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A comprehensive literature study of morphology, taxonomy, phylogeny and biochemical aspects of genus *Utricularia*

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Abstract
Utricularia L. (bladderworts) is one of the largest known carnivorous plant genera which come under Lentibulariaceae family. It comprises of about 240 species that are classified into three subgenera and 32 sections. *Utricularia* have unique morphology and can colonize in wide range of ecosystems such as lithophytes, epiphytes, rheophytes, etc. These plants are excellent specimens for future researches on physiology of carnivorous plants, trap evolution, biochemistry of pray capture, microbial symbiosis, aquatic phytoremediation and molecular phylogeny of angiosperm genome. Recent studies have shown that, some species of *Utricularia* and *Genlisea* have the smallest genome size in angiosperms. Three lineages in *Utricularia* genus have evolved independently which have genome size of less than 100 Mbp. Many researchers have also reported that submerged aquatic macrophytes of *Utricularia* can accumulate heavy metals at higher concentrations. The present review aimed to study the taxonomy, molecular phylogeny of *Utricularia* and its utilization for phytoremediation of polluted water bodies.

Keywords: *Utricularia*, phylogeny, phytoremediation, bladderworts, lentibulariaceae

1. Introduction

Earth's ecosystem is full with organisms that are very mysterious and hold many surprises. Few of these organisms are carnivorous plants which are widely distributed all around the world. Although the carnivorous plants are present around us since thousands of years, the first descriptions of these plants were reported in fifteenth century by Auslasser (1479) on *Pinguicula* [Lonning and Becker, 2004] [37]. More than500 species of carnivorous plants have been reported and are classified into different families since then.

Utricularia L., commonly called as bladderworts is one of the largest known carnivorous plant genera which come under Lentibulariaceae family of order Lamiales. It comprises of about 240 species that are classified into three subgenra and 32sections [Taylor, 1989; Müller *et al.*, 2006; Albert *et al.*, 2010; Fleischmann, 2012; Fleischmann, 2015] [69, 43, 3, 18, 17]. All the *Utricularia* species are classified on the basis of general trap morphology. But bladderwort traps have complex physiology which is not fully understand yet [Poppinga *et al.*, 2016] [53]. It shows high phonotypical plasticity (Inter as well as Intra specific) which makes it very difficult to identify all species. Mostly these plants get nutrition from minute preys like small crustaceans but some of the *Utricularia* species like *Utricularia vulgaris* L. can feed on larger preys which include nematodes, mosquito larva, etc [Harms and Johansson, 2000; Mette *et al.*, 2000] [41].

Utricularia was first described by, de Lobel during sixteenth century in the year 1591. And in India, *Utricularia* came into limelight with the publication of Nelipu by van Rheedein 1689. Myanmarn (1768) reported about *U. bifida* for the first time along with *U. caerulea*. In the year 1804, 34 species of *Utricularia* was reported by Vahl which included five species described from India. In 1859, Monograph of Indian *Utricularia* was published by Oliver. He reported 24 species, including four new species, two new varieties and a new name- *U. kumaonensis* Oliver. In 1868, the first discovery of the trap functions of *Utricularia* was reported by Holland.

In 1884, Claeke reported 22 species from different parts of India, Pakistan, Nepal, Bhutan, Sri Lanka, Malaya and Myanmar. In 1922, Haines listed nine species from Bihar and Odisha. Peter Taylor in 1989 published The Genus *Utricularia*- A Taxonomic Monograph which included 33 species from India [Taylor, 1989] [69]. In 1992, M.K. Janarthanam and A.N. Henry published Bladderworts of India in Flora of India, Series 4 which contains morphology and taxonomic keys of *Utricularia*.

2. Methodology

Using carefully chosen keywords and Boolean operators, a thorough literature search was carried out across several databases (including Google Scholar, PubMed, Scopus, and Web of Science). This stage guarantees that every pertinent study is recorded. After that, the retrieved articles are checked in two steps: first, titles and abstracts are examined, and then the whole text is evaluated to verify eligibility. To prevent duplication and guarantee correctness, the chosen studies are arranged methodically, frequently with reference management software. Key information from each study, such as authorship, publication year, study design, primary findings, and conclusions, is gathered through data extraction. After that, the collected data is either statistically (for quantitative or meta-analytic reviews) or narratively (for qualitative reviews) examined and synthesized. In order to evaluate the studies' validity, reliability, and any biases, a critical evaluation is also carried out.

A standardized structure called Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) was created to guarantee repeatability, accuracy, and transparency in systematic reviews and meta-analyses [Page *et al*., 2021] [46]. It entails a number of crucial processes, starting with the formulation of a precise research topic and the creation of a thorough protocol that specifies inclusion and exclusion criteria, databases to be searched, and analysis techniques.

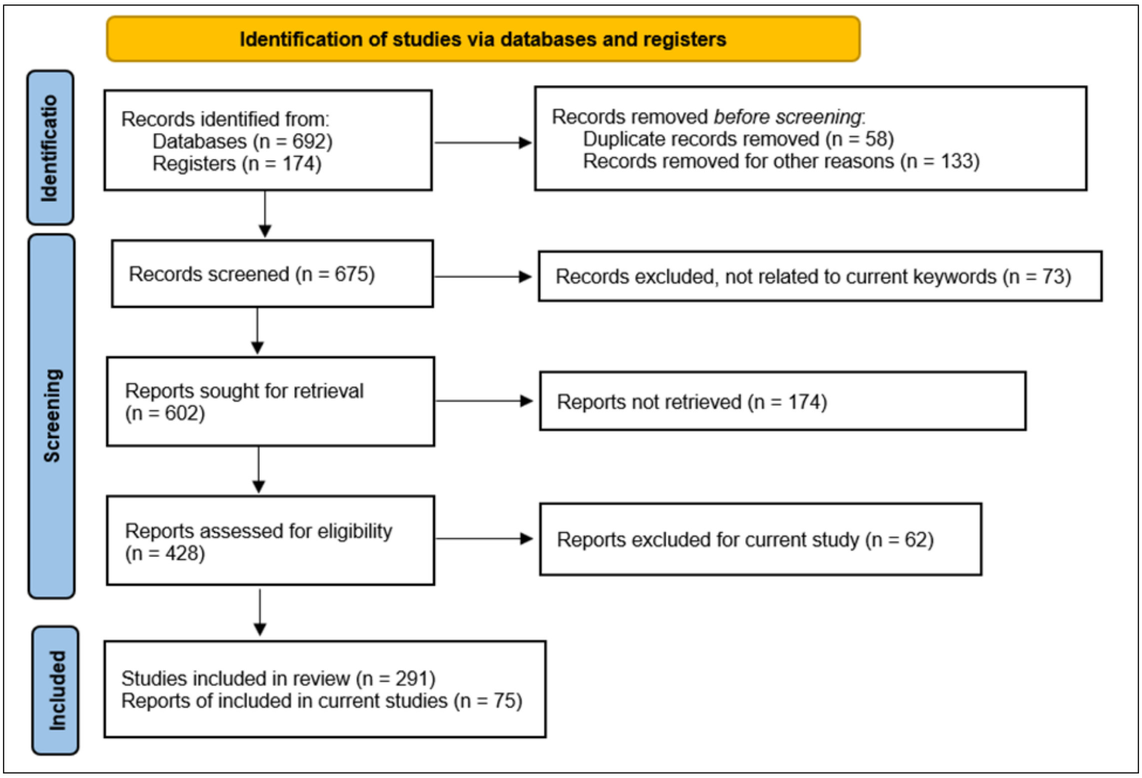

Fig 1: PRISMA flow chart which represent the systematic literature meta-analysis conducted for the current topic by using specific keywords

3. Results

In contrast to most plants, *Utricularia* uses its leaves and traps to directly absorb nutrients because it lacks actual roots. By pumping out water, the tiny bladder traps produce a vacuum. When tiny aquatic animals, such protozoa or small crustaceans, activate the trapdoor hairs, the door opens quickly, drawing in the prey. After the trap shuts, the prey is broken down by digestive enzymes, which enables the plant to absorb nutrients like phosphorus and nitrogen that are frequently lacking in their natural environments. *Utricularia* has pharmacological and ethnobotanical significance. Certain species have been used in traditional medicine to treat skin diseases, fevers, and respiratory and urinary conditions. Bioactive substances such flavonoids, terpenoids, and phenolic acids have been found in recent phytochemical research, indicating possible antibacterial, antioxidant, and anti-inflammatory qualities.

3a. Taxonomy of *Utricularia*

Utricularia is a very large and species-rich genus, and many species are often difficult to distinguish because of its unique morphology. A lot of different species and names have been published for over 200 years since Linnaeus put up the genus in 1753. The book published by Taylor, The Genus *Utricularia* is considered as base for the taxonomy of *Utricularia*. During his work, he came across more than 900 names for taxa of *Utricularia* that had been published. He studied and compared type specimens and descriptions, and finally was able to recognize that more than 3/4 of the names were actually representing synonyms of already described taxa, or invalid names [Fleischmann, 2012] [18].

Now a day's molecular phylogeny makes it easy to categories or identification of existing as well as newly discovered species [Jobson *et al*., 2003; Silva *et al*., 2018] [30, 66].

3. b. Morphology of *Utricularia*

Utricularia are herbaceous plants which cannot be classified on the basis of traditional methods based on morphological difference [Yadav *et al*., 2005] [75]. The vegetative parts of bladderworts are usually remain submerged in water or mud and due to this difference in habitat, variations in their morphology can be seen. Rutishauser and Isler (2001) stated that *Utricularia* do not have typical plant organs like stem, leaf or roots.

3. b. I. Rhizoids

Utricularia species do not have true roots, instead they have root like organs called rhizoids. They help in anchoring of the plant. In case of aquatic species rhizoids are not often present. Some species like *U. exoleta* have thick rhizoids where as some have branched rhizoids (*U. australis*). Branched rhizoids are mostly simple and papillose. In *U. aurea* the rhizoids are long and fusiform at the ends. In terrestrial and epiphytes, rhizoids are well developed at space base.

3. b. II. Stolon

Stolon is the pseudo-stem like structure present in *Utricularia* plants. Stolons in aquatic species remain submerged under water or free floating and can grow up to one meter in length. In case of terrestrial species, the stolons can be single or branched and are thread like (filiform) in appearance. Stolons in most of the species are soft and can be easily detachable. This makes it difficult to collects many species with intact stolons for taxonomical studies.

3. b. III. Foliar organs

True leaves are also absent in *Utricularia*. The shape, structure and venation of foliar organs vary from species to species. For example, in *U. aurea* the foliar organs range from 3-5 segments [Rahman, 2005] [55]. *U. minor* has polymorphic foliar organs.

3. b. IV. Inflorescence

Flowers (inflorescence) of *Utricularia* species are racemes and attached to the stolon. The size, shape and color of flowers differ species to species. In terrestrial species like *U. reticulata* or *U. scandens*, the flowers are twining. In species like *U. aurea* the inflorescence were attached to inflated rhizoids [Kumar *et al.*, 2018] [33]. The inflorescences of *Utricularia* are compared with beautiful orchids. The inflorescences of aquatic species like *U. vulgaris* are similar to small yellow snapdragons.

3. b. V. Traps

All carnivorous plant have traps to captured small preys. But the traps of *Utricularia* are very complex and also the fastest trapping device in the whole plant kingdom [Poppinga *et al.*, 2013; Poppinga *et al*., 2016] [52, 53]. The traps, also called as utricles, bladders or vesicular, are leaflike organs attached to the vegetative parts of the plants like stolon, rhiozoids and foliar organs [Janarthanam and Henry, 1992; Krol *et al*., 2012] [25, 31]. In case of epiphytes the traps are attached to stolon or rhiozoids. The opening (mouth) have trapdoors with several hair like structure (triggers) that makes the bladders watertight [Poppinga *et al.*, 2017] [49]. The walls of utricles have glands that pumps out the water, maintaining a negative hydrostatic pressure [Adamec, 2011; Sasago and Sibaoka, 1985a; 1985b; Vincent *et al*., 2011] [1, 62, 63, 72]. Due to this pressure the trap walls deflate and store elastic/potential energy like a spring. When a prey touches any trigger hair, the tarp inflates spontaneously, opening the door rapidly (>2 ms) [Poppinga *et al.*, 2017] [49].

Once the traps inflates, the water inside is pumped out again and the bladders are ready for next capture in about 10-15 minutes. The prey inside dies due to anoxia and get digested by hydrolytic enzymes [Adamec *et al*., 2010] [2]. According to many studies, a little is known about the diversity of traps and the effectiveness of prey capturing mechanism. In a broader prospective, such knowledge would indeed be essentially.

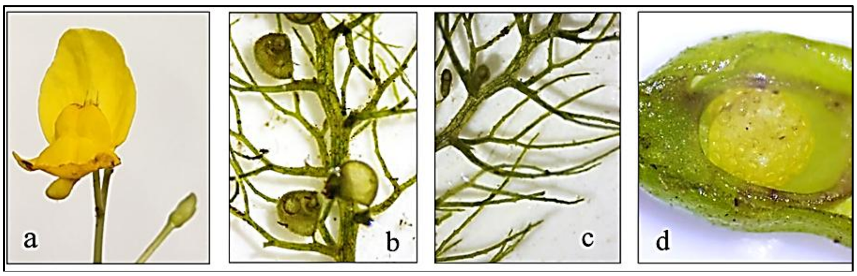

Fig 2: Morphology of *Utricularia aurea*: **a**. flower, **b**. traps, **c**. foliar organs, **d**. capsule and seeds.

3. c. Propagation in *Utricularia*

Most of the species *Utricularia* produced tiny dust like seeds which have small embryo [Płachno and Świątek, 2010; Eriksson and Kainulainen, 2011; Menezes *et al*., 2014] [47, 16, 40]. These seeds are dispersed by wind, insects, or by water. Capsule or fruit plays an important role in classification of species. In *U. aurea* the capsule are globose and circumscissile.Seeds also show great variation in *Utricularia*. Aquatic species like *U. aurea*, *U. minor and U. stellaris* are winged. Some species also form winter buds by modifying the shoot apices and leaves [Płachno *et al.*, 2014] [48]. These buds contain high protein and starch. Stolon fragments can also help in spreading of certain *Utricularia* species.

3. d. Interrelationship among the genera of the family Lentibulariaceae

Lentibulariaceae family comprises of above 300 species of carnivorous plants which are divided into three genera; *Utricularia*, *Genlisea* and *Pinguicula*. All the three genera are interrelated to each other on both morphological and molecular basis [Jobson*et* 2003]. *Utricularia* and *Genlisea* have evolved drastically with body orientation completely differing from classic root-shoot rules in angiosperms [Rutishauser, 2016] [61]. Where as in *Pinguicula* species, normal vegetative parts like shoot, root and leaves are present [Roccia *et al.*, 2016] [59]. *Pinguicula* plants have flypaper like traps which are covered with glandular trichomes. In case of *Genlisea*, specialized Y shaped organs called rhizophylls are present which helps in plant anchoring and traps small organisms. Great variations are seen in morphology of traps in all the species of *Utricularia*. The bladders (traps) are hollow, 1-6 mm long with trapdoors at the entrance [Vincent *et al*., 2011] [72].

3. e. Distribution and habitat of *Utricularia*

Except the Polar Regions, *Utricularia* grows all around the world. *It* can be found mostly in tropical and sub-tropical region with highest taxa concentrations in America, Australia and Asia [Taylor 1989; Jobson *et al*., 2003; Müller and Borsch 2005; Guisande *et al.*, 2007; McPherson, 2010] [69, 30, 42, 22, 39]. South America and Australia are regions with high taxa concentration (76% of Australia and 65%of South America). The highest region is Africa with more than 40 species. In India these species were found in different parts of Himalayan ranges, Western Ghats and Eastern Ghats. *Utricularia* mostly grows in warm climate with temperature ranging from 25º- 35º Celsius. But few species can grow in low temperature as well as high temperature. *Utricularia* grow on wet surfaces near water bodies or in nutrient poor pounds (free floating aquatic species), or in habitat with more or less permanent or seasonal high humidity. For example, *Utricularia vulgaris*, grows in meso-eutrophic waters (pH between 5 and 8) of the northern hemisphere and 'in both Africa and India some *Utricularia* species are commonly found in rice cultivations' [Taylor, 1989; Lonnig and Becker, 2004] [69, 37]. These plants may even be considered as invaders of a more or less artificial no oligotrophic environment. Species which grown on rocks have thin layer of water surrounding the bladders. On the basis of the habitat, *Utricularia* is differentiated into six different groups.

Species that grows on wet soil near water bodies like pond or streams comes under this group. Rhizoids (organs looking like roots) are well developed and able to fix the plants to the soil surface, but unable to absorb water and nutrients. Filiform stolons are developing; they exceed rarely a few centimeters long. Both stolons and rhizoids contribute to anchor the plant. The stolons may bear scatterred leaves (*U. arenaria*) or clumped leaves (*U. simulans*). Species which can grow on still water comes under this group. Free floating species mostly remain submerged under water. The only visible part of the plant is the inflorescence. Vegetative organs are squashy and include no, or nearly so, lignified tissues (sclerenchyma). The collenchyma is, too, scarce or absent [Roques and Jérémie, 2005] [60]. Air shoot are present which help sin keeping the plant suspended in water.

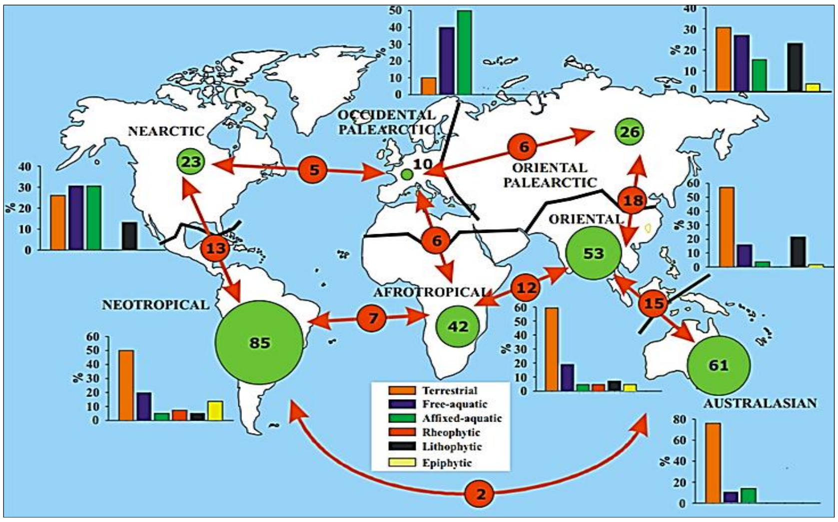

Fig 3: Biogeography of Utricularia. (Data collected from the research paper published by Guisande *et al*., 2007) [22]

Species which grows on still water but for better development fix itself to soil surface comes under this group. There are more than 50 such species whose trap-bearing stolon or rhizoids are anchored in thes oil, at bottom of the water (example, *U. minor*). Some species like *U. gibba*, though being floating plants, develop both specialized anchored parts while some others like *U. benjaminiana*, *U. rejlexa* produce tubers [Roques and Jérémie, 2005] [60]. Species which grows in swiftly moving water sources by anchoring onto a soil surface (*U rigida, U. tetraloba, U neottioides)*. Stolons and dissected leaves are reduced to filaments undulating in running water. Traps are rarely observed or not properly developed. Species that grows on moss covered trees or banks comes under this group. *U. jamesoniana, U. alpina, U. mannii*are examples of epiphytes which occurs in rain forests of very wet tropical climates. Species which grows on rocks comes under this group. Small ground species (i.e. *U. arenaria, U. prehensilis*) are found in shallow cavities, and ubiquitous semi-floating species (*U. gibba*sub sp. *exoleta*) in somewhat deeper hollows or cracks in therock.

3. f. Molecular phylogenetics and evolution

Recent studies had shown that some species of *Utricularia* and *Genlisea* have the smallest genome size in angiosperms [Ibarra-Laclette *et al*., 2013] [24]. The size of chromosome in these species is nearly equal to size of bacterial genome [Fleischmann *et al*., 2014; Greilhuber *et al*., 2006] [19, 21]. Three lineages in *Utricularia* genus have evolved independently which have genome size of less than 100 Mbp [Veleba *et al*., 2014] [70]. Therefore, these plants can be consider as extraordinary specimens to analysis the genome miniaturization process. In some studies, different molecular markers such as *matK*, *rps16*, *trnk* are used for conducting phylogenic analysis in *Utricularia* [Jobson and Albert, 2002; Jobson *et al*., 2003; Reut and Jobson, 2010; Westermeier *et al*., 2017] [26, 30, 58, 74]. Silva and his coworkers (2018) have elaborated the molecular phylogeny of bladderworts (*Utricularia*) in a wider approach.They conducted molecular analysis by using different plastid genome like *rbcL*, *matK*, *rps16*, etc and observed that the *rbcL* gene shows very low variable sites whose conservation is as essential as Rubisco enzyme that carries out dark reaction in photosynthetic plants. Raven, 2013 and Shivakumar *et al*., 2016 [64] reported similar observation.

They found that subgenus *Polypompholyx* is the sister group to the clade formed by subgenus *Utricularia* and *Bivalvaria* according to the combined sequences and also individual *matK*, *rps16* intron and *trnL*-F datasets. Previous studies based on *trnL*-F spacer, *rps16* intron [Jobson and Albert, 2002; Jobson *et al*., 2003; Reut and Jobson, 2010] [26, 30, 58], and on *matK* [Silva *et al*., 2016] [65] also support this tree topology (*Polypompholyx, Bivalvaria, Utricularia*); although Müller and Borsch (2005) had placed subgenus *Polypompholyx* as a sister group to subgenus *Bivalvaria*, and both as sister group to subgenus *Utricularia*. By taking pollen into consideration, Lobreau-Callen *et al*., (1999) [36] recognized shared characters of both sections and Taylor (1989) [69].

3. f .I. Phylogeny of Trap diversity

Until now, there are few reports available which provide a detail or brief knowledge on behavior of prey in the proximity of motile or non-motile carnivores plants trap during trapping [Bohn and Federle, 2004; Bauer *et al*., 2012; Poppinga *et al*., 2012] [10, 8, 51]. During recent studies, analyses of trap kinematics were performed with artificially triggering traps [Forterre *et al*., 2005; Poppingaand Joyeux, 2011; Volkov *et al*., 2014] [20, 50, 73]. All this leads to many unsolved questions regarding it phenotypic and genotypic diversity as well as trapping mechanism. Westermeier (2017) [74] in his study 'Trap diversity and character evolution in carnivorous bladderworts (*Utricularia*, Lentibulariaceae)' reported about functional morphology and trapdoor movement based on phylogenetic reconstruction of genes, derived from the rapidly evolving chloroplast regions *trnK*, *rps16*, and *trnQ-rps16*.

3. f. II. Evolution of *Utricularia*

Lbarra- Laclettle *et al*., (2013) [24] stated about molecular clock on the basis of *trnL*, *rps16*, *coxl* and *maK* sequencing. Based on molecular clock it was calculated that about 42 million years ago the common ancestor *Utricularia*, *Genlisea* and *Pinguicula* got diverged [Bell *et al*., 2010] [9]. The last common ancestor of *Genlisea-Utricularia* clade was found to bearose 39 mya (36 mya estimated by Ibarra-Laclette *et al*., 2013) [24], a lineage from South America. About 30 mya (31 mya according to Ibarra-Laclette *et al*., 2013) [24] *Utricularia* got separated from its sister genus and dispersed to Australia with the lineage represented by subgenus *Polypompholyx* (17 mya) and possibly to Africa afterwards (16 mya).The dispersal *Utricularia* to North America region may possibly happened from South America, around 11 mya (Ibarra-Laclette *et al*., 2013) [24] and to middle of Miocene between 12 mya [O'Dea *et al*., 2016] [45].

The colonization of *Utricularia* into Eurasia probably occurred via the Bering Strait to Northwestern Asia and also to Europe at around 4.7 mya [De Chaine, 2008] [13]. The lineage of *U. aurea*, *U. inflexa* and *U. reflexa* possibly reached the African continentfrom Tropical Asia very recently, around 3 mya, which would bestrongly supported if *U. cornelianawas* indeed *U. reflexa* [Jobson, 2012; Fleischmann, 2015] [28, 17].

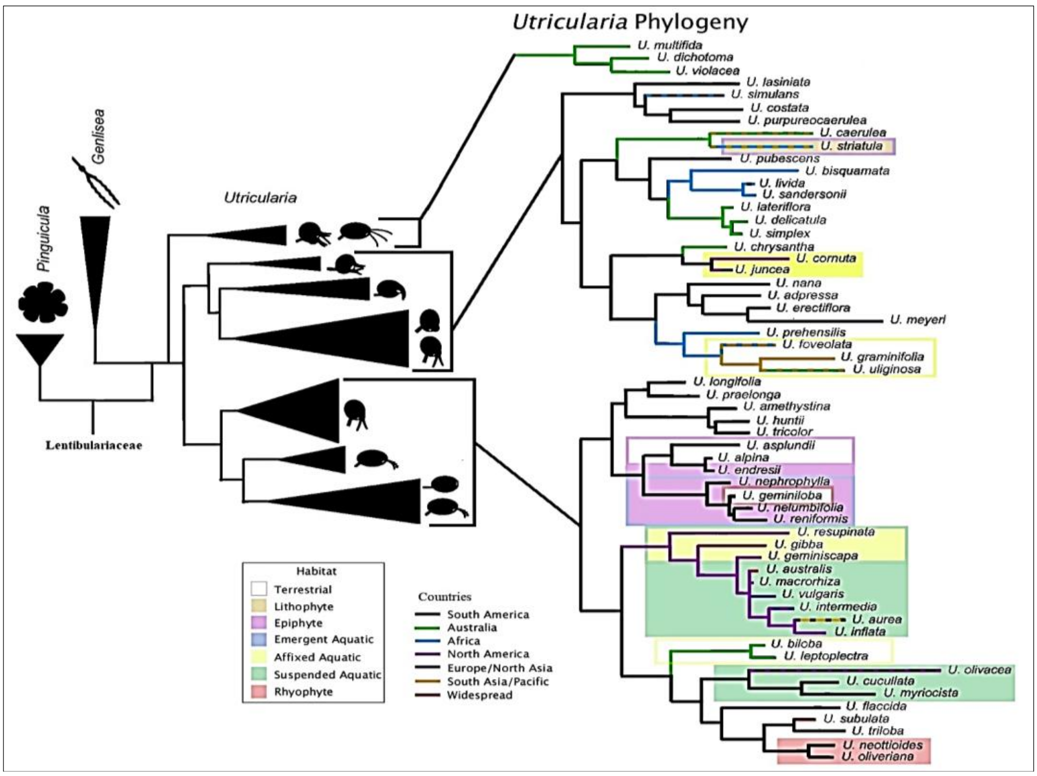

Fig 4: Pictorial representation of phylogeny linkage among different species of Utricularia along with the countries in which the species were reported as well as the habitats in which they grow by collecting the data from Victor *et al*., 2010; Jobson *et al*., 2003 [30] and Silva *et al*., 2018 [66].

3. g. Identification of new species

With the advancement in technologies and application of molecular phylogeny many new species of *Utricularia* are been discovered around the world. Yadav*et al*., (2005) [75] had identified a new *Utricularia* species (*Utriculariababui*) in the Western Ghats of India. In 2012, Fleischmen had presented many new species in the research paper "The new *Utricularia* species described since Peter Taylor's monograph". Jobson (2013, 2018) [27, 29] had identified five new species from Australia. In 2018, another new species of *Utricularia* (*Utriculariasunilii*) was found in Kerala, India.

3. h. Phytoremediation by *Utricularia*

Environmental pollution due to heavy metal pollutants has become a serious issue of modern society which have many hazardous effects [Prasad *et al*., 2006; Liu *et al*., 2007; Rai, 2009; Nouri and Haddioui, 2016] [54, 35, 56, 44]. Plants growing in heavy metal pollution have a spectrum of morphological and cellular changes, including reduced metabolism, degradation of biomolecules, change in proteins. These effects are caused due to stress by bioaccumulation of pollutants through root, stem or sprouts of plants growing in the polluted environment [Borišev *et al*., 2008; Babović *et al*., 2010] [11, 7].

Phytoremediation is the process of removing or detoxifying polluted water, soil and air by using plants. It has been proved by many researchers that plants can transfer pollutants into less harmful form as well as can accumulate metal pollutants in large quantities [Ali *et al*., 2013] [4]. Many aquatic species of plants can accumulate heavy metals without having any significant changes in their metabolism. Macrophytes and aquatic plants are often used for bioremediation of polluted water bodies [Borišev *et al*., 2008; Babović *et al*., 2010; Augustynowicz *et al*., 2010; Malec *et al*., 2011] [11, 7, 5, 38]. Submerged aquatic species of *Utricularia* such as *Utricularia vulgaris* and *Utricularia aurea* (macrophytes) can grow in heavy metal polluted water by phytoaccumilation.

Augustynowicz and his coworkers (2015) studied the bioremediation of chromium (VI) by *Utricularia gibba*. They observed that *Utricularia gibba* can accumulate Cr more effectively in comparison to other aquatic macrophytes like *Pistia stratiotes or Spirodelapolyrhiza*. *Utricularia aurea* helps in removal of heavy metal like zinc by biosorption method. Maksimovic (2019) [68] reported that *Salvinianatans* and *Utricularia vulgaris* have high bioaccumulation capacity to Fe, Zn, Mn, and Cu. The presence of common pioneer species (*Utricularia aurea* and *U. bifida*) indicates past disturbance in a habitat, such as that demonstrated in a paleonological study, with the first appearance of *U. aurea* pollen coinciding with the arrival of aborigines in Tasik Bera, Pahang. The presence of common *Utricularia* species in the suburban waysides can therefore be used as a rough prediction for water trophicity, succession stages, and the general health of the regenerating patches.

3. i. Medicinal properties of *Utricularia*

Although very little research has been conducted on medicinal values, it is still used traditional medicines. In Peninsular Malaysia, *Utricularia bifida* is used for treatment of urinary diseases. Divakar *et al*., (2013) [15] reported that Madayipara hillock tribals of Kerala use the *Utricularia reticulata* against urinary problems. In the year 2015, Deka and Devi reported that *Utricularia aurea* is used to cure diseases caused by mosquito. Choosawad *et al*., (2005) [12] reported the antioxidant activity of *Utricularia aurea*. Few research works have been conducted on medicinal properties of *Utricularia* species [Kumar *et al*., 2017; Singh *et al*., 2021] [32, 67].

Conclusion

From the above study we can conclude that, *Utricularia* is an intriguing genus which is now in focus of many researches related to phylogeny, taxonomy, trap biochemistry and many more. Largest portion of the genus ~84% comprises of terrestrial species such as lithophytes or epiphytes and ~16% are free floating aquatics. Recent studies have shown that, some species of *Utricularia* and *Genlisea* have the smallest genome size in angiosperms. Three lineages in *Utricularia* genus have evolved independently which have genome size of less than 100 Mbp. Many new species are also been identified all around the world. Different species of *Utricularia* have phytoremediation and medicinal properties. Still with all the development and research, many questions remain unsolved about its genome and trap pray interaction.

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Conflict of Interest

Authors have no conflict of interest.

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