



NOTE

New distribution of *Utricularia warburgii* (Lentibulariaceae) from Taiwan

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ABSTRACT: An *Utricularia* plant (Lentibulariaceae) was newly discovered in New Taipei, Taiwan. Characterized by the presence of horn-like processes corolla's lower lip distinguishes, a unique characteristic within the genus *Utricularia*, the plant is identified as *Utricularia warburgii* K.I.Goebel. *Utricularia warburgii* was endemic to China and holds horticultural value. Compared to the *U. warburgii* plants available in the market, the Taiwanese plant can be distinguished by its shorter pedicels and distinctive traits of corolla's lower lip, which include a semicircle and flat limb and spur nearly as long as the lower lip. Phylogenetic study, based on *rps16* and *trnK* regions, confirms that the Taiwanese plant clusters with other *U. warburgii* plants but present different genetic characters. We here provide a detailed description of the Taiwanese *Utricularia warburgii*, including habitat information and photographs. We also discuss the morphological and molecular diversity of *U. warburgii*.

KEY WORDS: aquatic plants, carnivorous plants, new records, Taiwan, *Utricularia*, taxonomy.

INTRODUCTION

The genus *Utricularia* L., also known as bladderworts, encompasses over 235 species worldwide (Müller *et al.*, 2006; Fleischmann, 2015). The carnivorous plant is famous for its lovely flowers and unique traps to catch small animals. Molecular research has confirmed the phylogeny of this genus and the relationship among the sections (Jobson *et al.*, 2003; Müller and Borsch, 2005; Jobson *et al.*, 2017). According to the latest checklist (Li, 1998; Hsu *et al.*, 2017; Chao and Hsu, 2018), 13 *Utricularia* species are documented in Taiwan, comprising nine native species, *U. aurea* Lour., *U. australis* R.Br., *U. bifida* L., *U. caerulea* L., *U. gibba* L., *U. heterosepala* Benj., *U. minutissima* Vahl, *U. striatula* Sm. and *U. uliginosa* Vahl; four naturalized species, *U. graminifolia* Vahl, *U. livida* E.Mey., *U. smithiana* Wight and *U. tricolor* A.St.-Hil.

During a floristic survey in the Mt. Beichatian, Taiwan, we encountered a *Utricularia* plant in wetlands (Fig. 1A), morphologically similar to *U. warburgii* K.I.Goebel because they share horn-like processes on corolla lower lip (Figs. 2, 3). *Utricularia warburgii*, classified within sect. *Nigrescentes*, is endemic to China (Taylor, 1989; Li, 2007) and has not been previously recorded in Taiwan. Based on monograph of *Utricularia* (Taylor, 1989), sect. *Nigrescentes* comprised only three species. The other two species being *U. bracteata* R.D.Good, endemic to southern tropical Africa, and *U. caerulea* L., widely distributed in tropical regions.

Utricularia warburgii is also valued as a horticulture plant. However, the Taiwanese *Utricularia* species presents some morphological differences compared to *U. warburgii* purchased from the market. Studying

Utricularia species is challenging due to their small size and fragility. Once pressed into specimens, many characteristics become difficult to observe, which highlights the importance of drawings and photographs for accurate identification. Online platforms such as iNaturalist (2024) and Plant Photo Bank of China (PPBC) (<https://ppbc.iplant.cn/>) can provide essential biodiversity data with photographic observations and precise locations.

In this study, we compared the Taiwanese *Utricularia* species with cultivated *U. warburgii* from China, using both morphological and genetic analyses. Additionally, we utilized open sciences projects to gather additional morphological data. As a result, we were able to confirm the species identification of the Taiwanese *Utricularia*.

MATERIALS AND METHODS

The *Utricularia* species was discovered in Mt. Beichatian, Taiwan, while a resembling plant, *U. warburgii*, was brought and cultivated in the lab. The voucher specimens were deposited at the herbaria of the Taiwan Forestry Research Institute (TAIF) and Provincial Pingtung Institute (PPI). General morphology and measurements were performed using both dissecting and compound microscopes, especially flowers, traps, and glands. Then we described following terminology of Taylor (1989). Additionally, information of all published species within sect. *Nigrescentes* were reviewed. To understand morphological diversity of *U. warburgii*, we check the photographs in iNaturalist (2024) and Plant Photo Bank of China (PPBC). The conservation status was assessed in accordance with the IUCN (2022) criteria.

To infer the phylogenetic position of the new species, our analysis incorporated known taxa from previous

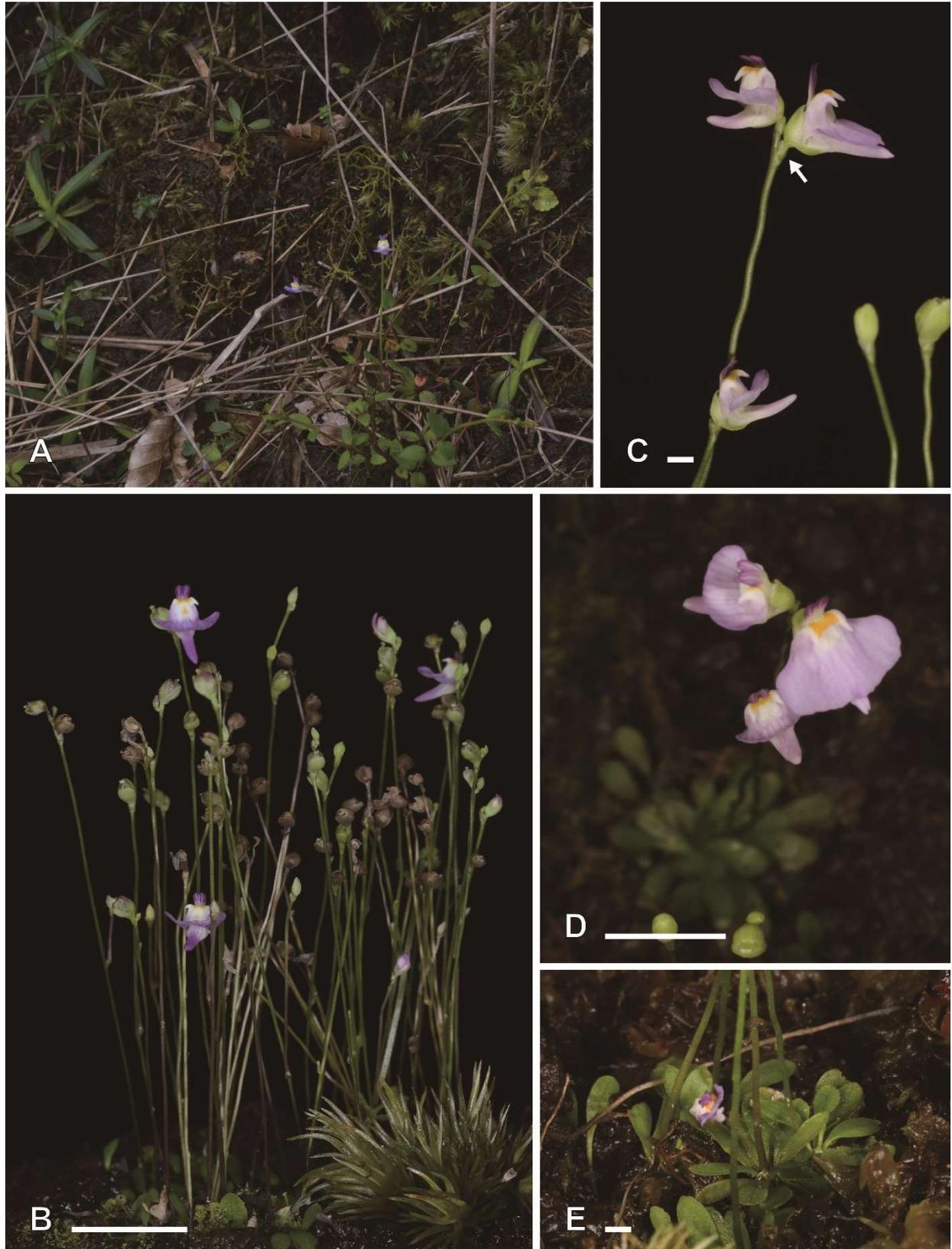


Fig. 1. *Utricularia warburgii* from Taiwan. **A.** Habit. **B.** Plant. **C–E,** same plant. **C.** Inflorescence with slightly twisting peduncle and two flowers; the flower, with pedicel 0.5 mm, bears a bract and 2 bracteoles (arrowed). **D.** Top view of the plant. **E.** Rosettes of 1-veined leaves. Scale bars for B = 1 cm, C, E = 1 mm, D = 5 mm.

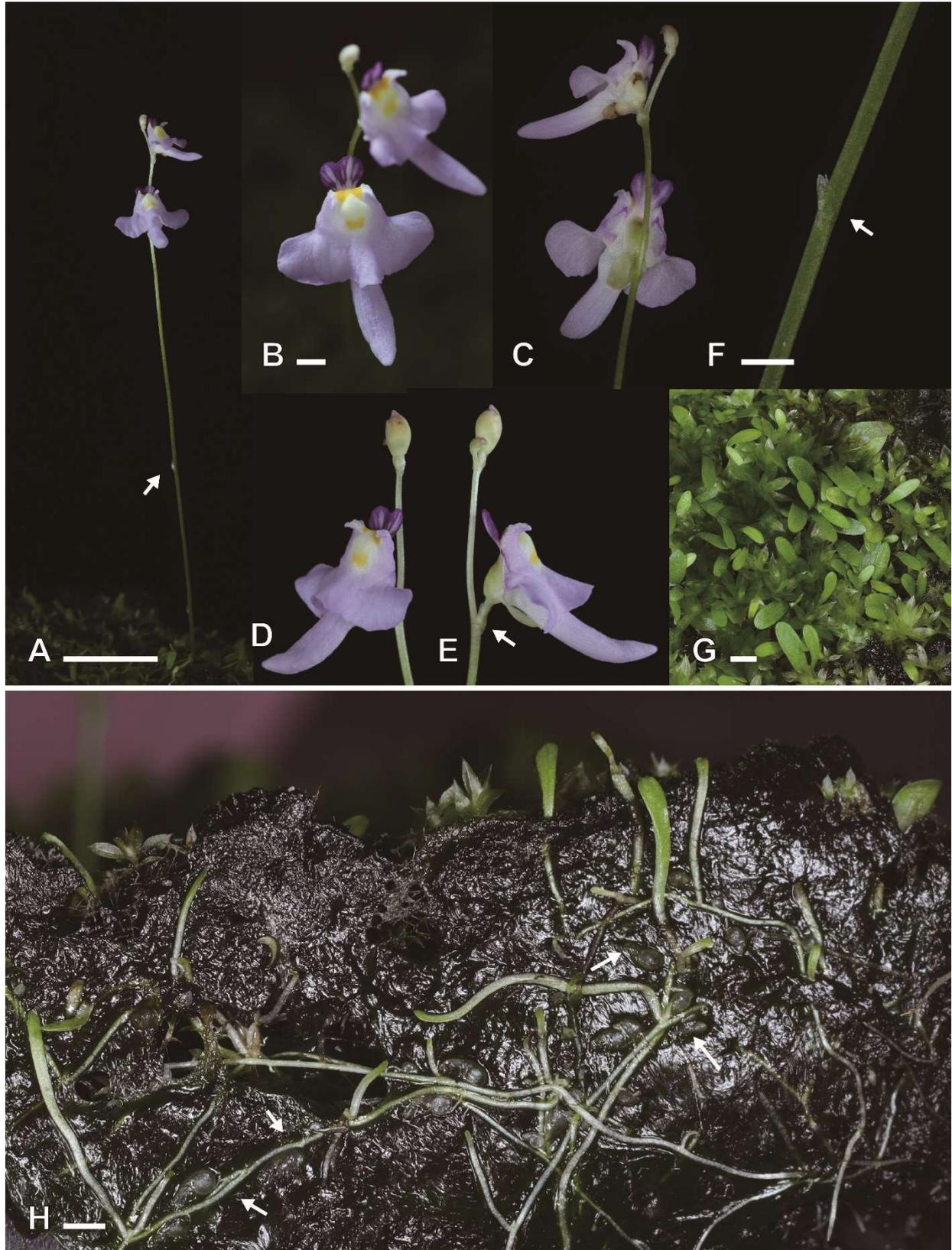


Fig. 2. *Utricularia warburgii* from China. **A.** Plant. A peduncle has a scale (arrowed). **B.** Corolla abaxial side. Lower lip limb transversely elliptic, reflexed. **C.** Corolla adaxial side. **D.** Corolla lateral view. **E.** Pedicel bears a bract and 2 bracteoles (arrowed). **F.** A scale (arrowed) on peduncle. **G.** Leaves. **H.** Rhizoids and stolons with traps (arrowed). Scale bars: A = 1 cm, B–H = 1 mm.

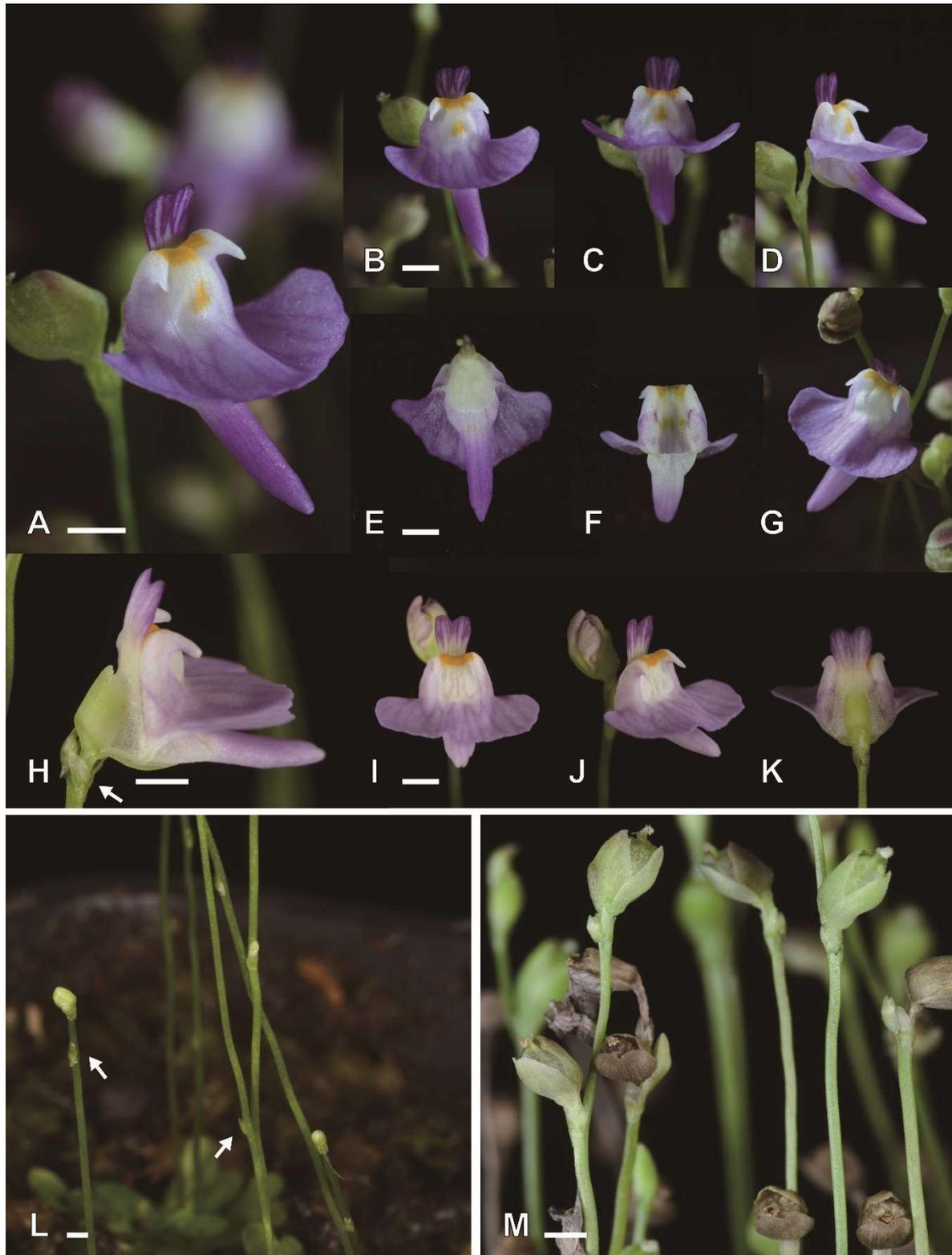


Fig. 3. Flowers and capsules of Taiwanese *Utricularia warburgii*. **A–E**, a flower has orange spot on palate of low lip. **A–C**, lower lip limb semicircle, involute. **D**. Corolla lateral view. **E**. Upward view, showing the low lobe of calyx. **F–G**. A flower without orange spot on palate of the low lip. **F**. Adaxial side of corolla low lip. **G**. Corolla abaxial side. **H–K**, a flower without distinct palate of low lip. **H**. Lateral view. A bract and 2 bracteoles on pedicel. The spur almost the as long as the lower lip. **I–J**. Corolla abaxial side, lower lip limb semicircle, flat. **K**. Corolla adaxial side. **L**. Bracts (arrowed) on peduncle. **M**. Mature and young capsules enclosed by calyxes, with short stalks. Scale bars: 1 mm.

**Table 1** Comparative table of morphological characters distinguishing *Utricularia warburgii* from Taiwan and China.

	from Taiwan	from China
Lamina width	0.5–2.5 mm	0.5–1.8 mm
Flower number	1–2(3)	2–4
Pedicel length	ca. 0.5 mm	1–3 mm
Corolla size	3–4 mm × 4–6 mm	4–6 mm × 6–8 mm
Corolla color	Violet	Pink, violet or purple
Corolla lower lip limb	Semicircle, flat or involute	Transversely elliptic, reflexed
Spur length	4–5 mm, usually almost as long as the lower lip limb	5–7 mm, twice longer than the lower lip limb

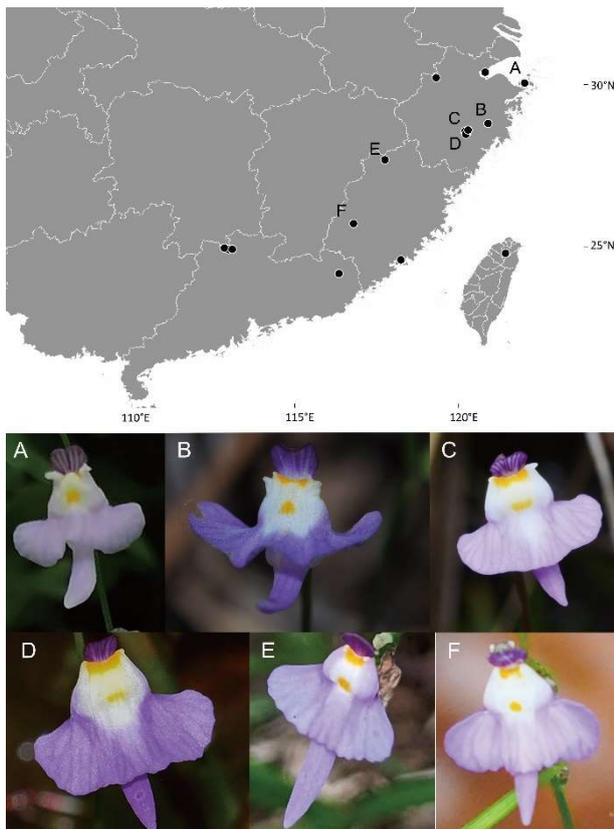


Fig. 4. Map showing the distribution of *Utricularia warburgii* (black circles) based on iNaturalist. The alphabets indicate multiple the flower morphology from specific localities. The map was produced by QGIS v. 3.6.0 (<https://qgis.org/en/site/index.html>) with maps and data from Global Administrative Areas ver. 2.8 (<https://gadm.org/maps.html>). The photographs copyrighted by liboheng_reborn (A), smalltown_huang (B), shiguangshi (C), xuc (D), zmp (E), Jianstargazer (F) CC-BY-NC.

phylogenetics studies of *Utricularia* sect. *Nigrescentes*, including *U. caerulea* and *U. warburgii*, and other species from Taiwan belonged to six more sections. They are sect. *Calpidsca* (*U. livida*), sect. *Foliiosa* (*U. tricolor*), sect. *Meionula* (*U. minutissima*), sect. *Oligocista* (*U. bifida*, *U. graminifolia*, *U. heterosepala*, *U. smithiana*, *U. uliginosa*), sect. *Phyllaria* (*U. striatula*), sect. *Utricularia*

(*U. aurea*, *U. australis*, *U. gibba*). *Utricularia tenella* R. Br. and *U. multifida* R. Br., in sect. *Polypompholyx* (Subg. *Polypompholyx*), were chosen as the basal group (Jobson *et al.*, 2017) to infer the phylogeny.

Following a modified cetyltrimethylammonium bromide (CTAB) method (Doyle and Doyle, 1990; Allen *et al.*, 2006), total genomic DNA was extracted from the silica-dried leaves. Two markers are applied for phylogenetic analysis: *rps16* and *trnK*, which encompass the *trnK* and *matK* gene. PCR primers used were as described by Oxelman *et al.* (1997) for *rps16* (*rps16*_F: GTG GTA GAA AGC AAC GTG CGA CTT; *rps16*_R2: TCG GGA TCG AAC ATC AAT TGC AAC) and by Johnson and Soltis (1995) for *trnK* (*trnK*3914F(dicot): GGG GTT GCT AAC TCA ACG G; *trnK*2R: AAC TAG TCG GAT GGA GTA G). Two primers were designed for sequencing the *trnK* region (*matK*781F: TATGCC TTT GCT CAT GAT CGC; *matK*905R: TGG GTT CGA ATC ATT ATG CG). Sequences obtained were aligned with MUSCLE (Edgar, 2004) and manually edited using BioEdit 7.1.3 (Hall, 1999).

A phylogeny was constructed using Maximum Likelihood (ML) analyses with IQ-TREE v. 2.2.0 (Nguyen *et al.*, 2015; Trifinopoulos *et al.*, 2016; Minh *et al.*, 2020), allowing each partition with its own evolutionary rate (Chernomor *et al.*, 2016). The best substitution model for each region was estimated with ModelFinder (Kalyaanamoorthy *et al.*, 2017), implemented in IQ-TREE v.2.2.0, following the BIC criterion. Branch support was evaluated using 1000 standard nonparametric Bootstrap iterations (Felsenstein, 1985). Phylogenetic trees were visualized using FigTree (Rambaut, 2009).

RESULTS AND DISCUSSION

Morphological analyses: *Utricularia warburgii* is the only known *Utricularia* species characterized by the presence of two horn-like processes on the lower lip of the corolla palate. When compared to the cultivated *U. warburgii* from China, the Taiwanese plant exhibits several distinguishing characteristics, including difference in lamina width, flower number per inflorescence, pedicel length, corolla size, corolla color, corolla lower lip limb shape, and spur length (Figs. 2 & 3). Notably, the Taiwanese plant typically has a shorter spur, nearly equal in length to the lower lip (Figs. 1C, 1D, 3F–K), as opposed to the Chinese plant, where the spur is twice the length of the lower lip (Fig. 2). The Taiwanese plant's corolla lower lip is semicircle and flat (vs. transversely elliptic and reflexed in the Chinese plant). Additionally, the pedicel of the Taiwanese plant is very short, almost stalkless (Fig. 1C), which differs from the Chinese *U. warburgii* (with pedicel lengths of 1–3 mm, Fig. 2E) but resemble *U. caerulea*. A comparative summary of these characteristics is provided in Table 1.

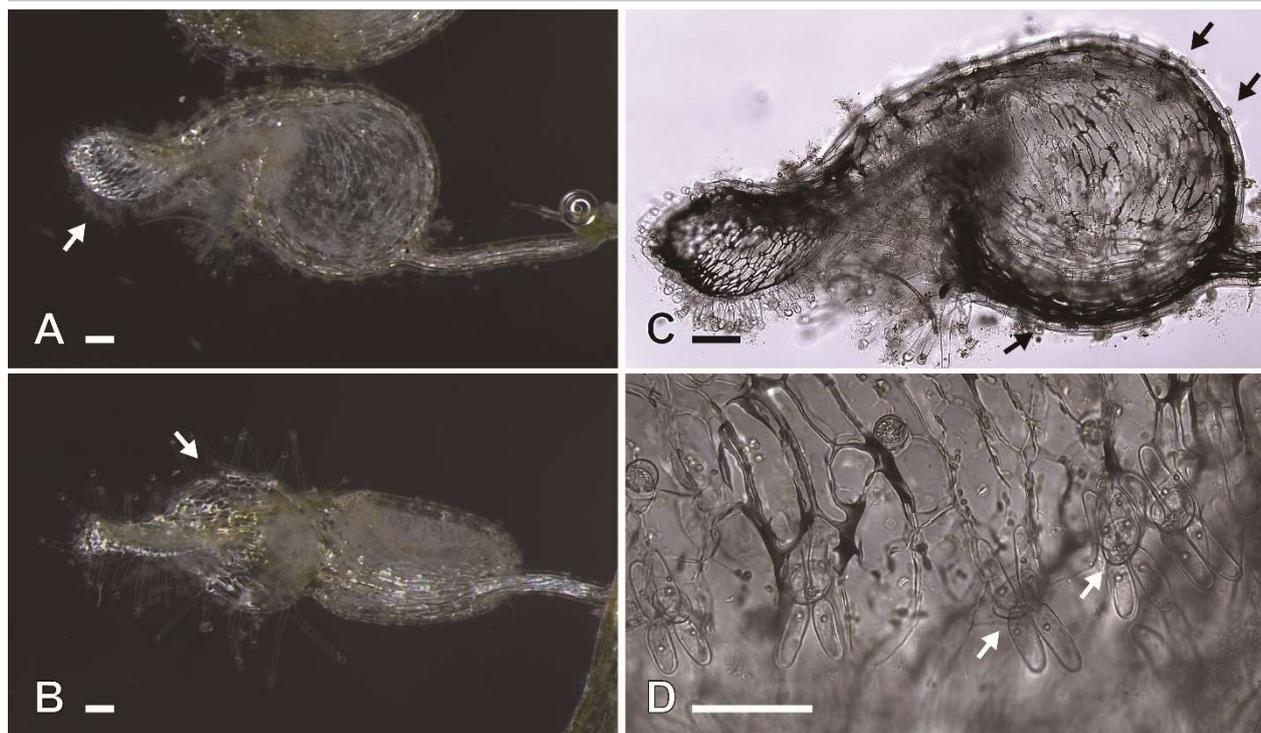


Fig. 5. Trap and gland hairs of Taiwanese *Utricularia warburgii*. **A.** Lateral view of trap, displaying obtuse beak (arrowed). **B.** Upward view, featuring a funnel-shaped rim around the mouth (arrowed). **C.** Lateral view, with domed glands (arrowed) on the outer lateral surface. **D.** Chamber glands, quadrifid (arrowed) within trap. A–B, under dissecting microscope; C–D, under compound microscope. Scale bars: 100 μ m.

Some morphological variations are observed among the Taiwanese plant. Some individuals have twisting peduncles rather than straight (Fig. 1C). The palate on the low lip, which usually has an orange spot, is a common trait in *Utricularia* (Figs. 3A–C), but this trait is less distinct in some flowers (Figs. 3F–G, 3H–K). The shape of the lower lip limb also varies, being either semicircle and involute (Fig. 3D) or flat (Fig. 3I).

Based on citizen science data, several morphological variations of *U. warburgii* are examined (Fig. 4). The purchased *U. warburgii* is similar to the morph in Figure 4A, while the Taiwanese plant resembles the morph in Figure 4C. It remains uncertain to which morph the type specimen belongs. According to Taxonomic Literature II (TLII) (Stafleu and Cowan, 1976), the type specimen collected by Otto Warburg was stored in the Berlin herbarium (B), but it has not been located, and Taylor (1989) also noted its absence. The Berlin herbarium was destroyed by fire during World War II, and the specimen may have been lost. The type specimen was originally collected in Zhenjiang. Among iNaturalist (2024) and Plant Photo Bank of China (PPBC), photographs closest to Zhenjiang were recorded on Zhoushan Island, where the morphology is most similar to the purchased plant. The protologue only provided illustrations of stolons, leaves, and traps, without any drawings of flowers. It was noted that the spur was only slightly longer than the lower lip, more similar to Figure 4C.

Despite the morphological differences between the Taiwanese plant and the purchased Chinese specimen, considering the morphological diversity of the species, we propose that the Taiwanese plant is indeed *U. warburgii*. With this addition, the total number of recorded *Utricularia* species in Taiwan is now fourteen.

Sect. *Nigrescentes* is characterized by its trap morphology, where a rim around the mouth is decurrent to form an obtuse beaked appendage, with both the appendage and the rim fringed with gland hairs (Taylor, 1989). The traps of the Taiwanese plant conform to this morphology, supporting its classification within sect. *Nigrescentes* (Figs. 5A–C). Furthermore, the Taiwanese *U. warburgii* has the same trap glands, with one-armed threshold glands and quadrifid chamber glands (Fig. 5D), resembling the trap glands of *U. caerulea*, another species within sect. *Nigrescentes* (Yang *et al.*, 2009).

Molecular phylogenetic analyses: The molecular research contributes to elucidate the taxonomic status of the *Utricularia* plant in Taiwan. Both the *rps16* and *trnK* regions of the Taiwanese and purchased *U. warburgii* are successfully amplified and sequenced, yielding four new sequences. To infer the phylogeny of the *Utricularia* species in Taiwan, the sequences of other species are obtained from GenBank, excluding *U. heterosepala* and *U. smithiana* due to the lack. The accession numbers of the DNA sequences were provided in Table 2. The phylogenetic tree (Fig. 6), constructed using an optimal



Table 2. *Utricularia* species samples used for the molecular phylogenetic analyses in this study. For each sample, the scientific name, collection number, country, GenBank accession numbers (*rps16* and *trnK*), and deposited herbarium are provided. New sequences are in bold.

Taxon	Specimen collection No.	Collection locality	GenBank accession No.		Herbarium
			<i>rps16</i>	<i>trnK</i>	
<i>U. aurea</i>	-	Australia	NC_084257	NC_084257	-
<i>U. australis</i>	R.W. Jobson 1391	Australia	MT278867	AF531823	NSW
<i>U. bifida</i>	-	India	MK560767	MF765522	-
<i>U. caerulea</i>	R.W. Jobson 1257	-	KY243543	MF765507	NSW
<i>U. gibba</i>	-	-	NC_021449	NC_021449	-
<i>U. graminifolia</i>	-	India	MK560774	MF765517	-
<i>U. livida</i>	R. W. Jobson 54A	-	AF482579	AF531833	NSW
<i>U. minutissima</i>	R.W. Jobson 2676	-	KY243558	MF765510	NSW
<i>U. aurea</i>	-	Australia	NC_084257	NC_084257	-
<i>U. striatula</i>	-	India	MK560770	-	-
<i>U. tenella</i>	D.J. Duval 1263	-	KY243523	-	-
<i>U. tricolor</i>	SRS106	-	OK187475	OK187475	-
<i>U. uliginosa</i>	T. Burson 92	-	AF482602	AF531849	BRI
<i>U. warburgii</i>	Y.-S. Chao 3556	China	PQ497690	PQ505708	TAIF
<i>U. warburgii</i>	L.-C. Wang 478	Taiwan	PQ497689	PQ505707	TAIF,PPI
<i>U. warburgii</i>	-	-	-	MF765506 (partial)	-

-. No data.

Table 3 Statistics for the ingroup DNA sequence alignments and the best partition scheme and their best-fit model determination by ModelFinder.

Dataset	Aligned length (bp)	Parsimony informative sites (bp)	Selected model
<i>rps16</i> intron	952	195 (20.5%)	TVM+F+G4
<i>trnK</i> intron	761	122 (16.0%)	K3Pu+F+G4
<i>matK</i> codon position 1	518	83 (16.0%)	TVM+F+G4
<i>matK</i> codon position 2	517	63 (12.2%)	TVM+F+I
<i>matK</i> codon position 3	517	124 (24.0%)	TVM+F+G4
<i>trnK</i> intron	227	29 (12.8%)	TN+F+G4
Concatenated	3492	616 (17.6%)	

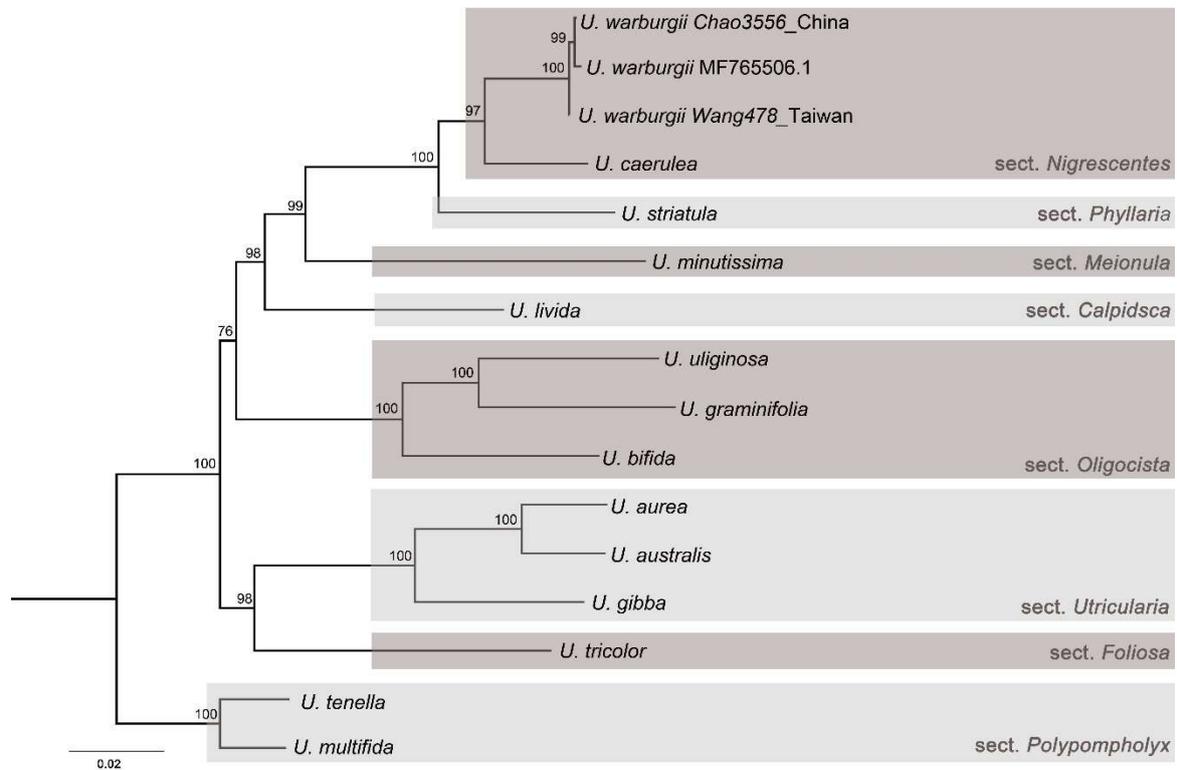


Fig. 6. Maximum-likelihood (ML) phylogenetic tree of *Utricularia warburgii* and related taxa in sect. *Nigrescentes*. Bootstrap support (BS) from ML is shown as percentages above each branch. Values below 50% are not shown.



partitioning scheme and the corresponding models (Table 3), is largely congruent with previous studies (Jobson *et al.*, 2017). It supports that the Taiwanese plant is grouped with Chinese *U. warburgii* and then clustered with *U. caerulea*. Molecular data show the genetic diversity of *U. warburgii*, and Taiwanese plant is the more phylogenetically distant to other Chinese plants.

Some *Utricularia* species, particularly within the sect. *Utricularia*, show low molecular diversity. For instance, *U. australis* R. Br., *U. macrorhiza* Leconte, and *U. vulgaris* L. exhibit only slight molecular differences and are difficult to identify based on morphology (Bobrov *et al.*, 2022). Considering both morphological and genetic diversity observed in *U. warburgii*, it is possible that the Taiwanese plant could be classified as a distinct variety. However, further taxonomic studies are required, involving enhanced sampling, more detailed morphological studies, and molecular analysis, to fully understand the diversity and classification of *U. warburgii* plants.

TAXONOMIC TREATMENT

Utricularia warburgii K.I. Goebel in Ann. Jard. Bot. Buitenz. 9: 66. 1890. **TYPE**: China, Zhejiang: Ningbo Warburg s.n. (B?, not located). Illustration, Goebel, Ann. Jard. Bot. Buitenz. 9, Pl. 7, Figs 22–27, Pl. 15, Figs. 118–121, stolons, leaves, traps.

瓦氏挖耳草 Figs. 1, 3, & 4

Description: Annual or perennial, terrestrial, subaquatic. **Rhizoids** few, capillary. Stolons numerous, capillary, 0.2–0.3 mm thick, branched. **Leaves** simple, numerous, rosulate at the peduncle base, 5–10 × 1.0–2.0 mm, petiolate; lamina narrowly obovate-cuneate, apex rounded, 1-veined. **Traps** on leaves, stolons, and rhizoids, stalked, ovoid, 0.5–0.8 mm × 0.8–1.4 mm; the mouth lateral, surrounded by an oblique funnel-shaped rim, the margin with radiating short-stalked glands; appendages 1, the dorsal side of trap decurrent to form a long, oblong-obovate, stipitate-glandular, carinate, obtuse beak about as long as the body of the trap. Grands on threshold one armed glands and on chamber glands quadrid. **Inflorescence** erect, solitary, simple, sometimes two, 3–6 cm long, peduncle straight or twisting terete, glabrous, 0.3–0.4 mm thick. Bract 1, attached at about the middle, ca. 1.2 mm long, ovate, with apex acute, the base acute. Bracteoles 2, a little shorter, ca. 0.8 mm, attached near the base, narrowly ovate, with apex acute, the base rounded. Pedicels filiform, terete, ca. 0.5 mm long. Calyx lobes subequal, ca. 1.5 mm long, upper lobe narrowly ovate, with apex rounded; lower lobe broadly ovate, with apex emarginate or erose. Corolla 4–6 mm long, 3–4 mm wide, violet, upper lip constricted below middle, the superior part obovate-cuneate with apex emarginate; lower lip limb semicircle, flat or involute, the apex rounded, the base white and swelling and orange at throat; palate with

a distinct distal transverse crest, the crest terminating at each end in an acute, curved forwardly, horn-like process; spur subulate, apex acute, 4–5 mm long, almost as long as the lower lip limb. **Capsule** ovoid, 1.5–1.8 mm × 2–2.5 mm, dehiscent by longitudinal, ventral slit. Seeds obovoid.

Specimens examined: TAIWAN. New Taipei City: Mt. Beichatian, under primary forest, 1000 m, 24 June 2023, Li-Chieh Wang 478 (TAIF, PPI).

Distribution and conservation status: At present, the reported population is located in wetlands on Mt. Beichatian. It grows intermixed with *Haloragis micrantha* (Thunb.) R.Br. and *Trichophorum subcapitatum* (Thwaites & Hook.) D.A.Simpson under primary forest. Twenty-five years ago, Mr. Wen-Hsien Chang has found a population in Linkou Plateau, New Taipei, but the voucher specimen could not be found.

This known population is no more than 250 individuals, and its occupancy area is very limited (< 1 km²). Because carnivorous plant is attractive, it is particularly vulnerable to over-collection. Following IUCN (2022) Red list categories and guidelines, a conservation code of Critically Endangered (CR, B2aC2a(ii)) is thus recommended.

Aquatic plants in Taiwan are facing a sharp decline in both population and species numbers, primarily due to over-collection, habitat destruction, and the invasion of alien species. Accurate and comprehensive scientific research serves as the foundation for any conservation efforts. However, we are concerned that the publication of this study may lead to immediate harvesting of this rare and beautiful plant. We urge everyone to focus on the protection of aquatic plants and take actions to ensure the survival of this species.

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