

By

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With 1 Figure

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Summary

Adamec L. 2016. The morphometry of quadrifid digestive glands in traps of three *Utricularia* species: does gland size correlate with trap size? – Phyton (Horn, Austria) 56 (1): 27–38, with 1 figure.

Quadrifid glands inside *Utricularia* traps consist of a basal cell and a tetrade of X-shaped terminal cells known as the long and short arms. They have digestive and absorptive functions associated with plant carnivory but their morphometry is commonly used for species determination. The interrelationship between the morphometric parameters of quadrifid glands in mature traps and trap length was estimated in three aquatic *Utricularia* species (*U. vulgaris*, *U. australis, U. stygia*). In these species, the ratio of trap length between the largest and smallest traps measured was 2.3–2.7. The total variability of width of both the long and short arms was relatively low in all species but the length of both the long and short arms was much greater; the ratio between the maximum and minimum lengths in each species was within 1.9–2.6. Linear regression models revealed significant correlations between long arm lengths and trap lengths in all species. This also applied for short arms except in *U. australis*. In *U. vulgaris* and *U. australis*, both the long and short arm widths correlated highly significantly with trap length, while the correlation was

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significant only in *U. stygia* short arms. In all species, the angles between the long arms did not correlate with trap length. With the short arms, the angles correlated highly significantly with trap length only in *U. stygia*, but not at all in the other species. For species determination purposes, only mature traps of uniform, mean size should be used to reduce the otherwise great variability of gland morphometry.

Zusammenfassung

Adamec L. 2016. The morphometry of quadrifid digestive glands in traps of three *Utricularia* species: does gland size correlate with trap size? [Morphometrie der vierteiligen Verdauungsdrüsen dreier *Utricularia* Arten: korrelieren die Drüsen- und Fallengröße?]. – Phyton (Horn, Austria) 56 (1): 27–38, mit 1 Abbildung.

Vierteilige Drüsen innerhalb von *Utricularia* Fallen bestehen aus einer Basalzelle und einer Tetrade von X-förmigen Endzellen, bekannt als „lange und kurze Arme". Sie haben Verdauungs- und Absorptionsfunktion im Zusammenhang mit dem Fleischfressen, ihre Morphometrie wird normalerweise zur Artbestimmung benutzt. Die Verhältnisse der morphomerischen Parameter der vierteiligen Drüsen in reifen Fallen und die Fallenlänge wurde anhand von drei *Utricularia* Arten (*U. vulgaris*, *U. australis, U. stygia*) bestimmt. Bei diesen Arten war das Verhältnis zwischen den kleinsten und den größten Fallen 2,3 bis 2,7. Die Unterschiede der Breite sowohl der kurzen als auch der langen Arme war relativ gering in allen Arten aber die Länge beider, des kurzen und des langen Armes, war viel größer; das Verhältnis lag bei 1,9 bis 2,6. Lineare Regressions-Modelle zeigten signifikante Zusammenhänge zwischen den Längen der längeren Arme und den Längen der Fallen bei allen Arten. Dies zeigte sich auch bei den kurzen Armen bis auf *U. australis*. In *U. vulgaris* und *U. australis* korrellierten die Breiten sowohl der kurzen, wie auch der langen Arme signifikant, während eine signifikante Korrelation der Breiten bei *U. stygia* nur bei den kurzen Armen auftrat. In allen Arten korrelierten die Winkel zwischen den langen Armen nicht mit der Fallenlänge. Bei den kurzen Armen korrelierten die Winkel nur bei *U. stygia* hochsignifikant mit der Fallenlänge, nicht aber bei den anderen Arten. Zum Zwecke der Artbestimmung sollten nur reife Fallen von gleichmäßiger Größe herangezogen werden, um damit die sonst große Variabilität in der Morphometrie der Drüsen zu verringern.

Introduction

The rootless carnivorous genus *Utricularia* L. (Lentibulariaceae) contains at least 214 species including around 50 aquatic or amphibious species which usually grow in standing, nutrient-poor humic waters (Taylor 1989, Guisande & al. 2007). The plants are able to capture fine animal prey, typically fine crustacean zooplankton, by their foliar traps (e.g., Friday 1989, Harms 1999, Richards 2001) and utilise certain mineral nutrients (N, P and K) from this prey for their growth (Friday & Quarmby 1994, Adamec 1997, 2008). It has also been recently discovered that some 'vegetarian' prey capture (pollen, algae) is also possible (Peroutka & al. 2008, Koller-Peroutka & al. 2015).

The traps are discoid, hollow bladders, usually 1-5 mm long with a typical wall thickness of two cells and they are filled with trap fluid. They con-

tain a variety of glands and trichomes on both the inner and outer surfaces, the functions of which are still partly unknown (Sydenham & Findlay 1973, Sasago & Sibaoka 1985a,b, Juniper & al. 1989). In its set state, when the trap is prepared for firing, a negative pressure relative to the ambient water is formed inside the trap (Sydenham & Findlay 1973, Sasago & Sibaoka 1985a, Singh & al. 2011). When trigger hairs situated on the trap door are touched by a prey species the door opens, the prey is aspirated into the trap lumen and the watertight door closes again. The trap is ready to fire again after 25–30 min (Sydenham & Findlay 1973, Sasago & Sibaoka 1985a), but the complete process of trap resetting (water pumping) lasts at least 6–10 h and can be interrupted by spontaneous firings (Adamec 2011a,b).

The inner surface of the *Utricularia* trap is covered by tens to hundreds of quadrifid glands (hairs) which are about 80–180 µm large (Fineran & Lee 1975, Sasago & Sibaoka 1985a, Thor 1988, Juniper & al. 1989, Taylor 1989). As demonstrated by various microscopic techniques, the main function of quadrifid glands is to secrete hydrolytic enzymes – mainly phosphatases and proteases – to the trap fluid for prey digestion (e.g., Vintéjoux 1993, Juniper & al. 1989, Vintéjoux & Shoar–Ghafari 2005) but they simultaneously function as absorptive glands for the products of prey digestion (Juniper & al. 1989). It is however possible that they partly shift their main function from digestive to absorptive with age (Sirová & al. 2009, 2010). Sirová & al. 2003, 2009 found that the hydrolytic enzyme production is constitutive, i.e., not stimulated by prey capture, but rather dependent on trap age. Quadrifid glands consist of a basal cell, which is embedded in the trap wall, a 'pedestal cell' (middle cell), and a tetrade of X-shaped terminal cells or 'arms' (Fineran & Lee 1975, Juniper & al. 1989, Płachno & Jankun 2004). The four terminal cells, consisting of pairs of long and short arms, are situated in parallel along the trap walls. The terminal cells form a short, narrow stalk sitting on the pedestal cell. Both terminal cells and the pedestal cell are very metabolically active, contain many mitochondria and have marked cell wall ingrowth (labyrinth architecture) as is typical for transfer cells (Fineran & Lee 1975, Sasago & Sibaoka 1985a, Juniper & al. 1989, Vintéjoux 1993, Płachno & Jankun 2004, Vintéjoux & Shoar-Ghafari 2005).

Utricularia traps are initiated in the shoot apex and the differentiation of young traps proceeds in the axils of young foliar filaments (Sattler & Rutishauser 1990, Cheema & al. 1992). As demonstrated in *U. vulgaris*, traps develop from trap initials (from the first appearance of leaves in the shoot apex) and increase their length for 26-28 days until they attain their first functional maturity – the ability to fire (Friday 1991). Functionally mature traps still increase their length by 12–14 % over the next two days and their further growth then stops. Moreover, regardless of their length, all traps on the same leaf attain functional maturity simultaneously. Throughout the growing season, the lifespan of *U. vulgaris* traps is only 30–32 days (Friday 1989). Traps within each aquatic *Utricularia* species can vary greatly in their

length: both within one leaf (by up to 4–5 times), at different sites, under different ecological conditions and during the growing season (e.g., Friday 1989, 1991, 1992, Guisande & al. 2000, Manjarrés-Hernández & al. 2006, Guiral & Rougier 2007, Adamec 2008, 2009, 2011c). As the ecological costs – structural, mineral, metabolic – associated with the production and maintenance of *Utricularia* traps are high (for the review see Adamec 2011d), the proportion of trap biomass to the total plant biomass (i.e., structural investment in carnivory) in many aquatic *Utricularia* species is under ecological regulation. As found in several species, this negative-feedback regulation is based on shoot N and/or P content and CO_2 availability in the water (Kibriya & Jones 2007, Adamec 2008, 2011d, 2015). In different species, this effect regulates both trap number and size, but trap size is usually regulated much more (cf. Friday 1992, Guisande & al. 2000, Manjarrés-Hernández & al. 2006, Guiral & Rougier 2007, Adamec 2009, 2011c, 2015).

The shape of quadrifid glands in *Utricularia* traps is species-specific and they have therefore been used for easy determination of related species, mostly between *U. ochroleuca* s. str., *U. stygia* and *U. intermedia* (Thor 1988, Taylor 1989, Schlosser 2003, Płachno & Adamec 2007). While the length and width of the long and short arms of the quadrifid glands were taken into account for species identification, the angles between the pairs of long and short arms were the main identification marks used. However, as reported in the literature (Thor 1988, Taylor 1989, Schlosser 2003, Płachno & Adamec 2007), the morphometric parameters are rather variable; even within a single trap. Moreover, no study has yet raised the question of whether these parameters in mature traps depend on trap size. The aim of this study was thus to estimate the interrelationship between the morphometric parameters of quadrifid glands in mature traps and trap length in three aquatic *Utricularia* species from the generic *Utricularia* section – *U. vulgaris*, *U. australis* and *U. stygia* – raised in an outdoor culture or collected in the field.

Material and Methods

Plant Material

Adult plants of *Utricularia vulgaris* L. (from Hodonínská Doubrava, S Moravia, Czech Rep.) and *Utricularia stygia* Thor (from Švarcenberk fishpond, Třeboň Basin, S Bohemia, Czech Rep.) were grown in a 750 l outdoor container with a water depth of ca. 30 cm and a litter of robust *Carex* species as a substrate (see Adamec 2011a,b). The water in the culture was considered oligotrophic and slightly humic (electrical conductivity 24.7 $mS.m^{-1}$, pH 7.18, total alkalinity 1.25 $meq.l^{-1}$, free CO_2 concentration ca. 0.19 mM). Adult plants of *Utricularia australis* R.Br. were collected from Mláka forest fishpond (Třeboň Basin; conductivity 48.0 $mS.m^{-1}$, pH 7.57, total alkalinity 1.55 $meq.l^{-1}$, free CO_2 concentration ca. 0.10 mM). All plant material was used from 4-9 June 2014. In *U. vulgaris* and *U. australis,* leaves from the 10^{th} adult leaf node (counted from the apex) were excised from each of 5 different plants. In *U. stygia*, carnivorous shoots 8–12 cm long from 5 different plants

were excised. From each of the 5 sampled leaves or carnivorous shoots, 5 traps of different sizes (free of prey) were excised, in order to cover the whole size gradient (giving 25 traps from each species). In *U. stygia*, traps were not sampled from young apical parts of the carnivorous shoots as they bore immature traps. For comparison with mature traps, one small immature trap of *U. stygia* was also used and processed.

Processing of Traps and Statistical Evaluation of Data

To estimate the maximum trap length (from trap rostrum to the distal end; Friday 1991, Adamec 2011b), each sampled trap was firstly photographed using a computer-controlled Olympus DP71 (Japan) microscope camera connected to an Olympus BX51 microscope at 40 × magnification. Wet traps were carefully longitudinally halved with a razor blade and a segment of ca. 1 × 1–1.5 mm from the relatively flat central part of the lateral wall was excised using fine scissors. Quadrifid glands were photographed at 400 × magnification. For each trap, one image including at least four undamaged representative glands was prepared and printed. On each print, two glands imaged with the greatest clarity and sharpness were selected for morphometric measurements to minimise geometric distortion of both sizes and angles. For one *Utricularia* species, morphometric measurements were conducted on 50 glands from 25 traps. The following parameters were measured using a ruler and a protractor: length and maximum width of both long and short arms and angles (to the nearest 0.3°) between the basal parts of long and also short arms (see Thor 1988, Schlosser 2003, Płachno & Adamec 2007). The accuracy of trap length estimation was ca. ± 20 μm, while that of the length or width estimation of the arms was ca. ± 0.4 μm. The length and width values for the pair of arms within the same gland were averaged.

Mean ± SE values and range of values are shown. As the morphology of *U. vulgaris* and *U. australis* quadrifid glands is very similar (Thor 1988), possible statistically significant differences in the parameters between these species were searched for using a two-tailed Student t-test (n = 50). Linear regression models were used to determine the statistical significance of relationships between all morphometric parameters and trap sizes, as well as between the length and width of the long and short arms within each species. In total, 25 regression models were identified for three species and are included in the results. Taking into account the Bonferroni correction to minimise interrelated factors, regressions of *U. vulgaris* and *U. australis* were significant at $P < 0.0063$, while those of *U. stygia* at $P < 0.0056$.

Results

In three *Utricularia* species, the ratio of trap length between the largest and smallest traps measured was 2.3–2.7, while the mean values were within 2.3–3.4 mm (Table 1). In all species, the mean length of the long arms was markedly greater (ca. 1.5–2.5 times) than that of the short arms. In comparison with a relatively low variability of the widths of both the long and short arms in all species, the variability of the length of both the long and short arms was much greater; the ratio between the maximum and minimum length in each species was within 1.9–2.6. Similarly, the difference between

the lowest and highest angles in the long arms was 31–51° and in short arms even 85–109°. *U. vulgaris* and *U. australis* differed significantly from each other ($P < 0.01$) in the length of the long and short arms and in the width of the long arms, while the other parameters were non-significant. In one immature *U. stygia* trap (trap length 2.18 mm), both long and short arms were much shorter (mean ± SD, n = 6; long arms 34.9 ± 7.0 µm; short arms 24.0 ± 3.7 µm) than those in mature traps of a similar size, but the widths of both the long arms (11.3 ± 0.32 µm) and the short arms (11.0 ± 0.35 µm) were comparable with those in mature traps (Fig. 1a,b).

Table 1. Morphometric characteristics of quadrifid glands in traps of *Utricularia vulgaris, U. australis* and *U. stygia* of different sizes. In the former two species, mature traps were collected from the 10th adult leaf nodes while from carnivorous shoots in *U. stygia*. n = 50 glands from 25 traps from 5 different plants; means ± SE intervals and range of values are shown. Asterisks denote statistically significant difference (Student t–test) between *U. vulgaris* and *U. australis*: ** – $P < 0.01$; ns – $P > 0.05$.

Species	Trap size (mm)	Length (µm)		Width (µm)		Angle (deg.)	
		Long arms	Short arms	Long arms	Short arms	Long arms	Short arms
U. vulgaris	2.76±0.10	87.7±2.8**	35.6±0.67**	10.2±0.13**	9.85±0.15^{ns}	29.3±1.6^{ns}	118.8±3.1^{ns}
	1.47-3.90	*57.6-143.8*	*27.2-50.6*	*8.3-12.5*	*7.5-12.1*	*10.8-54.4*	*54.0-158.8*
U. australis	2.26±0.08	104.1±3.1	41.5±1.1	10.7±0.11	10.2±0.12	28.6±1.1	121.4±3.0
	1.23-3.23	*59.1-155.9*	*27.1-63.4*	*8.7-12.2*	*8.7-11.8*	*15.3-46.0*	*73.7-182.6*
U. stygia	3.44±0.09	103.5±2.6	66.5±1.6	12.0±0.13	11.5±0.12	33.5±1.7	66.2±2.9
	2.00-4.50	*66.6-156.8*	*43.1-96.7*	*9.3-14.2*	*9.1-13.5*	*3.0-53.7*	*27.9-113.0*

Linear regression models revealed that the long arm lengths correlated significantly with trap length in all species (Table 2). This also held for short arm lengths with the exception of *U. australis*. In *U. vulgaris* and *U. australis*, both the long and short arm widths correlated highly significantly with trap length, while the correlation was significant only in *U. stygia* short arms. In all species, the long arm length correlated highly significantly with the short arm length. For the long arms, the length and width correlated highly significantly with each other only in *U. australis* and *U. stygia*, whereas only weakly, and non-significantly, in *U. vulgaris* ($P < 0.0079$). With the short arms, however, the length and width correlated highly significantly with each other only in *U. vulgaris* and *U. australis*, while they did not correlate in *U. stygia*. For all species, the width of the long arms correlated highly significantly with that of the short arms. In all species, the angles between the long arms did not correlate at all with trap length and for the short arms, the angles correlated highly significantly with trap length only in *U. stygia* (Table 2) and not at all in the other species.

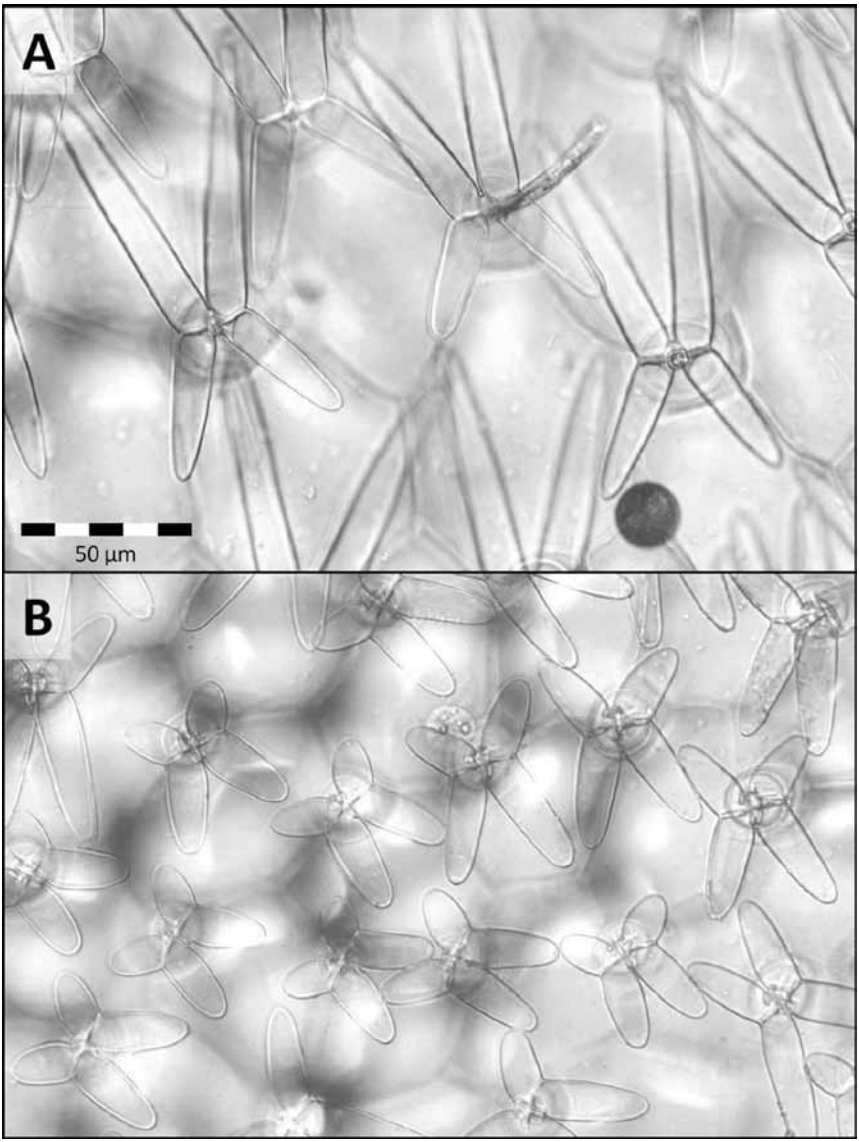

Fig. 1. A, Quadrifid glands in a small mature trap (length 2.51 mm) of *Utricularia stygia*. B, unripe quadrifid glands in a small immature trap (length 2.18 mm) of *U. stygia* from the same carnivorous shoot. Bar represents 50 µm.

Table 2. List of linear regression models on quadrifid glands of *Utricularia vulgaris, U. australis* and *U. stygia*. Statistically significant or meaningful models are shown; n = 50 glands from 25 traps from 5 different plants. Trap length in mm, other metric parameters in µm. As a result of Bonferroni correction, only values of P < 0.0063 (or P < 0.0056 for *U. stygia*) represent significant correlation (significant values are in bold for clarity); r^2, coefficient of determination.

No.	Linear regression models	r^2	P
	U. vulgaris		
1	Long arm length = 57.7 + 10.9 Trap length	0.169	**0.0030**
2	Short arm length = 28.5 + 2.58 Trap length	0.161	**0.0039**
3	Long arm width = 7.80 + 0.873 Trap length	0.475	**<0.0001**
4	Short arm width = 6.90 + 1.07 Trap length	0.552	**<0.0001**
5	Short arm length = 25.2 + 0.119 Long arm length	0.238	**0.0003**
6	Long arm width = 8.65 + 0.0178 Long arm length	0.138	0.0079
7	Short arm width = 4.25 + 0.157 Short arm length	0.490	**<0.0001**
8	Short arm width = 0.254 + 0.940 Long arm width	0.679	**<0.0001**
	U. australis		
1	Long arm length = 61.8 + 18.8 Trap length	0.211	**0.0008**
2	Short arm length = 32.1 + 4.15 Trap length	0.086	0.039
3	Long arm width = 8.76 + 0.879 Trap length	0.342	**<0.0001**
4	Short arm width = 8.33 + 0.840 Trap length	0.289	**<0.0001**
5	Short arm length = 14.7 + 0.257 Long arm length	0.548	**<0.0001**
6	Long arm width = 8.84 + 0.0182 Long arm length	0.246	**0.0002**
7	Short arm width = 7.57 + 0.0640 Short arm length	0.338	**<0.0001**
8	Short arm width = 1.11 + 0.849 Long arm width	0.667	**<0.0001**
	U. stygia		
1	Long arm length = 47.1 + 16.4 Trap length	0.347	**<0.0001**
2	Short arm length = 36.2 + 8.81 Trap length	0.266	**0.0001**
3	Long arm width = 10.4 + 0.465 Trap length	0.114	0.016
4	Short arm width = 9.76 + 0.497 Trap length	0.159	**0.0041**
5	Short arm length = 17.9 + 0.470 Long arm length	0.587	**<0.0001**
6	Long arm width = 9.46 + 0.0245 Long arm length	0.245	**0.0003**
7	Short arm width = 10.1 + 0.0213 Short arm length	0.085	0.040
8	Short arm width = 2.46 + 0.751 Long arm width	0.475	**<0.0001**
9	Short arm angle = 12.1 + 15.7 Trap length	0.265	**0.0001**

Discussion

In this study, trap length was selected as the best measure of trap size as it correlated best with the rates of *Utricularia* trap firing and resetting (Adamec 2011b). In all previous studies on the morphology of *Utricularia* quadrifid glands as a determination tool (Thor 1988, Taylor 1989, Schlosser 2003, Płachno & Adamec 2007), the interrelationship between gland morphometry and trap size has not been taken into account. Yet, these studies reported a great variability in all length and width parameters of the arms and angles

between the arms. It is thus plausible that a part of the variability was caused by different trap sizes.

As observed in *U. vulgaris,* traps develop and increase their length for 26–28 days until they attain the first functional maturity – their ability to fire – but they continue to increase in size during the next two days (Friday 1991). The stage of trap development where the quadrifid glands become mature, in terms of both their final size and physiological function, is not known for any *Utricularia* species. Moreover, the same question can be raised for the bifid glands. Preliminary observations on an obviously immature trap of *U. stygia* showed that for the quadrifid glands, both the long and short arms were around two times shorter than that found in mature traps of similar size (Fig. 1) and even three times shorter than in mature traps of the mean size, but the arm widths were the same.

Generally, the length of the long and short arms is much more variable in all species studied than the width of the arms (Table 1). Moreover, a significant correlation was proven between the length of the traps and the long arms in all species and also, except for *U. australis*, for the short arms (Table 2). Nevertheless, the linear regression models show that the quantitative interrelationships between trap length and the lengths and widths of both arms are different in traps of a single species. When compared with other species, the length of the long arms and especially of the short arms in *U. vulgaris* increases with increasing trap length relatively little, while the width of both arms increases relatively more. In *U. australis*, the lengths of both arms depend on increasing trap length much more markedly, while the widths of both arms correlate relatively less markedly; this trend is even more developed in *U. stygia*. Also in the latter species, the angles between the short arms, which are used for species determination (Thor 1988, Schlosser 2003, Płachno & Adamec 2007), correlated highly significantly and positively with trap length (Table 2). In spite of the great variability of the angles between short arms and a wide spectrum of trap lengths used for *U. stygia* in this study, the principal determination criterion for this species, as specified by e.g. Płachno & Adamec 2007 for main Czech populations, were not disturbed: "the mean angle between short arms is always below 85° but the maximum angle below 115°" (cf. Table 1). On the other hand, the highly significant length differences in long and short arms found between two very similar species, *U. vulgaris* and *U. australis*, cannot be recommended as a reliable determination criterion as these values overlap greatly with each other (cf. Thor 1988).

This study shows that the growth of quadrifid glands inside *Utricularia* traps is a typical example of allometric growth. In functionally immature traps, which are only somewhat shorter than their final length, both long and short arms are 2–3 times shorter than their final length (Fig. 1). However, at the next stage of trap development, trap growth is stopped (Friday 1991) while the elongation of both arms proceeds.

In conclusion, in mature aquatic *Utricularia* traps, the length of the terminal cells (arms) of quadrifid glands and also the angle between the short arms correlate significantly and positively with trap length. In several species, the morphometry of the glands is used as an advantageous determination mark but it is possible to only recommend the use of mature traps for species determination and, moreover, to select only traps of a uniform, mean size to reduce the otherwise great variability of gland morphometry.

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