Utricularia stygia in California, USA, and *U. ochroleuca* at its southern range

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What is *Utricularia stygia*?

Utricularia intermedia Hayne (1800) and *U. minor* L. (1753) are small, rootless, aquatic or semi-aquatic plants that are deeply anchored by colourless underground shoots with reduced leaves and numerous well developed traps. They have huge circumboreal distributions in the northern hemisphere (Hultén, 1986) and can easily be recognized.

However, plants can be found that show intermediate traits and are clearly distinct. These plants were first described as *U. ochroleuca* Hartman (1857)[1]. A great deal of literature is devoted to establishing this name and discussing the identity and distribution of this widespread but rare species (e.g. Ascherson, 1886; Celakovsky, 1886, 1887; Glück, 1902, 1913; Casper, 1974). A hybridogenic origin was postulated by L.M. Neuman in 1900 (i.e. that *Utricularia ochroleuca* = *U. intermedia* × *minor*), but no experimental evidence (e.g. controlled hybridisation) was presented, because the species rarely flowers.

More recently, *Utricularia ochroleuca* s. lat. was split into two species by Thor (1987, validly in 1988): A new species, *Utricularia stygia,* and a more exactly defined *Utricularia ochroleuca* s. str.[2], *Utricularia stygia* can be distinguished from *U. ochroleuca* s. str. by the darker yellow, larger, almost flat lower lip and a slightly larger number of teeth with bristles on each leaf segment. In contrast, *Utricularia ochroleuca* s. str. has paler, smaller flowers with a lower lip which is at first almost flat but that later becomes deflexed at the margins (Thor, 1988). Thor gave clear instructions on how to identify the six Nordic species[3] using two keys. One is based on the leaves, leaf segments and flowers and the other on the four-armed quadrifid glands inside the traps (see Table 1, page 114).

As flowers are rare, the best way to identify the species is indeed to look for traps on the green leaves and to check the teeth and tips of the ultimate segments of the green leaf and the

[1] *Utricularia bremii* Heer is closely related to *U. minor* and not considered here. However this taxon should be remembered when dealing with robust variations of *U. minor* or *U. ochroleuca*. The quadrifid gland arm angles for *U. bremii* are approximately S=190° L=20° (cf. Taylor, 1989).

[2] Botanists indicate the older, more inclusive concept of the species by writing *Utricularia ochroleuca* sensu lato, which means "in the broad sense" and which is abbreviated "s. lat." The more restrictive definition (which must include the type collection) is indicated by *Utricularia ochroleuca* sensu stricto, or "s. str." which means "in the strict sense." Only plants clearly in accordance with the description given by Thor (1988) are labeled s. str. here.

[3] Including *U. australis* and *U. vulgaris*, but excluding *U. bremii.* The latter is not known from Scandinavia (Thor, 1979), but was collected in Karelya, Russia (62°N, 35°E, Adamec, pers. comm. 2002).

quadrifids inside the trap with a microscope. The morphological differences (length and angle^{-1} of spur, size of shoots, number of teeth, number^{-1} of traps on green leaves, quadrifid angle^{-1} between short arms) may be ordered like this: *Utricularia intermedia* > *U. stygia* > *U. ochroleuca* > *U. minor.* The leaf segments of *U. intermedia* are typically obtuse and bear 5-12 bristles on minute teeth. *Utricularia stygia* (with 2-7 bristles) and *U. ochroleuca* s. str. (with 0-5 bristles) have fewer better developed teeth along the margins and acute leaf tips. *Utricularia minor* has one small bristle on the tip of each terminal leaf segment only.

	Angle S (in degrees)	Angle L (in degrees)	Teeth Number
U. intermedia	13 ± 8	8 ± 4	7.8 ± 1.6
U. stygia	74 ± 22	41 ± 15	4.7 ± 1.4
U. ochroleuca s. str.	171 ± 25	35 ± 17	2.2 ± 1.2
U. minor	271 ± 28	25 ± 11	0

Table 1: Statistic evaluation of the quadrifid glands and teeth of the ultimate leaf segments as given by Thor (1988). Angle S is the angle between the shorter pair of quadrifid glands arms, angle L is between the longer pair of quadrifid gland arms. Errors given as 1 standard deviation. A deviation of three standard deviations is significant.

The turions also have useful diagnostic characters. The hair density of the turions (see Figure 6) varies between species—the turions of *U. intermedia* are extremely furry (whitish when dry), while the turions of *U. minor* are bald except for very small terminal bristles. During the breaking of dormancy *U. intermedia* starts growing while the shape of the turion remains unchanged. The axes of the other species' turions become prolonged 3-5 times during this phase.

The observation of the small internal quadrifid glands requires the use of a microscope with about 150× magnification. Fresh, transparent, but mature traps are easiest to use, but traps preserved in spirits or dried without being pressed can also be used with reliable results. For this study the glands were studied with a microscope and photographed using a digital camera for computer evaluation (see Figures 1, 2, 3). For each species, 2-10 traps were opened to observe the internal glands, and 20-100 leaf segments were studied on 2-20 plants.

Variability

Thor's investigation was focused on Scandinavian material and he chose the most common type of *U. ochroleuca* s. str. in Scandinavia for his description and statistics (see Figure 1). He mentions that the type specimen of *U. ochroleuca* s. str. (from Hälsingland, Sweden) and most

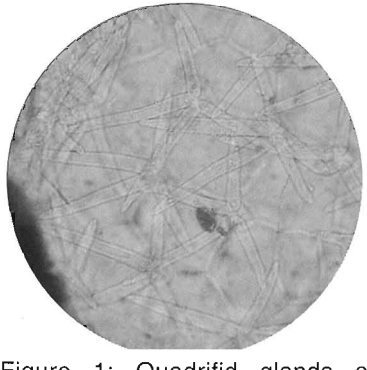

Figure 1: Quadrifid glands of *Utricularia ochroleuca* s. str., Itä-Uusima, Finland.

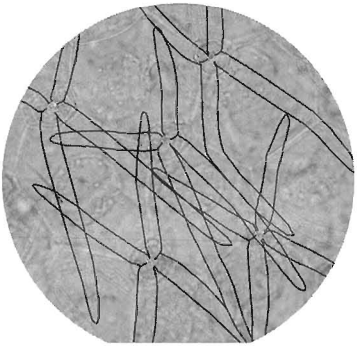

Figure 2: *Utricularia ochroleuca* s. lat., Trebon, Czechia. Some glands have been outlined to enhance visibility.

populations outside the Nordic countries have quadrifids with longer arms that are shorter and the angle between the shorter arms is less.

Herbarium specimens from East Germany and living plants from South Czechia were investigated and, indeed, they have a higher number of teeth (3-4), and the angles between the gland arms (angle L: 31°±10°, angle S: 85°±26°, N=20) are intermediate between the values given by Thor (see Figure 2, on p 114) for *U. ochroleuca* s. str. and *U. stygia*. Thus the difference between the more southern populations of *U. ochroleuca* s. lat. and *U. stygia* (see Figure 3, see on p 116) is not as large as could be expected when applying Thor's criteria.

The flower structure is often the most reliable feature to use when identifying *Utricularia* species, but some details are difficult to analyze in pressed specimens and frequently only sterile material is available. Field studies based upon living plants in situ are important to confirm herbarium findings on the form and color of inflorescences.

Utricularia ochroleuca s. lat. in Oregon and California

Utricularia ochroleuca s. lat. has a wide distribution in North America, but is quite rare (Ceska & Bell, 1973; NatureServe, 2001; Rondeau, 2002). I visited populations in Plumas Co., California, USA and Lane Co., Oregon, USA in 2000 and flowering specimens were found. Data on a third population in Clackamas Co., Oregon, USA, were kindly provided by B. Rice[4] and J.H. Rondeau.

Utricularia stygia, Plumas Co., California

Inflorescences of a plant similar to *Utricularia intermedia* were found within depressions of the floating meadows of a dystrophic lake (Willow Lake, 1650 m) in Plumas Co. late June 2000. These were distinctive because the peduncles were distinctly purplish and the spur of the corolla pointed downwards (see Front Cover). They were growing with *Utricularia minor*, *Sphagnum* spp., *Menyanthes trifoliata*, *Drosera anglica*, and in association with *Carex* spp., *Eriophorum* spp., *Scheuchzeria palustris*, *D. rotundifolia* and *D.* x *obovata* (see Figure 5). These plants were also found alongside *U. intermedia* at this site the year before by Rice and are similar to those found by Rondeau at the nearby Lake Almanor (1410 m) in 1994. Plants from both Willow Lake and Lake Almanor were regarded by both Rondeau and Rice as being *U. ochroleuca* s. lat.

The specimens from Willow Lake had purplish peduncles, that are 11.5-14.0 cm tall and bore 1-3 pale yellow flowers on straight, rather long (11 mm) pedicels. The lower corolla lip was 9 mm long and 11 mm wide, with margins distinctively curved upwards. The spur was rather long (5-6 mm) and narrow. It was pointed downwards at 15-25°. Rice examined nine plants from two of his herbarium sheets. Rhizoids were observed only at the base of one out of 6 inflorescences, while all had colourless shoots[4]. The plants were robust and single traps were found on every first to fifth green leaf. (Sometimes no traps were found on the green leaves[4]). Single (or paired) bristles were found on typically 4-7 small teeth along the margins of each ultimate leaf segment. The angle between the longer arms (61 µm) of the quadrifids was approximately 42°, between the shorter arms (50 µm) it was approximately 77° (see also Figure 1 in Rondeau, 2002).

Despite the determinations that the Californian specimens are *U. ochroleuca* s. lat., it is apparent they are best evaluated as being specimens of *U. stygia*. Even though the flowers were not dark yellow with reddish tinge, but pale yellow with reddish stripes on palate and spur, the upwards curved corolla margins in combination with the orientation of the spur (approximately 20°, an "acute angle" is also found in drawings by Thor (1988)) are characteristic for this species. The size of the plants, the number of bristles, and the orientation of the arms of the quadrifid glands are typical for *U. stygia*.

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[4]Rice provided data and observations based on plants collected by him and deposited at DAV.

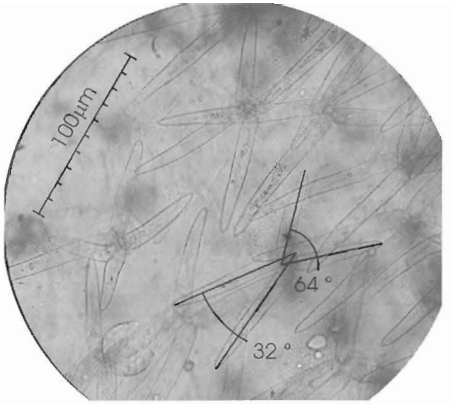

Figure 3: *Utricularia stygia*, Black Forest, Germany. One example on how the angles and lengths of the gland arms were measured is shown. In this example, S=64°, L=32°.

Utricularia ochroleuca s. lat., Lane Co., Oregon

Plants from this population were first collected here by Ingram, in 1926 (Ceska, 1973). In late June 2000, I found plants flowering frequently in seepages above the water table of the large fen along with *Drosera anglica* and *D. rotundifolia*. It lived in the open, water saturated hollows between the brown moss vegetation. In deeper water farther inside the fen *U. ochroleuca* s. lat. was replaced by *U. intermedia*. This suggests ecological niche partitioning for these two species (cf. Hoffmann, 2001; Adamec *et al.*, 2002).

This population was very unusual in lacking red pigments. Thus the peduncles (8-9 cm) were all green without any purplish coloration, even at the base. Usually two flowers were produced per inflorescence, on long 8-11 mm pedicels. The corolla was all light yellow with no red or brown markings. The lower lip was almost flat or had slightly deflexed margins. The spur was 3-4 mm long and distinctively curved and pointed downwards at approximately 40° relative to the lower lip (see Figure 4, see on p 117). Overall this was a small plant and the green leaves bore 0-2 traps. 2-5 bristles were found on sometimes prominent, curved teeth along the segment margins. Few, somewhat intermediate quadrifid glands were seen (angle S: 92-132°).

The corolla margins are deflexed which is characteristic for *U. ochroleuca* s. str. However, the plants differ from the description of *U. ochroleuca* s. str. given by Thor (1988): The large number of bristles (2-5, not 1-3) and the relatively low quadrifid gland angle S resemble *U. stygia*. Remarkable, but not unique to any species, is the absence of red pigments, the curved spur (not straight), and the pedicels, that were almost twice as long (not 4-7 mm).

Utricularia ochroleuca s.lat., Clackamas Co., Oregon

This plant was first collected in the Mt. Hood area by Thomson in 1927 (Ceska, 1973). Rice kindly described sterile herbarium specimens (DAV, 6 plants) that he collected at 1160 m, May 25th 2001 (pers. comm. 2002). He also provided two photographs of inflorescences (see Figure 7; see also the back cover illustration in Rondeau, 2002). Only five inflorescences were observed. He reported plants with purplish stalks, each very short, only approximately 5 cm tall, and bearing 2-3 flowers. The photographs show corollas that are yellow with some red-brown streaking on the palate, and with slightly deflexed margins. The spur is directed downwards from the lower lip at approximately 75°. Rice examined his collection and reported that the internodes were 4-7(10) mm, with 1(2) traps per leaf node. Leaf tips were acute, and the number of teeth

Figure 4: *Utricularia intermedia* (left) and *U. ochroleuca* s. lat. (right), Lane Co., Oregon, USA, June 26, 2000.

Figure 5: *Utricularia stygia*, Plumas Co., California, USA, June 20, 2000.

was very regularly seven. The values of the quadrifid arm angles are reported to be unstable, often most consistent with *U. stygia* (Rice, pers. comm. 2002). The number of teeth on the leaf segments is unusual for *U. ochroleuca* s. str. and approaches the value for *U. intermedia*. However the flower form and color clearly match *U. ochroleuca* s. str.

Conclusions

Compared to *U. ochroleuca* s. str., *U. stygia* is common in Europe and possibly in North America, too. The specimens of *U. ochroleuca* s. lat. observed in this study are not quite uniform in appearance. While Thor chose a form of *U. ochroleuca* s. str. common in northern Europe for his description, the type specimen of *U. ochroleuca* s. str. used by Hartman, and the form that may occur more often elsewhere in Europe, are reported to typically have smaller values for the quadrifid angle S, and more teeth along the margins of the terminal leaf segments. Thus it is less different from *U. stygia* and the casual observation of a few quadrifids is not foolproof.

Herbarium specimen and living plants, some of them in cultivation, from Germany, France, Czechia, Poland, Finland, Norway, and the USA were investigated and are presented in Table 2 for comparison.

The population of *U. ochroleuca* s. lat. from Plumas Co., California, can be identified as *U.*

		Angle S (in degrees)	Angle L (in degrees)	Teeth Number
1	*U. stygia*[1]	58	37	5 (3-6)
2	*U. stygia*[2]	45	21	6 (4-8)
3	*U. stygia*[3]	86 ± 26	44 ± 13	4.5 ± 1.2 (4-7)
4	*U. ochroleuca* s. lat.[4]	85 ± 26	31 ± 10	3 ± 1 (2-5)
5	*U. ochroleuca* s. lat.[5]	104 ± 20	34 ± 9	2 ± 1 (0-4)
6	*U. ochroleuca* s. lat.[6]	140 ± 26	44 ± 10	4 ± 1 (2-5)
7	*U. ochroleuca* s. str.[7]	155 ± 13	28 ± 4	1 (0-1)

[1]From the Black Forest, Germany
[2]From Hordalandet, Norway
[3]From Plumas Co., California, USA
[4]From the Trebon-Basin, Czechia
[5]From Lane Co., Oregon, USA
[6]From Park Co., Colorado, USA
[7]From Itä-Uusima, Finland

Table 2: Comparison between different populations: Angle S is the angle between the shorter pair of quadrifid glands arms, angle L is between the longer pair of quadrifid gland arms, number of teeth per ultimate leaf segment (counted without the tip).

stygia because of the form of the quadrifid glands, the ratio between the arm lengths (1.2), the number of teeth (4-7), the upwards curved rims of the corolla lower lip, and the size of the plants. Some features are different from the type description of *U. stygia*, specifically the long and narrow spurs, and long pedicels observed on these plants. However, these features are also atypical for *U. ochroleuca* s. str., and suggest an affinity to *U. intermedia*. The discovery of *U. stygia* in California extends the distribution of this species by approximately 3200 km, as the closest hitherto known collection sites are located on Richards Island, Northern Territories, Canada (N69°, W135°) and in the Kuskokwim river drainage basin, Alaska, USA (N62.5°, W154°) (Thor, 1988).

The population in Lane Co., Oregon, is *U. ochroleuca* s. lat., but is very unusual in being all green, and bearing bright yellow flowers without red or brown markings. While pure yellow flowers are also reported from Czechia (Celakovsky, 1887) and Japan (Wakabayashi, pers. comm. 2001), the plants from these populations have red pigmentation on at least the lower part of the peduncle, as is typical for the species. The spurs on the Lane Co. plants differ from the type description in being extremely short and curved.

The population in Clackamas Co., Oregon has very short inflorescences and flowers similar to *U.*

ochroleuca s. str. (cf. FloraWeb, 2001). But the number of marginal teeth on the leaf segments is extremely high (7) and the angle between the quadrifid arms is small. Therefore it is presently labeled as *U. ochroleuca* s. lat.. This site is located only approximately 80 km south of the type location of *U. occidentalis* A.Gray (1883) in Falcon Valley, Klickitat Co., Washington, USA. The collections made by Suksdorf reportedly have abnormally large inflorescences with tall scapes (10-25 cm tall), more numerous flowers (4-7) and frequently rhizoids. Thor considers this to be an aberrant population not included in his concept of *U. ochroleuca* s. str. The three USA populations of *U. ochroleuca* s. lat. discussed in this paper are very different from each other, although they are uniform within each population. It is unclear if this variability is a result of vegetative reproduction, geographic separation, or other factors. Most specimens of *U.ochroleuca* s. lat. seen show a higher number of teeth and smaller angles between the quadrifid gland arms than the sample from Finland, which is the only one at hand that is fully consistent with Thor's description. Therefore more (flowering) material from North America should be studied in greater detail[5].

Both *U. stygia* and *U. ochroleuca* are probably of hybridogenic origin, but the observed degree of variation does not support the idea that all of them are the direct result of a recent hybridisation between the quite uniform species *U. intermedia* and *U. minor*. Unfortunately these plants are threatened and disappearing at an alarming rate—this is especially true for the southern populations (that are probably evolutionary old) in Europe, Asia, and the USA. Loss of habitat may already have resulted in the destruction of other intermediate populations that may have been useful to understand the variation within these populations. These plants are worthy of protection—it is critical they continue to exist so they can be studied to reveal if more taxa (species, subspecies or hybrids) beside *U.stygia* are to be found among *U. ochroleuca* s. lat.

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Material Seen

Superscript key: a=seen alive, f=saw flowers, t=saw turions, *=did not see specimens personally.
Herbarium abbreviations: COLO=University of Colorado, Boulder, USA; DAV=University of California, Davis, USA; FR=Forschungsinstitut Senckenberg, Frankfurt, Germany; HEID=University of Heidelberg, Germany.

Utricularia ochroleuca:
1)[af] Lane Co., Oregon, USA (N44°, W122°, 1470m, E.S., 6/26/2000, HEID); 2)[af] Clackamas Co., Oregon, USA (N45°, W121°, 1160m, B.Meyers-Rice, 5/25/2001, DAV, MR010504*; J.H.Rondeau, HEID); 3) Southeast Fairbanks Co., Alaska, USA (N62°, W141°, J.H.Rondeau, HEID); 4) Park Co., Colorado, USA, (N39°, W106°, D.J.Cooper, 7/18/1991, COLO, No.448183) 4)[at] Jihocesky Kraij, Czechia (N49°, E15°, approximately 450m, Adamec, 1989); 5)[at] Itä-Uusima, Finland (N60°, E23°, approximately 20m, E.S., 7/26/2002, HEID); 6)[af] North East Ostrobothnia, Finland (N66°, E29°, FR); 7) Haute Saône, France (N48°, E7°, 450m, FR); 8) Kamenz, Sachsen, Germany (N51°, E14°, HEID); 9) Swinoujskie, Poland (N54°, E14°, FR); 10)[f] Lubsko, Poland (N52°, E15°, HEID).

Utricularia stygia:
1)[af] Plumas Co., California, USA (N40°, W121°, 1650m, E.S., 6/20/2000, HEID; B.Meyers-Rice & E.Salvia 7/18/1998, DAV, MR980701*); 2)[at] Hordaland Fylke, Norway (N61°, E6°, approximately 100m, E.S., 1996); 3)[at] Breisgau-Hochschwarzwald, Baden-Württemberg, Germany (N48°, E8°, 850-950m, E.S., 2001; FR); 4)[at] Weilheim-Schongau, Bayern, Germany (N48°, E11°, E.S., 2001, 590m);

[5]Out of four sterile herbarium specimens from Saguache and Park Co., Colorado, USA, only one could be confirmed being *U. ochroleuca*. (cf. Cooper, 1996)

Figure 6: *Utricularia stygia* forming turions, Black Forest, Germany, October 20, 2001

Figure 7: *Utricularia ochroleuca* s. lat., Clackamas Co., Oregon, USA, May 25, 2001. Photograph by B. Rice.

5) Garmisch-Patenkirchen, Bayern, Germany (N48°, E11°, FR); 6)[f] Kaiserslautern, Rheinland-Pfalz, Germany (N50°, E8°, FR, HEID); 7)[f] Ludwigshafen, Rheinland-Pfalz, Germany (N49.5°, E8.3°, approximately 110m, HEID); 8)[f] Zweibrücken, Rheinland-Pfalz, Germany (N49°, E7°, HEID).

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Front Cover: *Utricularia stygia*, Plumas Co., California, USA, green shoot with traps, inflorescence (one corolla detached). See article on page 113.

Back Cover: *Sarracenia purpurea* subsp. *venosa* var. *montana* in Georgia. See article on page 103.

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