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**ESTUDOS TAXONÔMICOS E SISTEMÁTICOS EM *UTRICULARIA*
L. (LENTIBULARIACEAE) DO BRASIL**

Tese (Doutorado)

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Tese apresentada ao Programa de Pós Graduação em Biologia Vegetal do Centro de Biociências, Universidade Federal de Pernambuco como parte dos requisitos parciais para obtenção do título de Doutor em Biologia Vegetal

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RESUMO

Lentibulariaceae é a maior família de plantas carnívoras, com cerca de 360 espécies divididas em três gêneros, *Pinguicula* (ausente no Brasil), *Genlisea* e *Utricularia*. Cada gênero possui especializações morfo-fisiológicas para captura e digestão de presas. Em território nacional foram registradas 90 espécies de *Genlisea* e *Utricularia*, reconhecidas pelo pequeno porte, armadilhas subterrâneas ou submersas, inflorescências emergentes em racemos ou flores solitárias, e corola bilabiada e calcarada. *Utricularia* é o maior em riqueza de espécies de plantas carnívoras, com cerca de 250 espécies, amplamente distribuído no globo, e com ancestral comum mais recente possivelmente surgido na América do Sul há aproximadamente 39 milhões de anos. Dessa forma, o continente, especialmente o território brasileiro, se configura como um importante centro de diversidade do grupo. O objetivo desse estudo foi empregar abordagens morfológicas e filogenéticas em espécies de Lentibulariaceae que ocorrem no Brasil, visando melhorar o conhecimento taxonômico, fitogeográfico, evolutivo e sistemático desse grupo. Aqui são apresentados um tratamento taxonômico para as 16 espécies de Lentibulariaceae registradas no estado do Espírito Santo; uma sinopse das 42 espécies da família ocorrentes no estado da Bahia, com padrões fitogeográficos, endemismos, raridades, ameaças aos seus habitats e esforços para conservação das mesmas profundamente discutidos; e uma hipótese filogenética bem suportada para a seção *Setiscapella*, um grupo de dez espécies morfolologicamente muito similares que vem sendo evidenciado com incongruências topológicas por estudos moleculares anteriores, e aqui combinamos dados moleculares de diferentes compartimentos genômicos (ITS, gene *matK*, espaçadores *rpl20-rps12* e *trnL-F*, e íntron *rps16*) e dados morfológicos, propondo uma nova seção, *U. sect. Diversicolor*, que engloba três espécies originalmente incluídas na seção *Setiscapella*.

Palavras-chave: Filogenia molecular. Lamiales. Nova seção. Plantas carnívoras. Taxonomia.

ABSTRACT

Lentibulariaceae is the largest carnivorous plant family, comprising about 360 species divided into three genera, *Pinguicula* (absent in Brazil), *Genlisea* and *Utricularia*. Each genus possesses morpho-physiological specializations to capture and digest their prey. In national territory, 90 species of *Genlisea* and *Utricularia* were registered, recognized by their small stature, underground or submerged traps, emergent inflorescences in racemes or solitary flowers, and bilabiate and spurred corolla. *Utricularia* is the most species-rich genus of carnivorous plants, with approximately 250 species widely distributed across the globe, and with the most recent common ancestor possibly arising in South America. Thus, the continent, especially the Brazilian territory, comprises an important center of diversity for the group. The objective of this study was to apply morphologic and phylogenetic approaches in species of the family Lentibulariaceae that occur in Brazil, aiming to improve the taxonomic, phytogeographic, evolutionary and systematic knowledge of this group. Here we present a taxonomic treatment for the 16 species of Lentibulariaceae recorded in the state of Espírito Santo; a synopsis of the family occurring in the state of Bahia, with phytogeographic patterns, endemisms, rarities, threats to their habitats and efforts to conserve them deeply discussed; and a well-supported phylogenetic hypothesis for the section *Setiscapella*, a group of ten morphologically very similar species that have been evidenced with topological incongruities in previous molecular studies, and here we combined molecular data from different genomic compartments (ITS, *matK* gene, *rpl20-rps12* and *trnL-F* spacers, and *rps16* intron) and morphological data, proposing a new section, *U. sect. Diversicolor*, which encompasses three species originally included in section *Setiscapella*.

Keywords: Carnivorous plants. Lamiales. Molecular phylogeny. New section. Taxonomy.

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1 INTRODUÇÃO

A carnivoría em plantas evoluiu independentemente, no mínimo, em 12 linhagens diferentes de Angiospermas, sendo uma adaptação às deficiências nutritivas dos substratos onde ocorrem. Por isso, essas plantas são capazes de colonizar os mais diversos habitats que muitos outros organismos vegetais não conseguem. Dentre essas linhagens, se destaca a família Lentibulariaceae, cujas espécies são ervas que ocorrem, geralmente, nas zonas mais úmidas e abertas de diversas fitofisionomias da Terra, sendo encontradas desde em formações pioneiras de terras baixas à campos de altitudes elevadas. Devido à essa habilidade de crescerem em ambientes muito específicos, juntamente com a sensibilidade a alterações ambientais (ex.: pH, poluição, temperatura), essas espécies têm potencial para agirem como bioindicadores de qualidade ambiental.

No histórico taxonômico da família, ao longo das últimas décadas muitos estudos filogenéticos foram realizados e estes evidenciam que ainda persistem alguns grupos que carecem de revisão sistemática. Isso é especialmente observável em *Utricularia*, que apesar uma significativa parte da classificação infragenérica baseada em características morfológicas ter sido corroborada por análises moleculares, diversas incongruências topológicas e problemas taxonômicos foram evidenciados, bem como rearranjos sugeridos e novos agrupamentos formalmente propostos. Contudo, a última revisão taxonômica é de três décadas atrás.

Notavelmente, existe uma complexidade na identificação de exemplares de Lentibulariaceae em coleções botânicas, sendo muitas amostras, por diversas vezes, determinadas somente à nível genérico ou erroneamente identificadas à nível genérico e/ou específico, inclusive como membros de outras famílias que possuem ocorrência nos mesmos habitats, como Burmaniaceae ou Xyridaceae. Isso é fortemente evidente em *Utricularia*, especialmente em grupos de espécies com morfologias florais muito similares.

Diante disso, o foco principal desta pesquisa consiste em estudos taxonômicos e sistemáticos de espécies de Lentibulariaceae que ocorrem no Brasil, combinando abordagens morfológicas, filogenéticas e fitogeográficas. Desse modo, o objetivo é contribuir para o melhor conhecimento sistemático da família, auxiliando no reconhecimento e delimitação de suas espécies pertencentes à flora brasileira, em

campo e/ou em herbário, com base em morfologia, e no entendimento das relações evolutivas entre algumas espécies de *Utricularia*, com base em análises filogenéticas. Assim, esta tese está organizada da seguinte forma:

A **Fundamentação Teórica** contendo uma breve discussão sobre a evolução da carnivoría em Angiospermas, culminando na caracterização da família Lentibulariaceae e de seus gêneros, bem como sua importância científica, ecológica e econômica. Além disso, inclui um aprofundamento no gênero *Utricularia*, discutindo seu histórico de classificação e circunscrição, características morfológicas, e por fim, a problemática da seção *Setiscapella* é apresentada.

O **Artigo 1** (publicado) consiste no tratamento taxonômico das 16 espécies de Lentibulariaceae registradas para o estado do Espírito Santo. O trabalho contém chave de identificação, descrições morfológicas, ilustrações, mapas de distribuição, lista de material examinado e comentários acerca da taxonomia e distribuição das espécies, além de uma tabela resumindo informações de status de conservação e unidades de conservação no Estado que englobam a distribuição natural das mesmas.

O **Artigo 2** (publicado) se trata da sinopse das 42 espécies de Lentibulariaceae no estado da Bahia, o qual se configura como o segundo maior em riqueza da família no País. Nesse trabalho são apresentados comentários diagnósticos curtos, fotografias de espécimes vivos, distribuição geográfica atualizada disposta em mapas, novos registros, e uma discussão aprofundada acerca de padrões fitogeográficos, endemismos, raridade e caracterização do atual cenário de ameaças e conservação. Os resultados corroboram com hipóteses prévias de conexões vegetais no passado e com estudos que apontam que o Rio São Francisco funciona como uma barreira geográfica influenciando em processos de especiação e diversidade genética no Nordeste do Brasil.

O **Artigo 3** (em construção) consiste na filogenia molecular de *Utricularia* sect. *Setiscapella* utilizando quatro regiões de DNA de cloroplasto (gene *matK*, espaçadores *rpl20-rps12* e *trnL-F*, e íntron *rps16*) e uma de núcleo (ITS1-5.8-2), combinadas com dados morfológicos suportando a não-monofilia da seção. Se fazendo necessária a proposta de uma nova seção para acomodar três espécies originalmente incluídas na seção *Setiscapella*, suportada por evidências filogenéticas e reconstrução de estados de caracteres ancestrais.

2 FUNDAMENTAÇÃO TEÓRICA

2.1 A EVOLUÇÃO DA CARNIVORIA EM PLANTAS

Uma planta se configura como carnívora preenchendo um conjunto de requisitos em adaptações morfológicas e fisiológicas, tais como a capacidade de atrair, capturar ou absorver nutrientes de organismos mortos em suas modificações foliares, denominadas armadilhas, de modo a beneficiar seu crescimento e reprodução (Givnish et al. 1984; Juniper et al. 1989; Ellison 2006; Ellison & Gotelli 2009; Rice 2010, 2011). Como já apresentado, essas plantas colonizam ambientes abertos, abundantes em umidade, porém, deficientes em nutrientes, onde os custos de desenvolver adaptações para a carnivoría são superados pelos benefícios da captura de presas (Givnish et al. 1984).

A carnivoría surgiu múltiplas vezes na história evolutiva das Angiospermas, em linhagens independentes, mais precisamente em cinco ordens, 12 famílias, 19 gêneros e ca. 850 espécies (Fleischmann et al. 2018). Cada tipo de armadilha apresenta adaptações morfológicas individuais para aprimorar a eficácia de captura conforme o ambiente e a disponibilidade de presas circundantes (Ellison & Gotelli 2009). Essas adaptações demonstram uma convergência evolutiva notória, pois apesar de ocorrerem em linhagens independentes, muitas apresentam similaridades nos sistemas de captura e digestão de presas (Fleischmann et al. 2018).

Há cinco tipos gerais de armadilhas carnívoras (Figura 1), o primeiro e mais comum consiste de folhas adesivas, devido ao indumento com tricomas glandulares secretores de mucilagem ou resina pegajosa. Presente nos gêneros *Byblis* Salisb. (Byblidaceae), *Drosera* L. (Droseraceae), *Drosophyllum* Link (Drosophyllaceae), *Philcoxia* P.Taylor & V.C.Souza (Plantaginaceae), *Pinguicula* L. (Lentibulariaceae), *Roridula* Burm. f. ex L. (Roridulaceae) e *Triphyophyllum* Airy Shaw (Dioncophyllaceae) (Cross et al. 2018; Fleischmann et al. 2018).

O segundo são folhas com epiascídias distais, ou folhas que formam tanques pela sua disposição em roseta, ou ainda folhas inteiramente tubulares com abertura no ápice, as quais acumulam água combinada com a secreção de enzimas digestivas produzidas pela planta ou através de relações mutualísticas com artrópodes ou bactérias que digerem as presas e a planta absorve os dejetos. Ocorre em *Nepenthes* L. (Nepenthaceae), *Cephalotus* Labill. (Cephalotaceae), *Brocchinia* Schult. f. e

Catopsis Griseb. (Bromeliaceae), *Paepalanthus* Mart. (Eriocaulaceae), *Darlingtonia* DC., *Heliamphora* Benth. e *Sarracenia* L. (Sarraceniaceae) (Cross et al. 2018; Fleischmann et al. 2018).

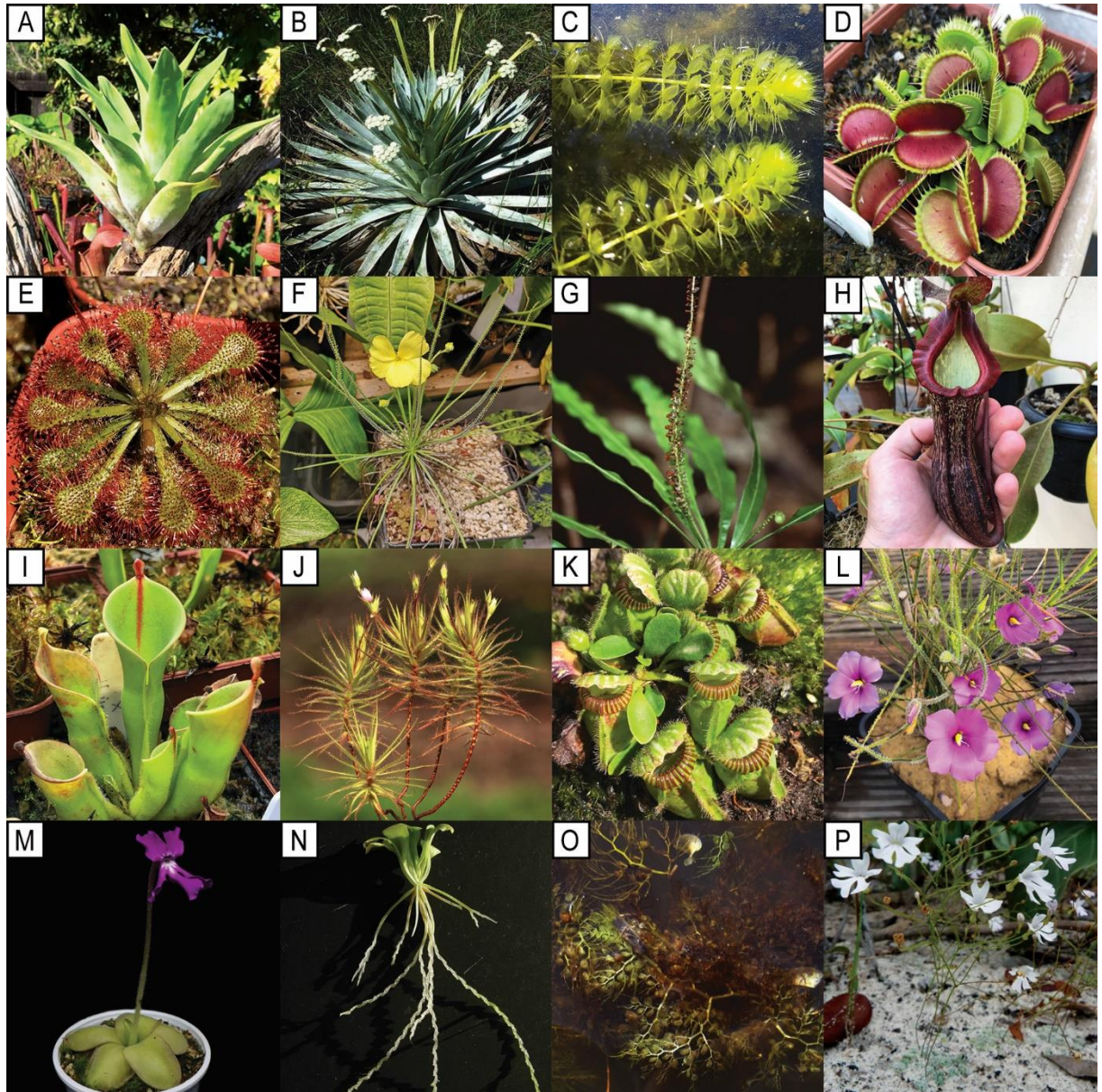


Figura 1 – Representantes de linhagens de plantas carnívoras. A. *Catopsis berteroniana* (Schult. & Schult. f.) Mez. B. *Paepalanthus bromelioides* Silveira. C. *Aldrovanda vesiculosa* L. D. *Dionaea muscipula* L. E. *Drosera intermedia* Hayne. F. *Drosophyllum lusitanicum* (L.) Link. G. *Triphyophyllum peltatum* (Hutch. & Dalziel) Airy Shaw. H. *Nepenthes maxima* Reinw. ex Nees. I. *Heliamphora minor* Gleason. J. *Roridula gorgonias* Planch. K. *Cephalotus follicularis* Labill. L. *Byblis gigantea* Lindl. M. *Pinguicula moranensis* Kunth. N. *Genlisea flexuosa* Rivadavia, A. Fleischm. & Gonella. O. *Utricularia foliosa* L. P. *Philcoxia goiasensis* P.Taylor. Fotos A por Manny Herrera, B por Marcelo Trovó, C por Teddy Vayssade, D, E, H e I por Bruno Garcia, F por Martine Hanna Loken, G por Cuauhtémoc Velázquez, J por David Wiles, K por Greg Bourke, L por Greg Allan, M por Fraser Anderson, N por Andreas Fleischmann, O por Valéria Sampaio, P por André Vito Scatigna.

O terceiro são armadilhas de disparo instantâneo, encontradas em *Aldrovanda* L. e *Dionaea* J.Ellis (Droseraceae), que consistem de folhas com dois lobos que se fecham rapidamente após o contato da presa com os tricomas sensitivos localizados na face interna dos lobos (Fleischmann et al. 2018). Enquanto os dois outros tipos, rizófilos e utrículos, são especializações foliares exclusivas dos gêneros *Genlisea* A.St.-Hil. e *Utricularia* L. (Lentibulariaceae), respectivamente. Os rizófilos são folhas aclorofiladas, tubulares, subterrâneas, internamente revestidas por tricomas retrorsos, e com dois braços distais helicoidais onde se localizam as aberturas passivas da armadilha. Por outro lado, os utrículos são vesículas de sucção ativa, subterrâneos ou submersos, que capturam as presas em frações de segundo após estas tatearem tricomas-gatilho sensitivos localizados na abertura da armadilha (Fleischmann et al. 2018).

Assim, apenas nas famílias Droseraceae e Lentibulariaceae evoluíram mais de um tipo de armadilha carnívora, todas possivelmente originadas a partir de armadilhas adesivas (Müller et al. 2004; Heubl et al. 2006; Fleischmann et al. 2010). Na ordem Lamiales, tricomas glandulares secretores de mucilagem adesiva são bastante comuns em diversas porções vegetativas ou reprodutivas das plantas, como uma adaptação contra a herbivoria, potencializando a hipótese da evolução da carnivoría nesse grupo, sendo alguns grupos (Martyniaceae e Orobanchaceae) consideradas “proto-carnívoras” por não possuírem absorção de nutrientes detectada (Givnish et al. 1984; Juniper et al. 1989; Rice 1999; Müller et al. 2004; Plachno et al. 2009).

2.2 A FAMÍLIA LENTIBULARIACEAE RICH.

Pinguicula, *Genlisea* e *Utricularia* são os três gêneros incluídos na família Lentibulariaceae, totalizando cerca de 380 espécies e configurando a maior família de plantas carnívoras (Fleischmann & Roccia 2018; Cross et al. 2020). Dentre os caracteres morfológicos compartilhados na família se observam: cálice gamossépalo, com duas ou cinco sépalas (raramente quatro); corola gamopétala, tubular, zigomorfa, bilabiada e calcarada; cálcar internamente coberto por glândulas nectaríferas; androceu com dois estames adnatos à corola e anteras uniloculares; gineceu bicarpelar e gamocarpelar com estigma bilabiado; e fruto capsular deiscente (Judd et al. 2009). Por outro lado, cada gênero apresenta adaptações morfológicas e fisiológicas distintas para captura e digestão de presas (Figura 2).

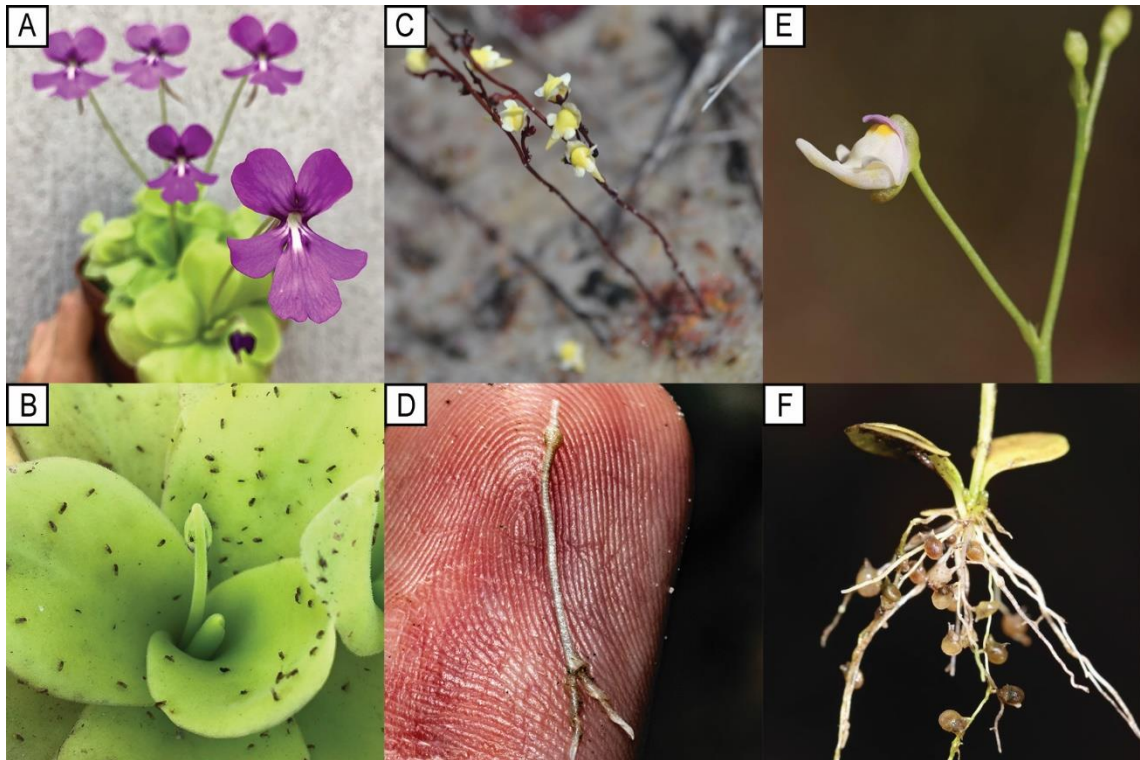


Figura 2 – Representantes dos três gêneros da família Lentibulariaceae, acima inflorescências ou flores solitárias, e abaixo armadilhas carnívoras. A-B. *Pinguicula moranensis* Kunth. C. *Genlisea oxycetron* P.Taylor. D. *Genlisea repens* Benj. E-F. *Utricularia amethystina* Salzm. ex A.St.-Hil. & Girard. Fotos A-B por Bruno Garcia, D por Hugo Dolsan, E-F por Juliano Fabricante.

O gênero *Pinguicula* está representado por cerca de 105 espécies, com distribuição nas Américas do Norte e Central, nos Andes da América do Sul, Antilhas, Europa e norte e leste da Ásia (Fleischmann & Roccia 2018; Cross et al. 2020). Seus representantes são reconhecidos por apresentarem raízes verdadeiras, folhas carnosas dispostas em uma roseta basal, com superfície adaxial recoberta por tricomas adesivos, constituindo suas armadilhas carnívoras; flores axilares, solitárias, e cálice com duas sépalas lobadas (três lobos na superior e dois na inferior) (Heslop-Harrison 2003; Cieslak et al. 2005; Fleischmann & Roccia 2018).

Ao contrário de *Pinguicula*, os outros dois gêneros são desprovidos de raízes, possuem armadilhas mais complexas e únicas, inflorescências racemosas eretas, simples, raramente ramificadas ou, em alguns casos, reduzidas a flores solitárias. Em geral, as flores são morfologicamente uniformes e similares, sendo o cálice pentâmero em *Genlisea* e dímero ou tetrâmero em *Utricularia* (Taylor 1989; Fleischmann 2012a).

Genlisea compreende 31 espécies que ocorrem nas zonas tropicais e subtropicais dos continentes africano e americano, incluindo o Brasil que abriga 19 espécies (Cross et al. 2020; Gonella et al. 2022). Caracterizadas por uma roseta basal de folhas aéreas simples, como em *Pinguicula*, contudo, as armadilhas carnívoras

consistem de modificações foliares subterrâneas, denominadas rizófilos (Fleischmann 2012a, 2018). Esses órgãos se originam de primórdios foliares cilíndricos com uma ponta invaginada (Rutishauser & Sattler 1989).

Os rizófilos são aclorofilados, em forma de Y invertido, com braços distais, tubulares e helicoidais, internamente recobertos por tricomas retróscos que direcionam a presa a uma câmara digestiva apical (ampola) por um caminho sem retorno, criando uma barreira para o sentido distal (Fromm-Trinta 1981; Fleischmann et al. 2010, 2011; Fleischmann 2012a, 2018). A superfície interna da ampola apresenta glândulas curtas, pediceladas, com organelas que sintetizam proteínas, e uma cutícula porosa para absorção de nutrientes das presas (Fromm-Trinta 1981; Adamec 2003; Płachno et al. 2007).

Utricularia é amplamente distribuído no planeta, compreende cerca de 250 espécies, englobando cerca de 35% de todas as plantas carnívoras existentes e configurando o maior táxon de plantas carnívoras (Cross et al. 2020; Guedes et al. 2021). Os utrículos, como são denominadas suas armadilhas carnívoras, são considerados as modificações foliares mais complexas do reino vegetal (Lloyd 1942; Rutishauser & Sattler 1989; Taylor 1989). Esses órgãos são formados a partir de primórdios foliares esféricos que culminam em vesículas microscópicas, submersas ou subterrâneas, seladas hermeticamente por uma porta articulada, que capturam as presas por um mecanismo de sucção à vácuo de diferença de pressão (Lloyd 1942; Vincent et al. 2011).

Os utrículos podem se formar nos estolões e folhas, raramente nos rizoides, e podem ser sésseis ou pedunculados, a porta articulada é munida de tricomas-gatilho sensitivos que disparam o sistema de sucção quando tateados (Lloyd 1942; Taylor 1989; Vincent et al. 2011). Sua superfície interna das armadilhas é densamente coberta por tricomas glandulares quadrífidos, os quais são responsáveis pela secreção de enzimas hidrolíticas e absorção de nutrientes. Ademais, ao redor da superfície interna da abertura são encontrados tricomas bífidos que atuam na evacuação de água após a sucção da presa (Reifenrath et al. 2006; Adamec et al. 2010; Poppinga et al. 2015).

Os representantes da família Lentibulariaceae têm atraindo a atenção de inúmeros pesquisadores desde que estudos reportaram algumas espécies de *Genlisea* e *Utricularia* como portadoras dos menores genomas (variando entre 1C =

60Mbp a 1.500Mbp) e das maiores taxas de substituição de bases (mutações) dentre todas as Angiospermas (Jobson & Albert 2002; Greilhuber et al. 2006; Ibarra-Laclette et al. 2013; Leushkin et al. 2013; Fleischmann et al. 2014; Carretero-Paulet et al. 2015; Lan et al. 2017). Tal fato, sobrepuja a tão postulada planta-modelo *Arabidopsis thaliana* (L.) Heynh., a qual permaneceu por mais de 30 anos como a angiosperma com menor genoma nuclear (Bennet & Leitch 2011). Assim, sendo consideradas importantes candidatas à plantas-modelo para estudos genéticos e evolutivos (Albert et al. 2010; Fleischmann et al. 2014).

Além disso, possuem um valor ornamental significativo, porém, sua importância ecossistêmica ainda não é totalmente elucidada (Zamudio 2003; Stumpf et al. 2012; Lemos 2016). Pott & Pott (2000) reportaram que algumas espécies fazem parte da alimentação de peixes e aves aquáticas, ao passo que também servem de abrigo para pequenos invertebrados aquáticos. E como já mencionado, algumas espécies com alta especificidade de habitat e distribuição restrita são potenciais bioindicadores de solos pobres e qualidade ambiental (Ellison & Gotelli 2001, 2002; Jennings & Rohr 2011).

2.3 O GÊNERO *UTRICULARIA* L.

2.3.1 Aspectos morfológicos

É difícil descrever e interpretar o desenvolvimento arquitetônico de *Utricularia* em termos de morfologia clássica, sendo a abordagem da ‘morfologia contínua’ (*continuum morphology*) e do pensamento de processo fornecedores de perspectivas complementares para compreender as particularidades nesse grupo de plantas (Rutishauser & Isler 2001; Rutishauser 2020). Para Agnes Arber (1920), o corpo vegetativo de *Utricularia* tem tanto uma natureza de caule quanto de folha, então é um mistério ainda não resolvido como tal condição surgiu historicamente de um ancestral possuindo órgãos caulinares e foliares bem definidos (Rutishauser 2015, 2020). O que se tornou um conceito conhecido como ‘Morfologia Arberiana Difusa’ (Fuzzy Arberian Morphology – FAM) (Rutishauser & Isler 2001; Rutishauser 2015).

As espécies de *Utricularia* exibem mosaicos de desenvolvimento (Figura 3) entre as categorias estruturais conhecidas como folhas e caules, sendo um primórdio capaz de formar utrículos, folhas, caules, rizoides ou inflorescência (Goebel 1981; Rutishauser & Isler 2001). Análises genômicas de algumas espécies de *Genlisea* e

Utricularia revelaram a presença de genes específicos de raízes (Ibarra-Laclette et al. 2011, 2013; Barta et al. 2015; Carretero-Paulet et al. 2015; Renner et al. 2018), então, a ausência de raízes verdadeiras pode ser resultado da não expressão desses genes, em vez da ausência deles (Rutishauser 2020). Em sua monografia, Taylor (1989) ressaltou a peculiaridade dos órgãos vegetativos do gênero em discrepância com as demais angiospermas, e acreditava que para propósitos práticos, descritivos e taxonômicos, era desejável aplicar uma terminologia própria consistente, e assim o fez.

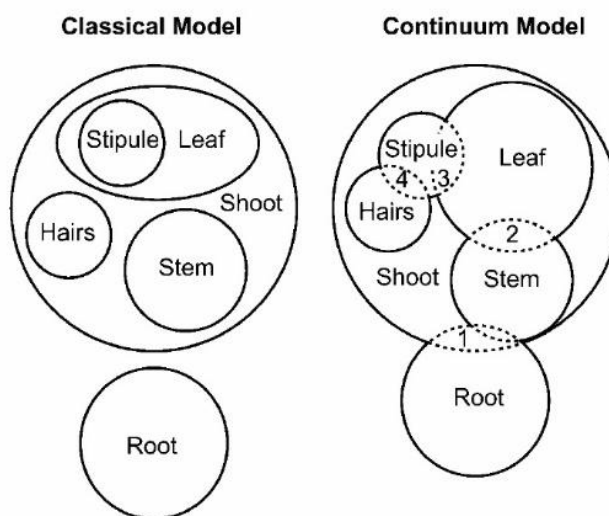


Figura 3 – Categorias estruturais de plantas vasculares de acordo com os modelos de morfologia Clássica e Contínua. No modelo Clássico os órgãos apresentam um sistema hierárquico sem sobreposições, enquanto no Contínuo, os órgãos se apresentam menos hierárquicos e com sobreposições parciais permitindo a percepção de mosaicos de desenvolvimento (intermediários) entre os mesmos. Extraído de Rutishauser & Isler (2001).

Nesse sentido, adotando a terminologia específica e prática de Taylor (1989), o plano corporal vegetativo de *Utricularia*, no geral, pode apresentar (Figura 4) rizoides, estolões, utrículos, folhas de diversos formatos e, em algumas espécies aquáticas suspensas de *U. sect. Utricularia*, um verticilo de flutuadores na base ou acima dos escapos florais. Segundo Jobson et al. (2018), esses órgãos flutuadores consistem de um caráter que, aparentemente, evoluiu uma única vez, com reversões para sua ausência no mínimo em duas espécies da seção.

Os estolões e rizoides têm sido apontados como homólogos à caules (Troll & Dietz 1954; Fleischmann 2012a), a folhas (Goebel 1891; Kumazawa 1967) ou como amálgamas no desenvolvimento de folhas e caules (Rutishauser & Sattler 1989; Rutishauser & Isler 2001). Rutishauser (2015) e Reut & Płachno (2020) detalham a simetria dorsiventral (Figura 5) dos estolões durante a organogênese da planta, onde a inflorescência, os ‘caules aéreos’ e as folhas surgem no setor dorsal de um nó no estolão principal, e este se ramifica em estolões secundários, rizoides ou flutuadores, enquanto os utrículos surgem no setor lateral do estolão principal. Reut & Płachno (2020) ainda concluíram que a determinação de um tipo de órgão diminui com o



Figura 4 – A. Rizoides de *Utricularia pusilla* Vahl. B. Estolões, utrículos e folhas capilares submersas de *U. intermedia* Hayne. C. Flutuadores de *U. breviscapa* C.Wright ex Griseb. D. Estolões e folhas aéreas laminares de *U. nigrescens* Sylvén. E. Folhas aéreas laminares e tubérculos de *U. jamesoniana* Oliv. F. Rizoides de ancoragem de *U. neottiioides* A.St.-Hil. & Girard. Fotos B por Fernando Rivadavia, C por Matheus Pestana, D por Marcos Ferramosca Cardoso, E por Josh Allen e F por Bartosz J. Plachno.

aumento da quantidade de primórdios na sucessão de desenvolvimento de órgãos em um nó de estolão, assim, a planta tem flexibilidade na produção do tipo de órgão apropriado em condições ambientais inconstantes.

Em algumas espécies epífitas e terrícolas de *U. sect. Orchidioides* e *Iperua*, os estolões formam tubérculos de armazenamento de água (Figura 4E), auxiliando na sobrevivência das espécies durante períodos de estresse hídrico (Taylor 1989). Tal caráter é homoplástico segundo Rodrigues et al. (2017), com pelo menos duas origens independentes, uma em *U. sect. Orchidioides*, com reversão em *U. cornigera*, e outra em *U. geminiloba* Benj. (*U. sect. Iperua*).

Os rizoides são também chamados de ‘estolões de ancoragem’ (Figura 4F), auxiliando na manutenção da inflorescência ereta ou emergente durante a antese (Lloyd 1942). Em espécies reófitas esses rizoides possuem aspecto de ‘garras’ com tricomas ventrais adesivos que auxiliam na ancoragem no substrato em habitats turbulentos (riachos e corredeiras) (Taylor 1989), uma convergência evolutiva encontrada também em Podostemaceae e Hydrostachyaceae (Rutishauser & Isler

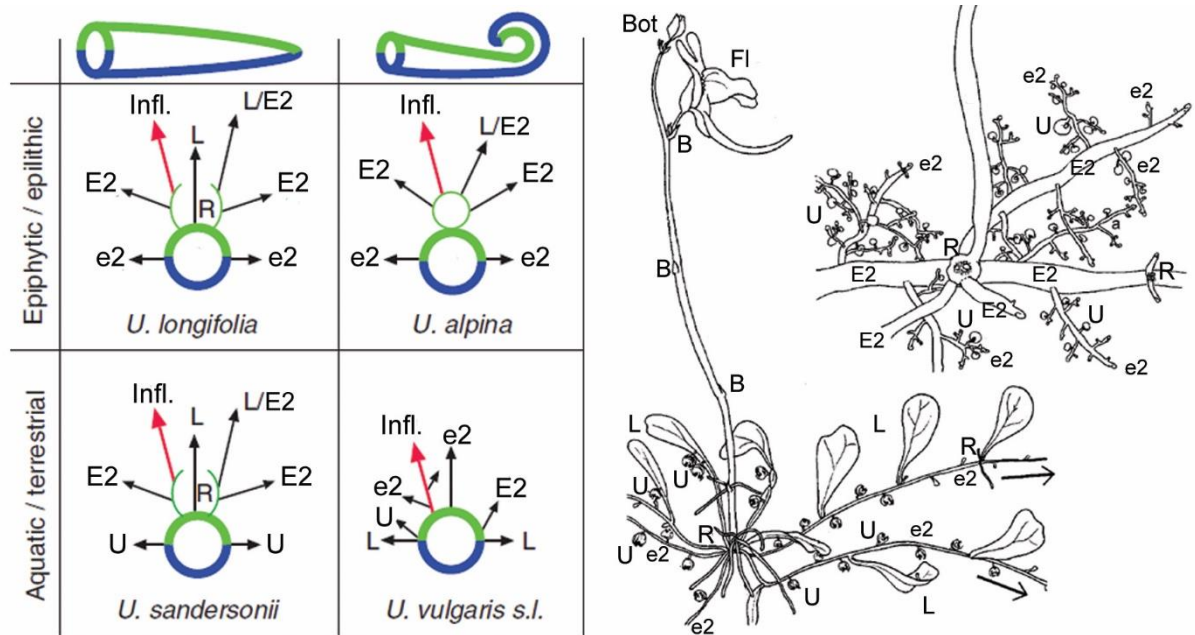


Figura 5 - Esquemas de desenvolvimento organogênico a partir de estolões primários em espécies de *Utricularia*, evidenciando a simetria dorsiventral dos estolões, em verde a porção dorsal e em azul, a ventral. Meristemas apicais podem ser retos ou circinados dependendo do subgênero e seção. R. Roseta de vários órgãos. L. Folha. E2 e e2. Estolões secundários espessos e delgados. L/E2. Folha e estolão secundário espesso surgindo da mesma posição. U. Utrículo. Infl. Inflorescência. B. Bráctea. Fl. Flor. Bot. Botão floral. Extraídos e modificados de Rutishauser (2015) e Rutishauser & Isler (2001).

2001). Płachno et al. (2020) evidenciaram que os rizoides de *U. neottioides* A.St.-Hil. & Girard possuem um esclerênquima bem desenvolvido e, além de ancoragem, desempenham múltiplas funções adicionais incluindo fotossíntese, armazenamento de nutrientes e reprodução vegetativa.

Os utrículos (Figura 6), como já mencionado, são estruturas vesiculares com uma abertura selada por uma porta articulada, essa abertura se apresenta em três configurações, quando posicionada adjacente à inserção do pedúnculo é dita basal, quando oposta à inserção do pedúnculo é dita terminal e, quando intermediária à essas duas posições, lateral (Taylor 1989). Lloyd (1932, 1942) descreveu a ocorrência de um velum nos utrículos, que consiste de uma estrutura cuticular produzida por tricomas especializados no epitélio pavimentoso do 'threshold', que, juntamente com mucilagem (Płachno et al. 2019), sela a porta das armadilhas, sendo necessário para o seu funcionamento adequado.

Externamente, esses órgãos podem ou não apresentar apêndices dorsais e/ou ventrais de diferentes formatos e ornamentações, cujas funções presumem-se estar relacionadas à atração e condução de presas à abertura (Taylor 1989; Reifenrath et al. 2006). Nas espécies terrícolas, rupícolas e epífitas, esses apêndices auxiliam na

retenção de umidade, agindo na prevenção de ressecamento dos utrículos em virtude do tipo de ambiente em que as plantas crescem (Reifenrath et al. 2006).

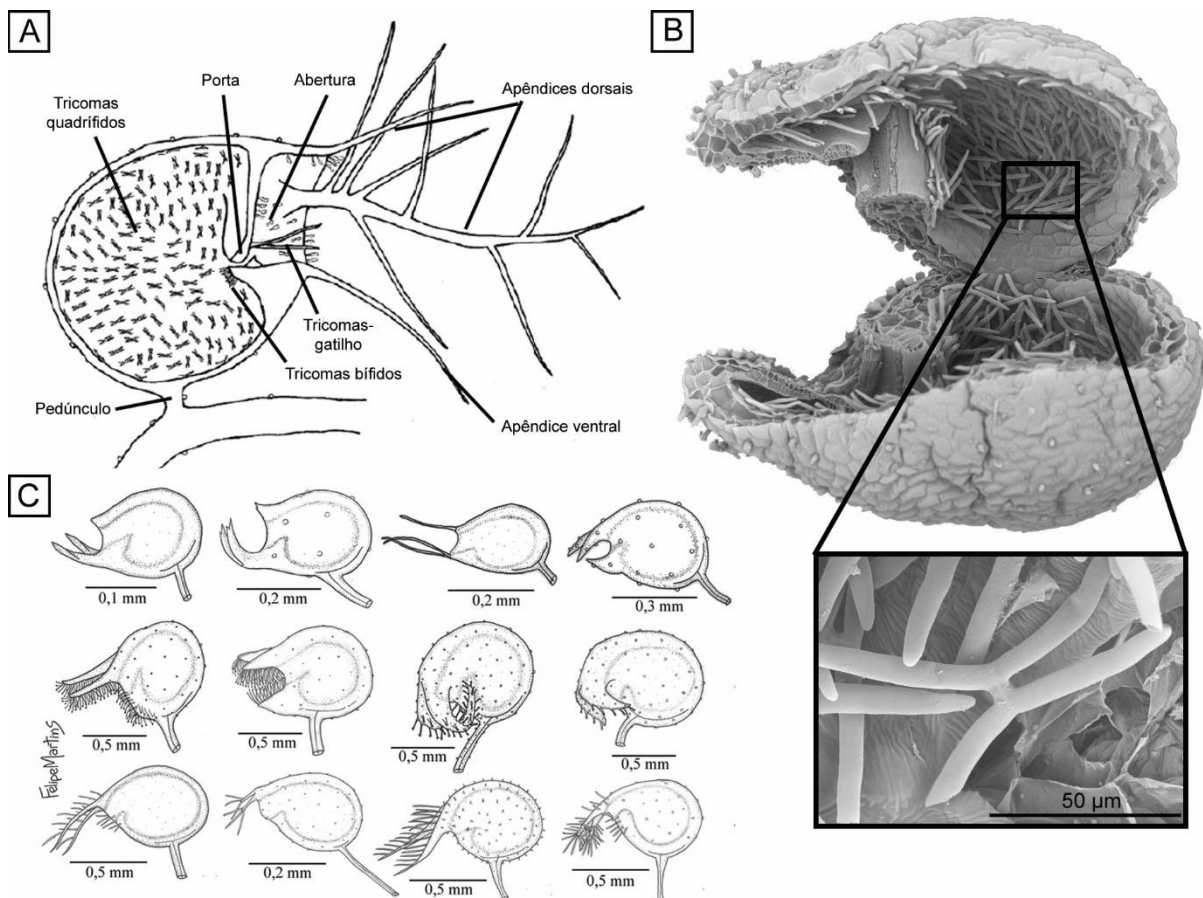


Figura 6 – A. Esquema de utrículo em corte longitudinal extraído e adaptado de Adamec (2011). B. Fotografia de Microscopia Eletrônica de Varredura de utrículo de *Utricularia cutleri* Steyererm. em corte longitudinal e destaque para um tricoma quadrífido (parte das mídias não publicadas de Guedes et al. 2019). C. Exemplos da diversidade morfológica de utrículos, ilustrados pelo presente autor, (esquerda para direita): *U. costata* P.Taylor, *U. simulans* Pilg., *U. tenuissima* Tutin, *U. adpressa* Salzm. ex A.St.-Hil. & Girard, *U. amethystina* Salzm. ex A.St.-Hil. & Girard, *U. trinervia* Benj., *U. longifolia* Gardner, *U. hispida* Lam., *U. resupinata* B.D.Greene ex Bigelow, *U. subulata* L., *U. trichophylla* Spruce ex Oliv., e *U. pusilla* Vahl.

Tricomas são caracteres-chave no mecanismo dos utrículos, realizando um papel significativo na captura e digestão de presas (Adamec 2011), e também possuem grande valor taxonômico em nível seccional e interespecífico (Taylor 1989). Existem três tipos funcionais principais presentes em diferentes porções dos utrículos (Figura 6). Como supracitado, os tricomas-gatilho se localizam na porta da armadilha e são sensíveis, responsáveis pela detecção de presas, acionando o processo de sucção. Os tricomas bifidos estão localizados na parte interna do ‘threshold’ (limiar interno da abertura), desempenhando função de efluxo de água após o processo de sucção, e possuem morfologia geralmente uniforme (Taylor 1989; Reifenrath et al. 2006; Adamec 2011).

Já os tricomas quadrífidos revestindo a parede interna dos utrículos possuem formatos similares aos de cromossomos, com os braços variando consideravelmente em disposição ou inclinação angular (conferindo silhuetas em forma de H, X ou π), comprimento, largura, textura e distância entre si (Taylor 1989). Essa variabilidade morfológica foi bastante investigada e usada com eficácia para propósitos taxonômicos (Lloyd 1942; Komiya 1972; Thor 1979, 1987, 1988; Taylor 1989; Doyle & Parnell 2003; Yang et al. 2009; Guedes et al. 2019, 2021).

As flores podem ser solitárias ou em inflorescência racemosa, cujos escapos apresentam variados arranjos de brácteas, bractéolas e escamas (brácteas estéreis, com gemas abortadas), as quais podem ser basifixas, peltadas ou subpeltadas, de diferentes formatos e ornamentações marginais (Figura 7). Escamas estão ausentes em representantes de *U.* subgen. *Polypompholyx* e *U.* sects. *Lecticula*, *Minutae*, *Vesiculina* e em alguns de *U.* sect. *Utricularia*. Ao passo que as brácteas estão sempre presentes, com ou sem um par de bractéolas adjacentes. As bractéolas estão ausentes nos membros de *U.* sects. *Avesicaria*, *Lecticula*, *Mirabiles*, *Nelipus*, *Setiscapella*, *Sprucea*, *Steyermarkia*, *Utricularia* e *Vesiculina*. Portanto, possuem importante valor taxonômico infragenérico (Taylor 1989).



Figura 7 – Variedade morfológica de brácteas e bractéolas em *Utricularia*. A. Bráctea e bractéolas basifixas, livres, margens laciniadas, de *U. hispida* Lam. B. Bráctea e bractéolas basifixas, basalmente conatas, margens inteiras, de *U. jamesoniana* Oliv. C. Bráctea basifixas, margem laciniada, de *U. praelonga* A. St.-Hil. D. Bráctea e bractéolas basifixas, conatas até $\frac{1}{4}$ de seu tamanho, margens inteiras, de *U. trinervia* Benj. E. Bráctea basifixas, tubular, de *U. resupinata* B.D.Greene ex Bigelow. F. Bráctea basifixas, margem fimbriada, auriculada, de *U. simulans* Pilg. G. Bráctea peltada, margens inteiras, de *U. pusilla* Vahl. H. Bráctea subpeltada, margens inteiras, de *U. viscosa* Spruce ex Oliv.

O cálice é persistente e acrescente nos frutos, formado por duas sépalas em *U.* subgen. *Utricularia* e *Bivalvaria* e quatro em *U.* subgen. *Polypompholyx* (Figura 8). Essas variam consideravelmente em forma, sendo uniformes ou diferentes entre si, com nervuras conspícuas ou não, com margens inteiras, laciniadas, erosas, denticuladas ou fimbriadas, e com ápices arredondados, agudos, obtusos, emarginados, truncados, bífidos, trifídeos, etc. (Figura 9). Portanto, configuram caracteres de grande valor taxonômico entre as espécies do gênero (Taylor 1989).



Figura 8 – Representantes dos três subgêneros de *Utricularia*, com ênfase no número de sépalas, quatro em (A) *U.* subgen. *Polypompholyx* e duas em (B, C) *U.* subgen. *Bivalvaria* e *Utricularia*. A. *Utricularia multifida* R.Br. B. *U. erectiflora* A.St.-Hil. & Girard. C. *U. amethystina* Salzm. ex A.St.-Hil. & Girard. Fotos A por Tim Entwisle, B por Gabriel Garcia e C por Juliano Fabricante.

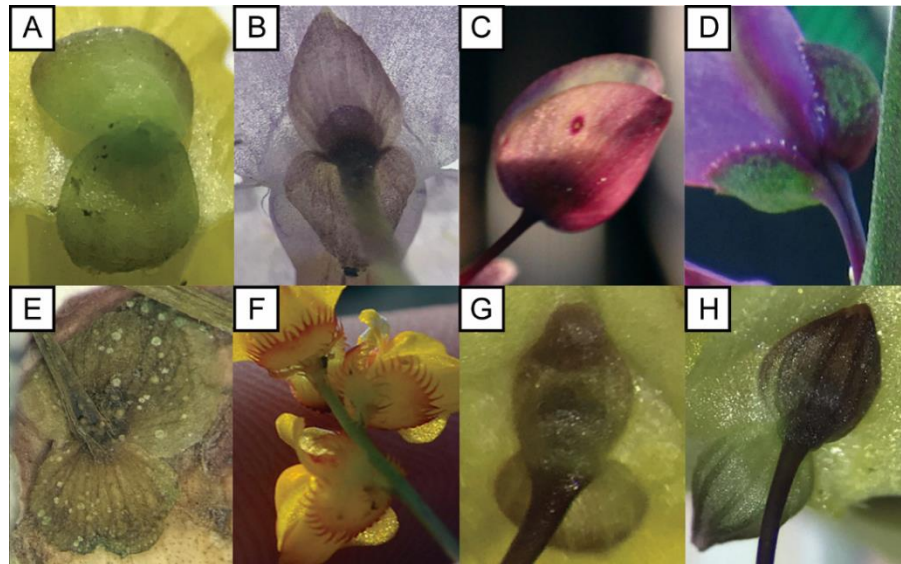


Figura 9 – Variabilidade morfológica das sépalas em *Utricularia*. A. Sépalas orbiculares, com margens inteiras, ápices arredondados e nervuras inconspícuas de *U. gibba* L. B. Sépalas ovais, com margens inteiras, ápices agudos e nervuras conspícuas não-proeminentes de *U. hydrocarpa* Vahl. C. Sépalas largo-ovais, com margens inteiras, ápices obtusos e nervuras conspícuas não-proeminentes de *U. jamesoniana* Oliv. D. Sépalas ovais, com margens denticuladas, ápices obtusos e nervuras conspícuas não-proeminentes de *U. longifolia* Gardner. E. Sépalas transversalmente elípticas, com margens erosas, ápices emarginados e nervuras conspícuas não-proeminentes de *U. praelonga* A.St.-Hil. F. Sépalas largo-ovais, com margens fimbriadas, ápices arredondados e nervuras inconspícuas de *U. simulans* Pilg. G. Sépalas ovais, com margens inteiras, ápices obtusos e nervuras conspícuas não-proeminentes de *U. subulata* L. H. Sépalas ovais, com margens inteiras, ápices agudos e nervuras conspícuas proeminentes de *U. triloba* Benj.

Da mesma forma, a morfologia e coloração da corola também fornecem caracteres cruciais na delimitação interespecífica. Essa consiste de um lábio superior com um arco basal dilatado (saco basal) que acomoda o androceu e o gineceu (Figura 10); um lábio inferior com limbo extremamente variável em forma entre as espécies, podendo ser inteiro, crenado, ou raso a profundamente lobado, plano, galeado ou ressupinado, além do palato ser giboso ou não; e um cálcio de diversos tamanhos, formatos, orientações e curvaturas, o qual pode produzir néctar através de glândulas na sua superfície interna (Taylor 1989).

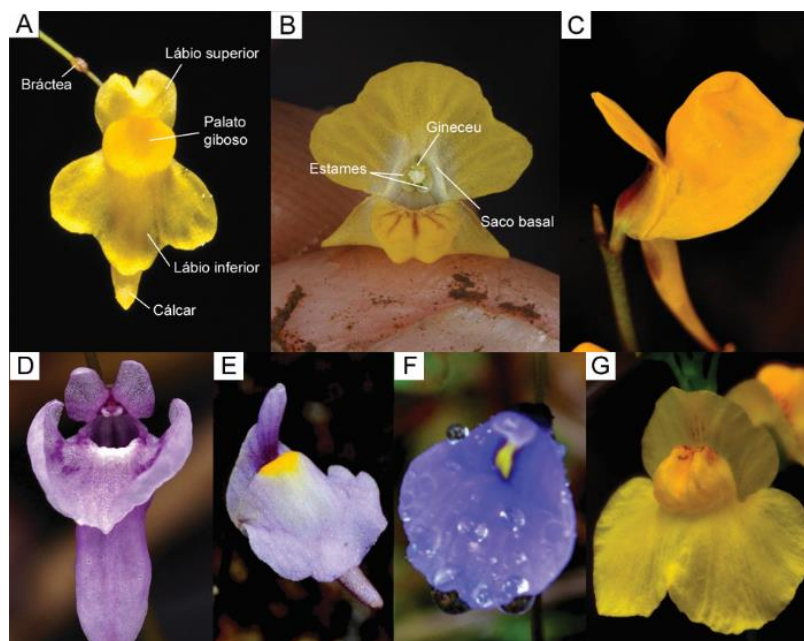


Figura 10 – Padrão morfológico geral em corolas de *Utricularia*. A. Elementos típicos na corola de *U. nervosa* G.Weber ex Benj., com lábio inferior trilobado, palato giboso, cálcio mais longo que o lábio inferior, com ápice agudo. B. Destaque no lábio superior da corola de *U. gibba* L. e órgãos reprodutivos acomodados no saco basal, os quais podem ficar escondidos quando o palato é giboso. C. Lábio inferior galeado de *U. juncea* Vahl, com cálcio perpendicular ao lábio inferior. D. Palato não-giboso de *U. benjaminiana* Oliv. e cálcio botuliforme. E. Lábio inferior crenado de *U. cutleri* Steyerl. com cálcio paralelo ao lábio inferior. F. Lábio superior diminuto e inferior inteiro e plano de *U. pubescens* Sm. G. Lábio inferior bilobado de *U. foliosa* L. Fotos A por Débora Ferreira, e C, D, F e G por Gabriel Garcia.

Por outro lado, os frutos não são um caráter taxonômico tão determinante à nível de espécies, mas tem grande valor nos agrupamentos de níveis taxonômicos superiores, como seções. Os frutos são do tipo cápsula e se apresentam em quatro configurações principais de deiscência (Figura 11): a bivalvar, restrita à *U. sect. Foliosa*; a circuncisa, exclusiva, embora não universal, de *U. sect. Utricularia*; a longitudinal é dominante nas demais seções, variando em tamanho do sulco de abertura e espessura das margens deste; ao passo que a deiscência por um poro

ventral é uma variação da longitudinal, encontrada em *U. sects. Setiscopella* e *Steyermarkia* (Taylor 1989).

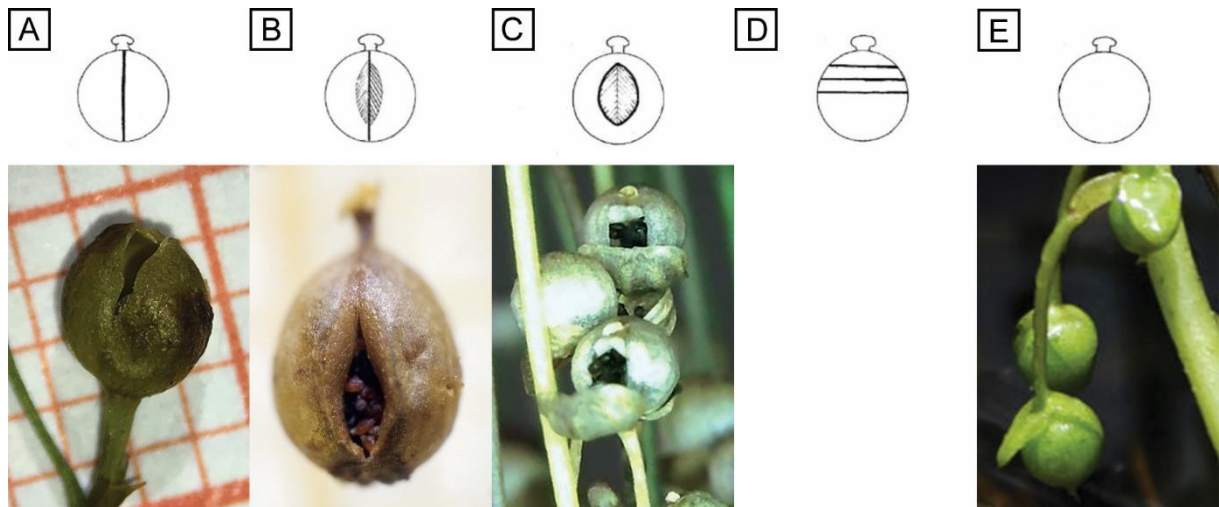


Figura 11 – Configurações principais de deiscência dos frutos (cápsulas) em *Utricularia*. A. Bivalvar (*U. trinervia* Benj.). B. Longitudinal (*U. juncea* Vahl). C. Poro ventral (*U. subulata* L.). D. Circuncisa. E. Indeiscente (*U. foliosa* L.). Esquemas extraídos de Taylor (1989). Fotos C por Sebastian Heimbach e E por Hermann Redies.

Já as sementes (Figura 12), são muito pequenas, variando de 0.2 a 1 mm compr., e sua grande variabilidade morfológica quanto a forma, tegumento (testa) e textura superficial as tornam relevantes na delimitação taxonômica à nível de espécie ou seção (Abraham & Subramanyan 1965; Taylor 1989). Contudo, tais caracteres são melhor observados por meio da Microscopia Eletrônica de Varredura (Taylor 1989; Menezes et al. 2014).

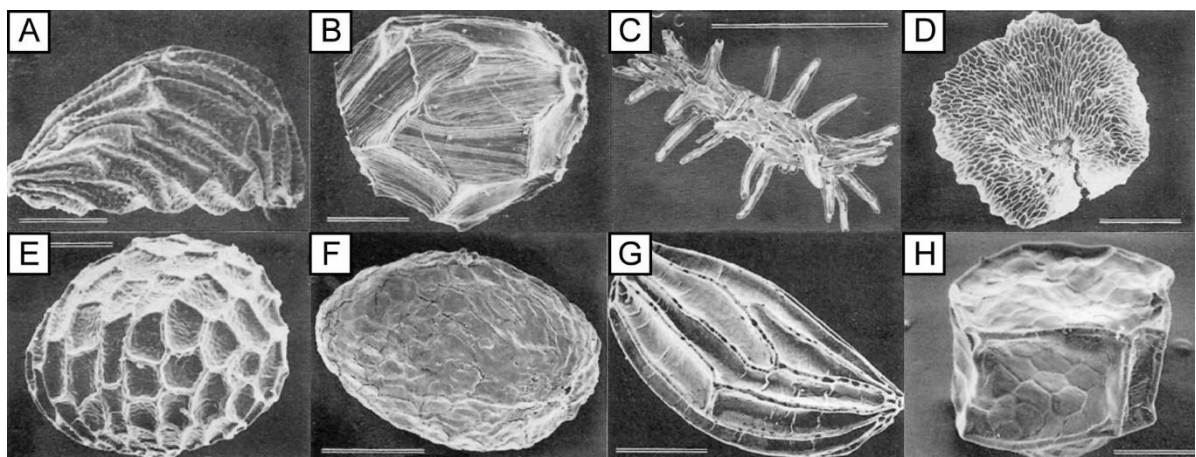


Figura 12 – Micrografias de sementes de *Utricularia* extraídas de Taylor (1989), evidenciando a diversidade em formas, tegumentos e ornamentações. A. *U. amethystina* Salzm. ex A.St.-Hil. & Girard. B. *U. laxa* A.St.-Hil. C. *U. reniformis* A.St.-Hil.. D. *U. humboldtii* R.H.Schomb.. E. *U. guyanensis* A.DC. F. *U. oliveriana* Steyerem. G. *U. pusilla* Vahl. H. *U. resupinata* B.D.Greene ex Bigelow.

Diante desse cenário de significativa variabilidade morfológica, a diversidade do gênero também se reflete na amplitude de habitats em que as espécies ocorrem e na

sua extrema especialização nutricional (Taylor 1989; Guisande et al. 2007). Um grande espectro de ambientes aquáticos e terrestres úmidos são colonizados por essas espécies, que apresentam diferentes formas de vida e de crescimento (Figura 13), desde hidrófitas (aquáticas suspensas), terrícolas, helófitas (anfíbias), reófitas, litófitas (rupícolas) a epífitas (Ellemberg & Mueller-Dumbois 1967; Taylor 1989; Cook 1996). Conforme os resultados de reconstruções filogenéticas, o ancestral de *Utricularia* teria sido terrícola, portanto, as demais formas seriam apomorfias (Jobson et al. 2003; Müller & Borsch 2005; Silva et al. 2018).

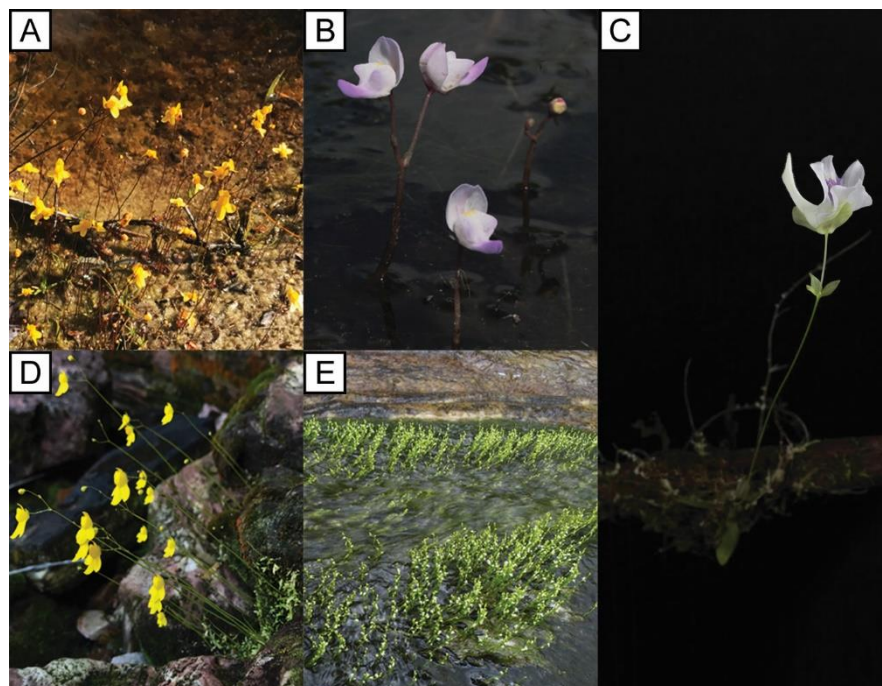


Figura 13 – Formas de vida/crescimento de *Utricularia*. A. Terrícola/Helófitas (*U. subulata* L.). B. Hidrófitas (*U. myriocista* A.St.-Hil. & Girard). C. Epífita (*U. jamesoniana* Oliv.). D. Litófitas/Rupícolas (*U. flaccida* A.DC.). E. Reófitas (*U. neottioides* A.St.-Hil. & Girard). Fotos B por Sergio Guzman, C por Josh Allen e E por Paulo Gabriel.

2.3.2 Histórico sistemático

Os primeiros registros de *Utricularia*, em forma de ilustrações, foram feitos pelo físico e naturalista suíço Conrad Gessner na sua obra 'Historia Plantarum', embora tenha sido compilada entre 1555 e 1565, só foi publicada, em parte, 200 anos depois de sua morte por Schmidel (1753) e finalizada por Zoller & Steinmann (1991) como 'Conradi Gessneri Historia Plantarum' (Casper 2002). Gessner inclusive originou os nomes Lentibulariaceae e *Pinguicula*, em suas anotações como "*Lentibullia*, vel *Lentibullaria*", contudo, o nome proposto desapareceu provavelmente pela obra não

ter sido completada, e permanece hoje levemente modificado (com um “l” a menos) (Casper 2002).

O gênero *Utricularia* foi estabelecido por Linnaeus (1753) em sua obra clássica ‘Species Plantarum’, na qual ele descreveu sete espécies apresentando duas sépalas, ovário uniovulado e placentação central-livre. Vahl (1804) propôs a primeira classificação infragenérica para o gênero, baseada principalmente na morfologia e disposição das folhas, na qual equivocadamente atribuiu algumas espécies em “*Aphyllae*” (sem folhas), possivelmente com base em material herborizado incompleto. Posteriormente, Brown (1810), Smith (1819), Saint-Hilaire (1830, 1833), Saint-Hilaire & Girard (1838, 1839) e diversos outros autores descreveram dezenas de espécies em vários continentes.

Rafinesque (1838) segregou *Utricularia* em 13 gêneros, baseando-se em diversos caracteres vegetativos sem consistência para esse nível taxonômico, ao passo que Lehmann (1844) propôs o gênero *Polypompholyx*, distinguindo-o de *Utricularia* pelo cálice com quatro sépalas. Paralelamente, De Candolle (1844) listou 131 espécies até então descritas, incluindo outras 26 propostas por ele, e as agrupou em cinco seções: *Megacista*, *Lentibularia*, *Stylotheca*, *Oligocista* e *Orchidioides*. Essa última classificação corroborou parcialmente com a de Vahl (1804), ainda em grande parte na ignorância da morfologia vegetativa da maioria das espécies. Benjamin (1847) contemplou uma monografia e propôs um novo sistema, dividindo o gênero em 11 seções com espécies de várias regiões do globo.

Na obra de Kamiénski (1895) o número de espécies se aproximava de 200, incluindo as 13 descritas por ele, onde ele agrupou a maior parte das espécies em *Utricularia* e outras em dois gêneros, *Biovularia* Kamiénski e *Polypompholyx* Lehm. Posteriormente, Barnhart (1916) realocou essas espécies em 13 gêneros, levando em consideração algumas propostas de Rafinesque (1838), baseando-se principalmente na posição e forma das brácteas e bractéolas nas inflorescências. Ademais, o número de estudos taxonômicos e florísticos com Lentibulariaceae crescia ao redor do mundo, com diversos autores tratando espécies de várias regiões e continentes (Luetzelburg 1910, 1926; Merl 1915; Kuhlmann 1940; Steyermark 1948, 1950, 1952, 1953; Dawson 1960; Fernández-Pérez 1964; Komiya 1972).

Peter Taylor foi considerado o maior especialista no gênero, começou suas pesquisas e trabalhos em *Utricularia* em 1949, quando o número de espécies listadas no *Index Kewensis* era cerca de 600. Foi autor de diversos estudos florísticos e

taxonômicos tratando de espécies da Índia, África e Américas Central e do Sul (Taylor 1964, 1967, 1973, 1977, 1980, 1986). A sua monografia (Taylor 1989) permanece como uma referência clássica para estudos abrangendo *Utricularia*. Essa obra reúne um intenso tratamento de aproximadamente 900 binômios, cuja grande maioria foi sinonimizada, culminando em 214 espécies reconhecidas por ele. Ademais, ele propôs uma classificação infragenérica respaldada em caracteres vegetativos.

Então, Taylor (1989) adotou dois subgêneros: *Polypompholyx* e *Utricularia*, distinguidos pelo número de sépalas, sendo quatro no primeiro e duas no segundo. Enquanto as seções (duas em *Polypompholyx* e 33 em *Utricularia*) foram embasadas na morfologia dos utrículos, levando como critérios posição da abertura, forma e ornamentação. As seções de *Polypompholyx* (Lehm.) P.Taylor estabelecidas foram *Polypompholyx* e *Tridentaria*. Ao passo que as 33 seções de *Utricularia* foram *Aranella*, *Australes*, *Avesicaria*, *Avesicarioides*, *Benjaminia*, *Calpidisca*, *Candollea*, *Chelidon*, *Choristothecae*, *Enskide*, *Foliosa*, *Iperua*, *Kamienskia*, *Lecticula*, *Lloydia*, *Martinia*, *Meionula*, *Mirabiles*, *Nelipus*, *Nigrescentes*, *Oligocista*, *Oliveria*, *Orchidioides*, *Phyllaria*, *Pleiochasia*, *Psyllosperma*, *Setiscapella*, *Sprucea*, *Steyermarkia*, *Stomoisia*, *Stylotheca*, *Utricularia* e *Vesiculina*.

Tal classificação foi parcialmente corroborada filogeneticamente por Jobson & Albert (2002), Jobson et al. (2003), Müller et al. (2004, 2006), Müller & Borsch (2005), Reut & Jobson (2010), Rodrigues et al. (2017), Westermeier et al. (2017), Jobson et al. (2017, 2018) e Silva et al. (2018). Entretanto, alguns rearranjos de seções foram sugeridos, novas seções foram formalmente propostas e uma nova classificação infragenérica foi estabelecida, mas nenhuma nova revisão taxonômica foi apresentada, possivelmente por se tratar de um gênero bastante numeroso e amplamente distribuído no planeta.

Müller & Borsch (2005) propuseram um rearranjo de algumas seções devido a resultados evidenciando grupos parafiléticos utilizando sequências plastidiais de *trnK* íntron + *matK* e, conseqüentemente, distinguiram três subgêneros (Figura 8): *U.* subgen. *Polypompholyx*, com duas seções (incluindo a seção *Pleiochasia* que anteriormente pertencia ao subgênero *Utricularia*); *U.* subgen. *Utricularia*, compreendendo oito seções de espécies majoritariamente epífitas e aquáticas; e *U.* subgen. *Bivalvaria*, englobando 11 seções de espécies terrestres, previamente incluídas em *U.* subgen. *Utricularia sensu* Taylor (1989). Essa topologia

(*Polypompholyx*, (*Bivalvaria*, *Utricularia*)) é atualmente adotada (Reut & Jobson 2010; Jobson et al. 2018; Silva et al. 2018).

Desde a monografia de Taylor (1989) três novas seções foram formalmente propostas. Lowrie et al. (2008) descreveram a monotípica *U. sect. Minutae* Lowrie, Cowie & Conran compreendendo *U. simmonsii* Lowrie, Cowie & Conran, a qual é conhecida por apresentar as menores flores do gênero e utrículos semelhantes aos de representantes de *U. sect. Enskide* (Raf.) P.Taylor, ambas seções do subgênero *Bivalvaria*. Em contrapartida, os resultados de Reut & Jobson (2010) apontaram a relação *U. simmonsii* + *U. chrysantha* R.Br. (*U. sect. Enskide*). Posteriormente, Jobson et al. (2018) adicionaram *U. fulva* F.Muell. e *U. jobsonii* Lowrie em suas análises filogenéticas, o que resultou em *U. sect. Minutae* formando um clado-irmão de *U. sect. Enskide*.

Outra seção proposta foi *U. sect. Lasiocaulis* R.W.Jobson & Baleeiro (Jobson et al. 2017), para o subgênero *Polypompholyx*, uma vez que os resultados de Reut & Jobson (2010) mostraram dois grandes clados principais dentre os representantes de *U. sect. Pleiochasia*, um englobando espécies com escapos glabros e outro, espécies com escapos indumentados. Este último clado configurando *U. sect. Lasiocaulis*, com *U. lasiocaulis* F.Muell. como espécie tipo, ao passo que o primeiro clado se manteve *U. sect. Pleiochasia*, com *U. dichotoma* Labill. como espécie tipo.

Quanto à grupos que tiveram rearranjos sugeridos com base em filogenias moleculares, mas que ainda carecem formalmente de propostas taxonômicas e nomenclaturais estão as seções *Iperua*, *Orchidioides*, *Oligocista*, *Benjaminia*, *Avesicarioides*, *Lloydia*, *Calpidisca*, *Utricularia*, *Foliosa*, *Psyllosperma*, *Setiscapella* e *Avesicaria*, sendo as duas últimas discutidas no próximo tópico por serem alvo de um dos capítulos deste trabalho.

O monofiletismo de *U. sects. Iperua* + *Orchidioides* foi evidenciado por Jobson et al. (2003) (Figura 14), utilizando sequências plastidiais de *rps16* íntron e região *trnL-F*. Posteriormente Müller et al. (2004) adicionaram amostras de *U. humboldtii* R.H.Schomb. (*U. sect. Iperua*) na filogenia, baseada em sequências de *trnK/matK*, e resultou no seu posicionamento em *U. sect. Orchidioides*, o que levou os autores a sugerirem que *U. sect. Orchidioides* fosse expandida englobando os membros de *U. sect. Iperua*. Recentemente, essa proposta foi ratificada com a inclusão de uma amostragem maior de espécies na filogenia, baseada em sequências de *rps16* íntron,

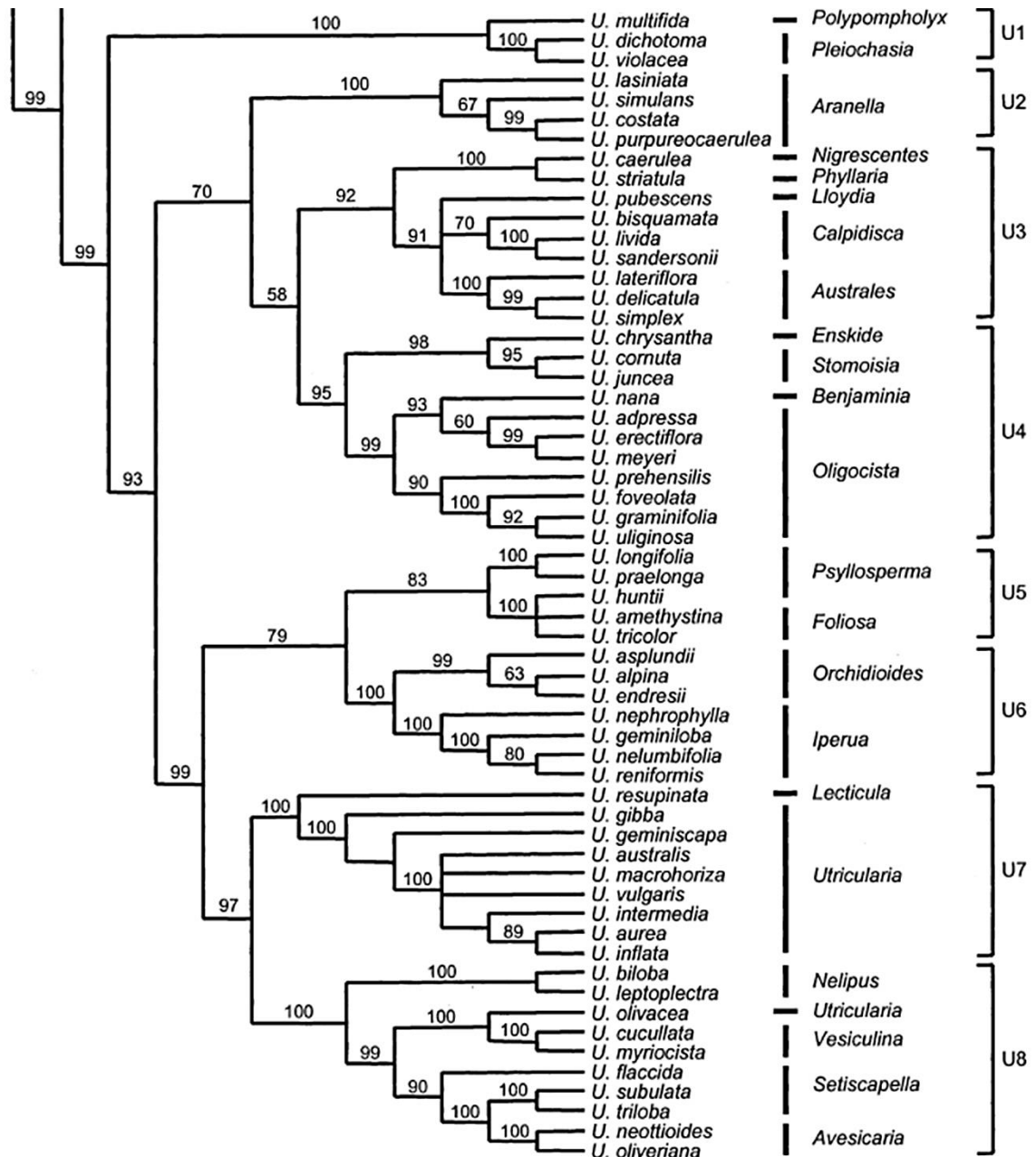


Figura 14 – Topologia consenso estrito das 24 árvores mais parcimoniosas apresentada por Jobson et al. (2003), com suportes Jackknife >50 acima dos ramos.

espaçador *trnL-F*, gene *matK* e região ITS (Figura 15), combinadas com caracteres morfológicos e anatômicos (Rodrigues et al. 2017).

A *U. sect. Oligocista* se mostrou parafilética (Figura 14), com base em sequências de *rps16* íntron e região *trnL-F*, com a inclusão de *U. nana* A.St.-Hil. & Girard, pertencente à monotípica *U. sect. Benjaminia* (Jobson et al. 2003). Müller et al. (2004) encontrou um resultado diferente, sendo *U. sect. Oligocista* monofilética e emergindo como grupo irmão de *U. sect. Avesicarioides*, e esse clado por sua vez, irmão de *U. sect. Benjaminia*. No entanto, os autores mesmos apontam que essas

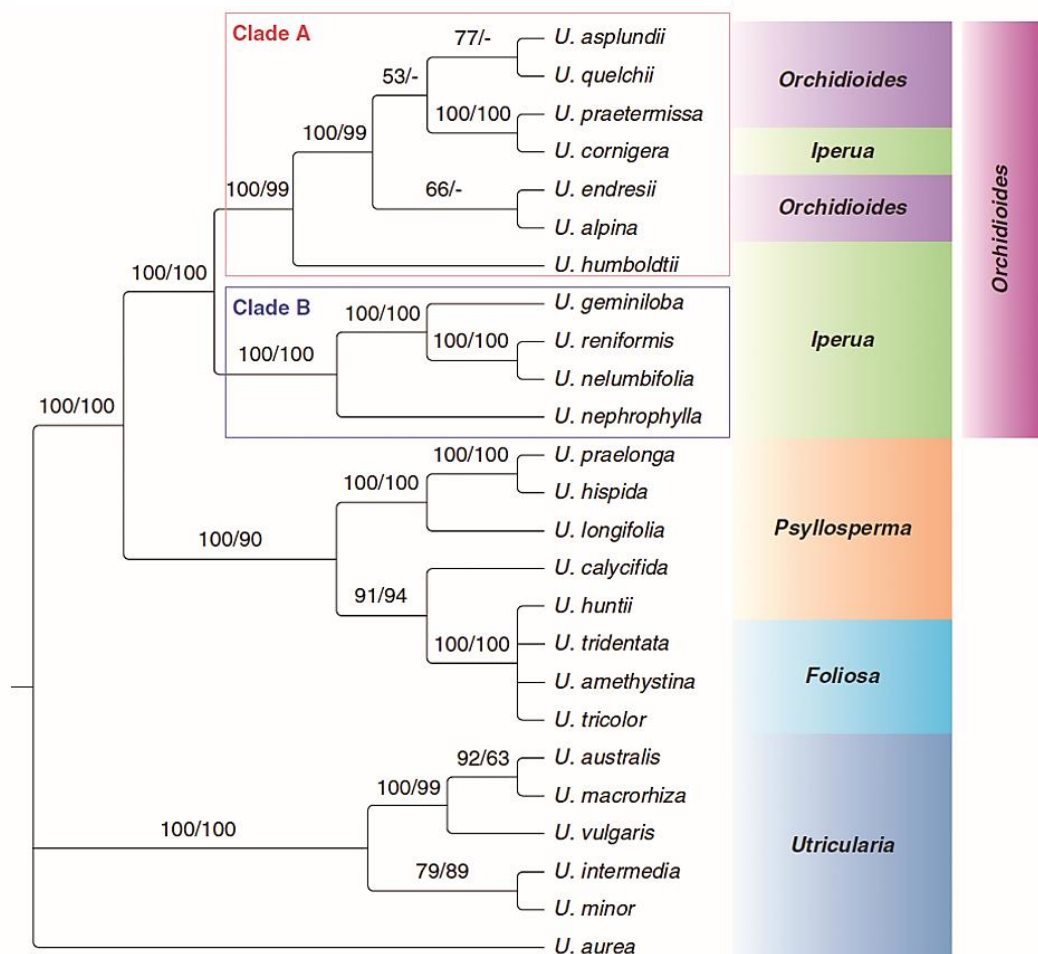


Figura 15 – Topologia da árvore consenso de Inferência Bayesiana apresentada por Rodrigues et al. (2017), baseada em três regiões plastidiais e uma nuclear. Números de suporte acima dos ramos consistem, respectivamente, de probabilidade posterior e bootstrap de máxima verossimilhança, e “-” para ramos com valores de suporte <50.

relações não podem ser confirmadas para o *trnK* íntron utilizado, por não terem a mesma amostragem taxonômica do primeiro trabalho (Müller et al. 2004).

Posteriormente, o parafiletismo de *U. sect. Oligocista* foi corroborado com altos suportes por Silva et al. (2018), em uma filogenia utilizando cinco marcadores plastidiais (genes *matK* e *rbcL*, espaçador *rpl20-rps12*, *rps16* íntron e espaçador *trnL-F*) e um nuclear (região ITS) (Figura 16), sugerindo a junção das seções *Benjaminia* e *Oligocista*. No entanto, a seção *Avesicarioides* não foi incluída na análise combinada de sequências por apresentar apenas uma sequência disponível (*matK*), que quando analisada isoladamente produziu uma topologia de *Avesicarioides* incluída em *Oligocista* (Silva et al. 2018). Dessa forma, essas relações não puderam ser confirmadas para outras regiões genéticas, além da subamostragem das espécies sul-americanas de *U. sect. Oligocista*, havendo assim um comprometimento nas inferências filogenéticas à nível de seções (Jobson et al. 2018).

A monotípica *U. sect. Lloydia*, estabelecida para abrigar a polimórfica *U. pubescens* Sm., emergiu bem suportada (Figura 16) entre as espécies de *U. sect. Calpidisca*, assim, os autores sugeriram a junção das seções suportadas pela sinapomorfia na forma dos utrículos (abertura terminal, apêndice dorsal e lábio ventral com fileiras de tricomas glandulares-estipitados) (Silva et al. 2018).

A numerosa e cosmopolita *U. sect. Utricularia* é formada por 34 espécies aquáticas *sensu* Taylor (1989) + *U. stygia* Thor e *U. tenuicaulis* Miki (Fleischmann 2012b), e foi evidenciada como parafilética (Figura 16) com base em análises de dados combinados e *rbcL* isolado, tendo *U. olivacea* C.Wright ex Griseb. emergido distante dos demais membros da seção, os quais formam um clado irmão de *U. resupinata* B.D.Greene ex Bigelow (*U. sect. Lenticula*) (Silva et al. 2018). Em contrapartida, Jobson et al. (2018) mostraram uma topologia diferente (Figura 17) com base em sequências de *rps16* íntron e região *trnL-F*, onde *U. olivacea* emerge como irmã de *U. sect. Vesiculina*.

Em um recente estudo utilizando a técnica de barcoding (ITS, *trnL-F* e *rps16*), Astuti et al. (2020) apontaram que a técnica falhou em discriminar espécies aquáticas problemáticas da Europa Central (*U. sect. Utricularia*). Esses autores encontraram uma grande variabilidade intraespecífica para quase todas as espécies, levantando hipóteses de possíveis hibridizações entre alguns táxons e apomixia em outros. Posteriormente, combinando o barcoding (ITS e *rps16*) e Inter Repetições de Sequência Simples (ISRR) com análises morfológicas de uma amostragem taxonômica mais ampla, Bobrov et al. (2022) obtiveram sucesso em discriminar esse grupo de espécies, evidenciando hibridizações. Por consequência, os autores sugeriram muitas novidades em status taxonômico e nomenclatura das mesmas.

Um dos casos mais problemáticos até os dias de hoje é o da Neotropical *U. sect. Foliosa* Kamiënski (*U. amethystina* Salzm. ex A.St.-Hil. & Girard, *U. tricolor* A.St.-Hil. e *U. tridentata* Sylvén), inicialmente apontado por Jobson et al. (2003) como parafilética (Figura 14), com a inclusão de membros de *U. sect. Psyllosperma* P.Taylor. O que também foi evidenciado por Müller & Borsch (2005) e Silva et al. (2018) (Figura 16), que sugeriram a junção dessas seções, utilizando apenas, respectivamente, seis e oito das doze espécies atualmente reconhecidas. Contudo, os resultados recentes contestam a união das seções, suportando o monofiletismo de *U. sect. Foliosa*, incluindo *U. biceps* Gonella & Baleeiro, recentemente descrita, e

evidenciando *U. sect. Foliosa* como grupo-irmão de *U. sect. Psyllosperma*, também monofilética (Baleeiro et al. 2018).

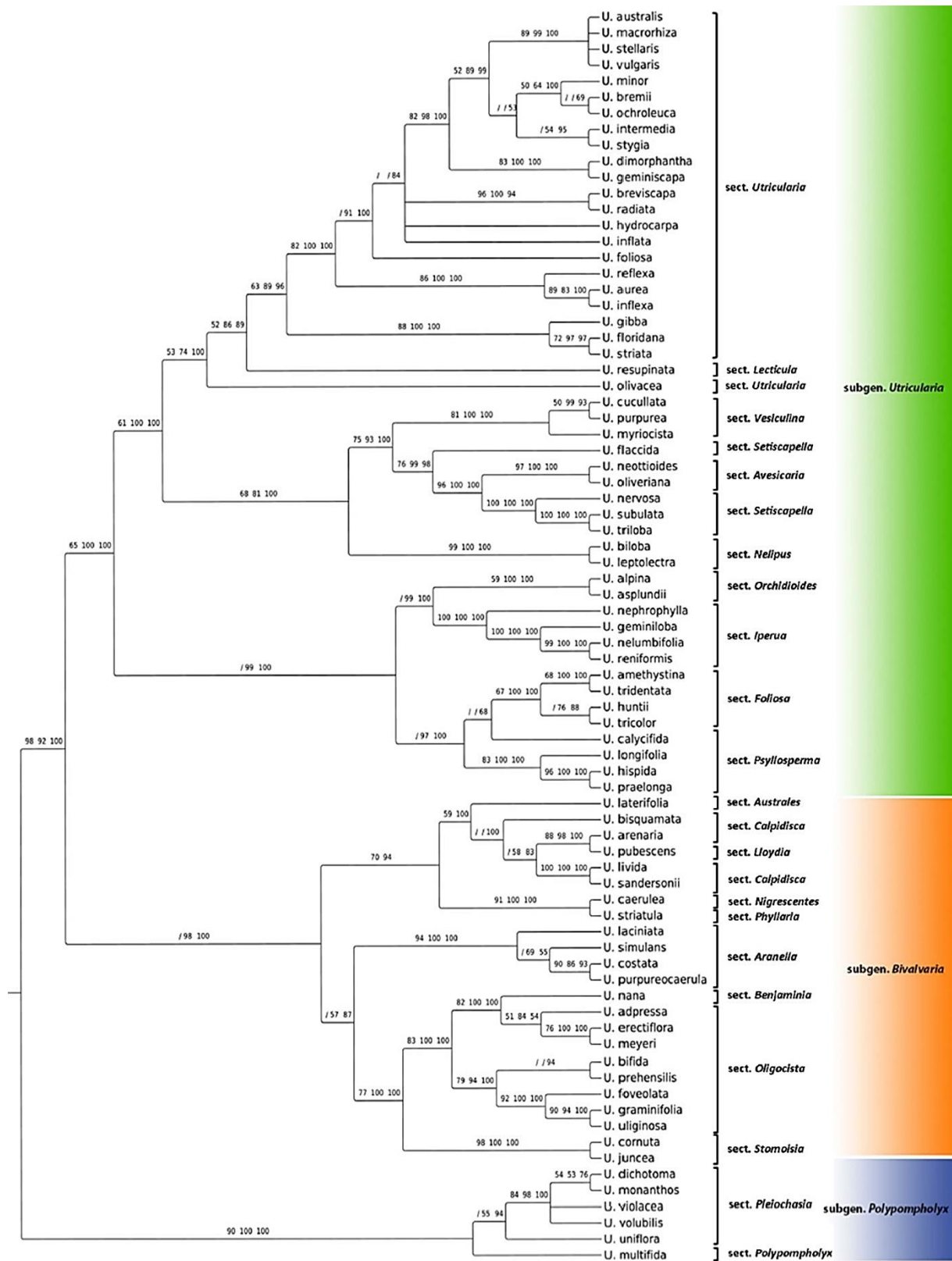


Figura 16 – Topologia da árvore consenso de Inferência Bayesiana apresentada por Silva et al. (2018), com suportes de bootstrap de máxima parcimônia, bootstrap de máxima verossimilhança e probabilidade posterior, respectivamente, acima dos ramos, e “/” denota valores <50.

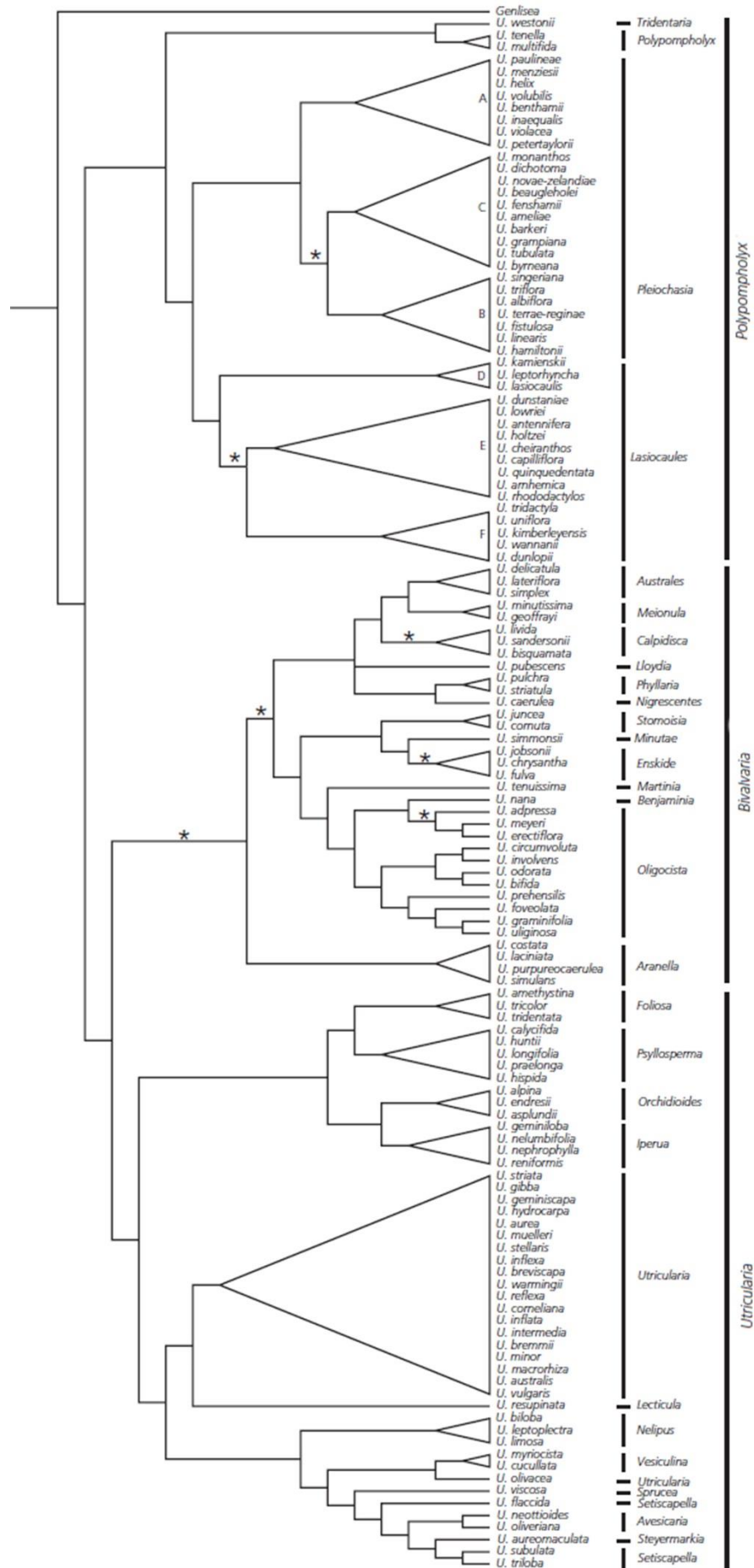


Figura 17 – Topologia da árvore consenso de Inferência Bayesiana baseada em sequências de *rps16* e *trnL-F* apresentada por Jobson et al. (2018), com “*” indicando suportes baixos de Jackknife (60-75%), demais ramos suportados >76%.

Os resultados de análises filogenéticas (Figura 18) e morfométricas de Baleeiro et al. (2016, 2019) mostraram que o táxon *U. amethystina*, considerado altamente polimórfico e possuindo 32 sinônimos (Taylor 1989), na realidade se tratava de um complexo de oito ou mais espécies. Esses autores delimitaram o táxon *U. amethystina sensu stricto*, de acordo com o holótipo e outras populações encontradas, que emergiu como monofilético. Tal cenário foi suportado pelos resultados de Silva et al. (2019), utilizando genomas de cloroplasto. Baleeiro et al. (2016, 2019) também sugeriram o reestabelecimento taxonômico de quatro dos sinônimos e apontaram outras quatro possíveis espécies novas.

Apesar dos esforços prévios, esse complexo taxonômico ainda carecia de resolução e circunscrição para cada espécie, ao passo que Guedes et al. (2021) contribuíram com o reestabelecimento de *U. trinervia* Benj., um dos 32 sinônimos de *U. amethystina sensu latu*. Os autores combinaram evidências macro- e micromorfológicas para justificar a distinção dos táxons, caracterizando de forma inédita os seus utrículos e grãos de pólen através da Microscopia Eletrônica de Varredura, bem como avaliando seu status de conservação.

Somente em 2022, a nova circunscrição da *U. sect. Foliosa* foi formalmente proposta, reconhecendo-a com 15 espécies, com a inclusão de outros sete reestabelecimentos taxonômicos (*U. bicolor* A.St.-Hil. & Girard, *U. damazioi* Beauverd, *U. lindmanii* Sylvén, *U. hirtella* A.St.-Hil. & Girard, *U. roraimensis* N.Br. and *U. velascoensis* Kuntze) e três novas espécies (*U. lunares* Baleeiro, Gonella & R.W.Jobson, *U. pantaneira* Baleeiro, Gonella & R.W.Jobson e *U. chapadensis* Baleeiro, Gonella & R.W.Jobson) (Baleeiro et al. 2022). Além disso, os autores ainda evidenciaram potenciais novos táxons a serem tratados em futuros estudos, bem como apontaram que existe um outro complexo de espécies dentro do binômio *U. hirtella* reestabelecido.

Além dos rearranjos infragenérico, desde a monografia de Taylor (1989) muitas espécies foram descritas, sinonimizadas ou reestabelecidas. Particularmente para o território brasileiro foram descritas oito espécies: *U. cochleata* C.P.Bove (2008), *U. cornigera* Studnička (2009), *U. rostrata* A.Fleischm. & Rivadavia (2009), *U. catolesensis* G.L.Campos, M.Cheek & Giul. (2010), *U. densiflora* Baleeiro & C.P.Bove

(2011), *U. biceps* Gonella & Baleeiro (2018), *U. ariramba* Gonella, Baleeiro & Andrino (2020) e *U. jaramacaru* Gonella, Baleeiro & Andrino (2020). Dessas, *U. cochleata* é sinônimo heterotípico de *U. subulata* L. e *U. catolesensis* de *U. rostrata* (Fleischmann 2012b).

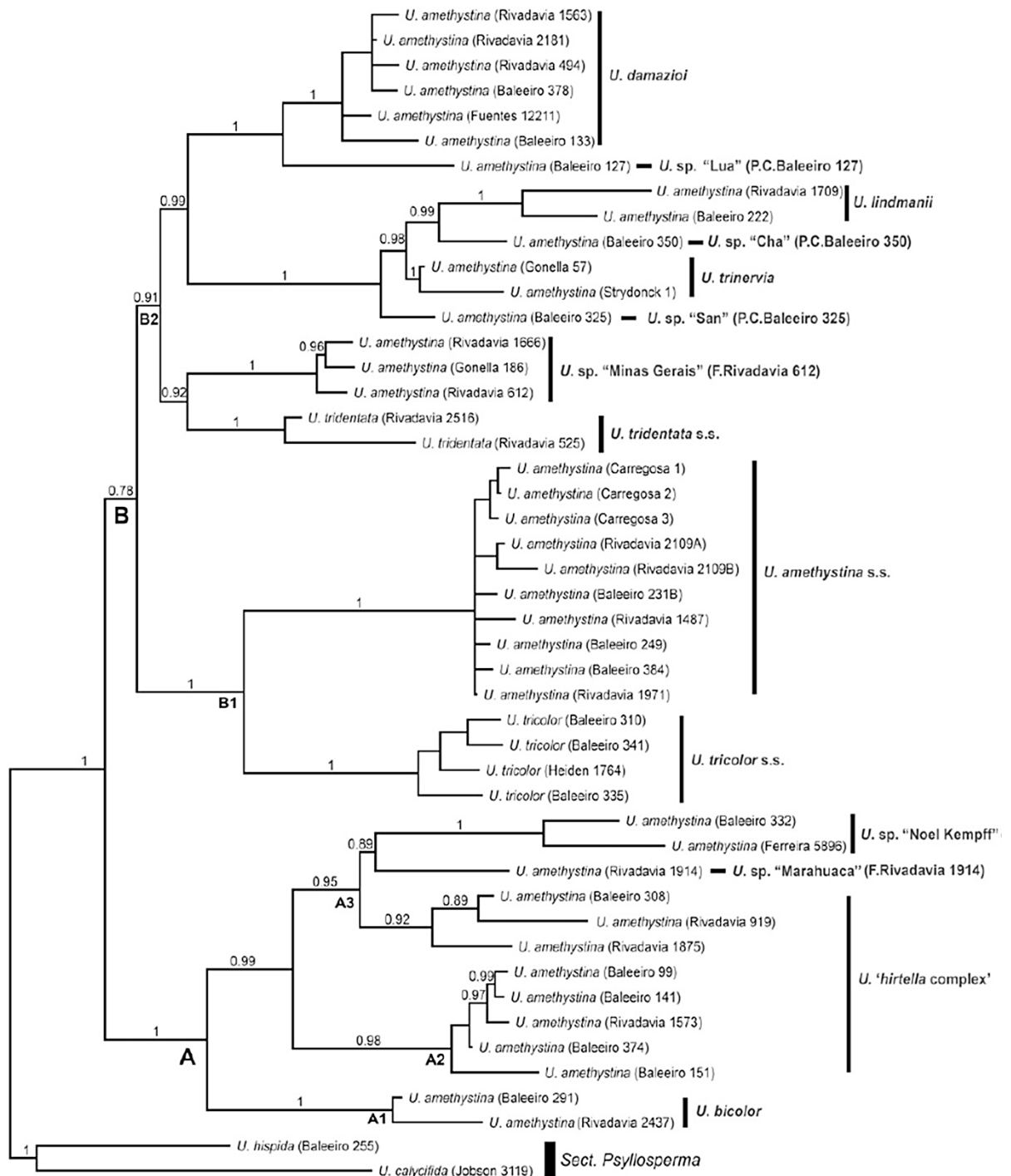


Figura 18 – Topologia da árvore consenso de Inferência Bayesiana baseada em sequências plastidiais e nucleares apresentada por Baleeiro et al. (2019), com suportes de probabilidade posterior acima dos ramos.

Quanto à reestabelecimentos taxonômicos, a previamente monotípica *U. sect. Sprucea*, passou a compreender *U. viscosa* Spruce ex Oliv. e *U. cutleri* Steyererm., sendo a última anteriormente considerada um sinônimo da primeira, reestabelecida por Guedes et al. (2019). Ademais, como já supracitado, *U. trinervia* passou a compor, juntamente com *U. biceps*, a *U. sect. Foliosa*, anteriormente com apenas três espécies sensu Taylor (1989) (Gonella & Baleeiro 2018; Guedes et al. 2021).

Diante desse cenário, por se tratar de um gênero numeroso (248 espécies), com copiosos nomes propostos ao longo de sua história (755) e por apresentar uma ampla distribuição mundial, novas revisões taxonômicas foram evitadas. Apesar disso, trabalhos pontuais com abordagens taxonômicas clássicas e filogenias moleculares menos abrangentes têm sido realizados, porém, diversos problemas ainda perduram, tanto na ótica taxonômica quanto nomenclatural. No território nacional, o projeto Flora do Brasil 2020 reuniu centenas de taxonomistas para colaborar com a catalogação e o tratamento taxonômico das espécies da flora do País (BFG 2021), o qual contou com Guedes et al. (2022) contribuindo com a ‘monografia’ de Lentibulariaceae. Das 90 espécies de Lentibulariaceae catalogadas em território nacional, 71 pertencem à *Utricularia*, das quais 21 são endêmicas (Guedes et al. 2022).

2.4 UTRICULARIA SECT. SETISCAPELLA (BARNHART) P.TAYLOR

Desde a primeira filogenia de Jobson & Albert (2002), que utilizou sequências da região *trnL-F* e *rps16* íntron, a *U. sect. Setiscapella* vêm sendo evidenciada como não-monofilética (Figura 19), com o posicionamento de *U. flaccida* A.DC. em clados com valores de suporte muito baixos e emergindo filogeneticamente distante das outras espécies da seção incluídas nas análises (Jobson et al. 2003; Westermeier et al. 2017; Jobson et al. 2018; Silva et al. 2018). Os resultados desses trabalhos são bastante semelhantes, para Jobson et al. (2003), que incluiu nas análises apenas três (*U. flaccida*, *U. subulata* L. e *U. triloba* Benj.) das dez espécies da seção e os mesmos marcadores supracitados, a *U. sect. Setiscapella* contém a *U. sect. Avesicaria* Kamiënski (*U. neottiioides* A.St.-Hil. & Girard e *U. oliveriana* Steyererm.).

Westermeier et al. (2017) apresentaram duas árvores filogenéticas, uma baseada em sequências de *trnK* íntron + gene *matK* e região *trnL-F* e incluíram *U. aureomaculata* Steyererm. (*U. sect. Steyermarkia* P.Taylor) e *U. nervosa* G.Weber ex Benj. (*U. sect. Setiscapella*) nessa análise. A outra baseada apenas na região

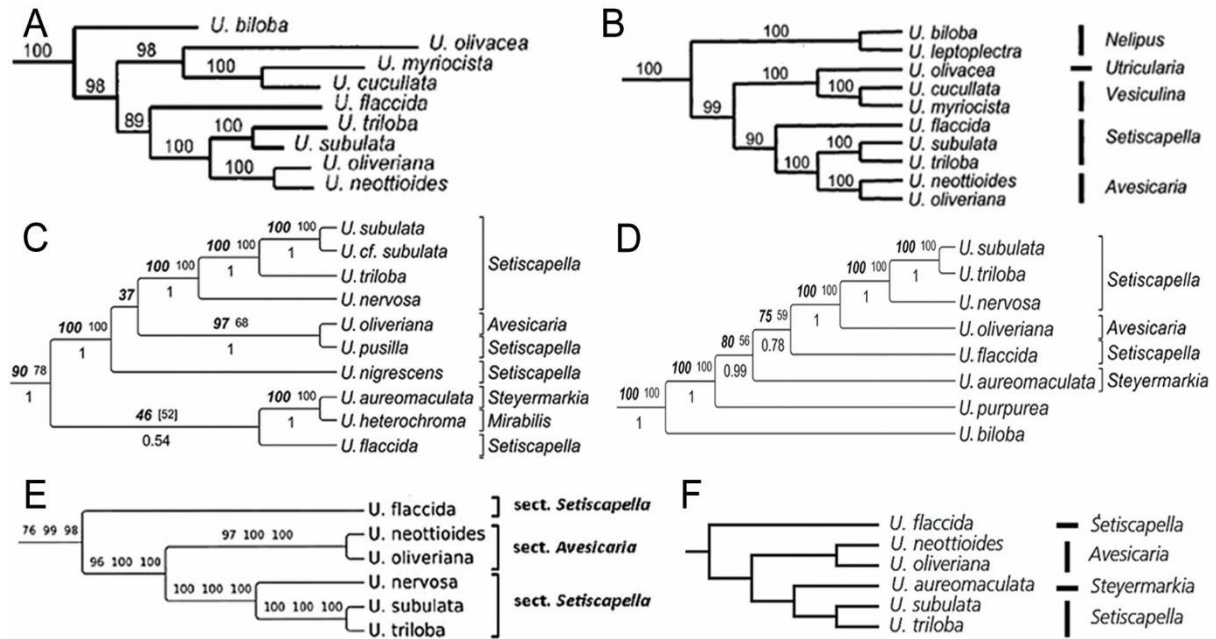


Figura 19 – Recortes de topologias de estudos filogenéticos incluindo membros da *U. sect. Setiscapella*. A. Árvore de consenso estrito de Máxima Parcimônia baseada em seqüências de *rps16* intron e região *trnL-F*, com suportes de Jackknife (Jobson & Albert 2002). B. Árvore de consenso estrito de Máxima Parcimônia baseada em seqüências de *rps16* intron e região *trnL-F*, com suportes de Jackknife (Jobson et al. 2003). C. Árvore consenso de Máxima Verossimilhança baseada em seqüências de *trnK/matK*, com suportes de bootstrap de máxima verossimilhança, bootstrap de máxima parcimônia e probabilidade posterior (Westermeyer et al. 2017). D. Árvore consenso de Máxima Verossimilhança baseada em dados combinados de *trnK/matK* e *trnL-F*, com suportes de bootstrap de máxima verossimilhança, bootstrap de máxima parcimônia e probabilidade posterior (Westermeyer et al. 2017). E. Árvore consenso de Inferência Bayesiana baseada em *rbcL*, *rps16*, *trnL-F*, *rpl20-rps12*, *matK* e ITS, com suportes de bootstrap de máxima parcimônia, bootstrap de máxima verossimilhança e probabilidade posterior (Silva et al. 2018). F. Árvore consenso de Inferência Bayesiana baseada em seqüências de *rps16* e *trnL-F*, com suportes de Jackknife >76 (Jobson et al. 2018).

trnK/matK, dessa vez aumentando a amostragem taxonômica com a inclusão de *U. nigrescens* Sylvén e *U. pusilla* Vahl (*U. sect. Setiscapella*). As duas topologias apresentadas mostram incongruências, uma vez que não possuem a mesma amostragem taxonômica e genética.

No geral, encontraram resultados similares aos de Jobson et al. (2003), ainda com *U. sect. Avesicaria* emergindo entre os táxons de *U. sect. Setiscapella*, em clados bem suportados, porém, para a região *trnK/matK* isolada, *U. oliveriana* e *U. pusilla* formam um clado bem suportado, que por sua vez forma um clado não suportado como grupo irmão de *U. nervosa*, *U. subulata* e *U. triloba*. Já *U. flaccida*, aparece como irmã do clado *U. aureomaculata* (*U. sect. Steyermarkia*) + *U. heterochroma* Steyerm. (*U. sect. Mirabilis* P.Taylor), embora não suportado, esse agrupamento por sua vez tem alto suporte como grupo irmão do clado *U. sects. Setiscapella* + *Avesicaria*.

Os resultados de Silva et al. (2018) também convergem com os dos autores acima, embora com uma amostragem mais ampla de táxons e de marcadores moleculares em suas análises, exceto para *U. flaccida*, a qual teve apenas sequências de *matK* incluídas. Por outro lado, Jobson et al. (2018), utilizando os mesmos marcadores de Jobson et al. (2003), incluíram *U. aureomaculata* nas análises e essa emergiu próxima ao clado *U. subulata* + *U. triloba*. Jobson et al. (2018) ressaltaram ainda que as espécies sul-americanas de *Utricularia* são frequentemente subamostradas e, por esse motivo, haveria comprometimento nas inferências filogenéticas a nível de seções.

Os membros de *U. sect. Setiscapella* e *Steyermarkia* são morfologicamente muito semelhantes (Figura 20), apresentando forma de vida terrícola ou rupícola, inflorescências laxas, geniculadas ou retas, brácteas peltadas, ausência de bractéolas, corola amarela (exceto *U. physoceras* P.Taylor e *U. jaramacaru* Gonella, Baleeiro & Andrino, branca), lábio inferior da corola trilobado ou rasamente trilobado, utrículos ovoides de abertura lateral, com dois apêndices dorsais subulados, ramificados, e cápsulas globosas com deiscência por um poro ventral. Taylor (1989) segregou essas duas seções com base na morfologia das sementes (oblíquo-elipsoides com células da testa muito alongadas em *Setiscapella* e globosas com células da testa isodiamétricas em *Steyermarkia*) e das folhas (uninérveas em *Setiscapella* e multinérveas em *Steyermarkia*).

Já os membros de *U. sect. Avesicaria* apresentam poucas similaridades morfológicas com essas seções (Figura 20), como brácteas peltadas, ausência de bractéolas, lábio inferior da corola trilobado, porém, possuem corola branca, forma de vida reófito, utrículos com pedicelos recurvados, abertura terminal, apêndices ventrais e/ou dorsais setiformes, cápsulas elipsoides e sementes viscosas, com células da testa não-alongadas (Taylor 1989).

No Brasil ocorrem nove das dez espécies atualmente aceitas de *U. sect. Setiscapella* (*U. flaccida*, *U. jaramacaru*, *U. nervosa*, *U. nigrescens*, *U. physoceras*, *U. pusilla*, *U. subulata*, *U. trichophylla* Spruce ex Oliv. e *U. triloba*), enquanto a décima é africana (*U. stanfieldii* P. Taylor). Dessas, seis podem ser encontradas na região Nordeste, duas na região Norte e outra na região Sudeste e Centro-Oeste. Em território nacional também ocorrem as duas espécies de *U. sect. Avesicaria* (*U. neottiioides* e *U. oliveriana*), enquanto as duas de *U. sect. Steyermarkia* (*U.*

aureomaculata e *U. steyermarkii* P. Taylor) são venezuelanas (Taylor 1989; Guedes et al. 2022).



Figura 20 – Espécies reconhecidas de *Utricularia* sects. *Setiscapella* (A-V), *Avesicaria* (W-Z) e *Steyrermakia* (A'-D'). A-D. *U. flaccida* A.DC. E-G. *U. jaramacaru* Gonella, Baleeiro & Andrino. H-I. *U. physoceras* P.Taylor. J-K. *U. nigrescens* Sylvén. N-P. *U. pusilla* Vahl. Q-R. *U. subulata* L. S-T. *U. trichophylla* Spruce ex Oliv. U-V. *U. triloba* Benj. W-X. *U. neottioides* A.St.-Hil. & Girard. Y-Z. *U. oliveriana* Steyerm. A'-B'. *U. aureomaculata* Steyerm. C'-D'. *U. steyrermakii* P.Taylor. Fotos E-H por Caroline O. Andrino, I-J por Pedro Lage Viana, J, T, W, X por Hugo Dolsan, K por Gabriel Garcia, L-M por Marcos F. Cardoso, N por Juliano Fabricante, Y por Mateusz Wrazidlo, Z por Ricardo Pereira, A' por Dani Piccione, B' por Nicole Rebbert, e D' por Fernando Rivadavia.

3 ARTIGO 1 – FLORA OF ESPÍRITO SANTO, BRAZIL: LENTIBULARIACEAE

Flora of Espírito Santo, Brazil

Flora of Espírito Santo: Lentibulariaceae

Felipe Martins Guedes^{1,3,5}, Vitor Fernandes Oliveira Miranda² & Marccus Alves^{1,4}

Abstract

The present study comprises the taxonomic treatment of the Lentibulariaceae species in Espírito Santo state, as a continuation of a series of studies focused on the Flora of Espírito Santo. Herein we present an identification key, morphological descriptions, illustrations, distribution map, list of analysed material and comments about taxonomy and distribution of the species. We confirmed the occurrence of 16 species in Espírito Santo state, of which four are new records and only three are not found in protected areas.

Key words: carnivorous plants, Flora of Brazil 2020, Genlisea, taxonomy, Utricularia.

Resumo

O presente estudo compreende o tratamento taxonômico das espécies de Lentibulariaceae no estado do Espírito Santo, como continuação de uma série de estudos focados na Flora do Espírito Santo. Aqui, apresentamos uma chave de identificação, descrições morfológicas, ilustrações, mapa de distribuição, lista de material analisado e comentários em taxonomia e distribuição das espécies. No Espírito Santo, confirmamos a ocorrência de 16 espécies, das quais apenas três não são encontradas em áreas de proteção.

Palavras-chave: plantas carnívoras, Flora do Brasil 2020, Genlisea, taxonomia, Utricularia.

Introduction

The Lentibulariaceae family consists of ca. 360 species of carnivorous plants with worldwide distribution (Fleischmann & Roccia 2018). In Brazil, it is represented by the genera *Genlisea* (19 spp.) and *Utricularia* (71 spp.), the former with 12 endemic species and the latter with 22 (Guedes *et al.* 2020). These species are easily recognized by their herbaceous habit, stoloniferous, leaves disposed in a basal rosette or alternate in stolons, or modified into dichotomous capillary segments, inflorescences 1-flowered or racemose and by their bilabiate and spurred, tubular corolla (Taylor 1989; Simpson 2010; Fleischmann 2012). However, the traps are completely distinct and unique among all carnivorous plants (Fleischmann *et al.* 2018).

In *Genlisea*, the traps are known as rhizophylls, consisting of achlorophyllous tubular leaves, subterranean, with two distal arms, helically twisted, internally covered with introrse trichomes that direct the prey to a proximal digestive chamber (Płachno *et al.* 2007; Fleischmann 2012). On the other hand, in *Utricularia*, the traps are known as bladder-traps or utricles, comprising foliar vesicles that are hermetically sealed by an articulated door, adorned with dorsal and/or ventral appendages, and with touch-sensitive trichomes that trigger the active mechanism of suction in fractions of seconds (Adamec 2011; Vincent *et al.* 2011; Whitewoods *et al.* 2019).

Like several other carnivorous plants, Lentibulariaceae are usually found in open, sunny, wet habitats with acidic and nutrient-poor soils, and

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free of urban waste (Givnish *et al.* 1984; Jennings & Rohr 2011; Cross *et al.* 2020; Guedes & Alves 2020). The family includes species with different growth forms, ranging from terrestrials, lithophytes (rupicolous), helophytes (amphibians) to epiphytes, rheophytes (haptophytes), and hydrophytes (aquatic free-swimming) (Ellenberg & Mueller-Dombois 1967; Taylor 1989; Cook 1996).

As a continuation of a series of studies focused on the Flora of Espírito Santo, we present the taxonomic treatment of the Lentibulariaceae from the state. This study includes an identification key, morphological descriptions, illustrations, distribution maps, list of analysed exsiccatae and comments about taxonomy and distribution of the species.

Material and Methods

The collections from BHCB, CEN, CEPEC, CVRD, EAC, ESA, HUEFS, GH, JABU, JPB, K, MBM, MBML, MOBOT, NY, OUPR, R, RB, P, SAMES, SP, SPF, UFP, UPCB, US, VIC and VIES (acronyms according to Thiers, continuously updated) herbaria were analysed. All specimens and nomenclatural types were analysed either in person or through virtual herbaria. The morphological descriptions were based on the specimens from the study area and, when necessary, supplemented with additional material from other areas considered most representative. The morphological terminology followed Harris & Harris (2001), and Fleischmann (2012) and Taylor (1989) for group specific terms. Vegetation characterization followed Garbin *et al.* (2017).

The distribution maps (Fig. 1) were created using QGIS v.3.16.3 (<<http://www.qgis.org>>), based on cartographic data obtained from the IBGE website (<<http://www.ibge.gov.br>>) and verified coordinates from the labels of the examined material. The identification key was based on morphological characters that are observable in both fresh and dried material, considering that several herbarium specimens are incomplete (*i.e.*, usually lacking leaves and traps).

Results and Discussion

The Lentibulariaceae family in Espírito Santo state is represented by 16 species: *Genlisea aurea* Saint-Hilaire (1833: 429), *G. lobata* Fromm-Trinta (1989: 152), *Utricularia erectiflora* Saint-Hilaire & Girard (1838: 870), *U. foliosa* Linnaeus (1753: 18), *U. gibba* Linnaeus (1753: 18), *U. hydrocarpa* Vahl

(1804: 200), *U. longifolia* Gardner (1842: 545), *U. myriocista* Saint-Hilaire & Girard (1838: 869), *U. nelumbifolia* Gardner (1842: 505), *U. nephrophylla* Benjamin (1847: 247), *U. pusilla* Vahl (1804: 202), *U. reniformis* Saint-Hilaire (1830: 244), *U. subulata* Linnaeus (1753: 18), *U. tricolor* Saint-Hilaire (1833: 418), *U. tridentata* Sylvén (1908: 28), and *U. triloba* Benjamin (1847: 248).

These species were recorded in different moister environments of the Atlantic Forest phytogeographic domain, including phytophysiognomies of Dense Ombrophilous Forest, Seasonal Semideciduous Forest and open formations of *campos de altitude*, rocky outcrop vegetation (granitic inselbergs), *campos nativos* and *restingas* (Garbin *et al.* 2017). All records cited in Dutra *et al.* (2015) and Guedes *et al.* (2020) for the Espírito Santo state were in conformity, except *Genlisea violacea* Saint-Hilaire (1833: 431), which does not occur in the state, and *Utricularia amethystina* Salzm. ex Saint-Hilaire & Girard (1838: 870) and *U. poconensis* Fromm-Trinta (1985: 139), both being equivocal identifications that are actually *U. tridentata* and *U. hydrocarpa*, respectively.

Thus, in this study, four species were considered new records for the state: *U. hydrocarpa*, *U. pusilla*, *U. triloba* and *U. tridentata*. The first three species are fairly common and widely distributed in the country (Guedes & Alves 2020). On the other hand, *U. tridentata* was only known from Argentina, Uruguay, and in Brazil from the states of Minas Gerais, Paraná, Rio de Janeiro, Rio Grande do Sul and Santa Catarina (Taylor 1989; Guedes *et al.* 2020). This species has only one record in the state, on a creek edge in an area of *campos de altitude* (> 1.600 msl) at the northern portion of Caparaó National Park (Fig. 1). This record fills an important gap, confirming its occurrence in both sides of Caparaó National Park (Minas Gerais and Espírito Santo), and these are the northernmost currently known populations of the species.

The Caparaó National Park (CNP) presents great botanical richness, and it is located in the Serra do Mar ecoregion, considered one of the most endangered areas in the Atlantic Forest domain, threatened by predatory agriculture and farming, fires, deterioration of watercourses, uncontrolled tourism, hunting and expansion of mineral exploration (ICMBio 2015; Moreira *et al.* 2020). The area is composed by a vegetation mosaic of Dense Ombrophilous Forest, Seasonal Semideciduous Forest and open formations of

campos de altitude (Mazine & Souza 2008; ICMBio 2015). Besides *U. tridentata*, the CNP is home to three other species with narrow geographic distribution and endemic to Brazil: *G. aurea*, *U. nephrophylla* and *U. reniformis*, thus, it can be

considered an important site for the diversity, endemism and conservation of Lentibulariaceae in the state, as well as from a phylogenetic point of view and preservation of their evolutionary processes.

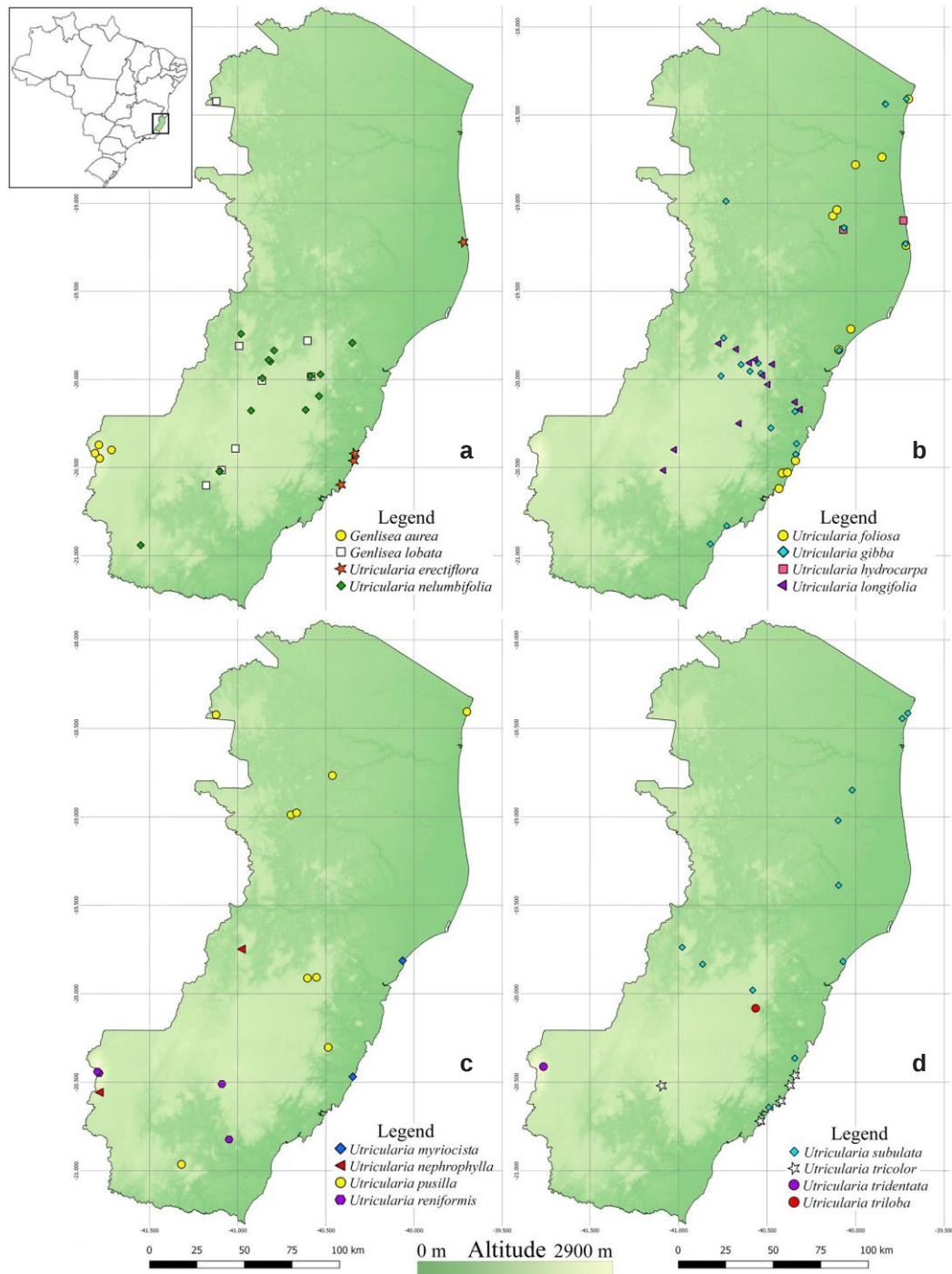


Figure 1 – Distribution map for the species of Lentibulariaceae in Espírito Santo state.

Genlisea aurea is found in rocky outcrops of *campos rupestres* and *campos de altitude* vegetation, in areas ranging from 350–2,500 msl, with disjunct distribution over 10 states of northeastern, central-western, southeastern and southern Brazil (Fleischmann 2012). In Espírito Santo state, however, it is known only from the Serra do Caparaó highlands (Fig. 1). *Utricularia nephrophylla* is known from few populations in Bahia, Minas Gerais, Rio de Janeiro and Espírito Santo (Taylor 1989; Guedes *et al.* 2020). Here we report another record further north-central in the state, in a granitic inselberg/rocky outcrop (Pedra do Caparaó) in the municipality of Itaguaçu (Fig. 1). *Utricularia reniformis*, on the other hand, is endemic to southern and southeastern Brazil (Taylor 1989; Guedes *et al.* 2020), and in Espírito Santo, it is known only from three granitic inselbergs/rocky outcrops ranging from 700 msl, in the municipality of Cachoeiro do Itapemirim, to 2,800 msl, in the Pico da Bandeira (Caparaó National Park) (Fig. 1).

Among the narrowly distributed species, *G. lobata* stands out for occurring only in highlands (800–1,800 msl) with *campos de altitude* vegetation, growing among *Sphagnum* spp. in boggy environments of granite/gneiss outcrops (Fleischmann 2012). In Espírito Santo state, this species was known only from populations at central and southern highlands (Fleischmann 2012), and here we report a record further north in the state, in a granitic inselberg/rocky outcrop surrounding the district of Santa Luzia do Azul, municipality of Água Doce do Norte (Fig. 1). There are populations known from Caparaó National Park, however, under Minas Gerais state territory (Fleischmann 2012).

Another area that can be considered important for the diversity of the family in the state is the Forno Grande State Park, which is home to five species: *G. lobata*, *U. longifolia*, *U. nelumbifolia*, *U. reniformis* and *U. tricolor*. The Forno Grande State Park is an area of Dense Ombrophilous Forest and *campos de altitude*, ranging from 1,000–2,200 msl, located in the municipality of Castelo (IDAF 2001). *Utricularia nelumbifolia* and *U. reniformis* stand out for their peculiar epiphytic growth form, inhabiting water filled leaf axils of *Vriesea* sp. and *Alcantarea* sp. (Bromeliaceae) (Taylor 1989). Both species are endemic to Brazil, *U. nelumbifolia* occurring only in southeastern Brazil, while *U. reniformis* has its distribution extended to southern Brazil (Guedes *et al.* 2020). In Espírito Santo, the only site where both species co-occur is at Forno

Grande State Park, *U. nelumbifolia* has records more concentrated in the central highlands of the state and only one record further south of Castelo (Fig. 1).

Utricularia longifolia and *U. tricolor* are species that can be found in both high- and lowlands, in areas of Ombrophilous Forest, Seasonal Semideciduous Forest, *campos rupestres* and *campos de altitude* (Taylor 1989; Zappi *et al.* 2003; Baleeiro *et al.* 2017; Guedes & Alves 2020). Besides the Forno Grande State Park, *U. tricolor* also occur in *restingas* in the municipality of Guarapari (Fig. 1). *Restingas* are coastal plains with pioneer formations, which are seasonally flooded habitats that present great richness of Lentibulariaceae species, and share several representatives found in *campos rupestres* and *veredas* from the Cerrado domain (Guedes *et al.* 2018; Guedes & Alves 2020). In Espírito Santo, these representatives are the widely distributed *U. erectiflora*, *U. foliosa*, *U. gibba*, *U. hydrocarpa*, *U. myriocista*, *U. pusilla* and *U. subulata* (Fig. 1).

Interestingly, *U. triloba* has only one record for the state, on a roadside in a Montane Dense Ombrophilous Forest area, in the municipality of Santa Leopoldina (Fig. 1). This is a fairly common and widespread species, frequently found sympatric with other congeners (Guedes & Alves 2020). Some fairly common species with only one to three records for the state (*U. hydrocarpa*, *U. myriocista*, *U. nephrophylla*, *U. reniformis*, *U. tridentata* and *U. triloba*) reinforce the need for a greater collection effort in several areas of low- and highlands in the state, with similar phytophysiognomies and conditions prone to the occurrence of the family.

It is also worth highlighting that 13 species were found in Conservation Units of Integral Protection and three in Units of Sustainable Use (Tab. 1). Only three species were not found in any protected areas, *U. erectiflora*, *U. myriocista* and *U. triloba*, all three in less than three localities throughout the state, but widely distributed with several populations in different environments in Brazilian territory and outside (Cross *et al.* 2020; Guedes & Alves 2020). On the other hand, *U. gibba* was found in 10 protected areas, this is one of the most common species with Pantropical distribution (Guedes & Alves 2020). Of all 16 species, *G. lobata* is classified as Endangered (EN) and *U. tridentata* as Vulnerable (VU) (CNCFlora 2020), *U. longifolia* is assessed as Near Threatened (NT) (Guedes & Alves 2020), and the remaining

Table 1 – Lentibulariaceae species found in Conservation Units in Espírito Santo and their conservation status. APA = Environmental Protection Area; APP = Permanent Protection Area; PARNA = National Park; PE = State Park; PM = City Park; REBIO = Biological Reserve; RN = Natural Reserve; RPPN = Private Reserve of Natural Heritage.

Species (Conservation Status)	Assessment Source	Conservation Unit of Integral Protection	Conservation Unit of Sustainable Use
<i>Genlisea aurea</i> (LC)	Cross <i>et al.</i> (2020)	PARNA Caparaó	–
<i>Genlisea lobata</i> (EN)	CNCFlora (2020); Guedes & Alves (2020)	PE Forno Grande	–
<i>Utricularia erectiflora</i> (LC)	IUCN (2020)	–	–
<i>Utricularia foliosa</i> (LC)	IUCN (2020)	PE Itaúnas, REBIO Sooretama	–
<i>Utricularia gibba</i> (LC)	IUCN (2020)	EB Santa Lúcia, PE Itaúnas, PM Recanto do Jacaré, REBIO Augusto Ruschi, REBIO Duas Bocas, REBIO Sooretama, RN Vale do Rio Doce	APA Mestre Álvaro, APP Lagoa Encantada, RPPN Vale do Sol
<i>Utricularia hydrocarpa</i> (LC)	IUCN (2020)	RN Vale do Rio Doce	–
<i>Utricularia longifolia</i> (NT)	Guedes & Alves (2020)	EB Santa Lúcia, PE Forno Grande, REBIO Augusto Ruschi	APA Mestre Álvaro
<i>Utricularia myriocista</i> (LC)	IUCN (2020)	–	–
<i>Utricularia nelumbifolia</i> (LC)	IUCN (2020)	EB Santa Lúcia, PARNA Caparaó, PE Forno Grande	–
<i>Utricularia nephrophylla</i> (LC)	Cross <i>et al.</i> (2020)	PARNA Caparaó	–
<i>Utricularia pusilla</i> (LC)	IUCN (2020)	REBIO Augusto Ruschi	–
<i>Utricularia reniformis</i> (LC)	IUCN (2020)	PE Forno Grande	–
<i>Utricularia subulata</i> (LC)	IUCN (2020)	PE Itaúnas, REBIO Sooretama, RN Vale do Rio Doce	APP Lagoa Encantada
<i>Utricularia tricolor</i> (LC)	IUCN (2020)	PE Forno Grande, PE Paulo César Vinha	–
<i>Utricularia tridentata</i> (VU)	CNCFlora (2020)	PARNA Caparaó	–
<i>Utricularia triloba</i> (LC)	Cross <i>et al.</i> (2020)	–	–

are widely distributed species, classified as Least Concern (LC) (Cross *et al.* 2020; IUCN 2020).

Taxonomic treatment

Lentibulariaceae Rich., in Poiteau & Turpin, Fl. Paris. 1: 23. 1808.

Herbs carnivorous; terrestrial, helophytes, lithophytes, rheophytes, epiphytes or hydrophytes. Rhizoids and stolons usually present. Leaves aerial or submerged, laminar or capillary, simple or dichotomously branched, in a basal rosette or alternate on stolons, basifixed or peltate. Traps (rhizophylls or utricles) subterranean

or submerged. Inflorescence 1-flowered to racemose, scape glabrous, pilose and/or glandular; scales, bracts and bracteoles basifixed, peltate or subpeltate, free or basally connate. Flowers dichlamydeous, bisexual, zygomorphic; calyx dipentamerous, dialisepalous; corolla pentamerous, gamopetalous, tubular, bilabiate, spurred, palate gibbous or not. Androecium with two stamens, epipetalous, anther monothecal, dehiscence longitudinal. Gynoecium bicarpelar, ovary superior, placentation free-central, style short, stigma bilabiate. Fruit capsule, seeds numerous (Taylor 1989; Simpson 2010; Fleischmann 2012).

Identification key to the species of Lentibulariaceae in Espírito Santo state, Brazil

1. Calyx pentamerous2
 2. Upper corolla lip entire, apex rounded; spur parallel to the lower lip1.1. *Genlisea aurea*
 - 2'. Upper corolla lip bilobed, apices bifid; spur parallel to the pedicel1.2. *Genlisea lobata*
- 1'. Calyx dimerous3
 3. Leaves coriaceous4
 4. Leaves peltate.....2.7. *Utricularia nelumbifolia*
 - 4'. Leaves basifixed5
 5. Lamina elliptical or narrowly obovate 2.5. *Utricularia longifolia*
 - 5'. Lamina reniform..... 2.10. *Utricularia reniformis*
 - 3'. Leaves membranaceous.....6
 6. Lamina reniform.....2.8. *Utricularia nephrophylla*
 - 6'. Lamina linear, spatulate, obovate, circular or capillary7
 7. Sepals with margins involute 2.1. *Utricularia erectiflora*
 - 7'. Sepals with margins flat8
 8. Bracteoles present.....9
 9. Corolla 15–20 mm long, lower lip entire to shallowly 3-crenate; both sepals with margin hyaline.....2.12. *Utricularia tricolor*
 - 9'. Corolla 6–10 mm long, lower lip distinctly trilobed; only the upper sepal with margin hyaline..... 2.13. *Utricularia tridentata*
 - 8'. Bracteoles absent10
 10. Bracts basifixed.....11
 11. Corolla pink, palate yellow 2.4. *Utricularia hydrocarpa*
 - 11'. Corolla yellow, palate sometimes with brown streaks12
 12. Scape inflated, pedicel deflexed in fruits....2.2. *Utricularia foliosa*
 - 12'. Scape slim, pedicel ascending in fruits2.3. *Utricularia gibba*
 - 10'. Bracts peltate or subpeltate13
 13. Hydrophytes, scape inflated, glandular; bracts subpeltate; corolla magenta2.6. *Utricularia myriocista*
 - 13'. Terrestrials or helophytes, scape slim, glabrous; bracts peltate; corolla yellow14
 14. Sterile bracts present on the raceme axis; spur up to twice as long as the lower corolla lip2.9. *Utricularia pusilla*
 - 14'. Sterile bracts absent on the raceme axis; spur as long as or slightly longer than the lower lip15
 15. Sepals with nerves prominent, converging to the apex; lower corolla lip shallowly trilobed.....2.14. *Utricularia triloba*
 - 15'. Sepals with nerves non-prominent, not converging to the apex; lower corolla lip deeply trilobed.... 2.11. *Utricularia subulata*

1. *Genlisea* A.St.-Hil., Voy. Distr. Diam. 2: 428. 1833.

Terrestrials, lithophytes or helophytes. Leaves aerial, laminar, simple, lamina obovate to obovate-spatulate, in a basal rosette, dense or sparse, covered or not with mucilage. Rhizophylls subterranean, tubular with two distal arms, helically twisted. Inflorescence racemose, erect, simple, lax or congest; scape flexible, thick or slim. Scales, bracts and bracteoles basifixed, free, margins entire. Calyx pentamerous, sepals

homomorphic, apex acute or obtuse, margins entire, nerves inconspicuous. Scape, scales, bracts, bracteoles, pedicels and sepals glabrous, subglabrous or pilose, trichomes simple and/or glandular. Corolla glabrous or irregularly pilose, trichomes simple and/or glandular, lips entire or lobed, palate gibbous or not; spur straight or curved, parallel to the lower lip (*G.* subgen. *Genlisea*) or to the pedicel (*G.* subgen. *Tayloria*). Capsule globose, glabrous or pilose, trichomes simple and/or glandular, dehiscence circumscissile (*G.* subgen.

Genlisea) or bivalvate (*G.* subgen. *Tayloria*). Seeds prismatic or pyramidal.

1.1. *Genlisea aurea* A.St.-Hil., Voy. Distr. Diam. 2: 429. 1833. Figs. 1a; 2a-d

Terrestrial or helophyte, 10–30 cm tall. Leaves in a dense rosette, usually covered with mucilage. Inflorescence lax or congest; scape 0.8–2.5 mm diam., thick. Scales and bracts 1.5–3 × 1–1.5 mm, ovate. Bracteoles 1–2.5 × 0.4–0.6 mm, lanceolate. Pedicels ascending in fruits. Sepals 2–4 × 1–2 mm, ovate, apex acute to obtuse. Scape, scales, bracts, bracteoles, pedicels and sepals pilose, trichomes glandular. Corolla 10–20 mm long, yellow, both faces glabrous, spur pilose, trichomes glandular, palate dark yellow; upper lip broadly ovate, entire, apex rounded, lower lip trilobed, apices rounded, palate gibbous; spur cylindrical to narrowly conical, as long as or longer than the lower lip, slightly curved, parallel to the lower lip, apex acute. Capsule 3–5 mm diam., globose, pilose, trichomes glandular, dehiscence circumscissile. Seeds ca. 0.3 mm long, pyramidal. **Examined material:** Iúna, Parque Nacional do Caparaó, arredores do Terreirão, 17.II.2000, fl., V.C. Souza 23307 (VIES); Rancho dos Cabritos, 18.II.2000, fl. and fr., V.C. Souza 23417 (ESA, RB); entre o acampamento Macieira e o Pico da Bandeira, 18.I.2019, fl., H.L. Silva 258 (VIES); Serra do Caparaó, 25.IX.1929, fl., Y.E.J. Mexia 4021 (NY, GH, US, P).

Genlisea aurea is easily recognized by its dense rosette of leaves with mucilage, thick scape (0.8–2.5 mm diam.), yellow corolla with dark yellow palate, pilose spur (trichomes glandular), entire upper lip, trilobed lower lip with rounded apices, spur parallel to the lower lip and pedicels ascending in fruits. This species is endemic to Brazil and has two recognized varieties, *G. aurea* var. *minor* is cited to the states of BA, GO, MG, MT and TO, and *G. aurea* var. *aurea* is cited to BA, ES, MG, PR, RJ, SC and SP (Fleischmann 2012; Guedes *et al.* 2020). In Espírito Santo, *G. aurea* has records restricted to a southwestern highland (Fig. 1a) at the Caparaó National Park, in areas of *campos de altitude*.

1.2. *Genlisea lobata* Fromm, Bradea 5: 152. 1899. Figs. 1a; 2e-h

Lithophyte, 7–16 cm alt. Leaves in a sparse rosette, not covered with mucilage. Inflorescence lax; scape 0.2–0.3 mm diam., slim. Scales and bracts 0.8–1.5 × 0.3–0.5 mm, oblong to lanceolate. Bracteoles 0.5–1 × 0.2 mm, linear to narrowly lanceolate. Pedicels strongly deflexed in fruits.

Sepals 1–1.3 × 0.4–0.5 mm, narrowly ovate to lanceolate, apex acute to obtuse. Scape, scales, bracts, bracteoles, pedicels and sepals pilose, trichomes simple and glandular. Corolla 6–9 mm long, white with purple streaks on the upper lip, abaxial face and spur pilose, trichomes simple and glandular, palate yellow and spur purple; upper lip bilobed, apices bifid, lower lip trilobed, apices bifid, palate gibbous; spur cylindrical, shorter than the lower lip, straight, parallel to the pedicel, apex obtuse. Capsule 2–3.5 mm diam., globose, pilose, trichomes simple and glandular, dehiscence bivalvate. Seeds 0.2–0.3 mm long, prismatic.

Examined material: Água Doce do Norte, Santa Luzia do Córrego Azul, 28.IV.2008, fl. and fr., L. Kollmann 11014 (MBML). Castelo, Parque Estadual do Forno Grande, trilha para o Forno, 17.VII.2008, fl. and fr., R. Goldenberg 1166 (CEPEC, MBML, RB, UPCEB), 26.III.2005, fl. and fr., L. Kollmann 7592 (MBML), 9.IV.2009, fl. and fr., R. Goldenberg 1428 (RB), afloramento por baixo do Mirante, 16.VII.2008, fl. and fr., A.P. Fontana 5376 (CEPEC, MBML, RB, UPCEB). Domingos Martins, Pedra Azul, BR-262, 16.VI.1984, fl. and fr., O.J. Pereira 307 (VIES), 29.X.1987, fl. and fr., O.J. Pereira 1336 (VIES). Itaguaçu, Serra do Sobreiro, Pedra do Caparaó, 10.IV.2004, fl. and fr., A.P. Fontana 842 (MBML), 23.IV.2005, fl. and fr., A.P. Fontana 1374 (MBML). Santa Leopoldina, Rio Bonito, 19.I.2002, fl. and fr., L. Kollmann 5328 (MBML), radar Cindactar, 22.XII.2001, fl. and fr., A.P. Fontana 276 (MBML). Santa Maria de Jetibá, Alto São Sebastião, 16.V.2005, fl. and fr., A.P. Fontana 2118 (RB). Santa Teresa, 25 de Julho, Bela Vista, 29.IV.2005, fl. and fr., L. Kollmann 7792 (MBML).

Genlisea lobata is easily recognized by its sparse rosette of leaves without mucilage, slim scape (0.2–0.3 mm diam.), white corolla with purple streaks on the upper lip and purple spur, bilobed upper lip with bifid apices, trilobed lower lip with bifid apices, spur parallel to the pedicel and pedicels strongly deflexed in fruits. This species is endemic to Brazil and it is cited to the states of BA, ES and MG (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *G. lobata* has records in the northwestern, central and southern highlands (Fig. 1a), in areas of granitic inselbergs/rocky outcrops of and *campos de altitude*.

2. *Utricularia* L., Sp. Pl. 1: 18. 1753.

Terrestrials, helophytes, epiphytes, lithophytes, rheophytes or hydrophytes. Leaves aerial or submerged, laminar or capillary, simple or branched, basifixed or peltate, membranaceous or coriaceous, 1- or multinerved. Utricles (traps) ovoid or globose, stalked or sessile, glabrous or



Figure 2 – a-d. *Genlisea aurea* – a. flower (back view); b. bract and bracteoles; c. corolla (front view); d. capsule. e-h. *Genlisea lobata* – e. flower (lateral view); f. bract and bracteoles; g. corolla (front view); h. capsule. i-l. *Utricularia erectiflora* – i. utricle; j. inflorescence; k. bract and bracteoles; l. sepals. m-q. *Utricularia foliosa* – m. utricle; n. bract; o. sepals; p. corolla (front view); q. capsule. r-v. *Utricularia gibba* – r. utricle; s. bract; t. sepals; u. corolla (front view); v. capsule. w-a'. *Utricularia hydrocarpa* – w. utricle; x. lowermost cleistogamous flower; y. bract; z. sepals; a'. corolla (front view). b'-f'. *Utricularia longifolia* – b'. utricle; c'. leaf; d'. bract and bracteoles; e'. sepals; f'. corolla (front view). g'-j'. *Utricularia myriocista* – g'. utricle; h'. inflorescence; i'. bract; j'. sepals.

glandular, entrance basal (when adjacent to the stalk), terminal (when opposite to the stalk) or lateral (when in intermediate position), with or without appendages, dorsal and/or ventral, simple or branched. Inflorescence 1-flowered or racemose, erect, simple or branched, lax or congest, presence or absence of cleistogamous flowers; scape stiff or flexible, inflated or slim, glabrous or pilose. Scales and bracts similar, basifixed, peltate or subpeltate, margins entire or laciniate-denticulate. Sterile bracts present or absent on the raceme axis (between the pedicels). Bracteoles, when present, basifixed or peltate, free or basally connate to the bracts, margins entire or laciniate-denticulate. Pedicels cylindrical or compressed, winged or not, glabrous, ascending or deflexed in fruits. Calyx dimerous, usually accrescent; sepals usually heteromorphic, margins entire or denticulate, flat or involute, hyaline or not, nerves conspicuous or inconspicuous, prominent or not, converging to the apex or not. Corolla glabrous or minutely glandular, lips entire or lobed, lower lip flat or galeate, palate gibbous or not; spur straight or curved, parallel or perpendicular to lower lip. Capsule globose, ovoid or ellipsoid, dehiscence bivalvate, circumscissile or longitudinal. Seeds cylindrical, ellipsoid, globose, ovoid or discoid, winged or not, with or without irregular peripheral projections.

2.1. *Utricularia erectiflora* A.St.-Hil. & Girard, *Compte Rend. Hebd. Séances Acad. Sci., Ser. D.* 7(21): 870. 1838. Figs. 1a; 2i-l

Terrestrial or helophyte, 11–23 cm tall. Leaves aerial, laminar, simple, lamina linear, basifixed, membranaceous, 1-nerved. Utricles 0.6–0.8 mm long, globose, sessile, glandular, entrance basal, with two dorsal appendages, simple, reflexed. Inflorescence racemose, simple or branched, congest, absence of cleistogamous flowers; scape 0.4–0.8 mm diam., stiff, slim, glabrous. Scales and bracts 1.5–2 × 1–2 mm, ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 1.5–2 × 0.4–0.5 mm, linear, basifixed, free, margins entire. Pedicels 1–2 mm long, cylindrical, winged, glabrous, ascending in fruits. Sepals ovate, margins entire, involute, non-hyaline, nerves inconspicuous, not converging to the apex; upper sepal 3–4 × 2.5–3 mm, apex acute to acuminate; lower sepal 3–4 × 3.5–4 mm, apex bifid. Corolla 8–10 mm long, yellow, glabrous; upper lip oblong, apex truncate, lower lip galeate, entire, palate non-gibbous; spur subulate, longer than the lower lip, curved, perpendicular to

the lower lip, apex acute. Capsule 2.8–3 × 1.8–2 mm, ovoid, dehiscence longitudinal. Seeds ca. 0.3 mm long, ovoid, non-winged, without peripheral projections.

Examined material: Guarapari, A.F.C.P. Saint-Hilaire (P holotype, K isotype). Linhares, Degredo, 15.III.2007, fl. and fr., L.F.T. Menezes 1646 (SAMES, VIES). Vila Velha, Barra do Jucu, 28.IX.1999, fl. and fr., C.N. de Fraga 490 (MBML); Interlagos, 6.VIII.2007, fl. and fr., F.B.C. Souza 45 (VIES).

Utricularia erectiflora is easily recognized by its sepals with involute margins and inconspicuous nerves, yellow corolla with a galeate lower lip, oblong upper lip and winged pedicels. This species is widely distributed in the Neotropics, and in Brazil, it is cited to the states of AL, BA, CE, DF, ES, GO, MA, MT, PB, PE, PI, PR, RJ, RN, RR, SC, SE, SP and TO (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. erectiflora* has few records in the southeastern and northeastern lowlands (Fig. 1a), in areas of *campos nativos* and *restingas*.

2.2. *Utricularia foliosa* L., *Sp. Pl.* 1: 18. 1753.

Figs. 1b; 2m-q

Hydrophyte, 10–25 cm tall. Leaves submerged, capillary, dichotomously branched, membranaceous, 1-nerved. Utricles 1–2 mm long, ovoid, stalked, glabrous, entrance lateral, with two dorsal appendages, simple or branched. Inflorescence racemose, simple, lax, cleistogamous flowers absent; scape 3–5 mm diam., stiff, inflated, glabrous. Scales absent. Bracts 4–5 × 3–3.5 mm, ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 10–20 mm long, compressed, non-winged, glabrous, deflexed in fruits. Sepals ovate, margins entire, flat, non-hyaline, nerves inconspicuous, not converging to the apex; upper sepal 2.8–3.2 × 2.5–3 mm, apex obtuse; lower sepal 3.5–4 × 2.8–3.2 mm, apex trifid. Corolla 10–15 mm long, yellow, glabrous, palate sometimes with brown streaks; upper lip broadly obovate, apex rounded, lower lip flat, bilobed, palate gibbous; spur conical, shorter than the lower lip, straight, parallel to the lower lip, apex obtuse to emarginate. Capsule 3–4 mm diam., globose, apparently indehiscent. Seeds ca. 1 mm long, discoid, winged, without peripheral projections.

Examined material: Aracruz, Barra do Riacho, 6.VII.1956, fl., J.G.F.S. 39 (RB), 15.V.1990, P.C. Vinha 1012 (CVRD, VIES); 8.VIII.2012, fl., A.M. Assis 3330 (VIES). Conceição da Barra, Parque Estadual de Itaúnas, 7.IV.2014, fr., W.O. Souza *et al.* 289 (VIES). Guarapari,

Parque Estadual Paulo César Vinha, 18.IV.1990, fl., *J.M.L. Gomes 1004* (VIES); Fazenda Bonanza, 18.V.2000, fl. and fr., *J.R. Pirani 4732* (CEN, HUEFS, RB, SPF); Lagoa do Milho, 19.XI.1987, fl., *O.J. Pereira 1370* (VIES); Setiba, 12.VII.1983, fl. and fr., *O.J. Pereira 206* (VIES). Linhares, 22.XI.1982, fl. and fr., *J.R. Pirani 198* (SP, SPF); 20.IV.2011, fl. and fr., *J. Meirelles 626* (CVRD, ESA, RB, SPF); Barra Seca, 7.III.1994, fl., *D.A. Folli 2236* (CVRD); Regência, 4.I.2007, fl. and fr., *M. Simonelli et al. 998* (VIES). São Mateus, 4.XI.1953, fl., *A.P. Duarte 3888* (RB); bairro Quadrado, próx. ao Rio São Mateus, 25.V.2011, fl., *M. Ribeiro 526* (SAMES); Rio Preto, 23.VI.2010, fl., *M.V. Amaral 13* (SAMES, VIES). Sooretama, Reserva Biológica de Sooretama, 20.I.2010, fl., *A.Q. Lobão 1564* (SAMES, VIES). Vila Velha, Lagoa do Milho, Barra do Jucu, 16.VI.1985, *M. Colledetti 355* (MBML).

Utricularia foliosa is easily recognized by its aquatic free-swimming growth form, absence of bracteoles, yellow corolla with a bilobed lower lip, broadly ovate upper lip, inflated scape and pedicels deflexed in fruits. This species is widely distributed in Africa and Americas, and in Brazil, it is cited to all the states (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. foliosa* is widely distributed (Fig. 1a) in permanent and temporary ponds and rivers, ranging from areas of Submontane Dense Ombrophilous Forest, Seasonal Semideciduous Forest to lowland areas of *campos nativos* and *restingas*.

2.3. *Utricularia gibba* L., Sp. Pl. 1: 18. 1753.

Figs. 1b; 2r-v

Hydrophyte, 5–15 cm tall. Leaves submerged, capillary, dichotomously branched, membranaceous, 1-nerved. Utricles 1–1.5 mm long, ovoid, stalked, glabrous or pilose, entrance lateral, with two dorsal appendages, branched. Inflorescence racemose, simple, lax, cleistogamous flowers absent; scape 0.5–1 mm diam., flexible, slim, glabrous. Scales and bracts 0.8–1 × 0.8–1 mm, semicircular, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 10–15 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals with margins entire, flat, non-hyaline, nerves inconspicuous, not converging to the apex; upper sepal 2–2.5 × 1.5–2 mm, obovate, apex rounded; lower sepal 1.5–2 × 1.5–2 mm, circular, apex rounded. Corolla 6–8 mm long, yellow, glabrous, palate sometimes with brown streaks; upper lip broadly ovate to circular, apex rounded to slightly 3-crenate, lower lip flat, similar to the upper lip, but smaller, palate gibbous; spur conical, longer

than the lower lip, slightly curved, parallel to the lower lip, apex obtuse to emarginate. Capsule 2–3 mm diam., globose, dehiscence bivalvate. Seeds ca. 1 mm long, discoid, winged, without peripheral projections.

Examined material: Águia Branca, estrada para São Gonçalo, 14.III.2016, fl. and fr., *R.C. Forzza 8762* (RB), Parque Natural Municipal Recanto do Jacaré, 23.IV.2004, fl. and fr., *A.M. Assis 1014* (MBML). Aracruz, área 103 da Aracruz Celulose S.A., 27.X.1992, fl. and fr., *O.J. Pereira 3986* (VIES). Cariacica, Reserva Biológica Duas Bocas, fl. and fr., *C.N. Fraga 2331* (CEPEC, MBML, RB, UPCEB). Conceição da Barra, Floresta Nacional do Rio Preto, 6.II.2019, fl. and fr., *B.S. Mendes et al. 151* (VIES); 4.XII.2019, *R. Nichio-Amaral et al. 1091* (VIES); Parque Estadual de Itáunas, 30.III.2000, fr., *O.J. Pereira 6139* (VIES). Linhares, Reserva Natural da Vale do Rio Doce, 16.VI.1998, fl. and fr., *D.A. Folli 3179* (CVRD); 13.III.2002, fl., *D.A. Folli 4209* (CVRD, MOBOT). Piúma, Lagoa da Piabanha, 23.I.1974, fl., *L.C. Abreu 01* (SP). Santa Cruz, 7.II.2000, fl., *F.A. Ferreira* (OUPR8593 e 8594). Santa Teresa, Estação Biológica Santa Lúcia, 21.XI.2015, fl. and fr., *M.O.O. Pellegrini 461* (RB); Jardim de Pedra, 1.II.2002, fl. and fr., *L. Kollmann 5472* (MBML); Reserva Biológica Augusto Ruschi, 19.II.2002, fl. and fr., *L. Kollmann 5572* (MBML); RPPN Vale do Sol, 17.I.2015, fl., *P.J. Coelho 131* (MBML); Serra do Gelo, nascente do Rio Santa Maria do Rio Doce, 16.VII.2003, fl., *A.M. Assis 943* (MBML); Vargem Alta, 2.VII.1985, fl., *W. Boone 558* (MBML). São Roque do Canaã, Alto Perdido, 24.VIII.2007, fl., *A.P. Fontana 3720* (MBML). Serra, Mestre Álvaro, 4.II.2011, fl., *A.M. Vago 53* (MBML); estrada entre Nova Almeida e Jacareipe, 19.VII.1973, fl. and fr., *D. Araújo 314* (RB). Sooretama, Lagoa do Macuco, 16.VII.1969, fl. and fr., *D. Sucre 5628* (RB). Vila Velha, APP Lagoa Encantada, Vale Encantado, 22.X.2018, fl. and fr., *R.T. Valadares 1910* (VIES); 30.VI.2014, fl., *R.T. Valadares 1210* (VIES); Barra do Jucu, Jaguarussu, 23.VIII.1991, fl., *O.J. Pereira 2384* (VIES); Morada do Sol, 23.VIII.2009, fl., *R.T. Valadares 871* (VIES).

Utricularia gibba is easily recognized by its aquatic free-swimming growth form, absence of bracteoles, yellow corolla with a broadly ovate to circular upper lip, rounded to slightly 3-crenate apex, lower lip similar to the upper lip, but smaller, slim scape and pedicels ascending in fruits. This species is Pantropical and, in Brazil, it is cited to all the states (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. gibba* is widely distributed (Fig. 1a) in permanent and temporary ponds and rivers, ranging from areas of Submontane Dense Ombrophilous Forest, Seasonal Semideciduous Forest to lowland areas of *campos nativos* and *restingas*.

2.4. *Utricularia hydrocarpa* Vahl, Enum. 1: 200. 1804. Figs. 1b; 2w-a'

Hydrophyte, 5–8 cm tall. Leaves submerged, capillary, dichotomously branched, membranaceous, 1-nerved. Utricles 1–2 mm long, ovoid, stalked, glabrous, entrance basal or lateral, with or without two dorsal appendages, simple or branched. Inflorescence racemose, simple, lax, lowermost flower cleistogamous; scape 0.8–1 mm diam., flexible, slightly inflated, glabrous. Scales, when present, and bracts 3–3.5 × 2–2.5 mm, ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 3–10 mm long, compressed, non-winged, glabrous, deflexed in fruits. Sepals ovate, margins entire, flat, non-hyaline, nerves inconspicuous, not converging to the apex; upper sepal 2–3 × 1.5–2 mm, apex acute; lower sepal 2–3 × 1.5–2 mm, apex bifid. Corolla 8–10 mm long, pink, glabrous, palate yellow; upper lip broadly obovate to circular, apex rounded, lower lip flat, bilobed, palate gibbous; spur conical, shorter than the lower lip, straight, parallel to the lower lip, apex obtuse. Capsule 2–3 mm diam., globose, dehiscence circumscissile. Seeds ca. 0.8 mm long, discoid, non-winged, with irregular peripheral projections.

Examined material: Aracruz, na divisa com Linhares, 22.XI.1982, fl., J.R. Pirani 194 (SP). Linhares, Reserva Natural da Vale do Rio Doce, 19.X.2000, fl. and fr., D.A. Folli 3714 (CVRD, R).

Utricularia hydrocarpa is easily recognized by its aquatic free-swimming growth form, absence of bracteoles, pink corolla with a yellow palate, broadly obovate to circular upper lip, bilobed lower lip, slightly inflated scape, pedicels deflexed in fruits and cleistogamous lowermost flower. This species is widely distributed in the Neotropics, and in Brazil, it is cited to all the states but AC, DF, ES, RO, RS, SC and TO (Guedes & Alves 2020; Guedes *et al.* 2020). Here we report a new record for the state. In Espírito Santo, *U. hydrocarpa* has only two records (Fig. 1a), in permanent and temporary ponds and rivers, in areas of *campos nativos* and *restingas*.

2.5. *Utricularia longifolia* Gardner in Hook., London J. Bot. 1: 545. 1842. Figs. 1b; 2b'-f'

Terrestrial or lithophyte, 13–83 cm tall. Leaves aerial, laminar, simple, lamina elliptical to narrowly obovate, basifixed, coriaceous, multinerved. Utricles 1–1.2 mm long, ovoid, stalked, glandular, entrance basal, with two dorsal appendages, simple, reflexed. Inflorescence

racemose, simple or branched, lax or congest, absence of cleistogamous flowers; scape 2–3 mm diam., slightly stiff, slim, glabrous. Scales and bracts 2.5–3.5 × 1–2 mm, narrowly ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 1.5–2 × 0.2–0.3 mm, linear, basifixed, free, margins entire. Pedicels 5–20 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals ovate, margins microscopically denticulate, flat, non-hyaline, nerves conspicuous, non-prominent, not converging to the apex; upper sepal 6–10 × 4–6 mm, apex acuminate; lower sepal 4–8 × 3–5 mm, apex acuminate bifid. Corolla 10–25 mm long, purple, glabrous, palate with one yellow crest; upper lip broadly ovate, apex truncate to rounded, lower lip flat, transversally elliptic, entire, palate gibbous; spur cylindrical, slightly longer than the lower lip, straight to slightly curved, parallel to the lower lip, apex bifid. Capsule 5–7 mm diam., globose, dehiscence longitudinal. Seeds ca. 0.5 mm long, pyramidal, non-winged, without peripheral projections.

Examined material: Castelo, Parque Estadual do Forno Grande, 12.X.2000, fl., L. Kollmann 3180 (MBML); 4.IX.2004, fl., L. Kollmann 6983 (MBML); 12.II.2008, fl. and fr., L. Kollmann 10570 (CEPEC, MBML, RB, UPCEB). Domingos Martins, Califórnia, III.1917, fl. and fr., P. von Luetzelburg 14025 (NY, US); Pedra Azul, 20.III.1983, fl., G. Hatschbach 46890 (CEPEC, MBM, US); 19.X.1985, fl., G. Hatschbach *et al.* 49960 (MBM, SP, US); 29.X.1987, fl. and fr., O.J. Pereira 1335 (VIES). Fundão, Goiapaba-Açu, 13.X.2002, fl. and fr., A.P. Fontana 418 (MBML). Itarana, Limoeiro do Caravaggio, 26.VII.2007, fl. and fr., J. Rossini 667 (MBML). Santa Leopoldina, Pedra Branca, Serra Santa Lucia, 1.XI.2006, fl., L.F.S. Magnago *et al.* 1558 (MBML). Santa Teresa, 29.VII.1990, fl. and fr., O.J. Pereira 2164 (VIES); cabeceira do Rio Bonito, 24.XI.2004, fl. and fr., L. Kollmann 7256 (MBML); Estação Biológica de Santa Lúcia, 23.II.2001, fl. and fr., L. Kollmann 3570 (MBML); REBIO Augusto Ruschi, 10.X.2004, fl. and fr., R.R. Vervloet 2622 (MBML); Serra do Gelo, nascente do Rio Santa Maria do Rio Doce, 16.VII.2003, fl., A.M. Assis 922 (MBML); Vale do Canaã, 15.VIII.1985, fl. and fr., W. Boone 674 (MBML). São Roque do Canaã, Alto Misterioso, 16.VII.2005, fl., A.P. Fontana 1566 (MBML); 16.IX.2005, fl., L. Kollmann 8314 (MBML); 7.XI.2007, fl., L. Kollmann 10152 (MBML). Serra, APA do Mestre Álvaro, Estação Biológica, 21.XI.1982, fl., J.R. Pirani 177 (P, SP, SPF).

Utricularia longifolia is easily recognized by its coriaceous, multinerved, elliptic to narrowly obovate leaves, purple corolla, palate with a yellow crest, transversally elliptic and entire lower lip, and sepals with microscopically denticulate margins.

This species is endemic to Brazil, and it is cited to the states of BA, ES, MG, RJ, SE and SP (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. longifolia* has records in the central and southern highlands and lowlands (Fig. 1a), in areas of granitic inselbergs/rocky outcrops and *campos de altitude*.

2.6. *Utricularia myriocista* A.St.-Hil. & Girard, *Compte Rend. Hebd. Séances Acad. Sci., Ser. D.* 7(21): 869. 1838. Figs. 1c; 2g'-j'

Hydrophyte, 5–8 cm tall. Leaves submerged, capillary, verticillate, branched, membranaceous, 1-nerved, apex bearing traps. Utricles 1–3 mm long, ovoid, stalked, glandular, entrance terminal, without appendages, with a central fascicle of stipitate-glandular trichomes. Inflorescence 1-flowered to racemose, simple, lax, absence of cleistogamous flowers; scape 2–3.5 mm diam., flexible, inflated, glandular. Scales absent. Bracts 2–2.5 × 1.5–2 mm, subpeltate, upper extremity obovate, lower extremity quadrate, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 3–5 mm long, compressed, non-winged, glandular, ascending in fruits. Sepals with margins entire, flat, non-hyaline, nerves inconspicuous, not converging to the apex; upper sepal 3–4 × 2.5–3 mm, ovate, apex obtuse; lower sepal 3–4 × 3–3.5 mm, circular, apex truncate. Corolla 13–15 mm long, magenta, glabrous, palate white and yellow; upper lip broadly obovate, concave, apex rounded, lower lip flat, trilobed, lateral lobes saccate and middle lobe broader, palate non-gibbous; spur subulate, slightly longer than the lower lip, curved, parallel to the lower lip, apex acute. Capsule ca. 3.5 mm diam., globose, dehiscence longitudinal. Seeds ca. 0.8 mm long, globose, non-winged, with irregular peripheral projections.

Examined material: Aracruz, Barra do Riacho, 25.V.1956, fl., J.G.F.S. (RB 102251). Vila Velha, Morada do Sol, 23.VIII.2009, fl., R.T. Valadares 870 (VIES). **Additional material:** BRASIL. BAHIA: Salvador, Parque Metropolitano de Pituáçu, 12.VII.2018, fl. and fr., F.M. Guedes 115 (UFP).

Utricularia myriocista is easily recognized by its aquatic free-swimming growth form, verticillate leaves bearing traps on the apex, inflated and glandular scape, subpeltate bracts, absence of bracteoles, magenta corolla with white and yellow palate, trilobed lower lip with saccate lateral lobes and broader middle lobe. This species is endemic to South America, and in Brazil, it is cited to the states of AM, AP, BA, ES, GO, MA, MG, MT, PA,

RR and SE (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. myriocista* has only two records (Fig. 1b) in coastal ponds in areas of *campos nativos* and *restinga*.

2.7. *Utricularia nelumbifolia* Gardner in Hook., *Icon. Pl.* 6: 505–506. 1843. Figs. 1a; 3a-e

Epiphyte, 55–115 cm tall. Leaves aerial, laminar, simple, lamina circular, peltate, coriaceous, multinerved. Utricles 1.5–2 mm long, ovoid, stalked, glandular, entrance lateral, with two dorsal appendages, simple, reflexed. Inflorescence racemose, simple, lax, absence of cleistogamous flowers; scape 3–5 mm diam., slightly stiff, slim, glabrous. Scales and bracts 3–6 × 1–2 mm, narrowly ovate to lanceolate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles, when present, 1.5–3 × 0.2–0.3 mm, linear, basifixed, free, margins entire. Pedicels 15–30 mm long, cylindrical, non-winged, glabrous, slightly deflexed in fruits. Sepals 6–18 × 5–15 mm, broadly ovate, apex acute, margins entire, flat, non-hyaline, nerves conspicuous, non-prominent, not converging to the apex. Corolla 25–40 mm long, pale lilac to purple, glabrous, palate with two yellow crests; upper lip broadly obovate, apex rounded, lower lip flat, trilobed, lateral lobes circular, middle lobe, diminutive, deltoid to obsolete, palate gibbous; spur subulate, longer than the lower lip, curved, parallel to the lower lip, apex acute. Capsule 8–12 × 6–10 mm, ovoid, dehiscence longitudinal. Seeds ca. 2 mm long, cylindrical, non-winged, without peripheral projections.

Examined material: Castelo, Parque Estadual do Forno Grande, 9.IX.2004, fl., L. Kollmann 6981 (MBML); 12.VIII.1948, fl. and fr., A.C. Brade 19256 (RB); 31.X.2012, fl., T.B. Flores 1737 (RB); Pedregulho, estrada entre Balança e Rio Manso, 16.X.2008, fl., C.N. Fraga 2259 (RB); Topo do Forninho 21.I.2009, fl., C.N. Fraga 2372 (CEPEC, MBML, RB, UPCB). Domingos Martins, Pedra Azul, 11.VII.2006, fl. and fr., A.P. Fontana 2201 (RB); 17.VII.2006, fl. and fr., A.P. Fontana 2208 (RB). Ibiraçu, Lombardia, 6.V.2005, fl., A.P. Fontana 1427 (MBML). Itaguaçu, Pedra do Caparaó, 23.IV.2005, fl., A.P. Fontana 1370 (MBML); 6.VI.2007, fr., A.P. Fontana 3510 (MBML). Itarana, São Sebastião, 5.IX.2012, fl., L. Kollmann 12478 (MBML). Mimoso do Sul, Pico dos Pontões, Pedra do Pontão, 22.VI.2008, fl. and fr., D.R. Couto 547 (MBML). Santa Leopoldina, Rio Bonito, 19.I.2002, fl., L. Kollmann 5344 (MBML). Santa Maria de Jetibá, Pedra do Garrafão, 25.I.2004, fl., M.V.S. Berger 132 (MBML); 9.VI.2006, fl., A.P. Fontana 2178 (RB). Santa Teresa, Estação Biológica de Santa Lúcia, 12.VIII.2005, fl. and fr., L. Kollmann 8222 (MBML); estrada para Alto Santo



Figure 3 – a-e. *Utricularia nelumbifolia* – a. leaf; b. utricle; c. bract and bracteoles; d. sepals; e. corolla (front view). f-j. *Utricularia nephrophylla* – f. leaf; g. utricle; h. bract and bracteoles; i. sepals; j. corolla (front view). k-o. *Utricularia pusilla* – k. leaf; l. utricle; m. inflorescence; n. bract; o. sepals. p-t. *Utricularia reniformis* – p. leaf; q. utricle; r. bract and bracteoles; s. sepals; t. corolla (front view). u-x. *Utricularia subulata* – u. utricle; v. bract; w. sepals; x. corolla (front view). y-b'. *Utricularia tricolor* – y. utricle; z. bract and bracteoles; a'. sepals; b'. corolla (front view). c'-f'. *Utricularia tridentata* – c'. utricle; d'. bract and bracteoles; e'. sepals; f'. corolla (front view). g'-i'. *Utricularia triloba* – g'. utricle; h'. sepals; i'. corolla (front view).

Antônio, 10.VIII.1999, fl. and fr., *G. Martinelli 15638* (RB); Pedra Alegre, 20.VI.2000, fl., *V. Demuner 1192* (MBML); Luxemburgo, Pedra Preta, 15.III.2005, fl., *A.P. Fontana 1148* (MBML); 15.III.2005, fl. and fr., *L. Kollmann 7440* (MBML); Pedra da Onça, 16.IV.1986, fl., *H.Q.B. Fernandes 1917* (MBML); 16.V.2000, fl., *V. Demuner 1079* (MBML); Pedra Paulista, 2.VI.2004, fl. and fr., *R.R. Vervloet 2655* (MBML); radar Cindactar, 3.XI.2000, fl., *A.P. Fontana 54* (MBML); 22.XII.2001, fl. and fr., *A.P. Fontana 269* (MBML).

Utricularia nelumbifolia is easily recognized by its epiphytic growth form, growing inside bromeliad tanks (*Vriesea* sp. and *Alcantarea* sp.), its peltate and circular leaves, pale lilac to purple corolla, palate with two yellow crests, trilobed lower lip with circular lateral lobes and diminutive, deltoid to obsolete middle lobe. This species is endemic to southeastern Brazil and it is cited to the states of ES, MG, RJ and SP (Taylor 1989; Guedes *et al.* 2020). In Espírito Santo, *U. nelumbifolia* has records in the central and southern highlands (Fig. 1b), in areas of granitic inselbergs/rocky outcrops and *campos de altitude*.

2.8. *Utricularia nephrophylla* Benj. in Mart., *Fl. bras.* 10: 247. 1847. Figs. 1c; 3f-j

Terrestrial or lithophyte, 7–16 cm tall. Leaves aerial, laminar, simple, lamina reniform, basifixed, membranaceous, multinerved. Utricles 0.5–1 mm long, globose, stalked, glandular, entrance basal, with two dorsal appendages, simple, reflexed. Inflorescence 1-flowered to racemose, simple, lax, absence of cleistogamous flowers; scape 0.5–1 mm diam., flexible, slim, glabrous. Scales, when present, and bracts 2–3 × 1–1.5 mm, narrowly ovate to elliptic, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 1.8–2.8 × 0.8–1.3 mm, narrowly ovate to elliptic, basifixed, free, margins entire. Pedicels 5–25 mm long, compressed, non-winged, glabrous, ascending in fruits. Sepals 4–6 × 2–4 mm, ovate, apex obtuse, margins entire, flat, non-hyaline, nerves conspicuous, non-prominent, not converging to the apex. Corolla 10–15 mm long, white to pale lilac, glabrous, palate with two yellow crests; upper lip ovate, apex truncate to emarginate, lower lip flat, trilobed, lateral lobes broadly obovate, middle lobe, diminutive, deltoid to obsolete, palate gibbous; spur cylindrical, shorter than the lower lip, curved, parallel to the lower lip, apex obtuse. Capsule 3–4 mm diam., globose, dehiscence longitudinal. Seeds ca. 0.6 mm long, globose, non-winged, with irregular peripheral projections.

Examined material: Itaguaçu, Serra do Sobreiro, Pedra do Caparaó, 23.IV.2005, fl., *A.P. Fontana 1375* (MBML).

Dores do Rio Preto, Parque Nacional do Caparaó, Cachoeira 2 Pilões, 22.III.2012, fl., *J. Kuntz 612* (ESA).

Additional material: BRASIL. RIO DE JANEIRO: Rio de Janeiro, Parque Nacional da Tijuca, estrada do Redentor, 26.II.1996, fl. and fr., *F. Rivadavia 552* (SPF).

Utricularia nephrophylla is easily recognized by its terrestrial or lithophytic growth form, reniform leaves, white to pale lilac corolla, palate with two yellow crests, trilobed lower lip with broadly obovate lateral lobes and diminutive, deltoid to obsolete middle lobe. Besides this set of characters, it differs from the closely related species, *U. reniformis*, in its much smaller corolla (10–15 mm long vs. 30–40 mm long). This species is endemic to Brazil, it is cited to the states of BA, ES, MG and RJ (Taylor 1989; Guedes *et al.* 2020). In Espírito Santo, *U. nephrophylla* has only two records in the southwestern highlands (Fig. 1b), in wet rocks and waterfalls in areas of granitic inselbergs/rocky outcrops and *campos de altitude*.

2.9. *Utricularia pusilla* Vahl, Enum. 1: 202. 1804. Figs. 1c; 3k-o

Terrestrial or helophyte, 3–12 cm tall. Leaves aerial, laminar, simple, lamina spatulate to obovate, basifixed, membranaceous, 1-nerved. Utricles 0.5–1 mm long, ovoid, stalked, glandular, entrance lateral, with two dorsal appendages, simple, hispid. Inflorescence racemose, simple, lax, absence of cleistogamous flowers; scape 0.4–0.5 mm in diameter, flexible, slim, glabrous above and glandular below. Scales and bracts 0.8–1 × 0.8–1 mm, broadly ovate, peltate, margins entire. Sterile bracts present on the raceme axis. Bracteoles absent. Pedicels 2–4 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals ovate, margins entire, flat, non-hyaline, nerves conspicuous, prominent, not converging to the apex; upper sepal 1–2 × 0.8–1 mm, apex rounded; lower sepal 1.2–2 × 1–1.5 mm, apex emarginate. Corolla 5–7 mm long, yellow, glabrous; upper lip oblong, apex retuse to emarginate, lower lip flat, deeply trilobed, palate gibbous; spur subulate, up to twice as long as the lower lip, straight to curved, parallel to the lower lip, apex acute. Capsule 2.5–3 mm diam., globose, dehiscence longitudinal. Seeds ca. 0.2 mm long, ellipsoid, non-winged, without peripheral projections.

Examined material: Águia Branca, Santa Luzia, 4.VII.2007, fl. and fr., *R.R. Vervloet 2784* (MBML); 26.IV.2008, fl. and fr., *L. Kollmann 10927* (MBML). Água Doce do Norte, Santa Luzia do Córrego Azul, Pedra da Torre, 28.IV.2008, fl. and fr., *A.P. Fontana 5116* (MBML). Cariacica, condomínio rural Cantinho do Céu, 8.VI.1999, fl. and fr., *C.N. Fraga 441* (MBML).

Mimoso do Sul, Conceição do Muqui, Pedra dos Pontões, 5.I.2011, fl., *D.R. Couto 1788* (VIES). Nova Venécia, Serra de Baixo, Pedra da Torre, 18.II.2008, fl. and fr., *A.P. Fontana 4840* (CEPEC, MBML, RB, UPCB); 19.II.2008, fl. and fr., *A.P. Fontana 4860* (CEPEC, MBML, UPCB). Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, 13.I.2003, fl., *L. Kollmann 5885* (MBML); Vale do Canaã, 22.VIII.2007, fl. and fr., *A.P. Fontana 3715* (MBML).

Utricularia pusilla is easily recognized by its sterile bracts on the raceme axis (between the pedicels), peltate bracts and scales, absence of bracteoles, spatulate to obovate leaves, yellow corolla with deeply trilobed lower lip and subulate spur, up to twice as long as the lower, and sepals with conspicuous and prominent nerves, but not converging to the apex. This species is widely distributed in the Neotropics, and in Brazil, it is cited to all the states but AP, DF, ES, MS, RO, RS and SC (Taylor 1989; Guedes & Alves 2020; Guedes *et al.* 2020). Here we report a new record for the state. In Espírito Santo, *U. pusilla* is widely distributed (Fig. 1b) in granitic inselbergs/rocky outcrops, *campos de altitude* and *restingas*.

2.10. *Utricularia reniformis* A.St.-Hil., Voy. Rio de Janeiro 1: 224. 1830. Figs. 1c; 3p-t

Terrestrial or epiphyte, 20–80 cm tall. Leaves aerial, laminar, simple, lamina reniform, basifixed, coriaceous, multinerved. Utricles 0.8–1.5 mm long, globose, stalked, glandular, entrance basal, with two dorsal appendages, simple, reflexed. Inflorescence racemose, simple, lax, absence of cleistogamous flowers; scape 2–6 mm diam., slightly stiff, slim, glabrous. Scales and bracts 6–8 × 2–3 mm, narrowly ovate to elliptic, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 4–6 × 0.6–1 mm, linear to narrowly lanceolate, basifixed, free, margins entire. Pedicels 10–40 mm long, compressed, non-winged, glabrous, slightly deflexed in fruits. Sepals 9–15 × 7–12 mm, ovate, apex obtuse, margins entire, flat, non-hyaline, nerves conspicuous, non-prominent, not converging to the apex. Corolla 30–40 mm long, purple, glabrous, palate with two yellow crests; upper lip broadly obovate, apex rounded or truncate, lower lip flat, trilobed, lateral lobes circular, middle lobe, diminutive, deltoid to obsolete, palate gibbous; spur subulate, longer than the lower lip, curved, parallel to the lower lip, apex acute. Capsule 5–8 mm diam., globose, dehiscence longitudinal. Seeds ca. 2 mm long, narrowly cylindrical, non-winged, with irregular peripheral projections.

Examined material: Cachoeiro de Itapemirim, Pedra do Cabrito, 28.III.2019, fl., *M.L. Brotto 3296* (MBM). Castelo, Parque Estadual do Forno Grande, 12.X.2000, fl., *L. Kollmann 3179* (MBML). Parque Nacional do Caparaó, entre o acampamento Macieira e o Pico da Bandeira, 18.I.2019, fl., *H.L. Silva 256* (VIES); Pico da Bandeira, 6.II.1985, *P.E. Berry 4537* (RB).

Additional material: BRASIL. RIO DE JANEIRO: Teresópolis, trilha para a Pedra do Sino, 13.XII.2015, fl. and fr., *V.F.O. Miranda 2049* (JABU).

Utricularia reniformis is easily recognized by its terrestrial or epiphytic growth form, growing inside bromeliad tanks (*Vriesea* sp.) like *U. nelumbifolia*, its reniform leaves, purple corolla, palate with two yellow crests, trilobed lower lip with circular lateral lobes and diminutive, deltoid to obsolete middle lobe. As aforementioned, it differs from the closely related species, *U. nephrophylla*, in its much larger corolla (30–40 mm long vs. 10–15 mm long). This species is endemic to southern and southeastern Brazil, and it is cited to the states of ES, MG, PR, RJ, RS, SC and SP (Taylor 1989; Guedes *et al.* 2020). In Espírito Santo, *U. reniformis* has few records in the southwestern highlands (Fig. 1a), in areas of granitic inselbergs/rocky outcrops and *campos de altitude*.

2.11. *Utricularia subulata* L., Sp. Pl. 1: 18. 1753. Figs. 1d; 3u-x

Terrestrial or helophyte, 5–10 cm tall. Leaves aerial, laminar, simple, lamina linear, basifixed, membranaceous, 1-nerved. Utricles 0.5–0.8 mm long, ovoid, stalked, glabrous to glandular, entrance lateral, with two dorsal appendages, branched. Inflorescence racemose, simple, lax, sometimes with cleistogamous flowers; scape 0.4–0.5 mm in diameter, flexible, slim, glabrous. Scales and bracts 0.8–1 × 0.8–1 mm, circular to ovate, peltate, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 5–8 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals circular, margins entire, flat, non-hyaline, nerves conspicuous, non-prominent, not converging to the apex; upper sepal 1–2 × 1–2 mm, apex rounded; lower sepal 1.2–2.2 × 1.2–2.2 mm, apex rounded to truncate. Corolla 6–10 mm long, yellow, glabrous; upper lip ovate-deltoid, apex obtuse, lower lip flat, deeply trilobed, palate gibbous; spur subulate, as long as to slightly longer than the lower lip, straight to slightly curved, parallel to the lower lip, apex acute or 2–4-denticulate. Capsule 2–2.5 mm diam., globose, dehiscence longitudinal. Seeds ca. 0.2 mm long, ellipsoid, non-winged, without peripheral projections.

Examined material: Conceição da Barra, área 157 da Aracruz Celulose S.A., 15.IV.1992, fl. and fr., *O.J. Pereira* 3305 (VIES); área 213 da Aracruz Celulose S.A., 24.III.1992, fl., *O.J. Pereira* 3053 (VIES); estrada sentido Riacho Doce, 28.VIII.2012, fl., *T.B. Flores* 1242 (ESA); Parque Estadual de Itaúnas, 18.XI.1999, fl. and fr., *C.N. Fraga* 536 (MBML); 30.III.2000, fl., *O.J. Pereira* 6100 (VIES); 15.VIII.2013, fr., *J.O. Machado* 106 (VIES). Guarapari, 8.II.1985, fl., *O.J. Pereira* 417 (VIES). Itaguaçu, Alto Limoeiro, 1.VI.1946, fr., *A.C. Brade* 18513 (RB); Serra do Sobreiro, Pedra do Caparaó, 23.IV.2005, fl. and fr., *A.P. Fontana* 1373 (MBML). Jaguaré, Giral, 17.I.2009, fl. and fr., *L. Kollmann* 11457 (MBML). Linhares, 18.IV.2011, fl., *J.C. Lopes* 220 (CVRD, ESA). Santa Teresa, cabeceira do Rio Bonito, 31.I.2002, fl. and fr., *L. Kollmann* 5446 (MBML). Sooretama, Reserva Natural Vale, 13.V.2009, fl., *G.D. Colletta* 281 (ESA). Vila Velha, Alagados do Vale, 1.IX.2014, fl., *R.T. Valadares* 1277 (VIES).

Utricularia subulata is easily recognized by its linear leaves, peltate bracts and scales, absence of bracteoles, yellow corolla with deeply trilobed lower lip and subulate spur, as long as to slightly longer than the lower lip, and sepals with conspicuous nerves, but non-prominent and not converging to the apex. This species is almost Pantropical, and in Brazil, it is cited to all the states but AC (Guedes & Alves 2020; Guedes *et al.* 2020). In Espírito Santo, *U. subulata* is widely distributed (Fig. 1b) in areas of granitic inselbergs/rocky outcrops, *campos de altitude*, *campos nativos* and *restingas*.

2.12. *Utricularia tricolor* A.St.-Hil., Voy. Distr. Diam. 2: 418. 1833. Figs. 1d; 3y-b'

Terrestrial or helophyte, 15–35 cm tall. Leaves aerial, laminar, simple, lamina obovate, basifixed, membranaceous, multinerved. Utricles 1.5–2 mm long, ovoid, stalked, glandular, entrance basal, with two dorsal appendages, simple, and a ventral chin-like projection, both dorsal and ventral structures covered with long inflexed glandular trichomes. Inflorescence 1-flowered to racemose, simple, lax, absence of cleistogamous flowers; scape 0.4–1.2 mm diam., flexible, slim, glabrous. Scales and bracts 1.5–2 × 1–2 mm, ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 1.5–2 × 0.4–0.5 mm, lanceolate, basifixed, basally connate with the bracts, margins entire. Pedicels 5–15 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals with margins entire, flat, hyaline, nerves conspicuous, non-prominent, not converging to the apex; upper sepal 4–5 × 4–5 mm, broadly ovate to circular, apex rounded; lower sepal 2–2.5 × 3–4 mm, transversally

elliptic, apex emarginate. Corolla 15–20 mm long, lilac to purple, minutely glandular, palate white and yellow; upper lip broadly ovate, apex rounded, lower lip flat, entire to shallowly 3-crenate, palate gibbous; spur narrowly conical, as long as or slightly longer than the lower lip, curved, parallel to the lower lip, apex obtuse to emarginate. Capsule 3–4 mm diam., globose, dehiscence bivalvate. Seeds ca. 1 mm long, narrowly cylindrical, non-winged, without peripheral projections.

Examined material: Castelo, Parque Estadual do Forno Grande, 13.V.1949, fl., *A.C. Brade* 19802 (RB). Guarapari, Nova Guarapari, 11.IX.1988, fl. and fr., *O.J. Pereira* 1802 (VIES); Parque Estadual Paulo César Vinha, 25.III.1991, fl., *J.M.L. Gomes* 1490 (VIES); 17.IV.1991, fl., *J.M.L. Gomes* 1512 (VIES). Vila Velha, Interlagos, 15.XI.2007, fl., *F.B.C. Souza* 92 (VIES); Lagoa do Milho, 20.VII.1973, fl., *D. Araújo* 375 (RB); 14.I.1975, fl., *A.L. Peixoto* 371 (RB); Ponta da Fruta, Setiba, 31.VIII.1982, fl., *O.J. Pereira* 152 (VIES).

Utricularia tricolor is easily recognized by its obovate leaves, bracteoles basally connate to the bracts, lilac to purple corolla with white and yellow palate, minutely glandular, entire to shallowly 3-crenate lower lip, and narrowly conical spur, as long as or slightly longer than the lower lip. This species is endemic to South America, and in Brazil, it is cited to the states of BA, DF, ES, GO, MG, MT, MS, PR, RJ, RS, SC and SP (Taylor 1989; Guedes *et al.* 2020). In Espírito Santo, *U. tricolor* has records in the southeastern highlands and lowlands (Fig. 1b), in areas of granitic inselbergs/rocky outcrops, *campos de altitude* and *restingas*.

2.13. *Utricularia tridentata* Sylvén, Ark. Bot. 8: 28. 1909. Figs. 1d; 3c'-f'

Terrestrial or helophyte, 5–12 cm tall. Leaves aerial, laminar, simple, lamina broadly obovate to circular, basifixed, membranaceous, multinerved. Utricles 1–1.5 mm long, ovoid, stalked, glandular, entrance basal, with two dorsal appendages, simple, and a ventral chin-like projection, both dorsal and ventral structures covered with long inflexed glandular trichomes. Inflorescence 1-flowered to racemose, simple, lax, absence of cleistogamous flowers; scape 0.4–0.6 mm diam., flexible, slim, glabrous. Scales and bracts 1–1.5 × 0.5–1 mm, ovate, basifixed, margins entire. Sterile bracts absent on the raceme axis. Bracteoles 1–1.5 × 0.3–0.4 mm, lanceolate, basifixed, basally connate with the bracts, margins entire. Pedicels 5–10 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals with margins entire, flat, hyaline, nerves conspicuous, non-prominent, not converging

to the apex; upper sepal 2–2.5 × 1.5–2 mm, ovate to oblong, apex rounded; lower sepal 1–1.5 × 1.3–1.8 mm, transversally elliptic, apex emarginate. Corolla 6–10 mm long, lilac to purple, minutely glandular, palate white and yellow; upper lip ovate, apex rounded, lower lip flat, distinctly trilobed, palate gibbous; spur narrowly conical, slightly longer than the lower lip, curved, parallel to the lower lip, apex obtuse. Capsule 2–2.5 mm diam., globose, dehiscence bivalvate. Seeds ca. 0.5 mm long, ovoid, non-winged, without peripheral projections.

Examined material: Iúna, Parque Nacional do Caparaó, Rancho dos Cabritos, beira do Córrego José Pedro, 18.II.2000, fl., V.C. Souza 23419 (ESA, RB).

Additional material: BRASIL. SANTA CATARINA: Campo Alegre, Campos do Quiriri, 17.XI.2012, fl. and fr., C.V. Silva 23 (JPB).

Utricularia tridentata is easily recognized by its broadly obovate to circular leaves, bracteoles basally connate to the bracts, lilac to purple corolla with white and yellow palate, minutely glandular, distinctly trilobed lower lip, and narrowly conical spur, slightly longer than the lower lip. This species is endemic to South America, and in Brazil, it is cited to the states of MG, PR, RJ, RS and SC (Taylor 1989; Guedes *et al.* 2020). Here we report a new record for the state. In Espírito Santo, *U. tridentata* has only one record in a southwestern highland (Fig. 1b), on a creek edge in an area of *campos de altitude*.

2.14. *Utricularia triloba* Benj. in Mart., *Fl. bras.* 10: 248. 1847. Figs. 1d; 3g'-i'

Terrestrial or helophyte, 3–13 cm tall. Leaves aerial, laminar, simple, lamina linear, basifixed, membranaceous, 1-nerved. Utricles 0.3–0.5 mm long, ovoid, stalked, glandular, entrance lateral, with two dorsal appendages, branched. Inflorescence racemose, simple, lax, sometimes with cleistogamous flowers; scape 0.1–0.2 mm in diameter, flexible, slim, glabrous. Scales and bracts ca. 1 × 0.6 mm, rhombic, peltate, margins entire. Sterile bracts absent on the raceme axis. Bracteoles absent. Pedicels 2–4 mm long, cylindrical, non-winged, glabrous, ascending in fruits. Sepals ovate, margins entire, flat, non-hyaline, nerves conspicuous, prominent, converging to the apex; upper sepal ca. 1 × 1 mm, apex acute; lower sepal ca. 1.2 × 1.2 mm, apex acute. Corolla ca. 10 mm long, yellow, glabrous; upper lip ovate, apex rounded, lower lip flat, shallowly trilobed, palate gibbous; spur subulate, slightly longer than the lower lip, straight, parallel to the lower lip, apex acute to 2–4-denticulate. Capsule 1.5–2 mm diam., globose,

dehiscence longitudinal. Seeds ca. 0.2 mm long, ovoid, non-winged, without peripheral projections. **Examined material:** Santa Leopoldina, Rio das Farinhas, 14.IV.2008, fl. and fr., A.P. Fontana 4921 (MBML).

Utricularia triloba is easily recognized by its linear leaves, peltate bracts and scales, absence of bracteoles, yellow corolla with shallowly trilobed lower lip and subulate spur, slightly longer than the lower lip, and sepals with conspicuous and prominent nerves, converging to the apex. This species is widely distributed in the Neotropics, and in Brazil, it is cited to all the states but CE, ES, MA, PE, RO, RS and SC (Guedes & Alves 2020; Guedes *et al.* 2020). Here we report a new record for the state. In Espírito Santo, *U. triloba* has only one record (Fig. 1b) on a roadside in an area of Montane Dense Ombrophilous Forest.

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List of Exsiccatae

Abreu LC SP 141206 (2.3). Amaral MV VIES 23888 (2.2), SAMES 2975 (2.2). Araújo D RB 203312 (2.3), RB 203077 (2.12). Assis AM MBML 29037 (2.2), MBML 21766 (2.3), MBML 30404 (2.3), MBML 21782 (2.5). Berger MVS MBML 21888 (2.7). Berry PE RB 205886 (2.10). Boone W MBML 2850 (2.3), MBML 2849 (2.5). Brade AC RB 203026 (2.7), RB 206227 (2.11), RB 205213 (2.12). Brotto ML MBM 422480 (2.10). Coelho PJ MBML 49756 (2.3). Colledetti M MBML 456 (2.2), MBML 461 (2.2). Colletta GD ESA 110440 (2.11). Couto DR MBML 39155 (2.7), VIES 33780 (2.9). Demuner V MBML 12553 (2.7), MBML 12845 (2.7). Duarte AP RB 203022 (2.2). Fernandes HQB MBML 1143 (2.7). Flores TB RB 998081 (2.7), ESA 12045 (2.11). Folli DA CVRD 4860 (2.2), CVRD 5931 (2.3), CVRD 7298 (2.3), MO 2997267 (2.3), CVRD 6649 (2.4), R 218143 (2.4). Fontana AP CEPEC 125401 (1.2), MBML 16609 (1.2), MBML 23197 (1.2), MBML 24461 (1.2), RB 582211 (1.2), RB 544702 (1.2), MBML 52377 (2.3), MBML 19084 (2.5), MBML 25197 (2.5), MBML 13739 (2.7), MBML 16603 (2.7), MBML 24321 (2.7), MBML 24459 (2.7), MBML 25148 (2.7), MBML 47026 (2.7), MBML 49200 (2.7), RB 562049 (2.7), RB 562056 (2.7), RB 562027 (2.7), MBML 24462 (2.8), MBML 45463 (2.9), CEPEC 125311 (2.9), CEPEC 125889 (2.9), MBML 34366 (2.9), MBML 34365 (2.9), MBML 52426 (2.9), RB 525395 (2.9), RB 52416 (2.9), UPBC 90393 (2.9), UPBC 90511 (2.9), MBML 24460 (2.11), MBML 35609 (2.14). Forzza RC RB 1115527 (2.3). Fraga CN MBML 12716 (2.1), CEPEC 133654 (2.3), MBML 38583 (2.3), RB 549171 (2.3), CEPEC 130779 (2.7), MBML 38750 (2.7), RB 549099 (2.7), RB 549208 (2.7), UPBC 66020 (2.7), MBML 12770 (2.9), MBML 12722 (2.11). Goldenberg R CEPEC 125888 (1.2), MBML 36013 (1.2), RB 532368 (1.2), RB 558090 (1.2), UPBC 76692 (1.2). Gomes JML VIES 4249 (2.2), VIES 5458 (2.12), VIES 6729 (2.12). Guedes FM UFP 85558 (2.6). Hatschbach G CEPEC 43498 (2.5), MBM 88493 (2.5), MBM 123288 (2.5), SP 249898 (2.5), US 3125454 (2.5), US 3172597 (2.5). JGFS RB 204613 (2.2), RB 203369 (2.3), RB 203787 (2.4), RB 102251 (2.6). Kollmann L MBML 16067 (1.2), MBML 23835 (1.2), MBML 24542 (1.2), MBML 35024 (1.2), MBML 16105 (2.3), MBML 16247 (2.3), CEPEC 125913 (2.5), MBML 13691 (2.5), MBML 14120 (2.5), MBML 22693 (2.5), MBML 23786 (2.5), MBML 25058 (2.5), MBML 32643 (2.5), MBML 34112 (2.5), RB 521945 (2.5), UPBC 63588 (2.5), MBML 16060 (2.7), MBML 22695 (2.7), MBML 23599 (2.7), MBML 24823 (2.7), MBML 49200 (2.7), MBML 19329 (2.9), MBML 34805 (2.9), MBML 13612 (2.10), MBML 16104 (2.11), MBML 36546 (2.11). Kuntz J ESA 121869 (2.18). Lobão AQ SAMES 2972 (2.2), VIES 23890 (2.2). Lopes JC CVRD (2.11), ESA 115157 (2.11). Machado JO VIES 37286 (2.2), VIES 43183 (2.11). Magnago LFS MBML 27943 (2.5). Martinelli G RB 968868 (2.2), RB 778163 (2.7). Meirelles J CVRD 16529 (2.2), ESA 115358 (2.2), RB 779236 (2.2), SP 222973 (2.2). Mendes BS VIES 42642 (2.3). Menezes LFT VIES 23889 (2.1), SAMES 2976 (2.1). Mexia YEJ GH 01973914 (1.1), NY 880033 (1.1), P 03575354 (1.1), US 1499187 (1.1). Miranda VFO JABU 2049 (2.10). Nichio-Amaral R VIES 47576 (2.3), VIES 47276 (2.3). Peixoto AL RB 203085 (2.12). Pellegrini MOO RB 1132592 (2.3). Pereira OJ VIES 451 (1.2), VIES 2005 (1.2), VIES 208 (2.2), VIES 2315 (2.2), VIES 8409 (2.3), VIES 5842 (2.3), VIES 15762 (2.3), VIES 2006 (2.5), VIES 4737 (2.5), VIES 711 (2.11), VIES 8410 (2.11), VIES 8411 (2.11), VIES 14804 (2.11), EAC 62897 (2.12), VIES 154 (2.12), VIES 3070 (2.12). Pirani JR CEN 93886 (2.2), HUEFS 226785 (2.2), RB 1163439 (2.2), SP 183299 (2.2), SP 46477 (2.2), SP 143042 (2.2), SP 183297 (2.4), P 04429016 (2.5), SP 183347 (2.5), SP 93538 (2.5). Ribeiro M SAMES 2974 (2.2). Rivadavia F SP 110510 (2.8). Rossini J MBML 31416 (2.5). Saint-Hilaire AFCP P00603321 (2.1). Silva CV JPB 52725 (2.13). Silva HL VIES 41858 (1.1), VIES 41856 (2.10). Simonelli M VIES 14662 (2.2). Souza FBC VIES 17079 (2.1), VIES 17163 (2.12). Souza VC ESA 64573 (1.1), RB 1169288 (1.1), VIES 13452 (1.1), ESA 64575 (2.13), RB 1169279 (2.13). Souza WO VIES 37286 (2.2). Sucre D RB 203403 (2.3). Vago AM MBML 41932 (2.3). Valadares RT VIES 19588 (2.3), VIES 29256 (2.3), VIES 35926 (2.3), VIES 19589 (2.6), VIES 35823 (2.11). Vervloet RR MBML 41415 (1.2), MBML 31553 (2.5), MBML 52013 (2.7), MBML 30577 (2.9). Vinha PC CVRD 2715 (2.2), VIES 4473 (2.2). von Luetzelburg P NY 400608 (2.5), US 1616069 (2.5).

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**4 ARTIGO 2 – DIVERSITY AND DISTRIBUTION OF
LENTIBULARIACEAE IN BAHIA STATE, BRAZIL: IMPLICATIONS FOR
PHYTOGEOGRAPHY AND CONSERVATION**



Diversity and distribution of Lentibulariaceae in Bahia state, Brazil: implications for phytogeography and conservation

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Abstract

Bahia state harbours an immense diversity of plant species with several cases of endemism, especially in the savanna wetlands, typical ecosystems where most Lentibulariaceae representatives occur. In this context, we aimed to improve the characterization of these savanna wetlands in terms of species richness of Lentibulariaceae, their phytogeographic patterns, endemism, forms of rarity, threats to their habitats, and conservation efforts. Herein we present the synopsis of the 42 species of Lentibulariaceae that occur in Bahia state, providing short diagnostic characterization, photographs of living specimens, updated geographic distribution displayed in maps, new records, and discussion concerning phytogeographic patterns, endemism, rarity, habitat characterization and current scenario of threats and conservation. Our results show a disjunct distribution and similarity in Lentibulariaceae species composition between savanna wetlands, corroborating previous hypotheses of vegetation connections during moister climatic conditions in the past. Moreover, differences in species composition among different restinga areas are consistent with biogeographical and paleomodelling studies pointing the São Francisco River as a geographic barrier influencing speciation and genetic diversity. Finally, we emphasize the situation of abandonment in some Protected Areas, lacking proper infrastructure, managers, management plans and board, and insufficient results for the effective conservation and protection of the environment and species.

Keywords: Carnivorous plants; conservation; distribution patterns; *Genlisea*; savanna wetlands; *Utricularia*

Introduction

Bahia is the largest state in northeastern Brazil, occupying 36.34% of the region, and hosts a great diversity of tropical megathermic climates, usually associated with different topographies and the effect of continentality (RADAMBRASIL 1981, Giuliatti *et al.* 2006). Three of the main Brazilian phytogeographic domains are represented in the state (Caatinga, Cerrado and Atlantic Forest), with many phytophysiognomies thus forming a massive vegetation mosaic with a rich flora and a high number of endemism (Giuliatti *et al.* 2006).

In these diverse phytophysiognomies of Bahia state, about 47% of the Lentibulariaceae Richard (1808: 23) (Lamiales, Eudicots) species from Brazil occur (Guedes *et al.* 2020). The family comprises three genera of carnivorous plants (ca. 360 species) with peculiar adaptations to attract, capture, digest and absorb nutrients from prey (Fleischmann 2018, Guedes *et al.* 2021). Only the rootless *Genlisea* Saint-Hilaire (1833: 428) and *Utricularia* Linnaeus (1753: 18) occur in Brazil, colonizing a wide range of permanently or seasonally wet habitats of lowland and highland open vegetation, in quartzitic/arenitic soils, marshy clay soils and in rocky granitic/gneissic outcrops (Taylor 1989, Fleischmann 2012, Guedes *et al.* 2018).

Their habitat diversity also reflects their diverse growth forms, i.e. terrestrial, amphibian (helophyte), suspended aquatic (hydrophyte), rupicolous (lithophyte), rheophyte and epiphyte species (Ellenberg & Mueller-Dombois 1967, Taylor 1989, Cook 1996). Habitats of many carnivorous plants, including Lentibulariaceae, are threatened around the world, mainly because of pollution, eutrophication, deforestation, agriculture, and industrial and urban expansion (Jennings & Rohr 2011, Cross *et al.* 2020, Guedes & Alves 2020).

As highlighted in previous studies (Guedes *et al.* 2018, 2019, 2021, Guedes & Alves 2020, Guedes & Matias 2020), northeastern Brazil is an important diversity centre of the family, which has been usually neglected in floristic surveys, and consequently little was known about its real richness in the area. The Flora of Bahia project started in 1997 and has been monographed at family or genus level through independent publications (Giulietti *et al.* 2006). No comprehensive papers on Lentibulariaceae has been published yet, except for local floras such as that of the Pico das Almas (Cheek & Taylor 1995), and single species newly described (Taylor & Fromm-Trinta 1983, Taylor 1986, Fleischmann & Rivadavia 2009, Campos *et al.* 2010, Fleischmann *et al.* 2011, Rivadavia *et al.* 2013).

Consequently, the present study aims at presenting the synopsis of the Lentibulariaceae species that occur in Bahia, providing short diagnostic characterization, photographs of living specimens, updated geographic distribution displayed in maps, new records, and discussion concerning phytogeographic patterns, endemism, rarity, and habitat characterization, including threats and conservation efforts.

Material and methods

Fieldwork was carried out in August and November 2017. The collections from ALCB, ASE, BAH, BHCB, BM, CEN, CEPEC, CESJ, E, EAC, ESA, FLOR, FUEL, G, HPL, HRB, HST, HTSA, HUEFS, HURB, HVASF, IPA, JABU, JPB, K, L, M, MAC, MBM, MBML, MO, NY, P, PEUFR, R, RB, SP, SPF, U, UB, UEC, UFP, US and W (acronyms according to Thiers 2022) herbaria were analysed. All the specimens, nomenclatural types and/or possible original material were analysed either in person or through virtual herbaria. Due to the great amount of examined material (1730 exsiccata ca.), only one specimen was selected from each municipality, deemed most representative.

The morphological diagnoses were based on the specimens from the study area, following Harris & Harris (2001) for the terminology, and Fleischmann (2012) and Taylor (1989) for group specific terms. Rarity was inferred following Rabinowitz's (1981) typology based on the geographic range, habitat specificity and local population size. Vegetation characterization followed Giulietti *et al.* (2006) and IBGE (2012). The distribution maps (Figs. 1–5 and Supplementary Material: Fig. A1) were created using QGIS v.3.16.3 (<http://www.qgis.org>), based on cartographic data obtained from the IBGE (<http://www.ibge.gov.br>) and the ICMBio (<https://www.icmbio.gov.br>) platforms, and verified coordinates from the labels of the examined material. The identification key was based on morphological characters that are observable in both fresh and dried material. Table 1 summarizes all the data concerning the conservation status and their source of assessment, type of Protected Area where the species are found, phytogeographic domains and phytophysionomies.

Results

The Lentibulariaceae family in Bahia state is represented by 42 species, 8 of *Genlisea* and 35 of *Utricularia*: *Genlisea aurea* Saint-Hilaire (1833: 429), *G. exhibitionista* Rivadavia & Fleischmann (2011: 19), *G. filiformis* Saint-Hilaire (1833: 428), *G. guianensis* Brown (1900: 2629), *G. lobata* Fromm-Trinta (1989: 152), *G. repens* Benjamin (1847: 254), *G. tuberosa* Rivadavia *et al.* (2013: 464), *G. uncinata* Taylor & Fromm-Trinta (1983: 365), *U. adpressa* Salzmann ex Saint-Hilaire & Girard (1838: 870), *U. amethystina* Salzmann ex Saint-Hilaire & Girard (1838: 870), *U. blanchetii* De Candolle (1844: 13), *U. breviscapa* Wright ex Grisebach (1866: 1), *U. costata* Taylor (1986: 7), *U. cucullata* Saint-Hilaire & Girard (1838: 869), *U. erectiflora* Saint-Hilaire & Girard (1838: 870), *U. flaccida* De Candolle (1844: 17), *U. foliosa* Linnaeus (1753: 18), *U. gibba* Linnaeus (1753: 18), *U. guyanensis* De Candolle (1844: 110), *U. hydrocarpa* Vahl (1804: 200), *U. jamesoniana* Oliver (1860: 169), *U. juncea* Vahl (1804: 200), *U. laxa* Saint-Hilaire & Girard (1838: 870), *U. longifolia* Gardner (1842: 545), *U. myriocista* Saint-Hilaire & Girard (1838: 869), *U. nana* Saint-Hilaire & Girard (1838: 870), *U. nelumbifolia* Gardner (1843: 505), *U. neottiioides* Saint-Hilaire & Girard (1838: 869), *U. nephrophylla* Benjamin (1847: 247), *U. nervosa* Weber ex Benjamin (1847: 247), *U. parthenopipes* Taylor (1986: 7), *U. poconensis* Fromm-Trinta (1985: 139), *U. praelonga* Saint-Hilaire & Girard (1838: 870), *U. purpureocaerulea* Saint-Hilaire & Girard (1838: 869), *U. pusilla* Vahl (1804: 202), *U. resupinata* Greene ex Bigelow (1840: 10), *U. rostrata* Fleischmann & Rivadavia (2009: 155), *U. simulans* Pilger (1914: 194), *U. subulata* Linnaeus (1753: 18), *U. trichophylla* Spruce ex Oliver (1860: 173), *U. tricolor* Saint-Hilaire (1833: 418) and *U. triloba* Benjamin (1847: 254).

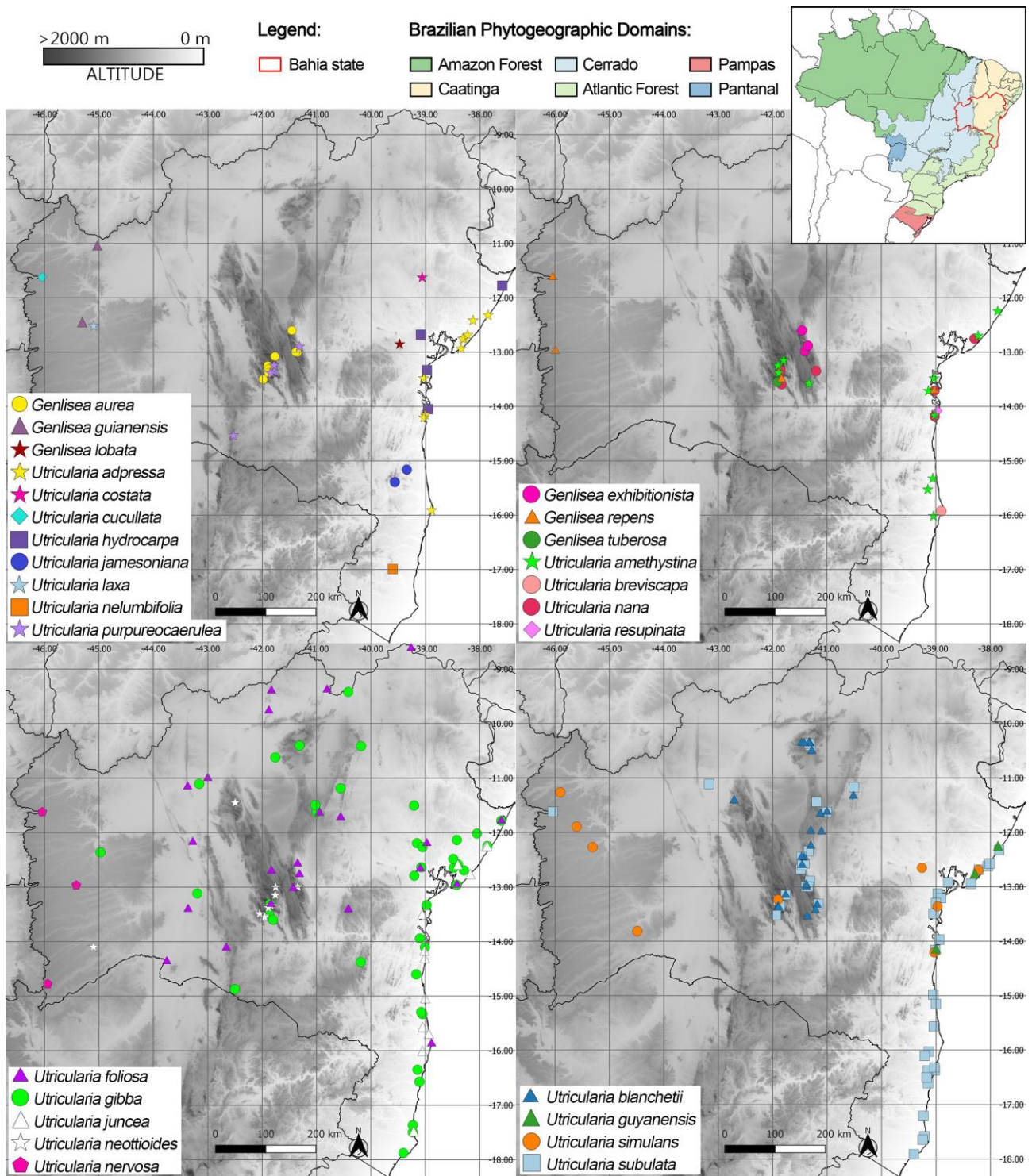


FIGURE 1. Distribution of Lentibulariaceae species in Bahia state.

These species were found in different moister environments of the Atlantic Forest, Caatinga and/or Cerrado domain, including phytophysionomies of lowland and highland open grassy-woody savannas with/without gallery forests (veredas/*Mauritia* swamps and campos rupestres), pioneer formations (restingas and paleodune fields), granitic/gneissic rocky outcrops (inselbergs), submontane Semideciduous Seasonal Forest, lowland Open Ombrophilous Forests and montane Dense Ombrophilous Forests (Giulietti *et al.* 2006, IBGE 2012). Most of the species (25 species) occur in campos rupestres, of which 5 (*G. exhibitionista*, *G. tuberosa*, *G. uncinata*, *U. purpureocaerulea* and *U. rostrata*) are endemic to this vegetation mosaic (Taylor 1989, Fleischmann & Rivadavia 2009, Fleischmann 2012). The restingas,

veredas and lowland Open Ombrophilous Forests are home to 20, 14 and 11 species, respectively; however, none is endemic to these phytophysiognomies (Guedes *et al.* 2020), whereas *G. lobata* is the only endemic to inselberg and campos de altitude vegetation of the Atlantic Forest domain (Fleischmann 2012, Guedes *et al.* 2018, Guedes & Alves 2020).

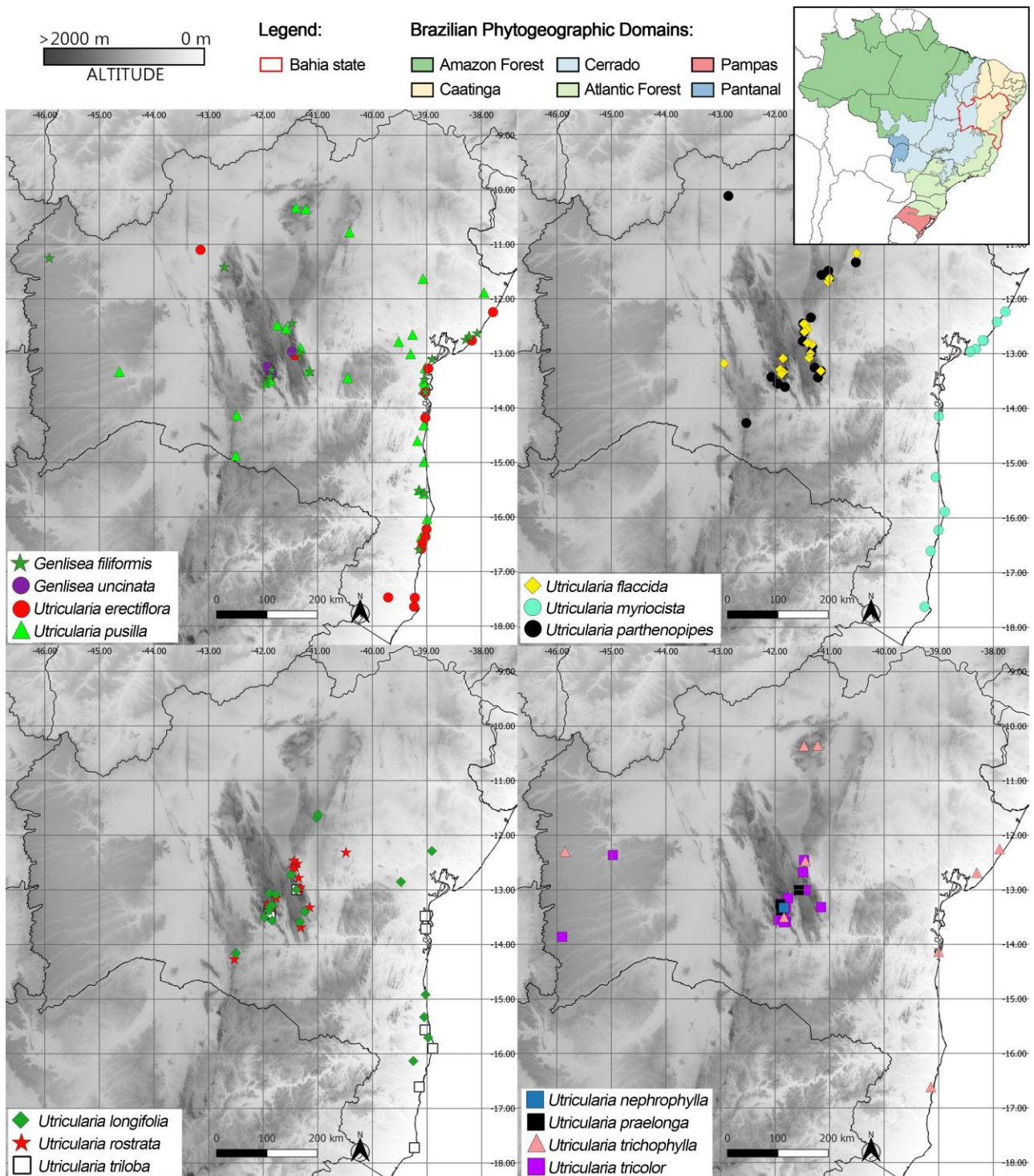


FIGURE 2. Distribution of Lentibulariaceae species in Bahia state.

Four species are endemic to Bahia: *G. exhibitionista*, *G. uncinata*, *U. parthenopipes* and *U. rostrata* (Guedes *et al.* 2020). These two *Genlisea* species are restricted to the campos rupestres of Chapada Diamantina highlands, *G. exhibitionista* occurs in the Serra do Sincorá and Cachoeira da Fumaça (sympatric with *U. rostrata*), while *G. uncinata* in the Serra da Mesa, Serra do Sincorá (but not sympatric with *G. exhibitionista*), Serra do Barbado and Serra dos Cristais (Figs. 1–4) (Fleischmann 2012). On the other hand, here we report the first record of *U. parthenopipes* outside

the Espinhaço Range (campos rupestres), in a paleodune field area of the lower middle São Francisco River (Figs. 1–4). Likewise, *U. rostrata* was previously considered restricted to the central portions of the Chapada Diamantina highlands (Fleischmann & Rivadavia 2009), but here we report two records from other localities of campos rupestres: Serra do Orobó and near a mining area in the municipalities of Ruy Barbosa and Caetité, which also represent the northernmost and southernmost known populations of the species, respectively (Figs. 1–4).

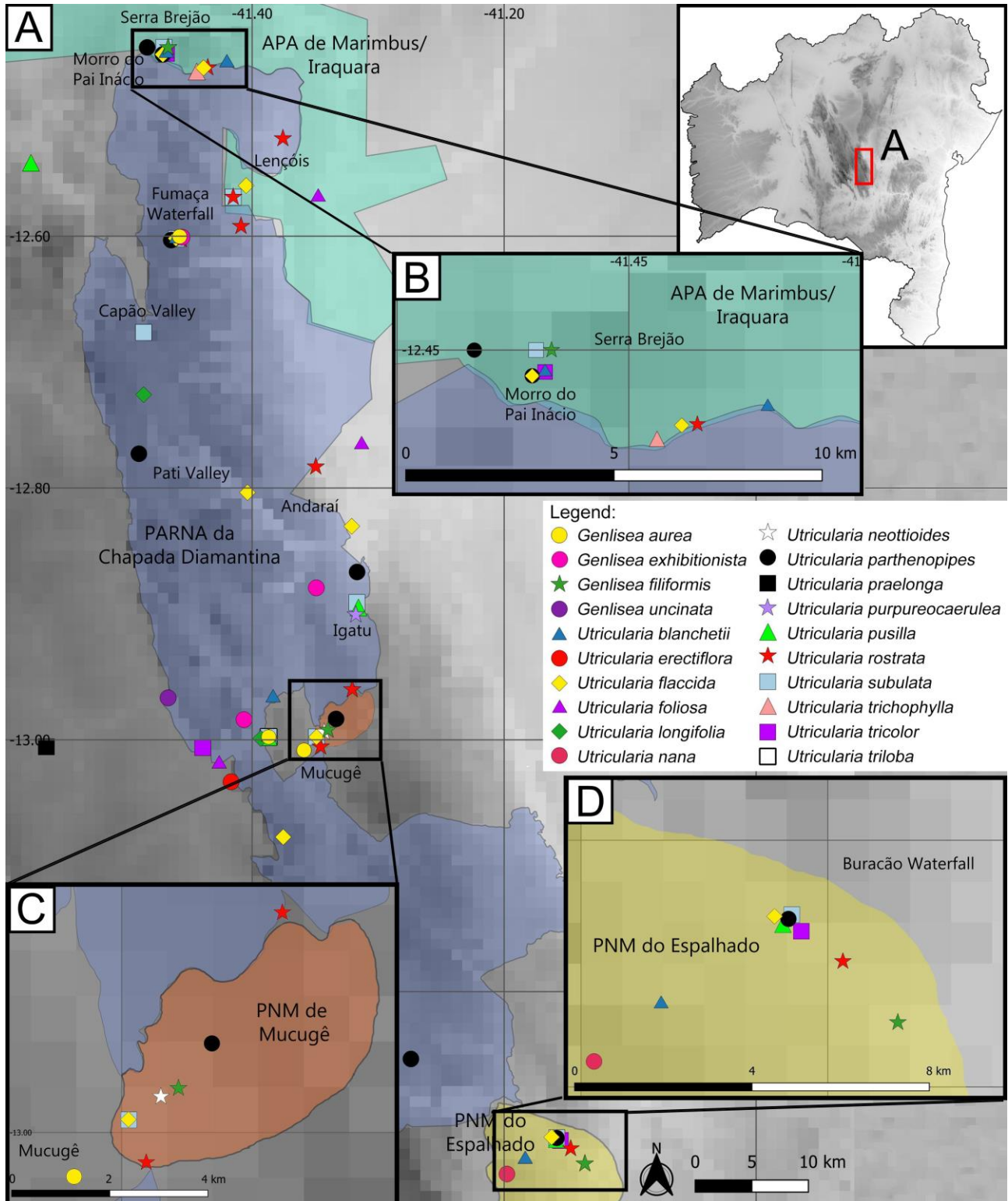


FIGURE 3. Distribution of Lentibulariaceae species in Protected Areas of Chapada Diamantina. APA = Environmental Protection Area, PARNA = National Park, PNM = Municipal Natural Park.

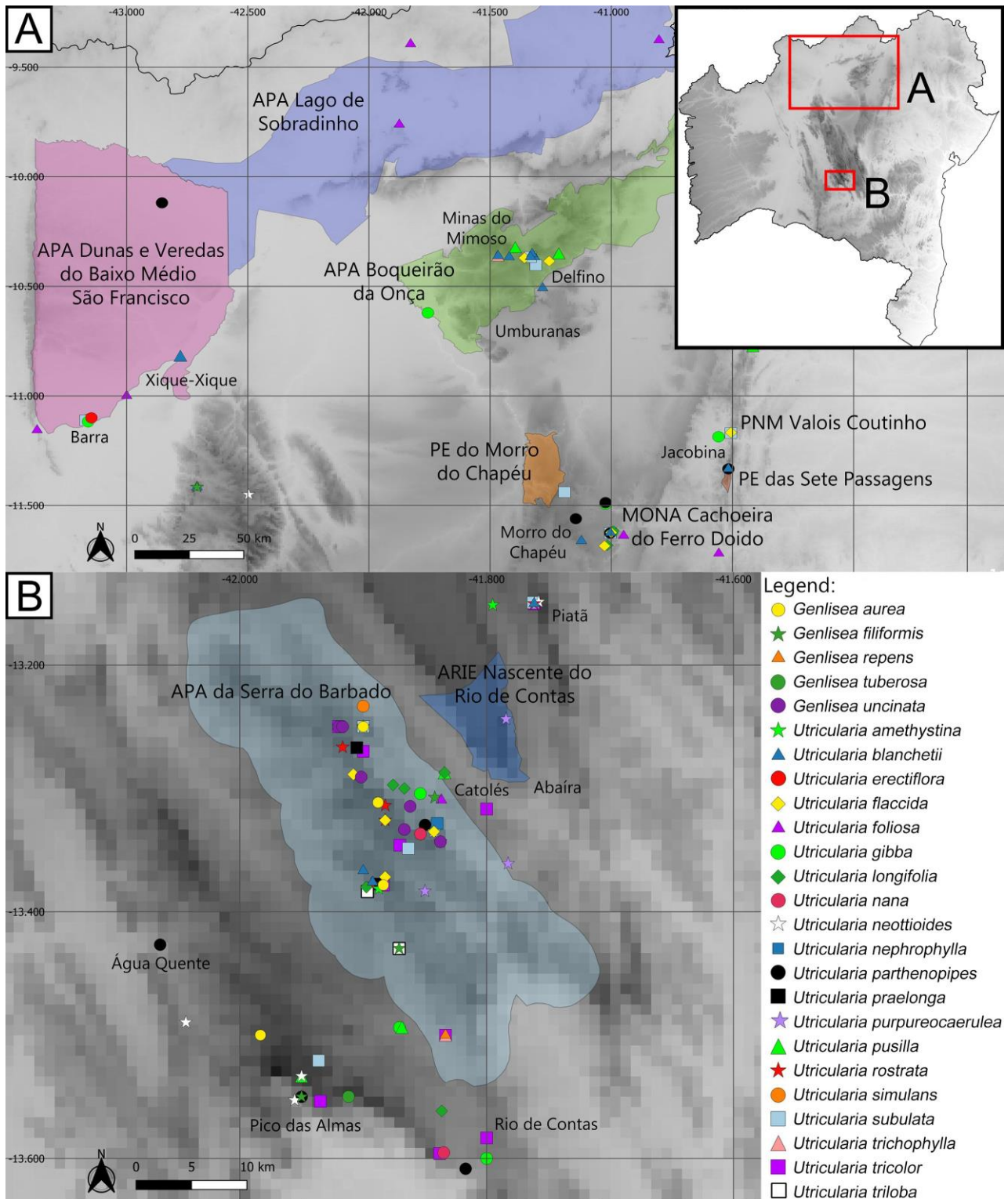


FIGURE 4. Distribution of Lentibulariaceae species in Protected Areas north (above) and southwest (below) of Chapada Diamantina. APA = Environmental Protection Area, ARIE = Area of Relevant Ecological Interest, MONA = Natural Monument, PE = State Park, PNM = Municipal Natural Park.

We also report here the first record of *G. repens* in an area of restinga. According to Fleischmann (2012), this species occurs in Paraíba state in a similar area, but those specimens actually correspond to *G. oxycetron* Taylor (1954: 288) (Guedes & Alves 2020). Furthermore, we indicate one equivocal citation, *G. pygmaea* Saint-Hilaire (1833: 431) (Gonella *et al.* 2020), and two new records, *U. laxa* and *U. nelumbifolia*, for Bahia state (Guedes *et al.* 2020). No voucher of *G. pygmaea* from Bahia was located. The first and only record of *U. laxa* in Bahia is from an area of vereda at the western portion of the state, in the municipality of São Desidério (Figs. 1 and 2). It is endemic to the southern

South America (Argentina, Brazil, Paraguay and Uruguay), where it occurs in lowland wet grasslands and savannas, campos limpos, veredas and lowland Open Ombrophilous Forests (Taylor 1989, Guedes *et al.* 2020). Whilst the first and only record of *U. nelumbifolia* in the state is from an inselberg at 605 m a.s.l., the northernmost known population of the species (Figs. 1, 2 and 5). It is endemic to Brazil and thus far has only been recorded in the Southeast region, in Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo states, in areas of montane Dense Ombrophilous Forests, inselbergs and campos de altitude vegetation, above 1000 m a.s.l. (Guedes *et al.* 2020, 2022).

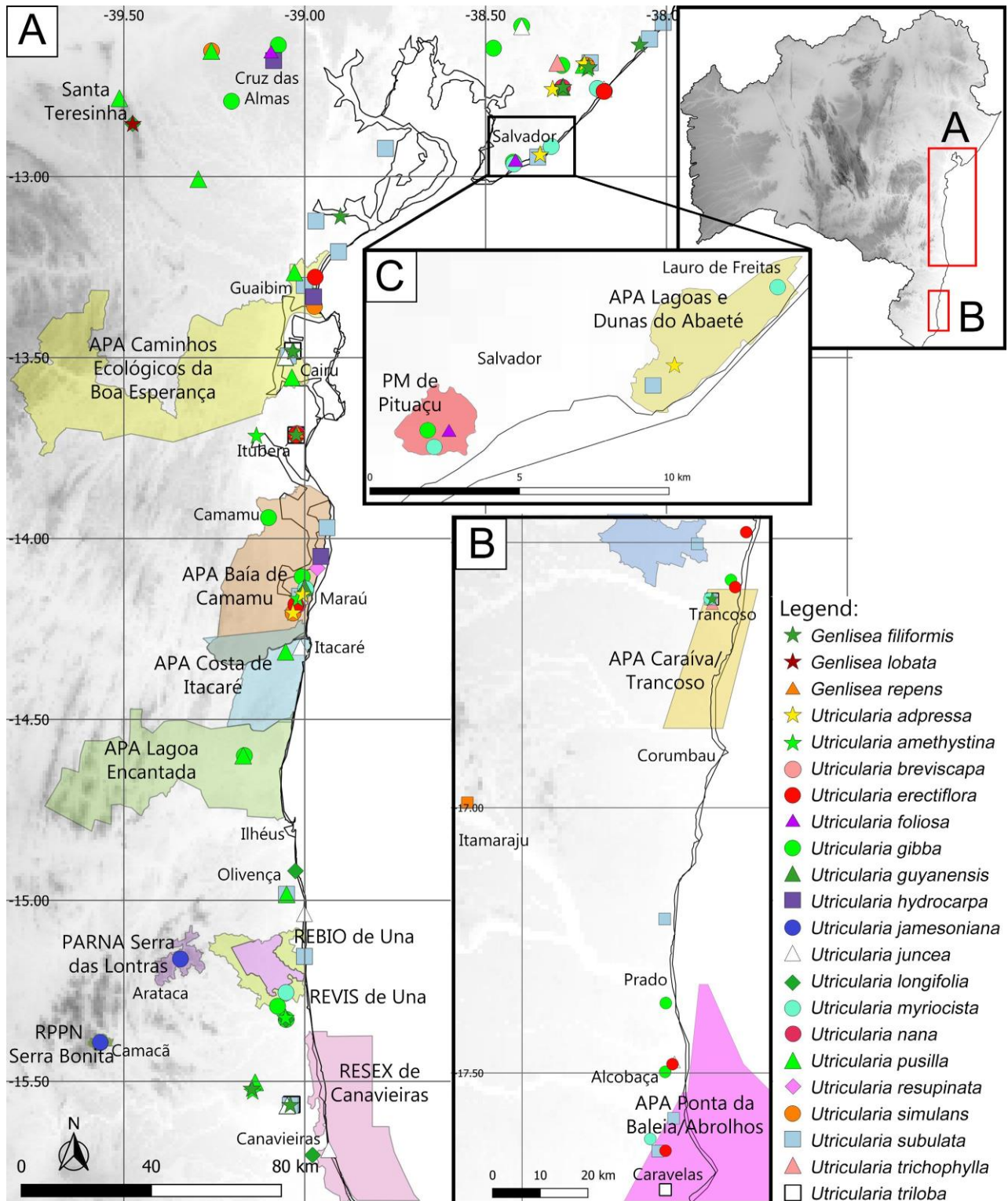


FIGURE 5. Distribution of Lentibulariaceae species in Protected Areas at northern and southern coast of Bahia. APA = Environmental Protection Area, ARIE = Area of Relevant Ecological Interest, MONA = Natural Monument, PARNA = National Park, PE = State Park, PM = City Park, PNM = Municipal Natural Park, REBIO = Biological Reserve, RESEX = Extractive Reserve, REVIS = Wildlife Refuge, RPPN = Private Reserve of Natural Heritage.

The areas that concentrate the greatest richness of Lentibulariaceae in the state are the Chapada Diamantina highlands (25 species), especially the southern portion, composed by the municipalities of Abaíra, Água Quente, Catolés, Piatã, Rio de Contas and their surroundings, which includes the Pico das Almas, Area of Relevant Ecological Interest of Nascente do Rio de Contas and Environmental Protection Area of Serra do Barbado, where 24 species occur (Figs. 1, 2 and 4), and the northern portion, composed by the municipalities of Andaraí, Igatu, Lençóis, Mucugê, Palmeiras and their surroundings, which includes the Chapada Diamantina National Park, Environmental Protection Area of Marimbus/Iraquara, and the Municipal Natural Parks of Mucugê and Espalhado, where 20 species can be found (Figs. 1 and 2). After these areas of campos rupestres, the entire coastline (restingas) is home to 20 species (Figs. 1, 2 and 5), of which 13 are shared with the campos rupestres (Table 1). Another area that is rich in Lentibulariaceae species is western Bahia, where the veredas predominate, hosting 14 species (Figs. 1 and 2), of which 9 are shared with the campos rupestres and 7 are shared with the restingas (Table 1).

TABLE 1. Lentibulariaceae species found in Conservation Units in Bahia state, with conservation status and phytophysiognomies where they occur. APA = Environmental Protection Area, ARIE = Area of Relevant Ecological Interest, MONA = Natural Monument, PARNA = National Park, PE = State Park, PM = City Park, PNM = Municipal Natural Park, REBIO = Biological Reserve, RESEX = Extractive Reserve, REVIS = Wildlife Refuge, RPPN = Private Reserve of Natural Heritage. EN = Endangered, DD = Data Deficient, LC = Least Concern, NT = Near Threatened, VU = Vulnerable.

Species (Conservation Status)	Source of Conservation Status Assessment	Conservation Unit of Full Protection	Conservation Unit of Sustainable Use	Phytogeographic domain	Phytophysiognomy
<i>Genlisea aurea</i> (LC)	Cross <i>et al.</i> (2020)	PARNA da Chapada Diamantina	APA Serra do Barbado	Cerrado	Campos rupestres
<i>Genlisea exhibitionista</i> (VU)	Fleischmann <i>et al.</i> (2011)	PARNA da Chapada Diamantina		Cerrado	Campos rupestres
<i>Genlisea filiformis</i> (LC)	Cross <i>et al.</i> (2020) Guedes <i>et al.</i> (2020)	PNM de Mucugê PNM do Espalhado	APA Caraíva/Trancoso APA do Rio Preto APA Marimbus/Iraquara APA Serra do Barbado	Atlantic Forest Cerrado	Lowland Open Ombrophilous Forests Restingas Campos rupestres Veredas
<i>Genlisea guianensis</i> (LC)	Cross <i>et al.</i> (2020)		APA do Rio Preto	Cerrado	Veredas
<i>Genlisea lobata</i> (EN)	Livro Vermelho Flora do Brasil (2013) Guedes <i>et al.</i> (2018, 2020)			Atlantic Forest	Inselbergs
<i>Genlisea repens</i> (LC)	Cross <i>et al.</i> (2020)		APA Serra do Barbado	Atlantic Forest Cerrado	Restingas Campos rupestres Veredas
<i>Genlisea tuberosa</i> (LC)	Rivadavia <i>et al.</i> (2013)			Cerrado	Campos rupestres
<i>Genlisea uncinata</i> (NT)	Fleischmann <i>et al.</i> (2011)		APA Serra do Barbado	Cerrado	Campos rupestres
<i>Utricularia adpressa</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu APA Lagoas e Dunas do Abaeté	Atlantic Forest	Restingas
<i>Utricularia amethystina</i> (DD)	Guedes <i>et al.</i> (2020)		APA Baía de Camamu APA Serra do Barbado	Atlantic Forest Cerrado	Restingas Lowland Open Ombrophilous Forests Campos rupestres
<i>Utricularia blanchetii</i> (LC)	IUCN (2021)	MONA Cachoeira do Ferro Doido PARNA da Chapada Diamantina PE das Sete Passagens PNM do Espalhado	APA do Boqueirão da Onça APA Marimbus/Iraquara APA Serra do Barbado	Cerrado	Campos rupestres

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TABLE 1. (Continued)

Species (Conservation Status)	Source of Conservation Status Assessment	Conservation Unit of Full Protection	Conservation Unit of Sustainable Use	Phytogeographic domain	Phytophysiognomy
<i>Utricularia breviscapa</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)			Atlantic Forest	Restingas
<i>Utricularia costata</i> (VU)	Guedes <i>et al.</i> (2020)			Atlantic Forest	Submontane Seasonal Semideciduous Forests
<i>Utricularia cucullata</i> (LC)	IUCN (2021)			Cerrado	Veredas
<i>Utricularia erectiflora</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu APA Caminhos Ecológicos da Boa Esperança APA Dunas e Veredas do Baixo Médio São Francisco APA Ponta da Baleia/Abrolhos	Atlantic Forest Caatinga Cerrado	Lowland Open Ombrophilous Forests Restingas Paleodune fields Campos rupestres
<i>Utricularia flaccida</i> (NT)	Guedes <i>et al.</i> (2020)	MONA Cachoeira do Ferro Doido PARNA da Chapada Diamantina PNM do Espalhado	APA do Boqueirão da Onça APA Marimbus/Iraquara APA Serra do Barbado	Cerrado	Campos rupestres
<i>Utricularia foliosa</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)	PARNA da Chapada Diamantina PM de Pituçu	APA Lago de Sobradinho APA Marimbus/Iraquara APA Serra do Barbado	Atlantic Forest Caatinga Cerrado	Lowland Open/Dense Ombrophilous Forests Lowland Seasonal Semideciduous Forests Restingas Park Steppe Savanna Paleodune fields Campos rupestres Veredas
<i>Utricularia gibba</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)	MONA Cachoeira do Ferro Doido PM de Pituçu REVIS de Boa Nova	APA Baía de Camamu APA Caminhos Ecológicos da Boa Esperança APA do Boqueirão da Onça APA Dunas e Veredas do Baixo Médio São Francisco APA Lagoa Encantada APA Serra do Barbado	Atlantic Forest Caatinga Cerrado	Lowland Open/Dense Ombrophilous Forests Lowland Seasonal Semideciduous Forests Restingas Park Steppe Savanna Paleodune fields Campos rupestres Veredas
<i>Utricularia guyanensis</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu	Atlantic Forest	Restingas
<i>Utricularia hydrocarpa</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu	Atlantic Forest	Lowland Open Ombrophilous Forests Restingas
<i>Utricularia jamesoniana</i> (NT)	Guedes <i>et al.</i> (2020)	PARNA da Serra das Lontras	RPPN Serra Bonita	Atlantic Forest	Montane Dense Ombrophilous Forests

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TABLE 1. (Continued)

Species (Conservation Status)	Source of Conservation Status Assessment	Conservation Unit of Full Protection	Conservation Unit of Sustainable Use	Phytogeographic domain	Phytophysionomy
<i>Utricularia juncea</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu APA Caminhos Ecológicos da Boa Esperança APA Costa de Itacaré/ Serra Grande RESEX de Canavieiras	Atlantic Forest	Lowland Open Ombrophilous Forests Restingas
<i>Utricularia laxa</i> (LC)	Cross <i>et al.</i> (2020)			Cerrado	Veredas
<i>Utricularia lloydii</i> (DD)	Cross <i>et al.</i> (2020)		APA Baía de Camamu	Atlantic Forest	Restingas
<i>Utricularia longifolia</i> (NT)	Guedes <i>et al.</i> (2020)	MONA Cachoeira do Ferro Doido PARNA da Chapada Diamantina	APA Serra do Barbado	Atlantic Forest Cerrado	Inselbergs Lowland Open Ombrophilous Forests Restingas Campos rupestres
<i>Utricularia myriocista</i> (LC)	Guedes <i>et al.</i> (2020)	PM de Pituaçu REBIO de Una	APA Baía de Camamu APA Caraíva/Trancoso APA Lagoas e Dunas do Abaeté	Atlantic Forest	Restingas
<i>Utricularia nana</i> (LC)	Guedes <i>et al.</i> (2020)	PNM do Espalhado	APA Baía de Camamu APA Serra do Barbado	Atlantic Forest Cerrado	Restingas Campos rupestres
<i>Utricularia nelumbifolia</i> (LC)	IUCN (2021)			Atlantic Forest	Inselbergs
<i>Utricularia neottioides</i> (LC)	IUCN (2021)	PNM de Mucugê	APA Serra do Barbado	Cerrado	Campos rupestres Veredas
<i>Utricularia nephrophylla</i> (LC)	Cross <i>et al.</i> (2020)		APA Serra do Barbado	Cerrado	Campos rupestres
<i>Utricularia nervosa</i> (LC)	IUCN (2021)			Cerrado	Veredas
<i>Utricularia parthenopipes</i> (LC)	IUCN (2021)	MONA Cachoeira do Ferro Doido PARNA da Chapada Diamantina PE das Sete Passagens PNM de Mucugê PNM do Espalhado	APA Dunas e Veredas do Baixo Médio São Francisco APA Marimbus/Iraquara APA Serra do Barbado	Caatinga Cerrado	Paleodune fields Campos rupestres
<i>Utricularia poconensis</i> (LC)	IUCN (2021)	-	-	Caatinga	-
<i>Utricularia praelonga</i> (LC)	IUCN (2021)		APA Serra do Barbado	Cerrado	Campos rupestres
<i>Utricularia purpureocaerulea</i> (LC)	Cross <i>et al.</i> (2020)	PARNA da Chapada Diamantina	APA Serra do Barbado ARIE Nascente do Rio de Contas	Cerrado	Campos rupestres

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TABLE 1. (Continued)

Species (Conservation Status)	Source of Conservation Status Assessment	Conservation Unit of Full Protection	Conservation Unit of Sustainable Use	Phytogeographic domain	Phytophysiognomy
<i>Utricularia pusilla</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)	PARNA da Chapada Diamantina PNM do Espalhado	APA Caminhos Ecológicos da Boa Esperança APA Costa de Itacaré/ Serra Grande APA do Boqueirão da Onça APA Lagoa Encantada RPPN Veracel/Estação Veracruz	Atlantic Forest Cerrado	Inselbergs Submontane Seasonal Semideciduous Forests Lowland/Submontane Open/Dense Ombrophilous Forests Restingas Campos rupestres Veredas
<i>Utricularia resupinata</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu	Atlantic Forest	Restingas
<i>Utricularia rostrata</i> (VU)	Cross <i>et al.</i> (2020)	PARNA da Chapada Diamantina PNM de Mucugê PNM do Espalhado	APA Marimbus/Iraquara APA Serra do Barbado ARIE Serra do Orobó	Cerrado	Campos rupestres
<i>Utricularia simulans</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)	PNM da Vida	APA Bacia do Rio de Janeiro APA Baía de Camamu APA Caminhos Ecológicos da Boa Esperança APA do Rio Preto APA Serra do Barbado	Atlantic Forest Cerrado	Restingas Campos rupestres Veredas
<i>Utricularia subulata</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)	MONA Cachoeira do Ferro Doido PARNA da Chapada Diamantina PARNA Pau Brasil PNM de Mucugê PNM do Espalhado PNM Valois Coutinho REVIS de Una	APA Baía de Camamu APA Caminhos Ecológicos da Boa Esperança APA Caraíva/Trancoso APA do Boqueirão da Onça APA Dunas e Veredas do Baixo Médio São Francisco APA Lagoas e Dunas do Abaeté APA Marimbus/Iraquara APA Ponta da Baleia/ Abrolhos APA Serra do Barbado RPPN Veracel/Estação Veracruz	Atlantic Forest Caatinga Cerrado	Lowland Open Ombrophilous Forests Restingas Paleodune Fields Campos rupestres Veredas
<i>Utricularia trichophylla</i> (LC)	Guedes <i>et al.</i> (2020) IUCN (2021)		APA Baía de Camamu APA do Boqueirão da Onça APA Marimbus/Iraquara	Atlantic Forest Cerrado	Restingas Campos rupestres Veredas
<i>Utricularia tricolor</i> (LC)	IUCN (2021)	PARNA da Chapada Diamantina PNM do Espalhado	APA Marimbus/Iraquara APA Serra do Barbado	Cerrado	Campos rupestres Veredas
<i>Utricularia triloba</i> (LC)	Cross <i>et al.</i> (2020) Guedes <i>et al.</i> (2020)		APA Caraíva/Trancoso APA Ponta da Baleia/ Abrolhos APA Serra do Barbado	Atlantic Forest Cerrado	Lowland Open Ombrophilous Forests Restingas Campos rupestres

In contrast, the areas with the lowest richness are the paleodune fields of the lower middle São Francisco River, where five species occur (*U. blanchetii*, *U. erectiflora*, *U. foliosa*, *U. gibba* and *U. parthenopipes*) (Figs. 1, 2 and 3), and the inselbergs where only one or two species can be found in Serra da Jiboia (municipality of Santa Teresinha) (*G. lobata* and *U. longifolia*) and Morro do Pescoço (municipality of Itamaraju) (*U. nelumbifolia*) (Figs. 1, 2 and 4), respectively. In addition, relief areas with submontane Semideciduous Seasonal Forest (municipality of Serrinha) and with montane Dense Ombrophilous Forest (municipalities of Arataca and Camacã) are home to *U. costata* and *U. jamesoniana*, respectively (Figs. 1, 2 and 4). The latter two are where the Serra das Lontras National Park and the Serra Bonita Private Reserve of Natural Heritage are located.

By using Rabinowitz's (1981) forms of rarity, the following species can be classified as rare: *G. exhibitionista*, *G. lobata*, *G. tuberosa*, *G. uncinata*, *U. blanchetii*, *U. flaccida*, *U. nelumbifolia*, *U. nephrophylla*, *U. parthenopipes*, *U. purpureocaerulea* and *U. rostrata* (sparse to locally abundant populations over a narrow geographic range in specific habitats); *G. guianensis* and *U. costata* (sparse populations over a large geographic range in several habitats).

Regarding the assessment of the conservation status according to the risk categories of the IUCN (2022) (Table 1), most species (32) are classified as at Least Concern, one (*G. lobata*) as Endangered, four (*G. uncinata*, *U. flaccida*, *U. jamesoniana* and *U. longifolia*) are considered Near Threatened, three (*G. exhibitionista*, *U. costata* and *U. rostrata*) are Vulnerable and one (*U. amethystina*) is assessed as Data Deficient (Fleischmann *et al.* 2011, Rivadavia *et al.* 2013, Guedes *et al.* 2018, Martinelli *et al.* 2018, Cross *et al.* 2020, Guedes & Alves 2020, IUCN 2022). On the other hand, the official regional assessment provided by the government of Bahia state (Salvador 2017) categorized five species as Endangered (*G. exhibitionista*, *G. uncinata*, *U. blanchetii*, *U. parthenopipes* and *U. rostrata*).

Moreover, 34 species occur in Protected Areas (Table 1), which means that 79% of the representatives of the family are under some level of protection effort in the state. There are 33 Protected Areas in the state that cover the natural distribution of Lentibulariaceae species (Supplementary Material: Fig. A1). Nonetheless, only 19 species are under major protection efforts, with intense inspection and maintenance of the habitat, controlling as much as possible human interference in areas categorized as Strictly Protected: National Parks (equivalent IUCN Category II), Municipal Natural Parks (II), State Parks (II), City Parks, Biological Reserves (Ia), Natural Monuments (III) and Wildlife Refuges (III) (Stolton *et al.* 2008, ICMBio 2022).

Unfortunately, the remaining 9 species are not found in any Protected Areas and have a unique record in the state (except *U. nervosa*), including three with a global restricted distribution. For instance, *G. lobata*, *G. tuberosa* and *U. nelumbifolia* are very narrowly distributed, found only on mountain-top sites in three (Bahia, Espírito Santo and Minas Gerais), four (Bahia, Distrito Federal, Goiás and Minas Gerais) and five states (Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo), respectively (Fleischmann 2012, Guedes *et al.* 2020). Overall, *G. lobata* has at least four populations in Protected Areas outside Bahia State, and *G. tuberosa* and *U. nelumbifolia* have both at least seven populations known so far (Fleischmann 2012, Guedes *et al.* in press).

Futhermore, *U. costata* occurs over a wider geographic range (Venezuela and Brazil), but less than 10 populations are known, and only three in Protected Areas (Guedes & Alves 2020). *Utricularia poconensis* also occurs in a wider range (Argentina, Bolivia and Brazil) with several populations known (Guedes *et al.* 2020), but only four of them in protected localities. On the other hand, *U. breviscapa*, *U. cucullata*, *U. laxa* and *U. nervosa* are fairly common and widely distributed species with several populations in protected localities (Guedes & Alves 2020, Guedes *et al.* 2020). Nonetheless, having a single record in the state, and on top of that not within a Protected Area, makes each of these species more susceptible to threats and local extinction processes.

Key to the Lentibulariaceae species in Bahia state

1. Calyx with 5 sepals *Genlisea* 2
- Calyx with 2 sepals *Utricularia* 9
2. Spur parallel to the pedicel 3
- Spur parallel to the lower corolla lip 5
3. Pedicels strongly circinate in fruits and spur uncinated *Genlisea uncinata*
- Pedicels ascending, recurved or abruptly recurved in fruits and spur straight 4
4. Corolla lips with lobe tips entire; palate non-gibbous *G. exhibitionista*
- Corolla lips with lobe tips divided; palate gibbous *G. lobata*
5. Corolla lilac *G. guianensis*
- Corolla yellow or pale yellow 6
6. Scape thick, succulent and slightly stiff *G. aurea*
- Scape slender and flexible 7
7. Stolons with tubers; bracts, bracteoles and sepals covered with eglandular and glandular trichomes *G. tuberosa*
- Stolons without tubers; bracts, bracteoles and sepals glabrous *G. repens*

9.	Hydrophytes.....	10
-	Terrestrial, helophytes, lithophytes, epiphytes or rheophytes	16
10.	Scape with a basal whorl of floats.....	<i>Utricularia breviscapa</i>
-	Scape without a basal whorl of floats.....	11
11.	Leaves verticillate; corolla magenta	12
-	Leaves dichotomous; corolla yellow, white or pink.....	13
12.	Traps with a ventral appendage recurved, ciliate	<i>U. cucullata</i>
-	Traps with a central fascicle of glandular-stipitate trichomes	<i>U. myriocista</i>
13.	Corolla yellow	14
-	Corolla white or pink	15
14.	Scape inflated and slightly stiff; corolla lower lip bilobed.....	<i>U. foliosa</i>
-	Scape slender and flexible; corolla lower lip orbicular to slightly 3-crenate.....	<i>U. gibba</i>
15.	Scape always bearing a basal cleistogamous flower; corolla pink.....	<i>U. hydrocarpa</i>
-	Cleistogamous flowers absent; corolla white.....	<i>U. poconensis</i>
16.	Bracts tubular; corolla lower lip reflexed (giving an aspect of resupinate flower).....	<i>U. resupinata</i>
-	Bracts non-tubular; corolla lower lip not reflexed	17
17.	Bracts peltate; bracteoles absent	18
-	Bracts basifixed; bracteoles present.....	24
18.	Rheophyte; corolla white	<i>U. neottioides</i>
-	Terrestrial, helophytes or lithophytes; corolla yellow	19
19.	Lithophyte; spur truncate, shorter than the lower lip.....	<i>U. flaccida</i>
-	Terrestrial or helophytes; spur subulate, bifid or quadrifid, as long as, longer or twice as long as the lower lip	20
20.	Presence of sterile bracts on the raceme axis; spur twice as long as the lower lip.....	<i>U. pusilla</i>
-	Absence of sterile bracts on the raceme axis; spur as long as or longer than the lower lip	21
21.	Sepals with nerves inconspicuous; leaves pinnatifid.....	<i>U. trichophylla</i>
-	Sepals with nerves conspicuous; leaves linear	22
22.	Scape with base pubescent.....	<i>U. nervosa</i>
-	Scape with base glabrous.....	23
23.	Sepals with nerves prominent, converging at the apices	<i>U. triloba</i>
-	Sepals with nerves non-prominent, not converging at the apices.....	<i>U. subulata</i>
24.	Bracts and bracteoles basally connate.....	25
-	Bracts and bracteoles free	28
25.	Epiphyte; stolons with tubers; spur curved upwards, 3-5 times longer than and perpendicular to the lower lip	<i>U. jamesoniana</i>
-	Terrestrial or helophytes; stolons without tubers; spur straight or curved, as long as or longer than and parallel to the lower lip	26
26.	Leaves linear; bracts with margins laciniate-denticulate; corolla yellow	<i>U. praelonga</i>
-	Leaves spatulate or orbicular; bracts with margins entire; corolla lilac, white or purple.....	27
27.	Corolla lilac or white, lower lip trilobed, spur straight and acute.....	<i>U. amethystina</i>
-	Corolla purple or lilac, lower lip entire to 3-crenate, spur curved and obtuse or emarginate	<i>U. tricolor</i>
28.	Spur obsolete	<i>U. guyanensis</i>
-	Spur non-obsolete	29
29.	Upper sepal with apex rostrate.....	<i>U. rostrata</i>
-	Upper sepal with apex non-rostrate.....	30
30.	Scales and bracts auriculate, with margins deeply fimbriate	<i>U. simulans</i>
-	Scales and bracts non-auriculate, with margins entire or denticulate	31
31.	Lower corolla lip galeate, spur perpendicular to the lower lip	32
-	Lower corolla lip plan, spur parallel to the lower lip	36
32.	Sepals with margins involute	<i>U. erectiflora</i>
-	Sepals with margins plan	33
33.	Sepals with nerves inconspicuous, non-prominent	34
-	Sepals with nerves conspicuous, prominent.....	35
34.	Upper corolla lip orbicular, spur longer than the lower lip	<i>U. adpressa</i>
-	Upper corolla lip oblong, spur as long as the lower lip	<i>U. laxa</i>
35.	Nerves prominent on both sepals, margins non-auriculate.....	<i>U. juncea</i>
-	Nerves prominent only on the upper sepal, margins auriculate.....	<i>U. nana</i>
36.	Sepals with margins denticulate or microscopically denticulate	37
-	Sepals with margins entire	39
37.	Leaves obovate to oblanceolate; sepals with margins microscopically denticulate; palate with a prominent crest.....	<i>U. longifolia</i>
-	Leaves linear; sepals with margins denticulate; palate with no crest	38
38.	Corolla purple to lilac, upper lip subreniform, spur slightly curved and subulate	<i>U. blanchetii</i>
-	Corolla white with purple streaks on the upper lip, upper lip cuneate and trilobed, spur straight to slightly curved and acute or bifid	<i>U. parthenopipes</i>
39.	Lower corolla lip entire to crenulate or shallowly trilobed, palate with no crest.....	40
-	Lower corolla lip trilobed, lateral lobes well-developed, middle one obsolete, palate with two prominent crests.....	41
40.	Lower lip shallowly trilobed; spur obtuse.....	<i>U. costata</i>
-	Lower lip entire to crenulate; spur subulate or bifid	<i>U. purpureocaerulea</i>
41.	Leaves circular, peltate; corolla purple to pale lilac.....	<i>U. nelumbifolia</i>
-	Leaves reniform; corolla white	<i>U. nephrophylla</i>

1. *Genlisea* A.St.-Hil., *Voyage dans le District des Diamans* 2: 429 (1833).

Terrestrial, lithophyte or helophyte herbs. Laminar leaves in a basal rosette, linear or obovate to spatulate. Subterranean tubular rhizophylls (traps), with two helically twisted arms. Basifixed and free scales, bracts and bracteoles. Glabrous scape, scales, bracts, bracteoles, pedicels, sepals and capsule or covered with eglandular and/or long-stalked glandular trichomes. Ascending, recurved, abruptly recurved or strongly circinate pedicels in fruits. Calyx with 5 homomorphic sepals. Corolla with gibbous or non-gibbous palate, spur parallel to the pedicel or to the lower corolla lip. Bivalvate or circumscissile capsule.

Comments:—The genus is divided into two clearly distinct subgenera, *G.* subgen. *Genlisea*, which is recognized by ascending pedicels in fruits, spur parallel to the lower corolla lip and circumscissile capsule, while *G.* subgen. *Tayloria* Fromm-Trinta (1977: 1) has recurved, abruptly recurved or strongly circinate pedicels in fruits, spur parallel to the pedicel and bivalvate capsules. Members of *G.* subgen. *Tayloria* are endemic to Brazil, and are purple/lilac flowered with the exception of *G. lobata* (white). *Genlisea* subgen. *Genlisea* is subdivided into three sections, of which two are African (*G.* sect. *Africanae* Fleischmann *et al.* (2010: 781) and *G.* sect. *Recurvatae* Fleischmann *et al.* (2010: 781) and one is Neotropical (*G.* sect. *Genlisea*). The Neotropical section is composed mainly by yellow flowered species with the exception of *G. guianensis*, *G. multiflora* Fleischmann & Costa (2017: 289) and *G. sanariapoana* Steyermark (1953: 534).

1.1. *Genlisea aurea* A.St.-Hil., *Voyage dans le District des Diamans* 2: 429 (1833). [Figs. 1 and 6A].

Terrestrial or helophyte. Scape, bracts, bracteoles, pedicels and sepals covered with long-stalked glandular trichomes. Thick, succulent and slightly stiff scape. Ascending pedicels in fruits. Yellow corolla, darker yellow and gibbous palate, glabrous lips, trilobed lower lip, glandular and acute spur, as long as or longer than and parallel to the lower lip. Circumscissile capsule, covered with long-stalked glandular trichomes.

Selected material:—Abaíra, Campo de Ouro Fino, 23 March 1992, fl. and fr., *T. Laessle* & *T. Silva* H 53311 (CEPEC, HUEFS, K, RB, SPF); Água Quente, Pico das Almas, 16 December 1988, fl., *R.M. Harley* 27267 (CEPEC, SPF); Mucugê, 20 July 1981, fl. and fr., *A.M. Giulietti* 1603 (SPF); Palmeiras, trilha p/ a cachoeira da Fumaça, 20 July 2005, fl., *F. Rivadavia* 2087 (SPF); Piatã, brejos ao redor do cruzeiro subindo a Serra do Santana, 27 July 1995, fl. and fr., *F. Rivadavia* 484 (SPF); Rio de Contas, Serra da Mesa, 18 July 2005, fl. and fr., *F. Rivadavia* 2076 (SPF).

Comments:—*Genlisea aurea* can be readily distinguished from the other yellow flowered congeners in Bahia by its thick and succulent scape, and scape, bracts, bracteoles, pedicels and sepals covered exclusively with long-stalked glandular trichomes. There are two recognized varieties, *G. aurea* var. *minor* Fleischmann (2012: 525) differs from *G. aurea* var. *aurea* by its longer pedicels (8–25 mm in anthesis and up to 30 mm in fruits), lax inflorescence and spur longer than the lower corolla lip (vs. shorter pedicels [5–8 mm in anthesis and up to 10 mm in fruits], congest inflorescence and spur as long as the lower corolla lip). Apparently, there is no clear boundaries between populations throughout the Chapada Diamantina highlands, *G. aurea* var. *aurea* is found in the municipalities of Abaíra, Catolés, Mucugê, Palmeiras (Fumaça Waterfall), Piatã and Rio de Contas, while *G. aurea* var. *minor* is found in Abaíra, Catolés, Água Quente (Pico das Almas) and Mucugê.

1.2. *Genlisea exhibitionista* Rivadavia & A.Fleischm., *Phytotaxa* 33: 19–21 (2011). [Figs. 1 and 6B].

Terrestrial or lithophyte. Scape, bracts, bracteoles, pedicels and sepals covered with eglandular and long-stalked glandular trichomes. Slender and flexible scape. Recurved pedicels in fruits. Pale lilac corolla, white and pale greenish-yellow, non-gibbous palate, sparsely glandular abaxial surface of the lips, bilobed upper lip, trilobed lower lip, glandular and obtuse spur, shorter than the lower lip and parallel to the pedicel. Bivalvate capsule, covered with eglandular and long-stalked glandular trichomes.

Selected material:—Andaraí, 15 km north of Mucugê on road to Andaraí, 18 February 1977, fl., *R.M. Harley* 18889 (RB); Palmeiras, Cachoeira da Fumaça, 20 June 2005, fl., *F. Rivadavia* 2086 (SPF); Mucugê, no alto da Serra ao norte da cidade, 24 July 1995, fl. and fr., *F. Rivadavia* 472 (SPF, holotype).

Comments:—*Genlisea exhibitionista* can be readily distinguished from the other congeners by its corolla with a non-gibbous palate, so that the stamens and pistil are exposed. This endemic species is so far known from only three locations, two in the Serra do Sincorá (municipalities of Andaraí and Mucugê) and one in the Fumaça Waterfall (municipality of Palmeiras).



FIGURE 6. **A.** *Genlisea aurea*; **B.** *G. exhibitionista*; **C.** *G. filiformis*; **D.** *G. guianensis*; **E.** *G. lobata*; **F.** *G. repens*; **G.** *G. tuberosa*; **H.** *G. uncinata*; **I.** *Utricularia adpressa*; **J–K.** *U. amethystina*; **L–M.** *U. blanchetii*; **N.** *U. breviscapa*; **O.** *U. costata*; **P.** *U. cucullata*; **Q.** *U. erectiflora*; **R.** *U. flaccida*; **S.** *U. foliosa*; **T.** *U. gibba*; **U.** *U. guyanensis*; **V.** *U. hydrocarpa*; **W.** *U. jamesoniana*; **X.** *U. juncea*; **Y.** *U. laxa*. (Photos A by J.C. Zamora; B by C. Rohrbacher; C by Z. Miranda; D, E, G, H by P.M. Gonella; F, Y by H. Dolsan; I–M, Q, R, U, X by F.M. Guedes; N, O by J. Fabricante; P by M. Hopkins; S. by Y. Canalli; T by A. Nepomuceno; V by G.S. Garcia; W by Y. Gouveia).

1.3. *Genlisea filiformis* A.St.-Hil., *Voyage dans le District des Diamans* 2: 430 (1833). [Figs. 2 and 6C].

Terrestrial or helophyte. Scape, bracts, bracteoles and sepals glabrous or with sparse eglandular and long-stalked glandular trichomes. Slender and flexible scape. Ascending pedicels in fruits, covered only with long-stalked glandular trichomes. Yellow corolla and pale-yellow spur, gibbous palate, glabrous lips, trilobed lower lip, glabrous or sparsely glandular and saccate spur, longer than and parallel to the lower lip. Circumscissile capsule, covered with eglandular trichomes.

Selected material:—Abaíra, Catolés, Campo do Bicota, 04 May 1999, fl. and fr., *G.L. Campos* 49 (HRB); Cairu, Garapuá, 12 August 2006, fr., *M.L. Guedes* 13595b (ALCB); Camaçari, Guarajuba, 06 September 1999, fl. and fr., *G.L. Campos* 106 (HRB); Canavieiras, km 11 da Rod. BA-270, 12 July 1978, fl., *T.S. dos Santos* 3272 (CEPEC); Formosa do Rio Preto, Fazenda Jhon Deere, 04 April 2018, fl. and fr., *E.O. Moura* 1949 (UB); Gentio do Ouro, Serra da Boa Vista, 27 May 2009, fl. and fr., *J.A. Siqueira Filho* 2092 (HVASF); Ibicoara, trilha para a cachoeira do Buracão, 12 July 2005, fl. and fr., *F. Rivadavia* 1991 (SPF); Ituberá, à direita do km15 da estrada p/a Praia de Pratigi, 08 October 2005, fl. and fr., *F. Rivadavia* 2113 (SPF); Jaguaripe, depois da estação da Petrobrás, 27 September 2014, fl. and fr., *G. Costa* 1031 (HURB); Livramento de Nossa Senhora, lower N.E. slopes of the Pico das Almas, 17 February 1977, fl. and fr., *R.M. Harley* 19565 (CEPEC, K, RB); Mucugê, PNM de Mucugê, 19 May 2004, fl. and fr., *J. Costa* 697 (HUEFS); Palmeiras, Serra dos Lençóis, lower slopes of Morro do Pai Inácio, 21 May 1980, fl. and fr., *R.M. Harley* 22264 (CEPEC, K, RB); Porto Seguro, Trancoso, 20 September 2013, fl. and fr., *P.C. Baleeiro* 360 (SPF); Rio de Contas, em capôs rupestres beirando a estrada para Caiambola, 18 July 2005, fl. and fr., *F. Rivadavia* 2060 (SPF); Santa Luzia, Estrada entre Una e Santa Luzia, 02 November 2017, fl. and fr., *F.M. Guedes* 86 (ALCB, UFP).

Comments:—*Genlisea filiformis* can be readily distinguished from the other yellow flowered congeners in Bahia by its saccate spur and capsule covered exclusively with eglandular trichomes. This species is found in a wide altitudinal range in the state, from campos rupestres to restingas and veredas.

1.4. *Genlisea guianensis* N.E.Br. in Hook., *Icones Plantarum* 27: t. 2629 (1900). [Figs. 1 and 6D].

Terrestrial or helophyte. Glabrous scape, sparsely eglandular bracts, bracteoles and sepals. Slightly thick and flexible scape. Ascending pedicels in fruits, covered with eglandular, rarely mixed with long-stalked glandular, trichomes. Lilac corolla, lilac or white and gibbous palate, glabrous lips, trilobed lower lip, glabrous or sparsely eglandular and obtuse spur, longer than and parallel to the lower lip. Circumscissile capsule, covered with eglandular trichomes.

Selected material:—Barreiras, Sumpf Rio das Femmeas, s.d., *P. von Luetzelburg* s.n. (M); Formosa do Rio Preto, VIII-1912, fr., *P. von Luetzelburg* 22 (M), *ibid.*, s.d., fl. and fr., *P. von Luetzelburg* 65 (M).

Comments:—*Genlisea guianensis* can be readily distinguished from the other lilac/purple flowered congeners in Bahia by its ascending pedicels in fruits, spur parallel to the lower corolla lip and capsule covered exclusively with eglandular trichomes. This is the only lilac flowered member of *G.* subgen. *Genlisea* in Brazil. *Genlisea guianensis* has records only from areas of veredas in the state.

1.5. *Genlisea lobata* Fromm, *Bradea* 5: 152 (1989). [Figs. 1 and 6E].

Terrestrial or lithophyte. Scape, bracts, bracteoles, pedicels and sepals covered with eglandular and long-stalked glandular trichomes. Slender and flexible scape. Abruptly recurved pedicels in fruits. White corolla with purple streaks on the upper lip, purple spur, yellow and gibbous palate, glabrous lips with divided lobe tips, bilobed upper lip, trilobed lower lip, sparsely eglandular and glandular and obtuse spur, longer than the lower lip and parallel to the pedicel. Bivalvate capsule, covered with eglandular and long-stalked glandular trichomes.

Selected material:—Santa Teresinha, Ápice da Serra, mata da antena de televisão, 09 October 2010, fl. and fr., *E. Melo* 8571 (HUEFS).

Comments:—*Genlisea lobata* can be readily distinguished from the other congeners by its white corolla with purple streaks on the upper lip, lips with divided lobe tips and abruptly recurved pedicels in fruits. This is the northernmost known record of the species, restricted to granite/gnaissic outcrops, and also the northernmost occurrence of any member of *G.* subgen. *Taylora*.

1.6. *Genlisea repens* Benj. in Mart., *Flora Brasiliensis* 10: 254 (1847). [Figs. 1 and 6F].

Terrestrial or helophyte. Glabrous scape, bracts, bracteoles, pedicels and sepals. Slender and flexible scape. Ascending pedicels in fruits. Yellow corolla, gibbous palate, glabrous lips, trilobed lower lip, glabrous and acute spur, longer than and parallel to the lower lip. Circumscissile and glabrous capsule.

Selected material:—Barreiras, Veredas do Rio Branco, 04 September 2005, fl., *E. Melo* 3994 (HUEFS); Ituberá, Jatimane, estrada para Pratigi, 05 May 2000, fl., *R.P. Oliveira* 554 (HUEFS); Rio de Contas, 9 km ao norte da cidade para o povoado de Mato Grosso, 26 October 1988, fl. and fr., *R.M. Harley* 25644 (CEPEC, K, SPF); São Desidério, 16 June 2006, fl., *F. Rivadavia* 2225 (SPF).

Comments:—*Genlisea repens* can be readily distinguished from the other yellow flowered congeners in Bahia by its glabrous scape, bracts, bracteoles, pedicels, sepals, corolla and capsule. This species was previously known to inhabit high altitude savannas in South America (Fleischmann 2012), and here we report the first record in an area of restinga (municipality of Ituberá). Fleischmann (2012) mentions a record from Paraíba state in a similar area; however, those specimens actually correspond to *G. oxycentron* Taylor (1954: 288) as reported by Guedes & Alves (2020). In Bahia, *G. repens* is also found in campos rupestres and veredas.

1.7. *Genlisea tuberosa* Rivadavia, Gonella & A.Fleischm., *Systematic Botany* 38: 464 (2013). [Figs. 1 and 6G].

Terrestrial or helophyte. Stolons with tubers. Scape, bracts, bracteoles and sepals covered with eglandular and long-stalked glandular trichomes. Slender and flexible scape. Ascending pedicels in fruits. Yellow corolla, gibbous palate, glabrous lips, shallowly trilobed lower lip, glandular and acute spur, longer than and parallel to the lower lip. Circumscissile capsule, covered with eglandular and glandular trichomes.

Selected material:—Rio de Contas, Lower NE slopes of the Pico das Almas, 17 February 1977, fl. and fr., *R.M. Harley* 19566 (K).

Comments:—*Genlisea tuberosa* can be readily distinguished from the other yellow flowered congeners in Bahia by its stolons with tubers, glandular and acute spur, and capsule covered with both eglandular and glandular trichomes. This species is endemic to Brazilian campos rupestres vegetation, and in Bahia is only found in Pico das Almas, municipality of Rio de Contas.

1.8. *Genlisea uncinata* P.Taylor & Fromm, *Bradea* 3(41): 365 (1983). [Figs. 2 and 6H].

Terrestrial or helophyte. Scape, bracts, bracteoles, pedicels and sepals densely covered with eglandular and long-stalked glandular trichomes. Thick and succulent scape. Strongly circinate pedicels in fruits. Purple corolla, yellow and gibbous palate, glandular lips, trilobed lower lip, glandular and uncinata spur, longer than the lower lip and parallel to the pedicel. Bivalvate capsule, covered with glandular trichomes.

Selected material:—Abaíra, Catolés, Serra dos Cristais, 20 May 1999, fl. and fr., *V.C. Souza* 22881 (ESA); Mucugê, Serra do Sincorá, 19 March 1988, fl. and fr., *R.M. Harley* 20980 (CEPEC holotype, K, NY, P, R, U isotypes); Piañã, trilha para o Campo da Mutuca, 16 July 2005, fl. and fr., *V.F.O. de Miranda* 1284 (JABU).

Comments:—*Genlisea uncinata* can be readily distinguished from the other purple/lilac flowered congeners in Bahia by its thick and succulent scape, strongly circinate pedicels in fruits and uncinata spur, parallel to the pedicel. Before the record of *G. lobata* reported for the state (Guedes *et al.* 2018), this species together with *G. exhibitionista* were considered the northernmost occurrence of any member of *G.* subgen. *Tayloria* (Fleischmann 2012). *Genlisea uncinata* is endemic to the highest summits of the Chapada Diamantina highlands.

2. *Utricularia* L., *Species Plantarum* 1: 18 (1753).

Terrestrial, helophyte, epiphyte, rheophyte, lithophyte or hydrophyte herbs. Aerial or submerged leaves, laminar, cylindrical or dichotomous and capillary. Utricles (traps) on stolons and leaves. Glabrous scape, few hydrophyte species bear a whorl of floats at the base of the scape. Basifixed or peltate scales, bracts and bracteoles (if present), free or basally connate. Ascending or deflexed pedicels in fruits. Calyx with 2 usually heteromorphic sepals, with entire, denticulate or deeply fimbriate margins, inconspicuous or conspicuous nerves, prominent or not. Corolla with gibbous or non-gibbous palate, spur parallel or perpendicular to the lower lip. Longitudinal, circumscissile, bivalvate or apparently indehiscent capsule.

2.1. *Utricularia adpressa* Salzm. ex A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 870 (1838). [Figs. 1 and 6I].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. Yellow corolla, non-gibbous palate, orbicular upper lip and longer than the upper sepal, galeate lower lip, straight and acute spur, longer than and perpendicular to the lower lip. Longitudinally dehiscing capsule.

Selected material:—s.l., s.d., fl. and fr., *P. Salzmann s.n.* (G, K, L, MO, R original material); Belmonte, 7 km SE de Belmonte, 05 January 1981, fl. and fr., *A.M. de Carvalho & J. Gatti 407* (CEPEC, K, R); Cairu, Baixo Sul, Garapua, 12 August 2006, fl. and fr., *M.L. Guedes 13593 and 13594* (ALCB); Camaçari, 30 November 2002, fl., *F. Rivadavia 1455* (SPF); Maraú, BR-030 entre Itacaré e Maraú, 05 November 2017, fl. and fr., *F.M. Guedes 94 and 97* (UFP); Salvador, Itapuã, 1951, fl. and fr., *A.L. Costa s.n.* (ALCB).

Comments:—*Utricularia adpressa* can be confused with *U. erectiflora*, *U. laxa* and *U. nana*, but it differs from *U. erectiflora* by its slender and flexible scape, sepals with plan margins and orbicular upper corolla lip (vs. thick and stiff scape, sepals with involute margins and oblong upper corolla lip); from *U. laxa* by its orbicular upper corolla lip and spur longer than the lower lip (vs. oblong upper corolla lip and spur as long as the lower lip); and from *U. nana* by its sepals with inconspicuous nerves, orbicular upper lip and longer than the upper sepal (vs. sepals with conspicuous nerves, oblong upper lip and shorter than the upper sepal). In the state, *Utricularia adpressa* has records only from areas of restinga.

2.2. *Utricularia amethystina* Salzm. ex A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 870 (1838). [Figs. 1 and 6J-K].

Terrestrial or helophyte. Aerial spatulate leaves. Slender and flexible scape. Basifixed and basally connate bracts and bracteoles, margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins, hyaline on the upper sepal. Lilac or white corolla, white and yellow gibbous palate, trilobed lower lip, straight and acute spur, constricted at the middle, twice as long as and parallel to the lower lip. Bivalvate capsule.

Selected material:—s.l., 1830, fl., *P. Salzmann s.n.* (P, K, R, original material); Abaíra, Catolés, Garimpo do Bicota, 02 March 1992, fl. and fr., *B. Stannard H51699* (CEPEC, HUEFS, K, NY, SPF); Barra da Estiva, 19 July 1981, fl. and fr., *A.M. Giulietti 1338* (SPF); Belmonte, Estrada Belmonte–Itapebi km 33, 13 August 1981, fl. and fr., *H.S. Brito & S.G. da Vinha 112* (CEPEC); Cairu, 14 September 1993, fl. and fr., *M.L. Guedes s.n.* (ALCB); Camaçari, estrada da CETREL, 06 September 1999, fl. and fr., *G.L. Campos & R.M.O. Alves 112* (HRB); Canavieiras, Estrada entre Santa Luzia e Canavieiras km 41, 18 July 2006, fl. and fr., *J. Paula-Souza 6161* (ESA, HPL); Ituberá, Mata de Burunganga, 15 September 2006, fl. and fr., *M.L. Guedes 12653* (ALCB); Maraú, Estrada sentido Itacaré/Maraú, 07 August 2005, fl. and fr., *J.L. Paixão 560* (CEPEC); Mata de São João, Km 94 da rodovia do Coco BA-099, próx. à praia de Massarandupió, 18 January 2003, fl. and fr., *F. Rivadavia 1523* (SPF); Piatã, Margem do Rio Veloso em direção ao Morro, 15 July 2005, fl. and fr., *V.F.O. de Miranda 1260* (JABU); Rio de Contas, PARNA da Chapada Diamantina, Serra das Almas, 06 July 2015, fl. and fr., *P.C. Baleeiro 378* (SPF); Santa Luzia, estrada entre Santa Luzia–Una, 02 September 2017, fl. and fr., *F.M. Guedes 85 and 87* (UFP).

Comments:—*Utricularia amethystina* can be confused with *U. tricolor*, but it differs by its trilobed lower corolla lip, straight and acute spur, constricted at the middle, twice as long as the lower lip, and hyaline margins only on the upper sepal (vs. entire to 3-crenate lower lip, curved and obtuse or emarginate spur, as long as or longer than the lower lip, and hyaline margins on both sepals). In Bahia state, this species is found in campos rupestres and restingas.

2.3. *Utricularia blanchetii* A.DC., *Prodromus Systematis Naturalis Regni Vegetabilis* 8: 13 (1844). [Figs. 1 and 6L-M].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, denticulate margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plant and denticulate margins. Purple to lilac corolla, yellow gibbous palate, subreniform upper lip, entire lower lip, slightly curved and subulate spur, longer than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, Campos da Mutuca, 23 March 1992, fl. and fr., *B. Stannard H52788* (HUEFS, NY, SPF); Andaraí, Cachoeira do Ramalho, 20 August 2002, fl., *E.C. Smidt 355* (HUEFS); Barra da Estiva, 10 July 2005, fl. and fr., *F. Rivadavia 1974* (SPF); Bonito, Estrada para Bonito, 10 October 2002, fl. and fr., *M.E.R. Junqueira 133*

(HUEFS); Campo Formoso, Água Preta, Estrada Alagoinhas–Minas do Mimoso km 15, 26 June 1983, fl. and fr., *L. Coradin* 6112 (CEN, CEPEC, NY, RB); Gentio do Ouro, Serra da Boa Vista, 27 May 2009, fl., *J.A. Siqueira Filho* 2091 (HVASF); Ibicoara, 12 July 2005, fl. and fr., *F. Rivadavia* 1992 (SPF); Iramaia, Estrada de terra sentido Raposa, 03 August 2017, fl., *M.M.T. Cota* 1065 (HUEFS); Lençóis, Chapadinha, próx. ao Rio Mucugezinho, 27 September 1994, fl. and fr., *G. Stam* 939 (CEPEC); Miguel Calmon, Piemonte da Diamantina, 04 March 1978, fl. and fr., *J.S. Santos* 139 (CEPEC); Morro do Chapéu, Fazenda Tocalha, BA-144, 31 August 2017, fl. and fr., *F.M. Guedes* 39 (UFP); Mucugê, 11 July 2005, fl. and fr., *F. Rivadavia* 1975 (SPF); Palmeiras, Morro do Pai Inácio, 26 September 1994, fl. and fr., *A.M. Giulietti* 784 (ALCB); Piatã, Serra do Santana, 13 July 2005, fl. and fr., *F. Rivadavia* 1995 (SPF); Rio de Contas, Serra da Mesa, 18 July 2005, fl. and fr., *F. Rivadavia* 2069 (SPF); s.l., Rio São Francisco, s.d., fl. and fr., *J.S. Blanchet* 2852 (G lectotype, BM, K, P, W isoelectotype); Sento Sé, APA Boqueirão da Onça, Cachoeira do Zé Leite, 16 April 2014, fl. and fr., *D.S. Fernandes* 190 (HVASF); Umburanas, Delfino, Serra do Curral Feio, 03 April 2002, fl., *A. Oliveira* 130 (HUEFS); Utinga, 4 km de Morro do Chapéu, 25 September 1985, fl. and fr., *M.G.L. Wanderley* s.n. (SP).

Comments:—*Utricularia blanchetii* can be confused with *U. parthenopipes* and *U. purpureocaerulea*, but it differs from *U. parthenopipes* by its purple to lilac corolla, subreniform upper lip, slightly curved and subulate spur, longer than and parallel to the lower lip (vs. white corolla with purple streaks on the upper lip, cuneate and trilobed upper lip, straight to slightly curved and acute/bifid spur, constricted above the middle, shorter than and perpendicular to the lower lip); and from *U. purpureocaerulea* by its sepals with conspicuous but non-prominent nerves and denticulate margins (vs. sepals with conspicuous and prominent nerves and entire margins). This species was previously considered endemic to the campos rupestres of the Chapada Diamantina highlands until it was also reported for Pernambuco state (Guedes *et al.* 2018).

2.4. *Utricularia breviscapa* C.Wright ex Griseb., *Catalogus Plantarum Cubensium* 161: 1-301 (1866). [Figs. 1 and 6N].

Hydrophyte. Submerged, dichotomous and capillary leaves. Inflated and flexible scape, with a basal whorl of floats. Basifixed bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. Yellow corolla, gibbous palate, deeply trilobed lower lip, straight and bifid spur, as long as and parallel to the lower lip. Circumscissile capsule.

Selected material:—Belmonte, Km 20 a 21 da Rodovia Belmonte/Itapebi, 26 July 1988, fl. and fr., *T.S. dos Santos* 4392 (CEPEC).

Comments:—*Utricularia breviscapa* can be confused with *U. foliosa*, but it differs by its whorl of floats at the base of the scape and trilobed lower corolla lip (vs. absence of floats and bilobed lower corolla lip). In Bahia state, this species is represented by only one record, in a flooded area of restinga alongside the road.

2.5. *Utricularia costata* P.Taylor, *Kew Bulletin* 41: 7 (1986). [Figs. 1 and 6O].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous and prominent nerves, entire margins, lower sepal becomes navicular in fruits. Lilac corolla, white and yellow gibbous palate, shallowly trilobed lower lip, straight and obtuse spur, longer than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Serrinha, Próximo à Torre da Embratel, Povoado Barra do Vento, 18 August 2006, fl. and fr., *L.P. de Queiroz* 12292 (HUEFS).

Comments:—*Utricularia costata* can be confused with *U. rostrata*, but it differs by its sepals with prominent nerves, upper sepal with non-rostrate apex, lower sepal becomes navicular in fruits, shallowly trilobed lower lip, straight spur, twice as long as the lower lip (vs. sepals with non-prominent nerves, upper sepal with rostrate apex, lower sepal does not become navicular in fruits, trapezoid and crenate lower lip, curved spur, shorter than or as long as the lower lip). In Bahia state, this species is represented by only one record, in an area of Submontane Seasonal Deciduous Forest.

2.6. *Utricularia cucullata* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7(21): 869 (1838). [Figs. 1 and 6P].

Hydrophyte. Submerged, verticillate capillary leaves. Traps with a ventral recurved and ciliate appendage. Slightly inflated and flexible scape. Basifixed bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with

inconspicuous nerves, plan and entire margins. Magenta corolla, white and yellow non-gibbous palate, trilobed lower lip with saccate lateral lobes, straight and obtuse/bifid spur, longer than and parallel to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Barreiras, s.d., fl., A. Cotrim 367 (HUEFS).

Additional material:—BRAZIL. **Tocantins:** Ponte Alta do Tocantins, 17 May 2006, fl. and fr., F. Rivadavia 2267 (SPF).

Comments:—*Utricularia cucullata* can be confused with *U. myriocista*, but it differs by its traps with a ventral recurved and ciliate appendage and smaller corolla, 1-1.5 cm long (vs. traps without appendages, with a central fascicle of glandular-stipitate trichomes instead, and larger corolla, 2-3 cm long). In Bahia state, this species is represented by only one record, in an area of vereda.

2.7. *Utricularia erectiflora* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 870 (1838). [Figs. 2 and 6Q].

Terrestrial or helophyte. Aerial linear leaves. Thick and stiff scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with inconspicuous nerves, involute and entire margins. Yellow corolla, non-gibbous palate, shallowly trilobed lower lip, straight and obtuse spur, longer than and parallel to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Alcobaça, between Alcobaça and Prado, 16 January 1977, fl. and fr., R.M. Harley 17992 (CEPEC); Barra, Vereda de Dois Riachos, XI-2009, fr., A.P. Prata 2167 (ASE); Camaçari, Aldeia Hippie de Arembepé, 20 September 2017, fl. and fr., G. Costa 2771 (HURB); Caravelas, 27 km SW de Alcobaça, 20 February 1986, fl. and fr., T.S. dos Santos 3366 (CEPEC); Entre Rios, Subauma, 20 April 2002, fl. and fr., M.L. Guedes 9552b (ALCB); Ituberá, 08 October 2005, fl. and fr., F. Rivadavia 2111 (SPF); Maraú, Estrada entre Itacaré e Maraú, 05 November 2017, fl. and fr., F.M. Guedes 96 (UFP); Mucugê, Serra do Sincorá, 07 February 1974, fl. and fr., R.M. Harley 16114 (CEPEC, NY, US); Porto Seguro, Arraial d'Ajuda, 15 January 2006, fl. and fr., C.P. Bove 1918 (R); Santa Cruz de Cabralia, Santo André, 02 November 2003, fl. and fr., M.L. Guedes 10637 (ALCB); Teixeira de Freitas, Sul da Bahia BR 101, 19 November 2013, fl. and fr., P.C. Baleeiro 356 (SPF); Valença, Guaibim, 17 August 1995, fl. and fr., G. Hatschbach 63350 (MBM).

Comments:—*Utricularia erectiflora* can be confused with *U. adpressa* (see comments section in that species), *U. juncea* and *U. laxa*, but it differs from *U. juncea* and *U. laxa* by its thick and stiff scape and sepals with involute margins. In the state, this species is found in campos rupestres and restingas.

2.8. *Utricularia flaccida* A.DC., *Prodromus Systematis Naturalis Regni Vegetabilis* 8: 17 (1844). [Figs. 2 and 6R].

Lithophyte. Aerial obovate leaves. Slender and flexible scape. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. Yellow corolla, gibbous palate, trilobed lower lip, straight and truncate spur, shorter than and parallel to the lower lip. Capsule dehiscent by a ventral pore.

Selected material:—Abaíra, Catolés, Serra da Mesa, 15 July 2005, fl., F. Rivadavia 2021 (SPF); Andaraí, estrada Andaraí-Mucugê, 21 July 1985, fl. and fr., M.G.L. Wanderley 958 (CEN); Bom Jesus da Lapa, 1913, fl., P. von Luetzelburg 470 (NY); Ibicoara, Chapada Diamantina, Caminho para a Cachoeira do Buracão, 13 October 2007, fl. and fr., M.L. Guedes 13814 (ALCB); Jacobina, “montibus Jacobinis”, 1830, fl. and fr., J.S. Blanchet 2541 (G-D, BM, FI, K, P, W original material); Lençóis, Serra da Chapadinha, 29 July 1994, fl. and fr., M.L. Guedes 288 (ALCB); Morro do Chapéu, Cachoeira do Ventura, 29 August 2017, fl. and fr., F.M. Guedes 36 (ALCB, UFP); Mucugê, Serra do Gobira, 10 June 2012, fl. and fr., L.P. Queiroz 15571 (HUEFS, SPF); Palmeiras, Morro do Pai Inácio, 26 October 1994, fl. and fr., A.M.V. Carvalho 1042 (SPF); Piatã, Cachoeira do Patrício, 17 November 2007, fl. and fr., J.L. Ferreira 208 (HUEFS); Pindobaçu, Cachoeira da Fumaça, 09 October 2011, fl. and fr., C.R.S. Oliveira 34 (HVASF, R); Rio de Contas, trilha para o Pico Itobira, 26 March 2000, fl. and fr., M.D. Moraes 517 (UEC); Sento Sé, 16 km NW of Lagoinha on side road to Minas do Mimoso, 04 March 1974, fl. and fr., R.M. Harley 16725 (CEPEC, K, MO, NY, P, US); Umburanas, Delfino, Cachoeirinha, 13 August 1999, fl. and fr., E. Melo 2796 (HUEFS); Utinga, 4 km de Morro do Chapéu, 25 September 1985, fl. and fr., M.G.L. Wanderley s.n. (SP).

Comments:—*Utricularia flaccida* can be confused with *U. nervosa*, but it differs by its lithophytic life form, sepals with non-prominent nerves and corolla with truncate spur, shorter than the lower lip (vs. terrestrial or helophytic life form, sepals with prominent nerves and corolla with subulate/bifid/quadrifid spur, longer than the lower lip). This

species is endemic to northeastern Brazil; besides the campos rupestres of Bahia, it is also found in Montane Dense Ombrophilous Forest in Ceará state and ecotones between Dense Ombrophilous Forest and Submontane Seasonal Deciduous Forest in Sergipe state (Guedes & Alves 2020).

2.9. *Utricularia foliosa* L., *Species Plantarum* 1: 18 (1753). [Figs. 1 and 6S].

Hydrophyte. Submerged, dichotomous and capillary leaves. Inflated and slightly stiff scape. Basifixed bracts, entire margins, absent bracteoles. Deflexed pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Yellow corolla, gibbous palate, bilobed lower lip, straight and obtuse or emarginate spur, shorter than and parallel to the lower lip. Apparently indehiscent capsule.

Selected material:—Abaré, Margem esquerda do Rio São Francisco, 04 July 2012, fl., V.M. Cotarelli 1902 (HVASF, R); Andaraí, Marimbus, 25 March 2005, fl. and fr., E. Melo 3765 (HUEFS); Barra, Estrada Barra-Ibotirama BA-161, 02 June 1999, fl. and fr., E. Melo 2714 (HUEFS); Belmonte, km 20 a 21 da Rod. Belmonte/Itapebi, 31 August 1985, fl. and fr., T.S. dos Santos 4391 (CEPEC); Bom Jesus da Lapa, 22 km S do entroncamento para Bom Jesus da Lapa na estrada para Malhada, 11 February 2000, fl. and fr., L.P. de Queiroz 5893 (HUEFS); Boninal, Rio Cochó, 30 June 2015, fl. and fr., N.X.M. Sousa 121 (HURB); Caetité, Lagoa da Barragem da Fazenda Porcos, 03 May 2002, fl. and fr., M.C. Ferreira 1248 (HUEFS); Casa Nova, BR 235, 15 July 2009, fl. and fr., J. Paula-Souza 10077 (SPF); Cascavel, entre Lagoa Encantada e Cascavel, 21 March 1999, fl. and fr., R.M. Harley 53576 (HUEFS, SPF, UB); Conde, Ilha das Ostras, 02 November 2001, fl. and fr., D.L. Santana 641 (ALCB, SPF); Cruz das Almas, Córrego Machado de Dentro, 29 September 2010, fl. and fr., L.Y.S. Aona 1358 (HUEFS, HURB, UEC); Feira de Santana, Campus da UEFS, 11 September 1985, fl. and fr., L.R. Noblick 4382 (HUEFS); Juazeiro, Maniçoba 1, 08 March 2014, fl. and fr., M.C. Tonizza s.n. (HTSA, HUEFS, PEUFR); Lençóis, Rio Santo Antônio, Povoado de Remanso, 19 February 1999, fl. and fr., M.P. Sena s.n. (HUEFS); Malhada, Rod. para o Distrito de Cana Brava, 02 May 1990, fl. and fr., J.G. Jardim 3392 (CEPEC); Maracás, 23 April 2002, fl. and fr., E.R. de Souza 212 (HUEFS); Morro do Chapéu, Lagoa do Angelim, 14 October 2017, fl. and fr., E. Melo 13631 (HUEFS); Mucugê, 02 November 2007, fl. and fr., E. Melo 5396 (HUEFS); Muquém de São Francisco, 19 July 2005, fl. and fr., F. Rivadavia 2078 (SPF); Piritiba, Fazenda Guanabara, 29 May 2011, fl. and fr., I.M. Souza 48 (HUEFS); Queimadas, local em beira do Rio São Francisco, quase em frente a Xique-Xique, 12 October 1990, fl. and fr., A.F. Fierro 1915 (CEN, HUEFS, RB, SPF); Salvador, Parque Metropolitano de Pituaçu, 28 March 1999, fl. and fr., G.L. Campos 29 (HUEFS); Sento Sé, APA Boqueirão da Onça, 11 August 2006, fl. and fr., J.A. Siqueira Filho 1656 (HVASF); Sobradinho, margens da barragem de Sobradinho, 12 July 2009, fl. and fr., J. Paula-Souza 10000 (HTSA, SPF).

Comments:—*Utricularia foliosa* can be confused with the other hydrophyte congeners, especially on herbarium material, but it differs as follows: from *U. breviscapa*, see comments section in this species; from *U. gibba* by its inflated and slightly stiff scape, deflexed pedicels in fruits and bilobed lower corolla lip (vs. slender and flexible scape, ascending pedicels in fruits and cucullate orbicular to slightly 3-crenate lower lip); from *U. hydrocarpa* by its yellow corolla and absence of cleistogamous flowers (vs. pink corolla with a yellow palate and presence of a cleistogamous flower at the base of the scape); from *U. poconensis* by its yellow corolla (vs. white to pale pink); and from *U. cucullata* and *U. myriocista* by its yellow corolla and deflexed pedicels in fruits (vs. magenta corolla and ascending pedicels in fruits). This species is widely distributed in the state, in a wide altitudinal range and diverse phytophysionomies.

2.10. *Utricularia gibba* L., *Species Plantarum* 1: 18 (1753). [Figs. 1 and 6T].

Hydrophyte. Submerged, dichotomous and capillary leaves. Slender and flexible scape. Basifixed bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Yellow corolla, gibbous palate, cucullate orbicular to slightly 3-crenate lips, slightly curved and obtuse or emarginate spur, longer than and parallel to the lower lip. Bivalvate capsule.

Selected material:—s.l., 1830, fl. and fr., P. Salzmänn 450 and 452 (G, original material); Abaíra, Catolés, 27 July 1995, fl. and fr., F. Rivadavia 481 (SPF); Alagoinhas, Fazenda Pimantel, 04 September 2007, fl. and fr., N.G. de Jesus 2287 (ALCB); Alcobaça, 23 km S de Prado, 8 December 1981, fl. and fr., G.P. Lewis 801 (CEPEC); Anguera, Lagoa 5, 06 April 1997, E. Melo 2334 (HUEFS); Barra, Vereda de Dois Riachos, XI-2009, fl. and fr., A.P. Prata 2164 (ASE); Boa Nova, Fazenda Cotermaia, 08 March 2003, fl. and fr., P. Fiaschi 1410 (CEPEC); Bom Jesus da Lapa, Basin of the Upper São Francisco River, Morrão, 20 November 1983, fl. and fr., R.M. Harley 21466 (CEPEC); Camaçari, 30 November 2002, fl. and fr., F. Rivadavia 1444 (SPF); Camamu, Enseada de Camamu, Ponta do Santo, 28 November 1992, fl. and fr., A.M. de Carvalho 763 (CEPEC); Candeias, Fazenda Lagoa Azul, 09 September 2004, fl. and fr., K.R.B. DIVERSITY AND DISTRIBUTION OF LENTIBULARIACEAE

Leite 436 (HUEFS); Conceição do Almeida, entre o trevo de C. Almeida e Dom Macedo Costa, 13 February 2011, fl. and fr., *L.Y.S. Aona* 1419 (HURB); Conceição do Coité, Salgadilha Serra do Mucambo, 28 September 2014, fl. and fr., *T. Vieira* 26 (HUEFS); Conde, Ilha das Ostras, Rio Crumai, 02 November 2017, fl. and fr., *D.L. Santana* 640 (ALCB); Entre Rios, Fazenda Rio do Negro, 21 January 2012, fl. and fr., *A.V. Popovkin* 1041 (HUEFS); Feira de Santana, Lagoa 1 km 3 BA 052, 08 December 1996, *F. França* 2041 (HUEFS); Ilhéus, Lagoa Encantada, Caldeiras, 17 January 1993, fl. and fr., *W.W. Thomas* 9529 (CEPEC, NY); Jacaraci, 16 July 1999, fl., *F. Rivadavia* 1146 (SPF); Jacobina, Lagoa Antônio Sobrinho, 12 October 2007, fl., *J.L. Ferreira* 113 (HUEFS); Juazeiro, 31 July 2013, fl., *M.J.A. Campelo* 219 (HVASF); Lamarão do Passé, Caraíba Metais, 18 December 2004, fl., *M.L. Guedes* 11396a (ALCB); Maraú, ca. 3km a E de Maraú, 02 February 2005, fl. and fr., *J.G. Jardim* 2663 (CEPEC); Mata de São João, próx. à praia de Massarandupió, 18 January 2003, fl. and fr., *F. Rivadavia* 1524 (SPF); Morro do Chapéu, Cachoeira do Agreste, 30 August 2017, fl. and fr., *F.M. Guedes* 38 (UFP); Muritiba, represa da Fazenda Capivari, 06 May 2010, fl. and fr., *L.Y.S. Aona* 1310 (HURB); Nova Viçosa, arredores, 20 October 1983, fl., *G. Hatschbach* 47082 (MBM); Porto Seguro, Trancoso, 20 November 2013, fl. and fr., *P.C. Baleeiro* 359 (SPF); Prado, Entroncamento da Rod. Prado/Alcobaça, 10 February 1972, fl. and fr., *T.S. dos Santos* 2232 (CEPEC); Rio de Contas, Ponte do Coronel, 27 September 2010, fl., *R.M. Harley* 56164 (HUEFS); Salvador, Parque Metropolitano de Pituaçu, 28 March 1999, fl. and fr., *G.L. Campos* 28 (HUEFS, HRB); Santa Cruz de Cabrália, PARNA Pau-Brasil, 09 October 1984, fl. and fr., *F.S. Santos* 433 (CEPEC, MBML, SPF); Santa Luzia, Estrada entre Una e Santa Luzia BA-270, 02 November 2017, fl. and fr., *F.M. Guedes* 92 (UFP); São Desidério, Povoado Ilhas do Vito, 22 December 2003, fl. and fr., *D.P. Saridakis s.n.* (FUEL); São Sebastião do Passé, 14 July 2015, fl. and fr., *G. Costa* 1435 (CESJ, HURB); Senhor do Bonfim, 25 December 1984, fl. and fr., *R. Mello-Silva* 36574 (HUEFS, SPF); Sento Sé, APA Boqueirão da Onça, Quixabá, 01 February 2010, fl. and fr., *A.P. Fontana* 6473 (HVASF); Umburanas, Serra do Curral Feio, 28 May 2010, fl. and fr., *L.P. de Queiroz* 14846 (HUEFS); Valença, 08 October 2005, fl. and fr., *F. Rivadavia* 2108 (SPF).

Comments:—*Utricularia gibba* can be confused with *U. foliosa* (see comments section in this species). This species, just as *U. foliosa*, is widely distributed in the state, in a wide altitudinal range and diverse phytophysiognomies.

2.11. *Utricularia guyanensis* A.DC., *Prodromus Systematis Naturalis Regni Vegetabilis* 8: 110 (1844). [Figs. 1 and 6U].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Yellow corolla, non-gibbous palate, galeate lower lip, obsolete spur, shorter than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Camaçari, 30 November 2002, fl. and fr., *F. Rivadavia* 1442 (SPF); Maraú, Estrada entre Itacaré e Maraú BR-030, 05 November 2017, fl. and fr., *F.M. Guedes* 100 (ALCB, UFP); Mata de São João, próx. à praia de Massarandupió, 18 January 2003, fl. and fr., *F. Rivadavia* 1525 (SPF).

Comments:—*Utricularia guyanensis* can be readily distinguished from all the other congeners in Bahia state by its yellow corolla with an obsolete spur. In the state, this species is found only in areas of restinga.

2.12. *Utricularia hydrocarpa* Vahl, *Enumeratio Plantarum* 1: 200 (1804). [Figs. 1 and 6V].

Hydrophyte. Submerged, dichotomous and capillary leaves. Slightly inflated and flexible scape, always bearing a basal cleistogamous flower. Basifixed bracts, entire margins, absent bracteoles. Deflexed pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Pink corolla, yellow gibbous palate, bilobed lower lip, straight and obtuse spur, shorter than and parallel to the lower lip. Circumscissile capsule.

Selected material:—s.l., 1830, fl. and fr., *P. Salzmann* 449 (G original material of *U. salzmanii*); Conde, Ilha das Ostras, 03 November 2001, fl. and fr., *D.L. Santana* 648 (ALCB); Cruz das Almas, Açude do Instituto Agrônomo do Leste, 20 February 1956, fl. and fr., *G. Pinto* 56-25 (ALCB); Maraú, Lago em propriedade particular, 12 January 2008, fl. and fr., *C.S.D. Souza* 230 (CEPEC); Valença, 08 October 2005, fl. and fr., *F. Rivadavia* 2107 (SPF).

Comments:—*Utricularia hydrocarpa* can be confused with *U. foliosa* (see comments section in this species) and *U. poconensis*, but it differs from *U. poconensis* by its pink corolla and presence of a cleistogamous flower at the base of the scape (vs. white to pale pink corolla and absence of cleistogamous flowers). In the state, this species is found only in areas of restinga.

2.13. *Utricularia jamesoniana* Oliv., *Journal of the Proceedings of the Linnean Society, Botany* 4: 169 (1860). [Figs. 1 and 6W].

Epiphyte. Stolons with tubers. Aerial obovate leaves. Slender and flexible scape. Basifixed and basally connate bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. White corolla, sometimes with lips and spur apex tinged in lilac, yellow non-gibbous palate, deeply trilobed lower lip, curved upwards and subulate spur, 3-5 times longer than and perpendicular to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Arataca, PARNA Serra das Lontras, Serra do Peito de Moça, 17 December 2005, fl. and fr., J.G. Jardim 4908 (CEPEC); Camacã, RPPN Serra Bonita, 26 July 2007, fl. and fr., A.M. Amorim 6980 (CEPEC).

Comments:—*Utricularia jamesoniana* can be readily distinguished from any congeners in Bahia state by its epiphytic life form, stolons with tubers and white corolla, sometimes with lips and spur apex tinged in lilac, and curved upwards spur, 3-5 times longer than the lower lip. This species is represented in the state by only two records in areas of Montane Dense Ombrophilous Forest.

2.14. *Utricularia juncea* Vahl, *Enumeratio Plantarum* 1: 202 (1804). [Figs. 1 and 6X].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous and prominent/ridged nerves, plan and entire margins. Yellow corolla, non-gibbous palate, galeate lower lip, straight to slightly curved and acute spur, shorter than and perpendicular to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Alcobaça, 12Km N on road between Alcobaça and Prado, 19 March 1984, fl. and fr., R.M. Harley 17975 (CEPEC); Belmonte, 26 km S da cidade, 07 January 1981, fl. and fr., A.M. de Carvalho 475 (CEPEC, R); Cairu, Beira da estrada BA 884, 24 November 2013, fl. and fr., P.C. Baleeiro 364 (SPF); Camaçari, Arembepe, 04 February 2006, fl. and fr., D. Cardoso 1127 (HUEFS); Canavieiras, 29 June 1996, fl. and fr., J.A. de Jesus 545 (CEPEC); Entre Rios, Subauma, 20 April 2002, fl., M.L. Guedes 9552a (ALCB); Ilhéus, 18 km S on road from Olivença to Una, 21 April 1981, fl. and fr., S.A. Mori 13698 (CEPEC, NY); Itacaré, Fazenda das Bromélias, 17 March 2006, fl. and fr., J.S. Santana 45 (ALCB); Lamarão do Passé, Caraíba Metais, 18 December 2004, fl. and fr., M.L. Guedes 11396b (ALCB); Maraú, Estrada entre Itacaré e Maraú BR 030, 05 November 2017, fl. and fr., F.M. Guedes 98 (UFP); Mata de São João, 18 January 2003, fl. and fr., F. Rivadavia 1522 (SPF); Santa Luzia, estrada entre Una e Santa Luzia BA 270, 02 November 2017, fl. and fr., F.M. Guedes 89 and 91 (UFP).

Comments:—*Utricularia juncea* can be confused with *U. erectiflora* (see comments section in this species), *U. laxa* and *U. nana*, but it differs from *U. laxa* by its sepals with conspicuous and prominent/ridged nerves (vs. sepals with inconspicuous nerves); and from *U. nana* by both of its sepals with prominent nerves and margins non-auriculate (vs. only the upper sepal with prominent nerves, margins auriculate). In Bahia state, this species is found only in areas of restinga.

2.15. *Utricularia laxa* A. St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7(21): 870 (1838). [Figs. 1 and 6Y].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Yellow corolla, non-gibbous palate, galeate lower lip, curved and acute spur, as long as and perpendicular to the lower lip. Longitudinally dehiscent capsule.

Selected material:—São Desidério, Manoel de Souza, Fazenda Palmeiral, 22 July 2007, fl., A. Cotrim 868 (HUEFS).

Additional material:—BRAZIL. **Tocantins:** Paranã, 30 March 2004, fl. and fr., A.C. Sevilha 4024 (CEN).

Comments:—*Utricularia laxa* can be confused with *U. adpressa*, *U. erectiflora* and *U. juncea* (see comments on each species). Here we report a new record for Bahia state, in an area of vereda.

2.16. *Utricularia longifolia* Gardner in Hook., *London Journal of Botany* 1: 545 (1842). [Figs. 2 and 7A-B].

Terrestrial or lithophyte. Aerial obovate to oblanceolate leaves. Slender and slightly stiff scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, DIVERSITY AND DISTRIBUTION OF LENTIBULARIACEAE *Phytotaxa* 556 (3) © 2022 Magnolia Press • 235

plan and microscopically denticulate margins. Purple corolla, gibbous palate with a yellow crest, entire lower lip, curved and acute spur, as long as or longer than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, Água Limpa, 21 December 1991, fl. and fr., *R.M. Harley* 50221 (CEN, HUEFS, MO, NY, SPF); Água Quente, Pico das Almas, 16 December 1988, fl. and fr., *R.M. Harley* 27261 (CEPEC, NY, SPF); Barra da Estiva, 22 November 1985, fl. and fr., *G. Hatschbach* 50085 (MBM); Belmonte, Barrolândia, Estação Experimental “Gregório Bondar” CEPLAC, 13 May 1993, fl. and fr., *W.W. Thomas* 9900 (CEPEC, SPF); Caetité, Serra Geral, 10 February 1997, fl. and fr., *L.A. Passos Júnior* 5389 (ALCB, HUEFS, SPF); Canavieiras, Região da Jararaca, 04 June 2011, fl. and fr., *E.N. de Matos* 107 (HUEFS); Feira de Santana, BR 324 estrada Feira/Salvador, 18 October 2001, fl. and fr., *E. Melo* 3479 (HUEFS); Ibicoara, Chapada Diamantina, Caminho para a Cachoeira do Buracão, 13 October 2007, fl. and fr., *M.L. Guedes* 13793 (ALCB); Ilhéus, Olivença, 25 January 2003, fl. and fr., *C. van den Berg* 937 (HUEFS); Morro do Chapéu, Rio Ventura, 29 August 2017, fl. and fr., *F.M. Guedes* 34 (ALCB, UFP); Mucugê, 26 October 2014, fl. and fr., *A.V. Scatigna* 549 (UEC); Palmeiras, Vale do Capão, 27 December 2016, fl. and fr., *J. Calvo* 7386 (ALCB, US); Piatã, Pai Inácio, Três Morros, 05 November 1996, fl. and fr., *D.J.N. Hind* 4108 (ALCB, HUEFS, SPF); Rio de Contas, Fazenda Brumadinho, 07 November 1988, fl. and fr., *R. Kral* 75548 (HUEFS); Santa Luzia, Estrada entre Una e Santa Luzia BR 270, 02 November 2017, fl. and fr., *F.M. Guedes* 93 (UFP); Santa Teresinha, Serra da Jiboia, Morro da Pioneira, 13 January 2015, fl. and fr., *D. Cardoso* 3549 (ALCB, HUEFS); Una, Rod. Una/Comandantuba, Fazenda Antonio Pimenta, 26 November 1971, fl. and fr., *R.S. Pinheiro* 1655 (CEPEC).

Comments:—*Utricularia longifolia* can be readily distinguished from all the other congeners in Bahia state by its long obovate to oblanceolate leaves, sepals with microscopically denticulate margins and purple corolla with a yellow crest on the palate, entire lower lip. This species is found in campos rupestres, restingas and Submontane Seasonal Deciduous Forest.

2.17. *Utricularia myriocista* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7(21): 869 (1838). [Figs. 2 and 7C].

Hydrophyte. Submerged, verticillate capillary leaves. Traps with a central fascicle of glandular-stipitate trichomes. Inflated and flexible scape. Basifixed bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Magenta corolla, white and yellow non-gibbous palate, trilobed lower lip with saccate lateral lobes, curved and acute spur, longer than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—s.l., s.d., fl. and fr., *J.S. Blanchet* 1519 (P original material); Alcobaça, 2 km após o trevo de Alcobaça, 25 December 1998, fl., *C.P. Bove* 378 (R); Belmonte, fazenda Belmonte, 04 August 2006, fl., *E.P. Queiroz* 1785 (HRB); Camaçari, Lagoa de Arembepé, 13 October 2000, fl. and fr., *D.L. Santana* 115 (ALCB); Caravelas, estrada para o Aeroporto de Caravelas após 3 km, 24 December 1998, fl., *C.P. Bove* 374 (R); Entre Rios, Subauma, 20 April 2002, fl. and fr., *M.L. Guedes* 9553 (ALCB); Maraú, Estrada de terra Itacaré-Barra Grande, 22 July 2015, fl., *P.C. Baleeiro* 381 (SPF); Mata de São João, Laguna Grande, Sauípe, 02 May 2004, fl. and fr., *E.P. Queiroz* 563 (HRB); Porto Seguro, Trancoso, 20 November 2013, fl., *P.C. Baleeiro* 358 (SPF); Salvador, Parque Metropolitano de Pituáçu, 12 July 2018, fl. and fr., *F.M. Guedes* 115 (UFP); Santa Cruz de Cabralia, Santo André, 02 November 2003, fl. and fr., *M.L. Guedes* 10665 (ALCB); Una, Estrada Una-Olivença, 30 December 1998, fl. and fr., *C.P. Bove* 385 (R).

Comments:—*Utricularia myriocista* can be confused with *U. cucullata* (see comments section in this species). In Bahia state, this species is found only in areas of restinga.

2.18. *Utricularia nana* A.St.-Hil. & Girard, *Compt. Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 869 (1838). [Figs. 1 and 7D].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous nerves, prominent/ridged only on the upper sepal, plan and entire margins, auriculate. Yellow corolla, non-gibbous palate, oblong upper lip and shorter than the upper sepal, galeate lower lip, straight and acute spur, longer than and perpendicular to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, Catolés, Campo do Bicota, 04 May 1999, fl. and fr., *G.L. Campos* 46 (HUEFS, HRB); Camaçari, km 15 da estrada Camaçari-Dias d'Ávila, 14 August 2003, fl., *F. Rivadavia* 1692 (SPF); Ibicoara, estrada para a cachoeira do Buracão, 12 July 2005, fl., *F. Rivadavia* 1994 (SPF); Ituberá, Jatimane, estrada para Pratigi, 05 May 2000, fl., *R.P. Oliveira* 553a (HUEFS); Maraú, estrada entre Itacaré-Maraú, 12 June 1979, fl., *S.A. Mori* 11928 (CEPEC); Rio de Contas, Serra do Marcelino, 02 February 1997, fl., *M.L. Guedes* 4860 (ALCB).



FIGURE 7. A–B. *U. longifolia*; C. *U. myriocista*; D. *U. nana*; E–F. *U. nelumbifolia*; G. *U. neottiioides*; H. *U. nephrophylla*; I. *U. nervosa*; J. *U. parthenopipes*; K. *U. poconensis*; L. *U. praelonga*; M–N. *U. purpureocaerulea*; O–P. *U. pusilla*; Q. *U. resupinata*; R. *U. rostrata*; S. *U. simulans*; T. *U. subulata*; U–V. *U. trichophylla*; W. *U. tricolor*; X–Y. *U. triloba*. (Photos A, B, D, G, I, J, L, N, O–Q, S, T, W–Y by F.M. Guedes; C, U, V by S. Guzmán; E, F by N.G. Silva; H by J. Allen; K by M.F. Cardoso; M by P.M. Gonella; R by N. Rebbert).

Comments:—*Utricularia nana* can be confused with *U. adpressa* and *U. juncea* (see comments section in these species). In Bahia state, this species is found in campos rupestres and restingas.

2.19. *Utricularia nelumbifolia* Gardner in Hook., *Icones Plantarum* 6: 504 (1843). [Figs. 1 and 7E–F].

Terrestrial, lithophyte or epiphyte. Aerial circular, peltate leaves. Slender and slightly stiff scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. Purple to pale lilac corolla, gibbous palate with two yellow crests, trilobed lower lip, circular well-developed lateral lobes and obsolete middle lobe, curved and acute spur, longer than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Itamaraju, Morro do Pescoço, 11 February 2007, bud., *A.M. Amorim* 6905 (CEPEC).

Additional material:—BRAZIL. **Espírito Santo:** Castelo, Parque Estadual do Forno Grande, 21 January 2009, fl. and fr., *C.N. Fraga* 2372 (CEPEC).

Comments:—*Utricularia nelumbifolia* can be confused with *U. nephrophylla*, but it differs from its circular and peltate leaves, and purple to pale lilac corolla (vs. reniform leaves, and white corolla). This species is endemic to Brazil and here we report a new record for Bahia state, located on an inselberg, and representing the northernmost known population of the species.

2.20. *Utricularia neottioides* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 869 (1838). [Figs. 1 and 7G].

Rheophyte. Submerged, verticillate and capillary leaves. Slender and slightly stiff scape. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. White corolla, non-gibbous palate, trilobed lower lip, obsolete spur, shorter than and parallel to the lower lip. Capsule dehiscing by a ventral pore.

Selected material:—s.l., “Habitat in udis ad R. Fermoze. Provinciae Pernambucanae” (currently Bahia territory), s.d., fl. and fr., *C.F.P. von Martius* s.n. (M); Abaíra, Serra da Mesa, 15 July 2005, fl. and fr., *F. Rivadavia* 2019 (SPF); Água Quente, Arredores do Pico das Almas, 30 October 1988, fl. and fr., *S.A. Mori* 13619 (CEPEC); Gentio do Ouro, Serra do Assuruá, 1839, fl. and fr., *J.S. Blanchet* 2864 (NY); Mucugê, PNM de Mucugê, rio Cumbuca, 25 September 2004, fl. and fr., *A. Rapini* 1151 (HUEFS); Piatã, Serra de Santana, 13 July 2005, fl. and fr., *F. Rivadavia* 2005 (SPF); Rio de Contas, Pico das Almas, 22 April 2004, fl. and fr., *A.M. Amorim* 4028 (HUEFS, SPF).

Comments:—*Utricularia neottioides* can be readily distinguished from all the other congeners in Bahia state by its rheophytic life form, white corolla with non-gibbous palate, trilobed lower lip and obsolete spur. In Bahia state, this species is found only in campos rupestres.

2.21. *Utricularia nephrophylla* Benj. in Mart., *Flora Brasiliensis* 10: 247 (1847). [Figs. 2 and 7H].

Terrestrial or lithophyte. Aerial reniform leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. White corolla, gibbous palate with two yellow crests, trilobed lower lip, obovate well-developed lateral lobes and obsolete middle lobe, curved and obtuse spur, shorter than and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, trilha para o Campo da Mutuca, 29 July 1995, fl. and fr., *F. Rivadavia* 496 (SPF).

Additional material:—BRAZIL. **Minas Gerais:** Alto Caparaó, Parque Nacional do Caparaó, 27 February 2005, fl. and fr., *F. Rivadavia* 1961 (SPF).

Comments:—*Utricularia nephrophylla* can be confused with *U. nelumbifolia* (see comments on that species). This species is endemic to Brazil and in Bahia state it is represented by only one record, in an area of campos rupestres, being the northernmost population known of the species.

2.22. *Utricularia nervosa* Weber ex Benj. in Mart., *Flora Brasiliensis* 10: 247 (1847). [Figs. 1 and 7I].

Terrestrial or helophyte. Aerial linear leaves. Slender and slightly stiff scape, pubescent base. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with conspicuous and prominent nerves, plan and entire margins. Yellow corolla, gibbous palate, trilobed lower lip, straight and subulate/bifid/quadrifid spur, longer than and parallel to the lower lip. Capsule dehiscing by a ventral pore.

Selected material:—Cocos, Fazendas Trijunção, estrada para a Sede do Guará, 11 December 2001, fl. and fr., B.M.T. Walter 4900 (CEN); Barreiras, s.d., fl., A. Cotrim 474 (HUEFS); São Desidério, 150 km SW of Barreiras, Rio Piau, 13 April 1966, fl., H.S. Irwin 14758 (US).

Comments:—*Utricularia nervosa* can be confused with *U. flaccida* (see comments section in this species) and *U. subulata*, but it differs from *U. subulata* by its scape with pubescent base and corolla larger (≥ 1.2 cm long) (vs. scape with glabrous base and corolla smaller [≤ 1 cm long]). In Bahia state, this species is found only in areas of veredas.

2.23. *Utricularia parthenopipes* P.Taylor, *Kew Bulletin* 41(1): 7 (1986). [Figs. 2 and 7J].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, denticulate margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and denticulate margins. White corolla with purple streaks on the upper lip, yellow gibbous palate, cuneate and trilobed upper lip, entire lower lip, straight to slightly curved and acute/bifid spur, constricted above the middle, shorter than and perpendicular to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Abaíra, Catolés, caminho Boa Vista para Bicota, 09 July 1995, fl. and fr., F. França 1318 (HUEFS); Água Quente, arredores do Pico das Almas, 26 March 1980, fl. and fr., S.A. Mori 13622 (CEPEC, NY); Andaraí, 10Km ao S de Andaraí, 19 April 1981, fl. and fr., R.M. Harley 18768 (CEPEC, K, MO); Brejinho das Ametistas, 10 January 2006, fl. and fr., A.K.A. Santos 577 (HUEFS); Ibicoara, Campo Redondo, 06 April 2005, fl. and fr., P.D. Carvalho 74 (HUEFS); Lençóis, Rio Mandassaia, Brarro Branco, PARNA da Chapada Diamantina, 09 March 2000, fl. and fr., A.A. Ribeiro-Filho 42 (HUEFS); Miguel Calmon, Piemonte da Chapada, Grota de Dona Antônia, 03 August 2006, fl. and fr., R.M. Valadão 91 (ALCB); Morro do Chapéu, Cachoeira do Ferro Doido, 01 September 2017, fl. and fr., F.M. Guedes 42 (UFP); Mucugê, PNM de Mucugê, 11 June 2004, fl. and fr., E.B. Souza 897 (HUEFS); Palmeiras, PARNA Chapada Diamantina, Vale do Capão, 03 July 2015, fl. and fr., P.C. Baleeiro 367 (SPF); Pilão Arcado, Barra do Iuiu, 07 September 2005, fl. and fr., L.P. de Queiroz 10914 (HUEFS); Pindobaçu, Cachoeira da Fumaça, 09 October 2011, fl. and fr., C.R.S. Oliveira 31 (HVASF, R); Rio de Contas, Lower N.E. slopes of the Pico das Almas, 17 February 1977, fl. and fr., R.M. Harley 19523 (CEPEC holotype, K, NY, P isotypes).

Comments:—*Utricularia parthenopipes* can be confused with *U. blanchetii* (see comments section in this species). This species is endemic to Bahia state, where was previously considered to be restricted to campos rupestres. However, here we report the first record outside the Espinhaço Range, in a paleodune field area of the lower middle São Francisco River.

2.24. *Utricularia poconensis* Fromm-Trinta, *Bradea* 4: 139 (1985). [Fig. 7K].

Hydrophyte. Submerged, dichotomous and capillary leaves. Slightly inflated and flexible scape. Basifixed bracts, entire margins, absent bracteoles. Deflexed pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. White to pale pink corolla, yellow gibbous palate, bilobed lower lip, straight and acute spur, as long as and parallel to the lower lip. Circumscissile capsule.

Selected material:—s.l., Lagoa Oiti, am Rio Palmyras, VIII-1914, fl., P. von Luetzelburg 12705 (M, NY, US).

Additional material:—BRAZIL. **Tocantins:** Paranã, Fazenda São João, 26 March 2004, fl. and fr., A.C. Sevilla 3828 (CEN).

Comments:—*Utricularia poconensis* can be confused with *U. hydrocarpa* (see comments section in this species). Despite an intense search in the available and accessible literature, we were not able to track the precise locality of occurrence of this species in the state; the only known datum comes from herbarium notes saying that it was collected in the Caatinga domain.

2.25. *Utricularia praelonga* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 870 (1838). [Figs. 2 and 7L].

Terrestrial or helophyte. Aerial linear leaves. Slender and slightly stiff scape. Basifixed and basally connate bracts and bracteoles, plan and lacinate-denticulate margins. Ascending pedicels in fruits. Glandular sepals with conspicuous and prominent nerves, erose-denticulate margins. Yellow corolla, gibbous palate, entire to shallowly trilobed lower lip, curved and acute spur, as long as or longer than and parallel to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Abaíra, Campo de Ouro Fino, 15 February 1992, fl. and fr., R.M. Harley 52064 (HUEFS, NY, R); Mucugê, Chapada Diamantina, Fazenda Pedra Grande estrada para Bonimal, 17 February 1997, fl. and fr., E. DIVERSITY AND DISTRIBUTION OF LENTIBULARIACEAE *Phytotaxa* 556 (3) © 2022 Magnolia Press • 239

Saar PCD5829 (ALCB); Rio de Contas, Pico do Itobira, 02 January 2003, fl., R.M. Harley 54539 (HUEFS).

Comments:—*Utricularia praelonga* can be readily distinguished from all the other congeners in Bahia state by its basifixed and basally connate bracts and bracteoles with lacinate-denticulate margins, and yellow corolla with entire to shallowly trilobed lower lip. In the state, this species is found only in campos rupestres.

2.26. *Utricularia purpureocaerulea* A.St.-Hil. & Girard, *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences* 7: 869 (1838). [Figs. 1 and 7M-N].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous and prominent nerves, plan and entire margins. Purple or lilac corolla, yellow gibbous palate, subreniform upper lip, entire to crenulate lower lip, straight and subulate/bifid spur, longer than and parallel to the lower lip. Longitudinally dehiscent capsule.

Selected material:—Abaíra, Caminho Boa Vista para Bicota, 09 July 1995, fl. and fr., F. França 1317 (CEPEC, HUEFS, NY); Andaraí, PARNA Chapada Diamantina, Córrego do distrito de Igatu, 04 July 2015, fl. and fr., P.C. Baleeiro 371 (SPF); Licínio de Almeida, 12 Km da cidade em direção a Brejinho das Ametistas, 12 March 1994, fl., N. Roque 15013 (CEPEC, HUEFS, RB, SPF); Piatã, Trilha para o Campo da Mutuca, 16 July 2005, fl., V.F.O. de Miranda 1265 (JABU); Rio de Contas, Kaiambola, Serra da Mesa, 19 April 2003, fl., A.M. Giulietti 2416a (HUEFS).

Comments:—*Utricularia purpureocaerulea* can be confused with *U. blanchetii* (see comments section in this species). This species is endemic to Brazil, and in Bahia state is found only in campos rupestres, representing the northernmost known populations of the species.

2.27. *Utricularia pusilla* Vahl, *Enumeratio Plantarum* 1: 202 (1804). [Figs. 2 and 7O-P].

Terrestrial or helophyte. Aerial spatulate leaves. Slender and flexible scape. Peltate bracts, entire margins, absent bracteoles. Sterile bracts on the raceme axis. Ascending pedicels in fruits. Sepals with conspicuous and prominent nerves, plan and entire margins. Yellow corolla, gibbous palate, trilobed lower lip, straight to slightly curved and subulate spur, up to twice as long as and parallel to the lower lip. Capsule dehiscent by a ventral pore.

Selected material:—Abaíra, Saindo de Catolés de baixo em direção a Ribeirão, 20 September 1999, fl. and fr., G.L. Campos 160 (HUEFS); Andaraí, PARNA da Chapada Diamantina, Córrego do distrito de Igatu, 04 July 2015, fl. and fr., P.C. Baleeiro 372 (SPF); Belmonte, km 71 da Rod. Itapebi/Belmonte, Fazenda Nova Vida, 20 November 1978, fl. and fr., T.S. dos Santos (CEPEC); Caetitê, Serra Geral de Caititê, 12 April 1980, fl. and fr., R.M. Harley 21267 (CEPEC, MO, NY, P, RB, US); Cairu, Beira da estrada BA-884, 24 November 2013, fl. and fr., P.C. Baleeiro 365 (SPF); Camaçari, BA-512, 14 August 2003, fl. and fr., F. Rivadavia 1686 (SPF); Castro Alves, Salgado, 27 July 1964, fl. and fr., E. Santos 1966 (R); Correntina, Chapadão Ocidental da Bahia, lado do Rio Corrente, 24 January 1980, fl. and fr., R.M. Harley 21652 (CEPEC, K, RB); Entre Rios, Fazenda Rio do Negro, 04 August 2008, fl. and fr., D. Cardoso 2323 (HUEFS); Ibicoara, trilha para a Cachoeira do Buracão beirando o Rio Espalhado, 12 July 2005, fl. and fr., F. Rivadavia 1988 (SPF); Ilhéus, Caldeiras, Lagoa Encantada, 17 January 1993, fl. and fr., W.W. Thomas 9528 (CEPEC, NY); Itacaré, 6 Km ao SW Itacaré, 30 March 1974, fl. and fr., R.M. Harley 17526 (CEPEC); Jacaraci, Morro do Chapéu, 16 July 1999, fl. and fr., F. Rivadavia 1145 (SPF); Maracás, 6 Km ao SW da cidade, 19 June 1984, fl. and fr., A.M. de Carvalho 221 (CEPEC, RB); Mucugê, beirando estrada para Barra da Estiva, 11 July 2005, fl. and fr., F. Rivadavia 1976 (SPF); Nilo Peçanha, 5.8 km na rod. para Cairú, entrada para Turrinha, 23 February 2000, fl. and fr., J.G. Jardim 2782 (CEPEC, RB); Palmeiras, beira de rio, 02 November 2007, fl. and fr., E. Melo 5343 (HUEFS); Pindobaçu, próx. ao Rio Itapicuru, 06 December 2003, fl. and fr., A.M. Miranda 4378 (HST); Porto Seguro, RPPN Veracel, 05 February 2000, fl. and fr., J.G. Jardim 2683 (RB); Rio de Contas, Ponte do Coronel, povoado de Mato Grosso, 18 July 2005, fl. and fr., F. Rivadavia 2057 (SPF); Santa Luzia, Estrada entre Una e Santa Luzia, BA-270, 02 November 2017, fl. and fr., F.M. Guedes 88 and 90 (ALCB, UFP); Santa Teresinha, Barragem Casa do Forte, 11 October 2016, fl. and fr., L.Y.S. Aona 4430 (HURB); Santo Antônio de Jesus, Rodovia entre Santo Antônio de Jesus e Gandú, 02 August 2009, fl. and fr., C.T. Lima 188 (HUEFS); Seabra, Rio Riachão ca. 27 km S de Seabra, 25 February 1971, fl. and fr., H.S. Irwin 31035 (NY); Sento Sé, entre Almas de Cima e Minas do Mimoso, 01 April 2002, fl. and fr., K.R.B. Leite 156 (HUEFS); Serrinha, próx. à Torre da Embratel, Povoado Barra do Vento, 18 August 2006, fl. and fr., L.P. de Queiroz 12294 (HUEFS); Umburanas, Delfino Serra do Curral Feio, beira do rio Tabuleiro, 12 April 1999, fl. and fr., L.P. de Queiroz 5455 (HUEFS); Valença, 32 km de Nazaré da Farinha, 03 January 1999, fl. and fr., T.B. Cavalcanti 2407 (CEN).

Comments:—*Utricularia pusilla* can be confused with *U. subulata*, but it differs by its sterile bracts on the

raceme axis, sepals with prominent nerves and spur up to twice as long as the lower lip (vs. absence of sterile bracts on the raceme axis, sepals with non-prominent nerves and spur as long as or longer than the lower lip). This species is found in a wide altitudinal range and different phytophysiognomies.

2.28. *Utricularia resupinata* B.D.Greene ex Bigelow, *Florula Bostoniensis* 3: 10 (1840). [Figs. 1 and 7Q].

Terrestrial or helophyte. Submerged/aerial cylindrical, circinate leaves. Slender and flexible scape. Basifixed tubular bracts, absent bracteoles. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Lilac or white, yellow gibbous palate, reflexed trilobed lower lip (giving an aspect of resupinate flower), curved and emarginate spur, shorter than and perpendicular to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Maraú, antes da entrada para Maraú, sentido Barra Grande–Maraú, 24 November 2013, fl. and fr., *P.C. Baleeiro* 366 (SPF).

Additional material:—BRAZIL. **Sergipe:** Estância, APA Sul, 09 March 2010, fl. and fr., *I.R.N. Menezes* 87 (ASE).

Comments:—*Utricularia resupinata* can be readily distinguished from all the other congeners in Bahia state by its tubular bracts and lilac or white corolla with reflexed trilobed lower lip, which gives an aspect of resupinate flower. This species is represented by only one record in the state, which is the southernmost known population of the species.

2.29. *Utricularia rostrata* A.Fleischm. & Rivadavia, *Kew Bulletin* 64(1): 155 (2009). Figs. 2 and 7R].

Terrestrial or lithophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins, upper sepal with rostrate apex. Pink, lilac or white corolla, yellow gibbous palate, trapezoid crenate lower lip, curved and bifid spur, as long as and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, Serra do Barbado, 14 July 2005, fl. and fr., *F. Rivadavia* 2011 (SPF); Andaraí, Serra do Sincorá, trilha para Cachoeira do Ramalho, 06 August 2001, fl. and fr., *F.R. Nonato* 1019 (HUEFS); Barra da Estiva, ao lado da estrada subindo morro com antenas de TV ao sul da cidade, 22 July 2005, fl. and fr., *F. Rivadavia* 2093 (SPF); Caetité, 1Km ao S de Brejinho das Ametistas perto da mineração, 02 February 1991, fl. and fr., *N.P. Taylor* 1530 (CEPEC); Ibicoara, Cânion da Cachoeira do Buracão, 12 July 2005, fl. and fr., *F. Rivadavia* 1990 (SFP); Lençóis, PARNA da Chapada Diamantina, 15 June 2005, fl. and fr., *A. Moraes* 1 (HUEFS); Mucugê, Cachoeira do Tiburtino, PNM Mucugê Projeto Sempre Viva, 11 July 2005, fl. and fr., *F. Rivadavia* 1983 (SPF holotype); Palmeiras, próx. ao Morro do Pai Inácio, BR-242, 26 January 2000, fl. and fr., *M. Alves* 1819 (CEPEC); Piatã, trilha para a capelinha no alto da Serra de Santana, 29 April 2010, fl. and fr., *P.M. Gonella* 333 (SPF); Rio de Contas, Serra da Mesa, 18 July 2005, fl. and fr., *F. Rivadavia* 2066 (SPF); Ruy Barbosa, ARIE Serra do Orobó, 07 January 2007, fl. and fr., *D. Cardoso* 1492 (HUEFS).

Comments:—*Utricularia rostrata* can be confused with *U. costata* (see comments in *U. costata*). This species is endemic to the campos rupestres of Bahia, and as aforementioned, it was previously considered restricted to the central portions of the Chapada Diamantina highlands (Fleischmann & Rivadavia 2009), and now its known distribution extends to Serra do Orobó (municipality of Ruy Barbosa) and near a mining area (municipality of Caetité), which are the northernmost and southernmost known populations of the species, respectively.

2.30. *Utricularia simulans* Pilg., *Notizblatt des Königlichen botanischen Gartens und Museums zu Berlin* 6: 194 (1914). [Figs. 1 and 7S].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Basifixed and free bracts and bracteoles, deeply fimbriate margins, auriculate bracts. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and deeply fimbriate margins. Yellow corolla, gibbous palate, entire lower lip, straight to curved and obtuse spur, as long as and parallel to the lower lip. Longitudinally dehiscing capsule.

Selected material:—Abaíra, Campo da Pedra Grande, 25 March 1992, fl. and fr., *R.M. Harley* 53336 (HUEFS, MO, NY, SPF); Barreiras, PNM da Vida, Cachoeira do Acaba Vida, 14 July 1983, fl. and fr., *M.L. Guedes* 798 (ALCB); Camaçari, área brejosa dentro da CETREL, 14 August 2003, fl. and fr., *F. Rivadavia* 1687 (SPF); Castro Alves, Salgado, 27 July 1964, fl. and fr., *E. Santos* 1965 (R); Coribe, 5 km ao N de Coribe, 16 June 2006, fl. and fr., *F. Rivadavia* 2224 (SPF); Formosa do Rio Preto, Fazenda Jhon Deere, Conglomerado BA-442, 04 April 2018, fl. and fr., *E.O. Moura* 1492 (HUEFS).

1950 (UB); Maraú, estrada de Ubaitaba para Barra Grande, 08 October 2005, fl. and fr., *F. Rivadavia* 2114 (SPF); Valença, estrada de Valença à Ponta do Curral, 08 October 2005, fl. and fr., *F. Rivadavia* 2105 (SPF).

Comments:—*Utricularia simulans* can be readily distinguished from all the other congeners in Bahia state by its bracts, bracteoles and sepals with deeply fimbriate margins and auriculate bracts. This species is found in a wide altitudinal range, in veredas, campos rupestres and restingas.

2.31. *Utricularia subulata* L., *Species Plantarum* 1: 18 (1753). [Figs. 1 and 7T].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with conspicuous but non-prominent nerves, plan and entire margins. Yellow corolla, gibbous palate, trilobed lower lip, straight and subulate/bifid/quadrifid spur, as long as or longer than and parallel to the lower lip. Capsule dehiscing by a ventral pore.

Selected material:—s.l., 1830, fl. and fr., *P. Salzmann* s.n. (P), 455 (G); Abaíra, Campo de Ouro Fino, 17 January 1992, fl. and fr., *D.J.N. Hind* 50063 (HUEFS, NY, SPF); Alcobaça, Rod. BA-001 a 5 km S de Alcobaça, 18 March 1993, fl. and fr., *S.A. Mori* 9645 (CEPEC, NY); Andaraí, PARNA da Chapada Diamantina, córrego do distrito de Igatu, 04 July 2015, fl. and fr., *P.C. Baleeiro* 370 (SPF); Barra, Veredas de Dois Riachos, XI-2009 (bot.), *A.P. Prata* 2166 (ASE); Barrolândia, Estrada entre Barrolândia e a BA-001 km 21, 17 July 2006, fl., *J. Paula-Souza* 6086 (ESA); Belmonte, Estação Experimental da CEPLAC “Gregório Bonder”, 27 July 2009, fl. and fr., *M.M. Saavedra* 1014 (RB); Cairu, 14 September 1993, fl. and fr., *M.L. Guedes* s.n. (ALCB 26049b); Camaçari, área brejosa dentro da CETREL, 14 August 2003, fl. and fr., *F. Rivadavia* 1685 (SPF); Caravelas, Estrada p/ o Aeroporto de Caravelas, 24 December 1998, fl. and fr., *C.P. Bove* 371 (R); Entre Rios, Restinga de Massarandupió, 30 August 1998, fl. and fr., *M.L. Guedes* 1101 (ALCB); Ibicoara, trilha para cachoeira do Buracão beirando o rio Espalhado, 12 July 2005, fl. and fr., *F. Rivadavia* 1986 (SPF); Ilhéus, road from Olivença to Serra das Trempes, 03 February 1993, fl. and fr., *W.W. Thomas* 9699 (RB, SPF); Jacobina, Piemonte da Diamantina, PNM Valois Coutinho, 03 June 2011, fl. and fr., *T.L. Vieira* 01 (ALCB); Jaguaripe, Areal Itapixacara, Fazenda de Carcinocultura do Seu Júnior, 27 August 2015, fl. and fr., *L.Y.S. Aona* 4225b (ALCB, HURB); Lençóis, PARNA da Chapada Diamantina, Rio Mandassaia, 09 March 2000, fl. and fr., *A.A. Ribeiro-Filho* 54 (HUEFS); Maraú, Estrada entre Itacaré e Maraú BR-030, 05 November 2017, fl. and fr., *F.M. Guedes* 99 (ALCB, UFP); Mata de São João, Praia do Forte, 24 January 2006, fl. and fr., *A.M. Miranda* 5407 (HUEFS, HST); Morro do Chapéu, Cachoeira do Ferro Doido, 01 September 2017, fl. and fr., *F.M. Guedes* 43 (UFP); Mucugê, PNM de Mucugê, 24 April 2004, fl., *A.C. Pereira* 94 (HUEFS); Nova Viçosa, 22 July 1979, fl. and fr., *V.D. Gomes* 57 (RB); Palmeiras, Vale do Capão, trilha do Pati, 25 December 2016, fl. and fr., *J. Calvo* 7383 (ALCB); Piaã, Serra de Santana, 13 July 2005, fl. and fr., *F. Rivadavia* 1996 (SPF); Porto Seguro, Reserva Indígena Pataxó da Jaqueira, 26 March 2005, fl. and fr., *F. Rivadavia* 1969 (SPF); Prado, Fazenda Riacho das Ostras, 28 November 2006, fl. and fr., *S.G. Rezende* 1741 (CEPEC); Rio de Contas, Pico das Almas, 17 July 2005, fl. and fr., *F. Rivadavia* 2036 (SPF); Salinas da Margarida, Estrada entre Encarnação e Salinas, 27 September 2011, fl. and fr., *E.N. de Matos* 540 (HUEFS); Salvador, APA Lagoas e Dunas do Abaeté, 14 June 1999, fl. and fr., *A.T.A. Rodarte* 06 (ALCB); Santa Cruz de Cabrália, 5 Km S of Santa Cruz de Cabrália, 18 March 1974, fl. and fr., *R.M. Harley* 17144 (CEPEC); Santa Luzia, Estrada entre Una e Santa Luzia BA-270, 02 November 2017, fl. and fr., *F.M. Guedes* 83 (ALCB, UFP); Sento Sé, 16 km NW of Lagoinha ons ide road to Minas do Mimoso, 08 March 1974, fl. and fr., *R.M. Harley* 16961 (CEPEC); Umburanas, Delfino, Serra do Curral Feio, 03 April 2002, fl. and fr., *A. Oliveira* 112 (HUEFS); Una, 43 km na estrada para Ilhéus, 15 September 1992, fl. and fr., *A.M. Amorim* 742 (CEPEC, MBM, NY); Valença, Estrada para Guaibim, Fazenda Macarina, 17 June 2000, fl. and fr., *F. França* 3419 (HUEFS).

Comments:—*Utricularia subulata* can be confused with *U. nervosa*, *U. pusilla* (see comments section in these species), *U. trichophylla* and *U. triloba*, but differs from *U. trichophylla* by its entire leaves and sepals with conspicuous nerves (vs. pinnatifid leaves and sepals with inconspicuous nerves); and from *U. triloba* by its sepals with non-prominent nerves and not converging at the apices and corolla with trilobed lower lip (vs. sepals with prominent nerves converging at the apices and corolla with shallowly trilobed lower lip). This species is widely distributed in the state, in a wide altitudinal range and different phytophysionomies.

2.32. *Utricularia trichophylla* Spruce ex Oliv., *Journal of the Proceedings of the Linnean Society, Botany* 4: 173 (1860). [Figs. 2 and 7U-V].

Terrestrial or helophyte. Aerial/submerged pinnatifid leaves. Slender and flexible scape. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins. Yellow

corolla, gibbous palate, trilobed lower lip, straight and subulate/bifid/quadrifid spur, as long as and parallel to the lower lip. Capsule dehiscing by a ventral pore.

Selected material:—Camaçari, 14 August 2003, fl. and fr., *F. Rivadavia* 1688 (SPF); Entre Rios, Aerial, 31 October 2012, fl. and fr., A.V. *Popovkin* 1257 (HUEFS); Lençóis, Estrada entre Lençóis e Seabra, 15 February 1994, fl. and fr., R.M. *Harley* 14094 (SPF); Luís Eduardo Magalhães, Estrada BR-020 a 23 km S da cidade, 28 January 2002, fl. and fr., C.P. *Bove* 1002 (R); Maraú, 5 Km ao SE de Maraú, rod. p/ Ponta do Mutá, 02 February 1994, fl. and fr., R.M. *Harley* 18955 (CEPEC, K, NY); Porto Seguro, Trancoso, 24 November 2013, fl. and fr., P.C. *Baleeiro* 363 (SPF); Rio de Contas, 9 km N estrada para o povoado de Mato Grosso, 26 October 1988, fl. and fr., R.M. *Harley* 25667 (CEPEC, SPF); Sento Sé, APA Boqueirão da Onça, 05 September 2013, fl. and fr., D.S. *Fernandes* 88 (R); Umburanas, Delfino, Serra do Curral Feio, 12 April 1999, fl. and fr., L.P. *de Queiroz* 5458 (HUEFS).

Comments:—*Utricularia trichophylla* can be confused with *U. subulata* (see comments section in this species). In Bahia state, this species is found in veredas, campos rupestres and restingas.

2.33. *Utricularia tricolor* – A.St.-Hil., *Voyage dans le District des Diamans* 2: 418 (1833). [Figs. 2 and 7W].

Terrestrial or helophyte. Aerial spatulate to orbicular leaves. Slender and flexible scape. Basifixed and basally connate bracts and bracteoles, entire margins. Ascending pedicels in fruits. Sepals with inconspicuous nerves, plan and entire margins, hyaline on both sepals. Purple or lilac corolla, white and yellow gibbous palate, entire to 3-crenate lower lip, curved and obtuse or emarginate spur, as long as or longer than and parallel to the lower lip. Bivalvate capsule.

Selected material:—Abaíra, Campos de Ouro Fino, 22 January 1992, fl. and fr., D.J.N. *Hind* 50940 (E, CEPEC, HUEFS, K, MO, SPF); Correntina, Fazenda Jatobá, 08 August 1992, fl. and fr., F. *França* 774 (CEN); Ibicoara, PNM do Espalhado, Riachão das Pedras, 14 June 2012, fl. and fr., J.A. *Siqueira-Filho* 2784 (HVASF); Mucugê, Serra de São Pedro, 17 December 1984, fl. and fr., G.P. *Lewis* 7078 (SPF); Palmeiras, Vale do Capão, trilha do Pati, 25 December 2016, fl. and fr., J. *Calvo* 7384 (ALCB); Piatã, capelinha na trilha da Serra do Santana, 13 July 2005, fl. and fr., F. *Rivadavia* 2001 (SPF); Rio de Contas, Pico das Almas, 12 December 2012, fl. and fr., G.C. *Delgado-Junior* 580 (UFP); São Desidério, Rio Piau ca. 150km SW of Barreiras, 13 April 1966, fl., H.S. *Irwin* 14768 (NY, UB).

Comments:—*Utricularia tricolor* can be confused with *U. amethystina* (see comments section in this species). In Bahia state, this species is found only in veredas and campos rupestres.

2.34. *Utricularia triloba* Benj. in Mart., *Flora Brasiliensis* 10: 248 (1847). [Figs. 1 and 6X-Y].

Terrestrial or helophyte. Aerial linear leaves. Slender and flexible scape. Peltate bracts, entire margins, absent bracteoles. Ascending pedicels in fruits. Sepals with conspicuous and prominent nerves, converging at the apices, plan and entire margins. Yellow corolla, gibbous palate, shallowly trilobed lower lip, straight and subulate spur, longer than and parallel to the lower lip. Capsule dehiscing by a ventral pore.

Selected material:—s.l., s.d., fl., P. *Salzmann* s.n. (P); Belmonte, fazenda Belmonte, 04 August 2006, fl. and fr., E.P. *Queiroz* 1773 (HRB); Cairu, Garapua, 12 August 2006, fl., M.L. *Guedes* 13595a (ALCB); Caravelas, between Alcobaça and Caravelas on the BA-001 highway 20 km S of Alcobaça, 17 January 1977, fl. and fr., R.M. *Harley* 18034 (K, NY, RB); Ituberá, à direita do km 15 da estrada p/ Praia de Pratigi, 08 October 2005, fl. and fr., F. *Rivadavia* 2110 (SPF); Jaguaripe, Areal Itapixacara, Fazenda de Carcinocultura do Seu Júnior, 27 August 2015, fl. and fr., L.Y.S. *Aona* 4225a (ALCB, HURB); Mucugê, beirando estrada para Barra da Estiva, 11 July 2005, fl. and fr., F. *Rivadavia* 1977 (SPF); Porto Seguro, Trancoso, 20 November 2013, fl. and fr., P.C. *Baleeiro* 361b (SPF); Rio de Contas, Estrada para o Pico do Itobira, 12 April 1999, fr., A.M. *Amorim* 2822 (CEPEC, NY); Santa Luzia, Estrada entre Una e Santa Luzia BA-270, 02 November 2017, fl. and fr., F.M. *Guedes* 84 (ALCB, UFP).

Comments:—*Utricularia triloba* can be confused with *U. subulata* (see comments section in this species). In Bahia state, this species is found only in campos rupestres and restingas.

Discussion

Phytogeography:—Bahia state is a very well-sampled and studied region, especially in the northern portion of the Espinhaço Range (e.g., Chapada Diamantina highlands, Pico das Almas, Catolés, Serra do Barbado) (Harley & Simmons 1986, Stannard 1995, Conceição & Giuliatti 2002, Zappi *et al.* 2003, Conceição & Pirani 2005, 2007,

Giulietti *et al.* 2006, Rapini *et al.* 2008, Neves & Conceição 2010), which is considered one of the most important centres of diversity of the South American flora, showing a vegetation mosaic with high degree of endemism (Harley & Simmons 1986, Giulietti *et al.* 1996).

The Chapada Diamantina highlands is composed by different types of ecosystems, where the campos rupestres stand out as mosaics of open vegetation with predominance of an herbaceous stratum at the highest parts, surrounded by forests and savannas at the lower parts (Giulietti *et al.* 2006). The herbaceous stratum lays upon a white sandy soil forming communities dominated by Poaceae, Cyperaceae, Eriocaulaceae and Xyridaceae, and, where the drainage is hampered, oligotrophic peat bogs may be formed with the predominance of Xyridaceae, Cyperaceae, Orchidaceae, Eriocaulaceae, Burmanniaceae, Gentianaceae, Droseraceae and Lentibulariaceae (Giulietti & Pirani 1988, Giulietti *et al.* 1996).

Most Lentibulariaceae species bloom massively synchronized with or after the rainy season, they may tolerate periods submerged in pools with emergent inflorescences or blossom when the water lamina is retrieved or decreased (Fleischmann 2012, Rutishauser 2015). From our results, the greatest richness of Lentibulariaceae is detected in areas with rivers, streams and waterfalls, which may be related to the presence of water courses periodically moistening the vegetation with water carried by the wind.

The difference in richness between the campos rupestres + restingas and the veredas of western Bahia reflects a heterogeneity in distribution of species in these habitats, which might be caused by collections made in more accessible localities compared to more expensive fieldtrips needed for the less accessible places. This trend can be observed mapping the existing collections from the state (Figs. 1 and 2): a large part of the records are from the Chapada Diamantina highlands, from the municipality of Rio de Contas up to the northernmost mountains of Jacobina and Delfino, the latter two being geographically close. Furthermore, this can be seen throughout the coastline, especially near the capital (Salvador) and the surroundings of Ilhéus and Porto Seguro, but with a slight decrease in richness towards the southern boundary of the state. This overall pattern is also observed in other families, especially those found in wetlands, such as Onagraceae (Sousa *et al.* 2021), Gentianaceae (Siqueira *et al.* 2014), Begoniaceae (Gregório *et al.* 2016), Iridaceae (Oliveira *et al.* 2016), Nymphaeaceae and Cabombaceae (Lima *et al.* 2012a,b).

Some species that are endemic to the Espinhaço Range occur throughout the entire Range, but few of them are microendemic (Giulietti *et al.* 1987). Therefore, only a small fraction of these species is shared between the portion of the Range falling in Bahia state and that falling in Minas Gerais state, and the floristic similarity is remarkably low, even in adjacent localities (Giulietti & Pirani 1988, Rapini *et al.* 2002, 2008, Zappi *et al.* 2003, Conceição *et al.* 2005). In case of Lentibulariaceae, species that are endemic to the Espinhaço Range, interestingly, are restricted to either Bahia, such as *G. exhibitionista*, *G. uncinata* and *U. rostrata*, or to Minas Gerais, such as *G. flexuosa* Rivadavia *et al.* (2011: 15), *G. metallica* Rivadavia & Fleischmann (2011: 5) and *G. oligophylla* Rivadavia & Fleischmann (2011: 10) (Fleischmann 2012, Guedes *et al.* 2020). This scenario can also be observed in species of *Minaria* (Apocynaceae), *Senna* and *Calliandra* (Fabaceae), *Pseudotrimezia* (Iridaceae), *Microlicia* and *Marcetia* (Melastomataceae), as well as in several genera of Bromeliaceae (Rapini *et al.* 2008, Versieux *et al.* 2008, Ribeiro *et al.* 2014).

Several widely distributed species that also occur in the Espinhaço Range are shared between the portions of the Range falling in Bahia and Minas Gerais (ca. 18 species). On the other hand, few other species with narrower distribution show peculiar patterns in Bahia state, such as *U. flaccida* and *U. blanchetii*, which do not extend further south of Serra do Barbado and Barra da Estiva, respectively (Figs. 1 and 2). *Genlisea aurea*, *G. tuberosa*, *U. praelonga* and *U. purpureocaerulea* are more common in the portion of the territory of Minas Gerais, and in Bahia they do not extend further north of Palmeiras, Pico das Almas, Mucugê and Andaraí, respectively (Figs. 1 and 2). Other species, such as *G. pygmaea*, *G. violacea* Saint-Hilaire (1833: 431), *U. hispida* Lamarck (1791: 50), *U. laciniata* Saint-Hilaire & Girard (1838: 870), *U. pubescens* Smith (1819: 53), *U. reniformis* Saint-Hilaire (1830: 224) and *U. tenuissima* Tutin (1934: 334), can be also found in the Range, but only in the Minas Gerais portion (Guedes, unpublished data.).

Many species of the campos rupestres flora also occur in the restingas, showing a disjunct distribution pattern. It is assumed that such species may have originated in the Espinhaço Range and reached the restingas during more favourable conditions in the past (Giulietti & Pirani 1988, Giulietti *et al.* 2006, Alves *et al.* 2007, Sobral-Souza *et al.* 2015). These environments share similar edaphic and climatic conditions, regarding drainage regime, nutritional deficiency and intense solar radiation, being areas where there is accumulation of water in sandy soils that allows the development of swamp-like vegetation (Harley 1995). The existence of similar phytogeographic patterns associated with adaptive morphological specializations in different taxa indicates a common history after the Quaternary, as a result of particular unceasing and severe selective pressures (Giulietti & Pirani 1988, Cerqueira 2000, Alves *et al.* 2007, Rapini *et al.* 2008). Some Lentibulariaceae species are shared by these two phytophysiognomies in Bahia state, despite not exclusive to them, such as *G. filiformis*, *G. repens*, *U. amethystina*, *U. erectiflora*, *U. foliosa*, *U. gibba*, *U.*

longifolia, *U. nana*, *U. pusilla*, *U. simulans*, *U. subulata*, *U. trichophylla* and *U. triloba* (Figs. 1 and 2, Table 1). On the other hand, *U. breviscapa*, *U. cucullata* and *U. nervosa* have records in the Minas Gerais portion of the Range (Guedes, unpublished data), but in Bahia state they only have records in areas of restinga and vereda, respectively (Figs. 1 and 2).

Moister climatic conditions in the past may have influenced the present distribution of moist-dependent species by increasing the number of suitable habitats for them, forming vegetation connections between several habitats such as the Guyana Tepuis with Amazon and Atlantic environments, and with Cerrado and coastal formations (Mori *et al.* 1981, Wang *et al.* 2004, Fiaschi & Pirani 2009, Sobral-Souza *et al.* 2015). The distribution of several Lentibulariaceae species (Fleischmann 2012, Guedes *et al.* 2018), as well as Bonnetiaceae, Eriocaulaceae, Gentianaceae, Humiriaceae, Melastomataceae, Oxalidaceae, Velloziaceae and Xyridaceae (Alves *et al.* 2007, Fiaschi & Pirani 2009, Andrino *et al.* 2020) corroborate this hypothesis.

Similar to the areas of campos rupestres, the coastline of Bahia state is also well-sampled (Britto *et al.* 1993, Giulietti *et al.* 2006, Menezes 2007, Menezes *et al.* 2012, Martins 2012, Queiroz *et al.* 2012, Silva & Menezes 2012, Gomes & Guedes 2014, Alves *et al.* 2015, Fernandes & Queiroz 2015). The coast of Bahia is composed by wetlands along quaternary plains where the groundwater level is close to the surface of the land or it is flooded by shallow waters, comprising a large number of natural environments on the banks of rivers, streams, coastal lagoons, peat bogs and mangroves (Lyrio 1996, Dominguez 2004). These wetlands comprise the Pleistocene Alluvial Fans, which were originated with the reshaping of the Barreiras Formation sediments in a past drier climate, and the Pleistocene Marine Terraces, which were generated with deposits influenced by a higher relative sea level during the penultimate transgression (Lyrio 1996, Accioly 1997, Dominguez 2004). Such open areas are exposed to the action of winds and are characterized by soils poor in organic matter. In addition, they are under a permanent or seasonal influence of water saturation of the soil, either because of rainfall or due to changes in the groundwater level, which regulates a dynamic herbaceous vegetation cover where small-sized species occur, many of them rhizomatous or stoloniferous, such as species of Cyperaceae, Xyridaceae, Eriocaulaceae, Gentianaceae, Fabaceae, Droseraceae and Lentibulariaceae (Menezes 2007, Amaral *et al.* 2008). As aforementioned, 20 species of Lentibulariaceae occur in restingas of Bahia, of which 13 also occur in campos rupestres and 7 of them are found in veredas as well (Figs. 1 and 2, Table 1). Overall, 28 Lentibulariaceae species have records in several areas of restingas along the Brazilian coast (Guedes & Alves 2020, Guedes *et al.* 2020), suggesting that at some level this vegetation might play a role as an ecological corridor among different phytogeographic domains, with which a certain floristic composition is shared (Alves *et al.* 2007, Fernandes & Queiroz 2015, Marques *et al.* 2015, Silva *et al.* 2021).

Analysing the Brazilian Atlantic coast, the species composition of Lentibulariaceae in the restingas of Bahia is more similar to that found in restingas of Sergipe, Espírito Santo and Rio de Janeiro than those of Alagoas, Paraíba, Pernambuco and Rio Grande do Norte (Baleeiro *et al.* 2017, Guedes & Alves 2020, Guedes *et al.* 2022). This pattern is consistent with biogeographical and paleomodelling studies on the Atlantic Forest (Carnaval & Moritz 2008, Peres *et al.* 2020). The São Francisco River is considered a natural geographic barrier influencing the genetic diversification and speciation of different animal and plant taxa (Nascimento *et al.* 2013, Maciel *et al.* 2020). Furthermore, in Bahia state, the restinga is known to be clustered into two different groups, located north and south of Todos os Santos Bay (Salvador), respectively, with a floristic composition influenced by seasonality in the northern portion (Fernandes & Queiroz 2015). In the case of Lentibulariaceae, *G. repens*, *U. breviscapa*, *U. resupinata* and *U. triloba* were found only in the southern portion; however, *U. resupinata* also occurs in the restingas of Rio Grande do Norte and Sergipe, and *U. triloba* in Alagoas, Paraíba and Rio Grande do Norte (Guedes & Alves 2020).

Of the 7 species that, in Bahia state, were only found in areas of restinga, *U. resupinata* stands out for being the southernmost known record of the species. It occurs only in coastal environments of North, Central and South America (pine savannas, floodplain fields and restingas) (Taylor 1989, Guedes *et al.* 2020). On the other hand, *U. adpressa* also occurs in campos rupestres in Goiás state, campo limpo in Mato Grosso state and other savanna vegetation in Central and South America (Taylor 1989, Guedes *et al.* 2020). *Utricularia guyanensis* can be also found in campinaranas, Amazonian savannas, campo limpo and lowland Semideciduous Seasonal Forests, whereas *U. juncea* also occurs in campo limpo, gallery forests and lowland Semideciduous Seasonal Forests, and *U. breviscapa*, *U. hydrocarpa* and *U. myriocista* occur in pools in several types of vegetation on a wide altitudinal range (Taylor 1989, Guedes *et al.* 2020).

In contrast, the veredas of western Bahia comprise areas of hydromorphic soil, slightly depressed, located in flat areas or flattened by erosion, associated with sedimentary plateaus, resulting from processes of exudation from the groundwater (Passo *et al.* 2010). These savanna physiognomies are characterized by the presence of *Mauritia flexuosa* L. palm trees among herbaceous stratum, also known as *Mauritia* swamps (Fagundes & Ferreira 2016). Whilst the

paleodune fields of the lower middle São Francisco River are aeolian dunes originated by the sediments from the river and blown by the wind, during the last glacial stage of the northern hemisphere (Costa 1984, Pacheco & Oliveira 2016). These areas have been poorly sampled and studied (Rocha *et al.* 2004, Queiroz 2006, Queiroz & Cardoso 2008, Sátiro & Roque 2008, Oliveira *et al.* 2015).

Of the 14 Lentibulariaceae species found in veredas of western Bahia (Figs. 1 and 2, Table 1), four stand out for their distribution pattern: *G. guianensis* inhabits wet savannas of the Guyana Highlands of Venezuela and Guyana, eastern Bolivia, and Brazilian campinaranas (Roraima) and veredas (Bahia, Distrito Federal, Goiás, Mato Grosso, Minas Gerais and Tocantins) (Fleischmann 2012, Guedes *et al.* 2020); *Utricularia cucullata* occurs in ponds in several phytophysionomies of South America, except in restingas (Guedes *et al.* 2020); *U. laxa* and *U. nervosa* are also found in lowland and highland savanna physiognomies of South America, such as Amazonian savannas, campos rupestres and campos limpos (Taylor 1989, Guedes *et al.* 2020).

Palynological studies indicate that during the Late Pleistocene climate there has been a great expansion of the Amazonian and Atlantic rainforests, which invaded the Icatu River Valley (northwestern Bahia), and that could explain the distribution patterns of rainforest species in the Caatinga (Oliveira *et al.* 1999, Cassino *et al.* 2018). Overall, areas of veredas, paleodune fields and campos rupestres share several Lentibulariaceae species with areas of restingas, supporting past connections during moister climatic conditions (Sobral-Souza *et al.* 2015). The distribution patterns of *G. filiformis*, *G. repens*, *U. amethystina*, *U. erectiflora*, *U. foliosa*, *U. gibba*, *U. longifolia*, *U. nana*, *U. pusilla*, *U. simulans*, *U. subulata*, *U. trichophylla* and *U. triloba* corroborate this hypothesis.

Endemism, rarity and conservation:—When comparing these different environments, but with similar edaphic conditions, it is important to consider the diversity and variety of physiognomic aspects in each area. This may directly affect species richness as well as vegetation structural and taxonomic composition, culminating in different species composition (Silva *et al.* 2021). The absence of endemic taxa in veredas, paleodune fields and restingas contrasts with the high endemism rate observed in campos rupestres. Species that settle in geologically recent habitats, such as restingas, adapt to different climatic and nutritional conditions available in these areas (Silva *et al.* 2021). This highlights the importance of genetic richness, which is lacking the proper attention in biological conservation strategies in the country (Scarano 2006). Therefore, it is crucial that the savanna physiognomies in Bahia continue to be considered a priority for biodiversity conservation in the state.

It is well known that many savanna plant species occur in small populations, whilst others are endemic or narrowly distributed in restricted habitats (Maciel 2020). This scenario is commonly observable here with the Lentibulariaceae species: *G. exhibitionista* and *G. uncinata* are microendemic to few mountain-top localities with less than eight populations known for each of them (Figs. 1 and 2), and *U. parthenopipes* and *U. rostrata* are endemic to Bahia state with more than 10 populations known for each species (Figs. 1 and 2). Moreover, *G. lobata*, *G. tuberosa*, *U. blanchetii*, *U. flaccida*, *U. nelumbifolia*, *U. nephrophylla* and *U. purpureocaerulea* are Brazilian endemics with very narrow Areas of Occupancy (AOO), restricted to specific habitats and with less than 20 or 30 sparse populations known for each species (Fleischmann 2012, Guedes & Alves 2020, Guedes *et al.* 2020). While *G. guianensis* and *U. costata* are South American endemics also with narrow AOO and less than 20 and 10 sparse populations known, respectively (Fleischmann 2012, Guedes & Alves 2020, Guedes *et al.* 2020).

South American savannas are under different environmental conditions and threats that influence species on different scales and affect their forms of rarity, with higher extinction rates likely to happen for species with more restricted distribution, low abundance and higher habitat specificity (Maciel 2020). The percentage of these officially protected areas is much lower than those present in the Amazon Forest domain (Oliveira *et al.* 2017). Although rare species are important for conservation policies, no previous study has assessed the conservation efforts for species in each form of rarity in protected areas of the South American savannas (Maciel 2020).

Rare species can contribute significantly to the functioning of communities and, consequently, to the maintenance of their biodiversity (Lyons *et al.* 2005), which is remarkably true in campos rupestres, where a large portion of the flora is composed by endemic or microendemic species (Rapini *et al.* 2008). These species are often represented by small populations and therefore more susceptible to stochastic natural episodes or anthropogenic impact, which makes campos rupestres rich in vulnerable species needing special protection (Rapini *et al.* 2008).

Despite the existence of Protected Areas such as the Chapada Diamantina National Park, the Environmental Protection Areas of Serra do Barbado and Marimbus-Iraquara, as well as many others, in fact the rich biodiversity of the region is not protected (Neves & Conceição 2010). Several threats afflict these important diversity centres, such as the progression of agriculture, mining, fires, pasture, deforestation for wood removal, ornamental plant collection and touristic overexploitation (Harley 1995, Conceição 2000, Franca-Rocha *et al.* 2005). The effect of fire on Lentibulariaceae species, which are often overlooked in surveys and studies that address fires and regeneration

of vegetation, is still unknown (Neves & Conceição 2010, Gonçalves *et al.* 2011, Mesquita *et al.* 2011, Leite *et al.* 2017). The main fires in the Protected Areas of the Chapada Diamantina highlands are anthropogenic, being used in agriculture and livestock by local inhabitants for the renewal of pastures and cleaning of crop residues (ICMBio 2007).

The campos rupestres have been attracting several visitors every year, being localities full of natural beauty, breathtaking landscapes and great species richness (Salimena 2000). Notably, the practice of the so-called ecotourism has been taking place practically without any inspection by competent organs, thus threatening the integrity of Protected Areas in Chapada Diamantina (Conceição 2000). In these environments, Ecotourism practitioners find waterfalls, canyons, walls, and a multitude of ecological trails for trekking, abseiling and climbing (Salimena 2000). Among the problems related to tourist overexploitation there are the intensification of erosion processes on trails, landslides, drainage silting and impact on quartzite caves (Salimena 2000). The impact on vegetation caused by these activities has not been evaluated yet (Conceição 2000), however, this represents a potential threat to the Lentibulariaceae species, since they inhabit the moister zones of these environments, in sites flooded by rain and/or ground water, near and in waterfalls and streams.

On the other side of the state, the coastal zones are also identified as critical areas due to the unique and important ecosystems, where several economic activities (industrial, commercial, food production, and touristic), as well as disorderly occupation and construction of condominiums are recurrent (Menezes 2007, Martins 2012, Queiroz *et al.* 2012). Other aggravating aspects are the effect of the increasing change of vegetation and the illegal eradication of species, causing fragmentation of habitat that interfere in several important ecological processes, such as pollination and seed dispersal (Queiroz *et al.* 2012). Due to the delicate balance that exists between the different processes operating in the coastal zone, human activity can have a very negative effect on its environmental quality (Menezes 2007).

Several Lentibulariaceae records in the restingas are within Protected Areas (Fig. 5, Table 1), and these representatives are fairly common and widely distributed species: *G. filiformis*, *U. adpressa*, *U. erectiflora*, *U. foliosa*, *U. gibba*, *U. guyanensis*, *U. hydrocarpa*, *U. juncea*, *U. myriocista*, *U. nana*, *U. pusilla*, *U. resupinata*, *U. simulans*, *U. subulata*, *U. trichophylla* and *U. triloba* (Guedes & Alves 2020, Guedes *et al.* 2020). However, of the 13 coastal Protected Areas included in this study (Fig. 5, Supplementary Material: Fig. A1), one has no management plan (Una Wildlife Refuge), two are currently lacking managers (Environmental Protection Areas of Baía de Camamu and Caminhos Ecológicos da Boa Esperança) (INEMA 2021, Menegassi 2021), and servers have denounced the situation of abandonment in most of them, with managements not properly executed yet (Menegassi 2021).

Since these Protected Areas are not Strictly Protected, the occupation of the area is allowed, theoretically, for sustainable use (Sustainable Use Units; ICMBio 2022), lacking, however, proper infrastructure for that, and in fact, impacted by deforestation, disorderly occupation, pollution and drainage of flooded areas for the implementation of condominiums (INEMA 2021, Menegassi 2021). Following our surveys, the Environmental Protection Areas of Baía de Camamu and Caminhos Ecológicos da Boa Esperança contain 75% of the Lentibulariaceae species found in the restingas of Bahia (Fig. 5, Table 1). As aforementioned, *U. resupinata* has only one record in the state, the southernmost population known of the species, and it happens to be within the territory of the Environmental Protection Area of Baía de Camamu, being hence at great risk of local extinction if the circumstances will not change.

Meanwhile, the western Bahia region, where is located the most important fluvial system of northeastern Brazil (São Francisco river basin), is one of the main areas of intense agricultural growth of the Cerrado domain (Oliveira *et al.* 2015). Due to the flat topography, deep soils and water availability from rainfall, rivers and groundwater, this region is very suitable for agricultural mechanization (Oliveira *et al.* 2017). Consequently, the remaining vegetation with high environmental relevance of western Bahia, such as veredas, have become priority areas for conservation as well (MMA 2002). Only three (*G. filiformis*, *G. guianensis* and *U. simulans*) of the 14 species found in veredas are within Protected Areas (Vida Municipal Natural Park, Environmental Protection Areas of Bacia do Rio de Janeiro and Rio Preto). Nevertheless, these areas lack management plans and are currently supervised by a single manager (INEMA 2021, Menegassi 2021). In the state, *Genlisea guianensis*, *U. cucullata*, *U. laxa* and *U. nervosa* are represented by a single or no more than three populations each, which leaves them at greater risk of local extinction.

In this context, the management of several Protected Areas in the state perpetuates with insufficient results for the effective conservation and protection of the environment and species (Menegassi 2021). In addition to the lack of managers, other major bottleneck for the effective implementation of protected areas are the management plan and board: the former is the document that constitutes a critical pillar, with zoning, rules and guidelines, while the latter is the instrument of dialogue between the society and a protected area (Menegassi 2021).

Moreover, in many cases, protected areas do not have an adequate arrangement for biological conservation due to the lack of connectivity between each other (Oliveira *et al.* 2017). Ecological corridors are able to reduce the

consequences of human impact and to provide interconnectivity between protected areas, serving as fundamental platforms for wildlife fluxes of communities that suffer from agricultural activities (Uezu *et al.* 2005). It would be crucial to use spatial analysis of landscape combined with environmental policies to demarcate legal reserves, expanding permanent protection areas, and establish strategies to maintain ecological interactions in these savanna environments that are highly sought for agricultural, urban and industrial expansion (Oliveira *et al.* 2017). On top of that, the lack of public policies to assure the conservation of these environments reinforce the worsening of this situation (Fagundes & Ferreira 2016).

Conclusions

Bahia state is home to 46% of the Lentibulariaceae species of Brazil, this great richness is due to the diversity of wet habitats and phytophysionomies suitable for these taxa. Four species (*G. exhibitionista*, *G. uncinata*, *U. parthenopipes* and *U. rostrata*) are endemic to the state, one (*G. pygmaea*) was wrongly reported, and two (*U. laxa* and *U. nelumbifolia*) constitute new records for the state. *Utricularia parthenopipes* is here reported for the first time outside the campos rupestres, in a paleodune field area, and *U. rostrata* sees its geographic range expanded for other localities outside the Chapada Diamantina highlands.

The campos rupestres, especially the Chapada Diamantina highlands, hold the greatest richness of the family in the state (25 species) and is the only phytophysionomy with endemic Lentibulariaceae species (*G. exhibitionista*, *G. tuberosa*, *G. uncinata*, *U. purpureocaerulea* and *U. rostrata*). While restingas configure the phytophysionomy with the second greatest richness (20 species), followed by veredas (14 species), lowland Open Ombrophilous Forests (11 species.), paleodune fields (5 species), inselbergs (2 species), submontane Semideciduous Seasonal Forest (2 species) and montane Dense Ombrophilous Forest (1 species). The disjunct savanna wetlands share several Lentibulariaceae species, and their distribution patterns, as well as of other moist-dependent taxa, endorse hypotheses of vegetation connections during moister climatic conditions in the past. In addition, the restingas of Bahia share more of Lentibulariaceae with the restingas south of the São Francisco River than with those in the north, consistent with biogeographical and paleomodelling studies pointing the River as a geographic barrier influencing speciation and genetic diversity.

Most of the species (33) occur within Protected Areas, but only 19 of them are under greater protection efforts in Areas Strictly Protected. However, they are still under threats and human interference. The remaining nine species are not found in protected localities, and, unfortunately, they represent those with unique records in the state, of which three have more restricted geographic distribution. This scenario makes these species more susceptible to threats and local extinction processes. In addition, 11 species can be classified at some level of rarity due to their endemism, geographic range and habitat specificity.

In this context, we address the need of scientific studies with improved characterization of these savanna wetlands in terms of species richness, forms of rarity and ecological services in order to promote public policies and actions for conservation of genetic diversity, as well as restoration of degraded areas. In such way, biodiversity and ecosystem services are not lost before they are even known. In general, we hope this work contributes to advancement in the effective management and conservation strategies related to savanna wetlands, which are important environments for Lentibulariaceae species. Moreover, we also expect that this work serves as a platform for a better understanding of the Lentibulariaceae species and their distribution patterns, so that it is possible to seek a deeper comprehension of their ecological services and the threats they face, favoring conservation strategies.

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Supplementary material

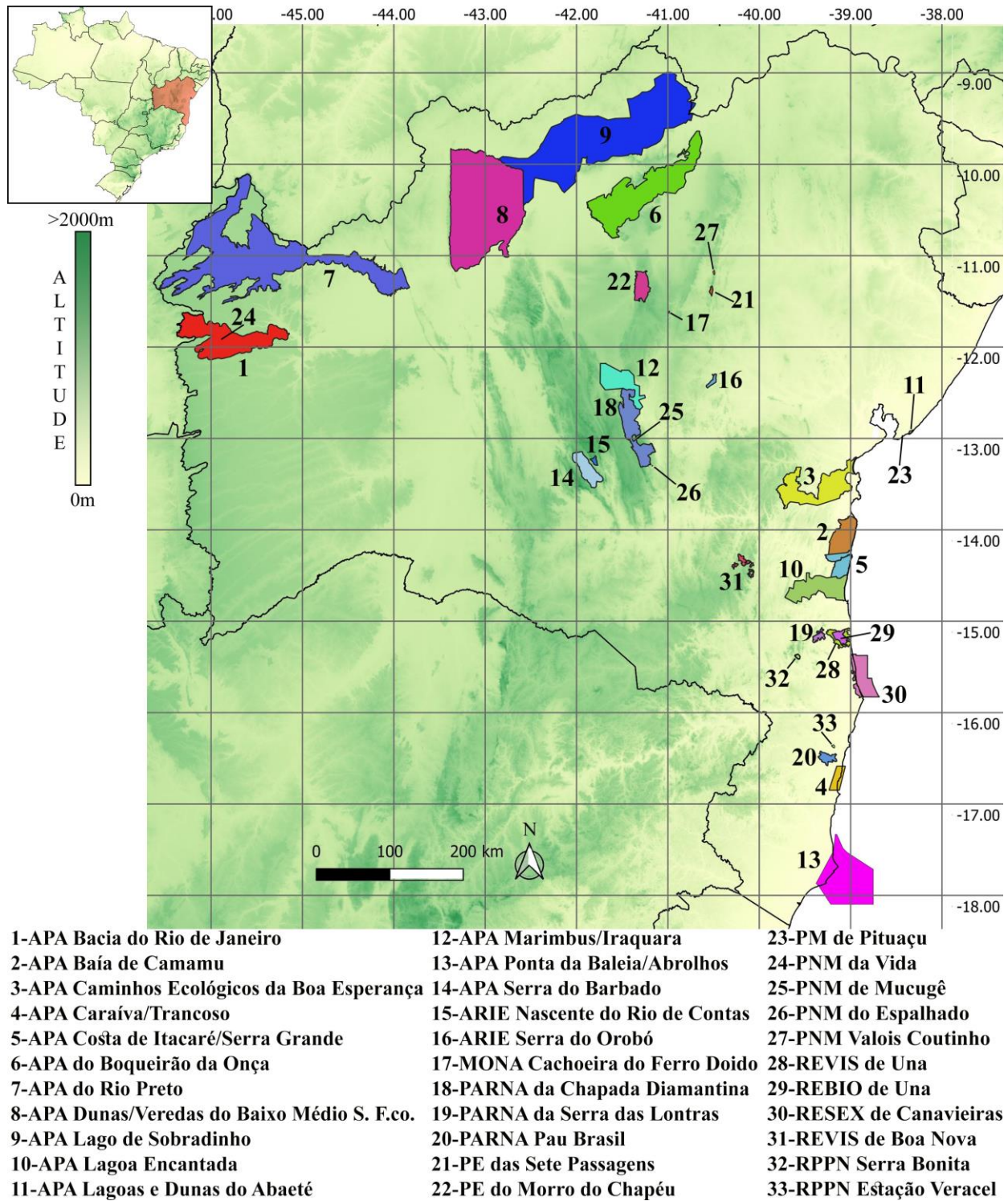


FIGURE A1. Protected Areas in Bahia state that cover the natural distribution of Lentibulariaceae species. **Strictly Protected Areas:** MONA = Natural Monument (II), PARNA = National Park (II), PE = State Park (II), PNM = Municipal Natural Park (II), REBIO = Biological Reserve (Ia), REVIS = Wildlife Refuge (III). **Areas of Sustainable Use:** APA = Environmental Protection Area (V), ARIE = Area of Relevant Ecological Interest (IV), PM = City Park (V), RESEX = Extractive Reserve (VI), RPPN = Private Reserve of Natural Heritage (IV).

- 5 **ARTIGO 3 – MOLECULAR PHYLOGENY OF *UTRICULARIA* SECT. *SETISCAPELLA* (LENTIBULARIACEAE) REVEALED ITS NON-MONOPHYLY AND THE NEED FOR A NEW SECTION**

Molecular phylogeny of *Utricularia* sect. *Setiscapella* (Lentibulariaceae) revealed its non-monophyly and the need for a new section

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Abstract

Utricularia is the most species-rich genus of carnivorous plants, it is widely distributed throughout the globe and exhibiting a great morphological variability that reflects on its adaptation to grow in different life forms. Although Taylor's infrageneric classification system is a remarkable literature, many phylogenetic studies evidenced incongruences in different taxonomic levels and suggested modifications to that system over the last decades. The paraphyly of *U.* sect. *Setiscapella* has been retrieved in previous molecular analyses, when samples of *U.* sect. *Avesicaria* and *U.* sect. *Steyermarkia* were included, using few plastid markers and 30-60% of the currently recognized taxa, however, with topological incongruities between the different analyses. Here we generated a new phylogenetic hypothesis with improved molecular datasets (*matK*, *rpl20-rps12* and *trnL-F* spacers, *rps16* intron and ITS1-5.8S-2) and nearly complete sampling of *U.* sect. *Setiscapella* (80%), *U.* sect. *Avesicaria* (100%) and *U.* sect. *Steyermarkia* (50%), including closely related taxa and four species (*U. cutleri*, *U. physoceras*, *U. trichophylla* and *U. viscosa*) never before sampled. We also assessed potential synapomorphies tracing the evolution of morphological characters through ancestral state reconstruction. Our phylogenetic analyses provided strong support for the majority of the clades, the isolated and combined datasets revealed the non-monophyly of section *Setiscapella*. We recognize *U.* sect. *Avesicaria* as a natural group based on phylogenetic placement and synapomorphies retrieved through ancestral character state reconstruction. On the other hand, *U.* sect. *Setiscapella* is here recognized by seven species and a new section, *U.* sect. *Diversicolor*, is proposed to include three species previously placed in section *Setiscapella*, based on molecular and morphological evidence.

Keywords: Bladderworts, carnivorous plants, infrageneric classification, multi-locus phylogeny, taxonomy.

1. Introduction

The rootless genus *Utricularia* L. (Lentibulariaceae, Lamiales) is the largest carnivorous plant taxon, it is worldwide-distributed and represented by c. 250 species (Rutishauser and Isler, 2001; Cross et al., 2020; Guedes et al. 2021). These small plants showcase a remarkable variety of life and growth forms (i.e., hydrophytes, terrestrials, helophyte, epiphytes, lithophytes and rheophytes), which reflects on a great morphological variation and unusual structures that do not fit in the traditional body plan found in other spermatophytes (Taylor, 1989; Rutishauser

and Isler, 2001). The vegetative body of *Utricularia* is a developmental mosaic between structural categories known as leaves and shoots, which is a concept known as Fuzzy Arberian Morphology (FAM) (Goebel, 1981; Rutishauser and Isler, 2001; Rutishauser, 2015). For practical purposes, descriptive and taxonomic, Taylor (1989) proposed a consistent terminology that is widely used to date.

The infrageneric classification system, also proposed by Taylor (1989) based mainly on number of sepals (for subgenus) and trap morphology (for sections), has always been controversial, although it is the most important taxonomic literature for *Utricularia*. Throughout the years, several modifications and rearrangements regarding sectional level have been suggested or proposed (Jobson et al., 2003, 2017; Müller and Borsch, 2005; Reut and Jobson, 2010; Rodrigues et al., 2017; Westermeier et al., 2017; Silva et al., 2018a; Baleeiro et al., 2019, 2022).

Despite the number of phylogenetic analyses performed for the genus, many issues persist, whether from systematic or nomenclatural point of view, concerning mostly the Neotropical species, frequently undersampled (Jobson et al., 2018). For instance, some cases have been addressed with efforts towards taxonomic resolution, such as the cases of *U. sect. Utricularia* P.Taylor), involving possible hybridization events and reticulate evolution (Astuti and Peruzzi, 2018; Astuti et al., 2020; Bobrov et al., 2021) and the *U. amethystina* complex (*U. sect. Foliosa* Kamiński), which very recent has been partially resolved (Baleeiro et al., 2016, 2019, 2022; Silva et al. 2019; Guedes et al., 2021).

Among the persisting problematics that has not been given much attention or efforts towards taxonomic resolution is the *U. sect. Setiscapella* (Barnhart) P.Taylor. This section is currently composed by ten species, of which nine occur in Brazil (*U. flaccida* A.DC., *U. jaramacaru* Gonella, Baleeiro and Andrino, *U. nervosa* G.Weber ex Benj., *U. nigrescens* Sylvén, *U. physoceras* P.Taylor, *U. pusilla* Vahl, *U. subulata* L., *U. trichophylla* Spruce ex Oliv. e *U. triloba* Benj.), and one is African (*U. stanfieldii* P.Taylor) (Taylor, 1989; Guedes et al., 2023). These species are morphologically very similar, often confused with each other and misidentified in herbarium collections (Guedes et al., 2018). Section *Setiscapella* is recognized by their terrestrial life/growth form (except *U. flaccida*, lithophyte), yellow corolla (except *U. jaramacaru* and *U. physoceras*, white with pale yellow and white with pink, respectively) with shallowly to deeply trilobed lower lip, peltate bracts, absence of bracteoles, globose capsules dehiscing by a ventral pore and obliquely ellipsoid seeds, ridged, with very elongate testa cells (Taylor, 1989; Guedes et al., 2023).

In all molecular phylogenetic studies developed for the genus so far (Jobson and Albert, 2002; Jobson et al., 2003; Müller and Borsch, 2005; Westermeier et al., 2017; Silva et al., 2018a), there were sampled only three to six of the ten currently recognized species of section *Setiscapella*. These studies indicated that this section is paraphyletic, showed divergences of topology when samples of *U. sect. Avesicaria* Kamiński and *U. sect. Steyermarkia* P.Taylor were included, and *U. flaccida* has always emerged in unsupported clades. The two members of *U. sect. Avesicaria* (*U. neottioides* A.St.-Hil. and Girard and *U. oliveriana* Steyerm.) also occur in Brazil, while the two members of *U. sect. Steyermarkia* (*U. auromaculata* Steyerm. and *U. steyermarkii* P.Taylor) are endemic to Venezuela (Taylor, 1989; Guedes et al., 2023).

Back then, *U. flaccida* was known to be restricted to the Chapada Diamantina highlands, in Bahia state, and recently it was reported for two other states in northeastern Brazil (Ceará and Sergipe), thus being endemic to this region (Guedes et al., 2018; Guedes and Alves, 2020; Guedes and Matias, 2020). The individuals from populations of Ceará and Sergipe states are notably smaller than the ones from populations of Bahia, with less flowers and slightly smaller corollas (Guedes et al., 2018; Guedes and Alves, 2020; Guedes and Matias, 2020).

Most of these aforementioned phylogenetic studies were based solely in two to three plastid markers, only Silva et al. (2018a) included nuclear ribosomal DNA data in their analyses. Using only genes inherited uniparentally (plastid DNA), which suffer events of recombination and gene conversion, may bias and introduce errors to phylogenetic reconstruction (Davis et al., 2014). In contrast, including genes that are inherited biparentally (nuclear ribosomal DNA), and are present in numerous copies, can provide alternative evidence for relationships retrieved, usually supporting previous hypotheses based on plastid genes (Zeng et al., 2014).

Among the main reasons why most researchers still use Taylor's classification system is the lack of consensus to propose a new system due to distinct topologies found in the phylogenetic proposals presented so far. In this context, we aimed to: (1) infer a consensus phylogenetic tree using plastid and nuclear markers and a nearly complete sampling (80%) of *U. sect. Setiscapella*, including *U. sect. Avesicaria* (100%) and *U. sect. Steyermarkia* (50%); (2) assess potential morphological synapomorphies for the retrieved clades and trace the evolution of these characters through ancestral state reconstruction; and (3) propose a new sectional division.

2. Material and Methods

2.1. Taxon sampling and DNA extraction

This study is based on newly generated DNA sequences and the available ones from GenBank (NCBI), and it includes eight of the ten recognized members of *U. sect. Setiscapella* and 15 other *Utricularia* species (Table 1) belonging to the sections *Aranella*, *Avesicaria*, *Foliosa*, *Lecticula*, *Mirabiles*, *Sprucea*, *Steyermarkia*, *Utricularia* and *Vesiculina* (Taylor 1989). Six *Genlisea* A.St.-Hil. species (*G. aurea* A.St.-Hil., *G. filiformis* A.St.-Hil., *G. guianensis* N.E.Br., *G. repens* Benj., *G. tuberosa* Rivadavia, Gonella and A.Fleischm. and *G. violacea* A.St.-Hil.) were selected as outgroup based on available sequences on GenBank for the selected molecular markers.

DNA was isolated from leaves, scapes and flowers stored in silica gel, from natural populations (in Brazil) collected by the authors. Multiple accessions (43 specimens) were used for 11 species (Table 2) of *U. sect. Avesicaria*, *U. sect. Setiscapella* and *U. sect. Sprucea* to encompass their morphological variation and distribution. Extractions were performed according to the Doyle and Doyle (1987) protocol, with modifications by Lodhi et al. (1994). The infrageneric classification follows Taylor (1989) with recent additions of taxonomic reestablishment (Guedes et al. 2019) and recently described species (Gonella et al. 2020). All materials collected for this study were deposited at the JABU, SPF, UFP and UFRN herbaria [acronyms according to Thiers (2023), continuously updated].

2.2. PCR amplification and Sequencing

Four plastid DNA regions and one nuclear ribosomal DNA region were amplified. The *matK* gene (3F_KIM and 1R_KIM; Li et al., 2011), the *rps16* intron (RPSF and RPSR2; Oxelman et al., 1997), the intergenic spacers *rpl20-rps12* (*rpl20* and 5'-*rps12*; Hamilton, 1999) and *trnL-F* (*trnL*-fwd and *trnF*-rev; Taberlet et al., 1991), and the ITS1-5.8S-2 (ITS5 and ITS4; White et al., 1990 / ITS18d and ITS28cc; Hillis and Dixon, 1991).

PCR amplifications were achieved in PTC-100 thermocycler (MJ Research) using 25 µL reactions containing (protocols for each amplified region in the Supplementary Material: Table S1) ultra-filtered autoclaved water, *Taq* DNA polymerase, nucleotides (dNTPs) at 100 µM, 10x buffer (containing 20 mM MgCl₂), primers at 10 µM and, when necessary, the adjuvant dimethyl sulfoxide (DMSO), as recommended by Miranda et al. (2010).

PCR products were purified using absolute isopropanol and 70% ethanol. DNA sequencing reactions were obtained in PTC-100 thermocycler (MJ Research), each 10 µL

reaction containing 4 μ L of ultra-filtered autoclaved water, 1 μ L of primer (forward strand), 1 μ L of DNA template, 3 μ L of Big Dye buffer and 1 μ L of Big Dye (Big Dye Terminator Cycle Sequencing Kit, Applied Biosystems). Reaction products were further cleaned using 75% isopropanol and 70% ethanol, and drying at room temperature, before taken to the Centro de Recursos Biológicos e Biologia Genômica (CREBIO) for sequencing. Sanger sequencing procedures were conducted at the Laboratório de Sistemática Vegetal (LSV) of the Biology Department at the São Paulo State University, campus of Jaboticabal.

2.3. Sequence assembly, Alignment and Phylogenetic analyses

The electropherograms resulted from the sequencing were analysed for possible errors in BioEdit v.7.2.5 (Hall, 1999) and then, the newly generated sequences were edited. Data matrices of each DNA region and combined (plastid + nuclear) were assembled, including 72 previously published sequences (available at NCBI database) (Table 1), and then aligned in MAFFT v.7 (Katoh and Standley, 2013) using default parameters.

The best fitting nucleotide substitution models for each matrix were selected using MrModelTest v.2.4 (Nylander, 2004) on PAUP* v.4.0 (Swofford, 2002) under the Akaike Information Criterion (AIC; Akaike, 1973), and the selected models were GTR+I+G for ITS and GTR+G for each of the plastid regions. Maximum Likelihood (ML) analyses for each sequence alignment and for the concatenated matrices (ptDNA and ptDNA + rDNA) were performed using RAxML v.8.2.12 (Stamatakis, 2014) in CIPRES Science Gateway (Miller et al., 2010), with branch supports obtained through rapid bootstrap (RBS) (Stamatakis et al. 2008) based on the majority-rule consensus tree from 1000 pseudo-replicates.

Bayesian Inference (BI) analyses were executed using MrBayes v.3.2.7 (Huelsenbeck and Ronquist, 2001; Ronquist et al., 2012), also in CIPRES (Miller et al., 2010). Two parallel runs with four Metropolis-coupled Markov chain Monte Carlo (MCMCMC; Geyer, 1991; Gilks and Roberts, 1996; Yang and Rannala, 1997) chains were performed for 9 million generations, with sampling frequency at each 1000 generation and the first 25% of sampled trees discarded as burn-in (Huelsenbeck and Ronquist, 2001). Convergence diagnostics of runs provided by MrBayes were verified, such as effective sample size (ESS) ≥ 200 and potential scale reduction factor (PSFR) approaching 1.0. Posterior probabilities (PP) were obtained from the 50% majority-rule consensus tree. Support values were considered high for RBS ≥ 85 and for PP ≥ 0.90 (Cummings et al., 2003; Erixon et al., 2003; Simmons et al., 2004; Stamatakis et al. 2008). All resulting tree files from ML and BI were visualized in FigTree v.1.4.3 (Rambaut, 2009).

2.4. Ancestral Character State Reconstruction

We traced the evolution of 10 morphological characters (life/growth form, pustulate leaves, trap appendages, color of corolla, palate color, palate type, spur shape, seed shape, seed testa cells, seed texture) selected as diagnostic for *Utricularia* and that are very variable among the species (Taylor, 1989; Guedes et al., 2023). Character states were based on the examination of herbarium material from ALCB, ASE, CEN, CEPEC, EAC, EAN, FLOR, HEPH, HRB, HST, HTSA, HUEFS, HUFU, HUMC, HURB, IAC, ICN, INPA, IPA, JABU, JPB, K, MAC, MG, MUFAL, NY, PEUFR, PISF, R, RB, SP, SPF, UB, UEC, UFJF, UFP, UFRN and VEN collections (acronyms according to Thiers, 2023); and complemented with data from the literature (Taylor, 1989; Guedes et al., 2023).

Analyses of ancestral character state were carried out using the Bayesian binary MCMC method (BBM) as implemented in RASP v.4.3 (Yu et al., 2020) onto the majority-rule consensus tree generated by the Bayesian Inference of the combined dataset (plastid + nuclear) without outgroups. To account for uncertainties in tree topologies, the frequencies of ancestral ranges at nodes were averaged for all post-burn-in trees sampled in the BI analysis. The analyses were performed using default parameters in RASP, two MCMC chains were run simultaneously for 500,000 generations with sampling frequency every 1000 generations.

3. Results

3.1. Molecular datasets

This study generated 129 new sequences for *Utricularia*, which were combined with 72 previously published sequences (Jobson and Albert, 2002; Jobson et al., 2003; Müller and Borsch, 2005; Kondo and Shimai, 2006; Westermeier et al., 2017; Silva et al., 2018a, 2018b). The plastid matrix has a length of 3170 bp (*matK* region = 747 bp, *rpl20-rps12* = 872 bp, *rps16* intron = 1009 bp and *trnL-F* spacer = 542 bp) and the combined matrix has 4245 bp (ITS region = 1075 bp).

3.2. Phylogenetic inferences

Phylogenies retrieved to date suggested that *U. sect. Vesiculina* is sister to *U. sect. Setiscapella* + *Avesicaria*, however, our plastid and combined datasets (Figs. 1 and 2) strongly support a close relationship between *U. sect. Vesiculina* and *Sprucea* (RBS = 100 / PP = 1.0), and this clade placed as sister to the clade *U. sect. Steyermarkia* + *Setiscapella* + *Avesicaria*. The BI tree from the ITS dataset (Fig. 1) also showed this topology, although not supported (PP

= 0.52), and the ML tree (Supplementary Material: Fig. S1), in turn, placed *U. sect. Vesiculina* + *U. sect. Sprucea* as sister to *U. sect. Foliosa* (RBS = 46).

There were no other significantly conflicting topologies among trees generated by each approach in each matrix, except the incongruity in the placement of *U. sect. Avesicaria* recovered by the plastid and ITS datasets. The plastid tree (Fig. 1) retrieved *U. sect. Avesicaria* as sister to *U. pusilla* (RBS = 92 / PP = 0.94). On the other hand, the ITS tree (Fig. 1) recovered *U. sect. Avesicaria* as sister to a clade containing most members of *U. sect. Setiscapella* (RBS 98 = / PP = 1.0). Both plastid and ITS datasets support the close relationship between *U. flaccida* and *U. physoceras*, but these, in turn, emerged in unsupported clades as sister to the clade containing *U. sect. Avesicaria* + other members of *U. sect. Setiscapella*.

The ML and BI phylogenetic trees obtained from of the combined matrix (plastid + nuclear) were congruent in their topologies, with most clades well supported by bootstrap (RBS $\geq$ 85) and posterior probabilities (PP $\geq$ 0.90) (Fig. 2). The BI tree from the combined dataset recovered an unresolved topology with *U. sect. Steyermarkia* + *U. sect. Mirabiles* in a polytomy with *U. sect. Setiscapella* and *U. sect. Avesicaria*. Furthermore, *U. sect. Setiscapella* was recovered as non-monophyletic and it can be divided into two supported subclades: A consisting of *U. flaccida* and *U. physoceras* (RBS = 100 / PP = 1.0) and B containing the other members of *U. sect. Setiscapella* (*U. pusilla*, *U. trichophylla*, *U. nervosa*, *U. nigrescens*, *U. subulata* and *U. triloba*) (RBS = 33 / PP = 0.98). The clade B, in turn, is sister to *U. sect. Avesicaria*, which is composed by *U. neottiioides* and *U. oliveriana* (RBS = 100 / PP = 1.0).

However, the ML tree (Supplementary Material: Fig. S1) retrieved clade A as sister to the clade *U. sect. Steyermarkia* + *U. sect. Mirabiles*, although not supported (RBS = 55), and that group, in turn, as sister to B + *U. sect. Avesicaria* (RBS = 87). In all approaches and datasets, four taxa of clade B were retrieved as well-defined lineages with supported relationships (Figs. 1 and 2): *U. subulata* as sister to *U. triloba* and *U. nervosa* as sister to *U. nigrescens*, and these, in turn, as sister groups.

3.3. Ancestral State Reconstruction

Most characters yielded potential synapomorphies defining the clade B, *U. sect. Avesicaria* (*U. neottiioides* and *U. oliveriana*) (Figs. 3–5), such as the rheophytic life/growth form, traps with numerous dorsal setiform appendages, non-gibbous palate, obsolete spur, and obliquely ovoid seeds with elongate testa cells and smooth texture. While other characters states were potentially homoplastic for the rest of the taxa.

Terrestrial life/growth form was retrieved as the ancestral state for these taxa (Fig. 3A), and according to previous studies it is the ancestral state for the genus, with other states as apomorphies that have evolved independently many times among the *Utricularia* species (Müller and Borsch, 2005; Silva et al., 2018). The presence of pustulate leaves is an apomorphic trait that arose at least twice in these lineages (Fig. 3B). Traps with two dorsal, filiform, branched appendages is the plesiomorphic state (Fig. 3C), conserved in *U.* sect. *Steyermarkia* and *U.* sect. *Setiscapella*. The ancestral state for the color of corolla was possibly white (Fig. 3D), assuming two reversions, one in *U. neottiioides* and *U. oliveriana* (*U.* sect. *Avesicaria*) and the other in *U. heterochroma* Steyererm. (*U.* sect. *Mirabiles*).

The presence of blotches in the palate causing it to have a different color from the corolla is a plesiomorphic state lost in the lineage that originated *U.* sect. *Avesicaria* and most members of *U.* sect. *Setiscapella* (Fig. 4A). Whilst the non-gibbous palate arose in *U.* sect. *Avesicaria* (Fig. 4B). The ancestral spur was possibly conical with the other states apomorphic (Fig. 4C). Globose seeds with isodiametric testa cells are plesiomorphic states conserved in *U.* sect. *Steyermarkia* and *U.* sect. *Mirabiles* (Figs. 4D and 5A). And seed with smooth texture is a plesiomorphic state with reversion to *U.* sect. *Avesicaria* (Fig. 5B).

4. Discussion

Setiscapella was initially described as a genus by Barnhart (1916), comprising only *S. subulata* (L.) Barnh. (*U. subulata*) and, decades later, Komiya (1973) reduced it to a subgenus of *Utricularia*. Steyermark (1953) described *U. aureomaculata* and stated that it could be placed in the group of *Setiscapella*, together with *U. pusilla*, *U. nervosa*, *U. subulata* and *U. triloba*, based on the peltate bracts. Few years later, Taylor (1967) described *U. steyermarkii* stating that it is closely related to *U. aureomaculata* and *U. heterochroma*, based on the pustulate surface of the leaves and trap morphology.

In 1986, he made a new combination and new status as *U.* subgen. *U.* sect. *Setiscapella*, where he also described *U. physoceras*, including it in this section comprising eleven species (*U. aureomaculata*, *U. flaccida*, *U. physoceras*, *U. pusilla*, *U. nervosa*, *U. nigrescens*, *U. stanfieldii*, *U. steyermarkii*, *U. subulata*, *U. trichophylla* and *U. triloba*) (Taylor, 1986). Then, three years later, Taylor (1989) established section *Steyermarkia* segregating *U. aureomaculata* and *U. steyermarkii* from section *Setiscapella*, based on leaf and seed morphology: multinerved leaves and globose seeds with isodiametric testa cells in *U.* sect. *Steyermarkia*, and 1-nerved

leaves and obliquely ellipsoid seeds with very elongate testa cells in *U.* sect. *Setiscapella*. At last, the most recent addition to section *Setiscapella* was *U. jaramacaru* (Gonella et al., 2020).

Utricularia sect. *Setiscapella* sensu Taylor (1989) is non-monophyletic according to all phylogenetic trees retrieved so far, based on *matK* region, *rps16* intron and *trnL-F* spacer (Jobson and Albert, 2002; Jobson et al., 2003; Müller and Borsch, 2005; Westermeier et al., 2017; Silva et al., 2018a) and our combined and isolated datasets. According to our Bayesian estimates, the combined dataset do not resolve the relationships between *U.* sect. *Setiscapella* and *U.* sect. *Steyermarkia*, resulting in polytomy (Fig. 2). While in the ML analysis, *U.* sect. *Steyermarkia* + *U.* sect. *Mirabiles* are sister to *U. flaccida* + *U. physoceras*, although unsupported (RBS = 55). Furthermore, our combined dataset support the relationship of *U.* sect. *Avesicaria* as sister to the *U.* sect. *Setiscapella* subclade B (Fig. 2), containing *U. pusilla*, *U. trichophylla*, *U. nervosa*, *U. nigrescens*, *U. subulata* and *U. triloba*.

Members of *U.* sect. *Setiscapella* and *U.* sect. *Steyermarkia* are morphologically very similar (Figs. 2–6), sharing features such as ovoid traps with lateral entrance and bearing two dorsal, filiform, branched appendices, yellow corolla (with exception of *U. physoceras* and *U. jaramacaru*, white with pink blotches and white with pale yellow, respectively), trilobed lower corolla lip with gibbous palate (enclosing the reproductive organs) and globose capsules dehiscing by a ventral pore (Taylor, 1989; Guedes et al., 2023).

On the other hand, members of *U.* sect. *Avesicaria* show less morphological similarities with the aforementioned sections (Figs. 2–6), such as peltate bracts, absence of bracteoles, trilobed lower corolla lip. However, these rheophyte species are entirely white flowered, with a non-gibbous palate (exposing the reproductive organs), their traps have terminal entrance with ventral and/or dorsal setiform appendices, their capsules are ellipsoid and seeds are viscid with elongate testa cells (Taylor, 1989; Guedes et al., 2023). Therefore, considering such morphological distinctiveness and its phylogenetic position, we recognize *U.* sect. *Avesicaria* as a natural group.

Our results also point out to *U. flaccida* and *U. physoceras* as genetically and morphologically distant from the other members of *U.* sect. *Setiscapella*. *Utricularia flaccida* shares morphological traits with *U. aureomaculata* and *U. steyermarkii* (*U.* sect. *Steyermarkia*) (Figs. 2–6), such as lithophytic life/growth form, pustulate adaxial surface of the leaves (due to the presence of large stomata, Fig. 6B), palate with blotches of different color from the corolla and cylindrical spur, shorter than the lower lip, with non-acute apex (rounded, retuse or

truncate). The latter two traits, also shared with *U. physoceras* and *U. jaramacaru* (Taylor, 1989; Gonella et al., 2020; Guedes et al., 2023). Which led us to propose a new sectional division to accommodate *U. flaccida*, *U. physoceras* and *U. jaramacaru* (discussed further).

Regarding improvements on taxonomic sampling, *U. physoceras*, endemic to Pará state in Brazil, and *U. trichophylla*, with Neotropical distribution, had their first DNA sequences generated in this study. *Utricularia trichophylla*, in turn, is sister to *U. pusilla* based on our combined and ITS datasets (Figs. 1 and 2). In addition, *U. nigrescens* and *U. pusilla* had only *matK* sequences published (Westermeier et al., 2017) and here we generated sequences for other markers (except *rpl20-rps12* for *U. nigrescens*). Moreover, *U. flaccida* was previously sampled for only three plastid markers (GenBank accession numbers: AF531830.1, AF482569.1, AF482644.1), and these accessions are apparently from two distinct populations from Bahia state in Brazil (Jobson and Albert, 2002; Müller and Borsch, 2005). At that time, the distribution of this species was known to be restricted to the Chapada Diamantina highlands, in Bahia state, and recently it has become known to also occur in Ceará and Sergipe states, being endemic to northeastern Brazil (Guedes et al., 2018; Guedes and Alves, 2020, Guedes and Matias, 2020).

The populations from Ceará (FMG 154 and 155) and Sergipe states (FMG 123) are more closely related to each other than with the populations from Bahia state (VFOM 1683, VFOM P53 and GB), which is shown in our individual and combined datasets (Figs. 1 and 2). Individuals from populations observed in Ceará and Sergipe are much smaller than the ones from Bahia, inflorescences are considerably shorter, less flowered, and with slightly smaller corollas. This variation may be correlated with different selective pressures, once populations from Ceará and Sergipe are under the climate regime of Atlantic Forest phytophysiognomies, while those from Bahia are under conditions of Cerrado phytophysiognomies (Guedes et al., 2018; Guedes and Alves, 2020; Guedes and Matias, 2020).

5. Proposal for new sectional division

Taylor (1989) distinguished section *Setiscapella* from all other sections of the genus based on a combination of characters as mentioned above, but in his monograph he stated that the obliquely ellipsoid seeds, ridged, with very elongate testa cells are unique in the genus. Here, we delimit section *Setiscapella* (Figs. 1, 2 subclade B and 3) as always possessing a yellow corolla with a palate of the same color as the corolla and a subulate spur, as long as, longer or twice as long as the lower lip, with apex acute, bi- or quadrifid. Whereas the subclade A (Figs. 1–3) comprising section *Diversicolor*, endemic to Brazil, always possessing a palate

with different color from the corolla (blotches) and a cylindrical spur, shorter than or as long as the lower lip, with apex rounded or truncate.

Utricularia* section *Diversicolor Guedes and Alves, *sect. nov.* (Fig. 6A–I).

Type: *Utricularia flaccida* A.DC. Prodr. Syst. Nat. Reg. Veg. 8, 17. 1844.

Annual herbs. Terrestrial, helophyte or lithophyte. Leaves aerial, laminar, simple or branched, 1-nerved, adaxial surface pustulate or not. Traps ovoid, stalked, glabrous, entrance lateral, with two dorsal, filiform branched or very short denticulate appendages. Inflorescence racemose, geniculate, erect, lax; scape flexible, slender, glabrous. Scales and bracts similar, peltate, margins entire, sterile bracts absent. Bracteoles absent. Pedicels cylindrical, glabrous, ascending in fruits. Sepals heteromorphic, margins entire, flat, non-hyaline, nerves inconspicuous or conspicuous, non-prominent, not converging to the apices. Corolla glabrous, yellow with brown/orange blotches on the palate, white with a pale yellow palate, or white/pale pink with pink blotches on the palate; upper lip entire or bilobed, lower lip flat, crenate, trilobed or shallowly trilobed; palate gibbous, with a different color from the corolla; spur cylindrical, straight, parallel to the lower lip, shorter than or as long as the lower lip, apex rounded or truncate. Capsule globose, dehiscent by a ventral pore. Seeds obliquely ellipsoid, ridged, with very elongate testa cells.

Etymology: The epithet “*diversicolor*” refers to the different color of the palate in relation to the rest of the corolla.

Distribution: All species are endemic to Brazil. *Utricularia flaccida* is endemic to northeastern Brazil, in Ceará (known only from few populations in the Ibiapaba plateau, in Montane Dense Ombrophilous Forest), Sergipe (known only from few populations in the Serra de Itabaiana, in an ecotone of Submontane Dense Ombrophilous Forest and Seasonal Deciduous Forest) and Bahia states (several populations along the Chapada Diamantina highlands, in *campos rupestres* vegetation). Whereas *U. jaramacaru* and *U. physoceras* are endemic to northern Brazil, in Pará state, the first one known only from two populations in the Campos do Ariramba (*campinarana* vegetation) and the second known from few populations in the mountains of Carajás (*cangas* vegetation) (Mota and Zappi, 2018; Guedes et al., 2018, 2023, 2022; Guedes and Matias, 2020; Guedes and Alves, 2020; Gonella et al., 2020).

Key to *Utricularia* section *Diversicolor*

1. Leaves pustulate; corolla yellow; spur with apex truncate..... *U. flaccida*

- Leaves non-pustulate; corolla white or pale pink; spur with apex rounded 2
2. Traps with two dorsal, very short, denticulate appendages; corolla white with pale yellow palate, upper lip bilobed *U. jaramacaru*
- Traps with two dorsal, filiform, branched appendages; corolla white or pale pink with pink blotches on the palate *U. physoceras*

Utricularia* section *Setiscapella (Barnh.) P.Taylor (Fig. 6J –V).

Type: *Utricularia subulata* L., Sp. Pl. 1, 18. 1753.

Annual herbs. Terrestrial or helophyte. Leaves aerial, laminar, simple or branched, 1-nerved, adaxial surface non-pustulate. Traps ovoid, stalked, glabrous, entrance lateral, with two dorsal, filiform, branched appendages. Inflorescence racemose, geniculate or straight, erect, lax; scape flexible, slender, glabrous or pubescent below. Scales and bracts similar or not, peltate, margins entire (lowermost scales, sometimes, ciliate), sterile bracts, when present (*U. pusilla* and *U. stanfieldii*), on the raceme axis (between the pedicels). Bracteoles absent. Pedicels cylindrical, glabrous, ascending in fruits. Sepals homo- or heteromorphic, margins entire, flat, non-hyaline, nerves inconspicuous or conspicuous, prominent or not, converging to the apices or not. Corolla glabrous, entirely yellow; upper lip entire, lower lip flat, trilobed, shallowly or deeply trilobed; palate gibbous, same color as the corolla; spur subulate, straight or curved, parallel to the lower lip, as long as, longer or twice as long as the lower lip, apex acute, bi- or quadrifid. Capsule globose, dehiscent by a ventral pore. Seeds obliquely ellipsoid, ridged, with very elongate testa cells.

Distribution: *U. subulata* is almost Pantropical, *U. stanfieldii* is endemic to West Africa (Sierra Leone, Liberia, Ivory Coast, Togo, Nigeria), and the others are Neotropical (*U. pusilla*, *U. nervosa*, *U. nigrescens*, *U. trichophylla* and *U. triloba*). All of them are found in wet sandy savannas, wetter portions of rocky outcrops, near waterfalls from lowland to highland vegetation (Taylor, 1989; Guedes et al., 2023).

Key to *Utricularia* section *Setiscapella*

1. Sterile bracts on the raceme axis (between the pedicels) 2
- Sterile bracts absent on the raceme axis 3
2. Leaves narrowly linear; sepals with nerves prominent, converging to the apices; spur longer than the lower corolla lip *U. stanfieldii*

- Leaves obovate or spatulate; sepals with nerves prominent, not converging to the apices; spur twice as long as the lower corolla lip *U. pusilla*
3. Spur twice as long as the lower corolla lip *U. nigrescens*
- Spur as long as or longer than the lower corolla lip 4
4. Inflorescence straight; sepals with nerves inconspicuous *U. trichophylla*
- Inflorescence geniculate; sepals with nerves conspicuous 5
5. Sepals with nerves prominent, converging to the apices; lower corolla lip shallowly trilobed *U. triloba*
- Sepals with nerves prominent or not, not converging to the apices; lower corolla lip deeply trilobed 6
6. Scape pubescent below and glabrous above; corolla >1 cm long *U. nervosa*
- Scape glabrous; corolla $\leq$ 1 cm long *U. subulata*

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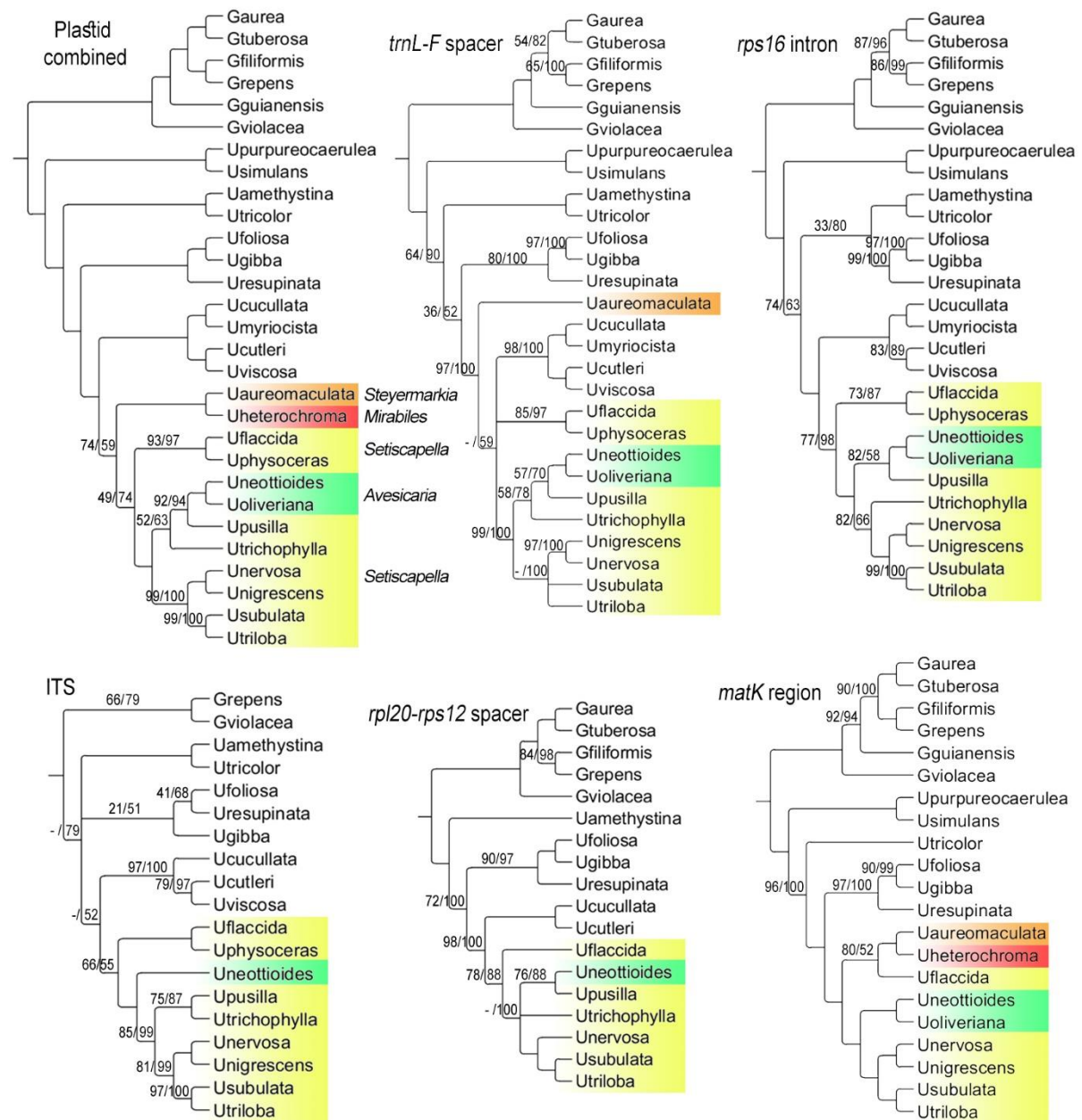


Figure 1. Majority-rule consensus trees obtained from Bayesian Inference (BI) of the plastid and individual datasets. Support values above branches indicate likelihood bootstrap (RBS) and posterior probabilities (PP), respectively, and - denotes clades absent in the Maximum Likelihood (ML) topology.

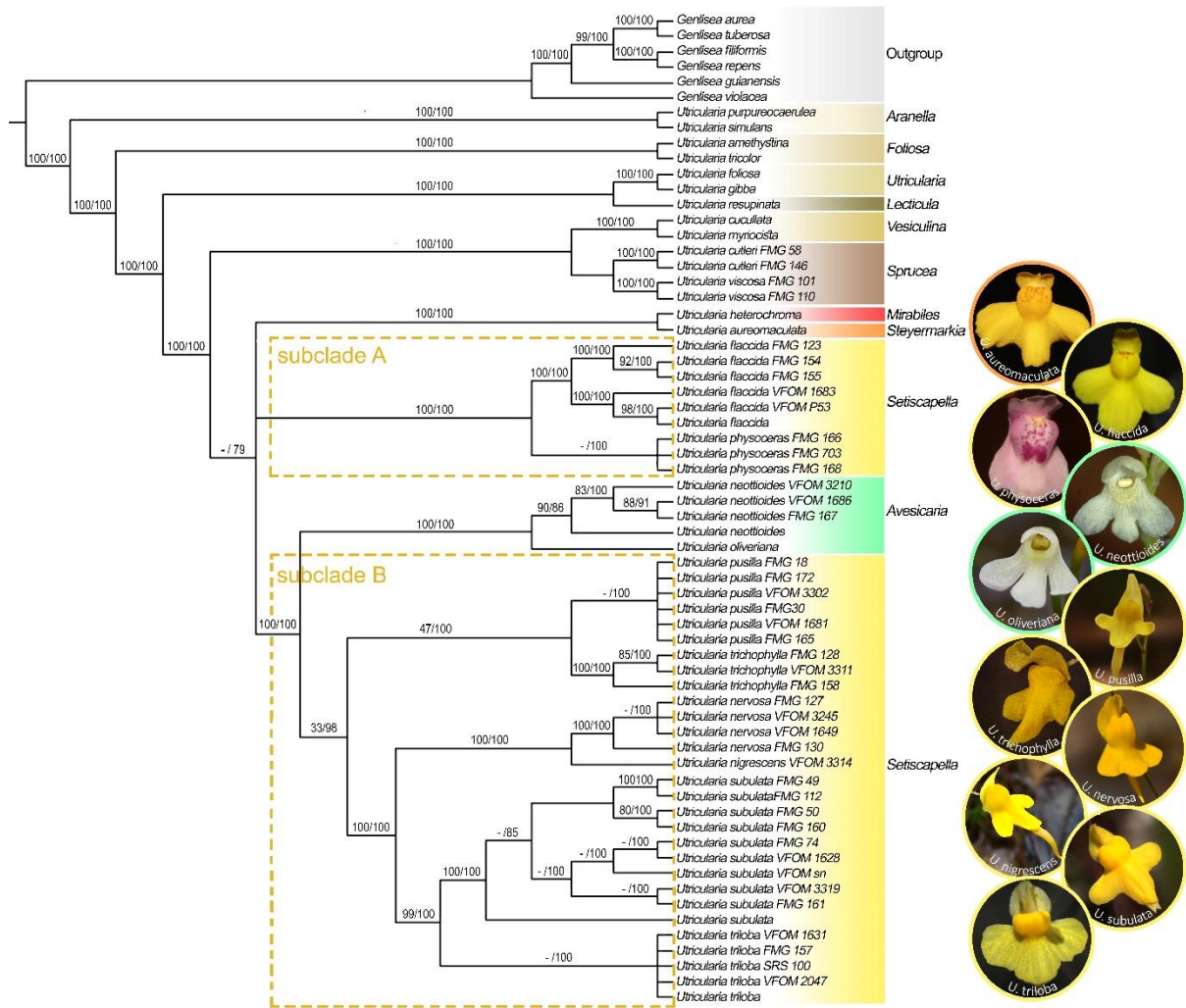


Figure 2. Majority-rule consensus tree obtained from Bayesian Inference (BI) of the combined dataset based on sequences of ITS, *matK*, *rpl20-rps12* spacer, *rps16* intron and *trnL-F* spacer. Support values above branches indicate likelihood bootstrap (RBS) and posterior probabilities (PP), respectively, and - denotes clades absent in the Maximum Likelihood (ML) topology. Photos by Nicole Rebbert, Caroline Andrino, Andreas Fleischmann, Hugo Dolsan, Gabriel Garcia and the present authors.

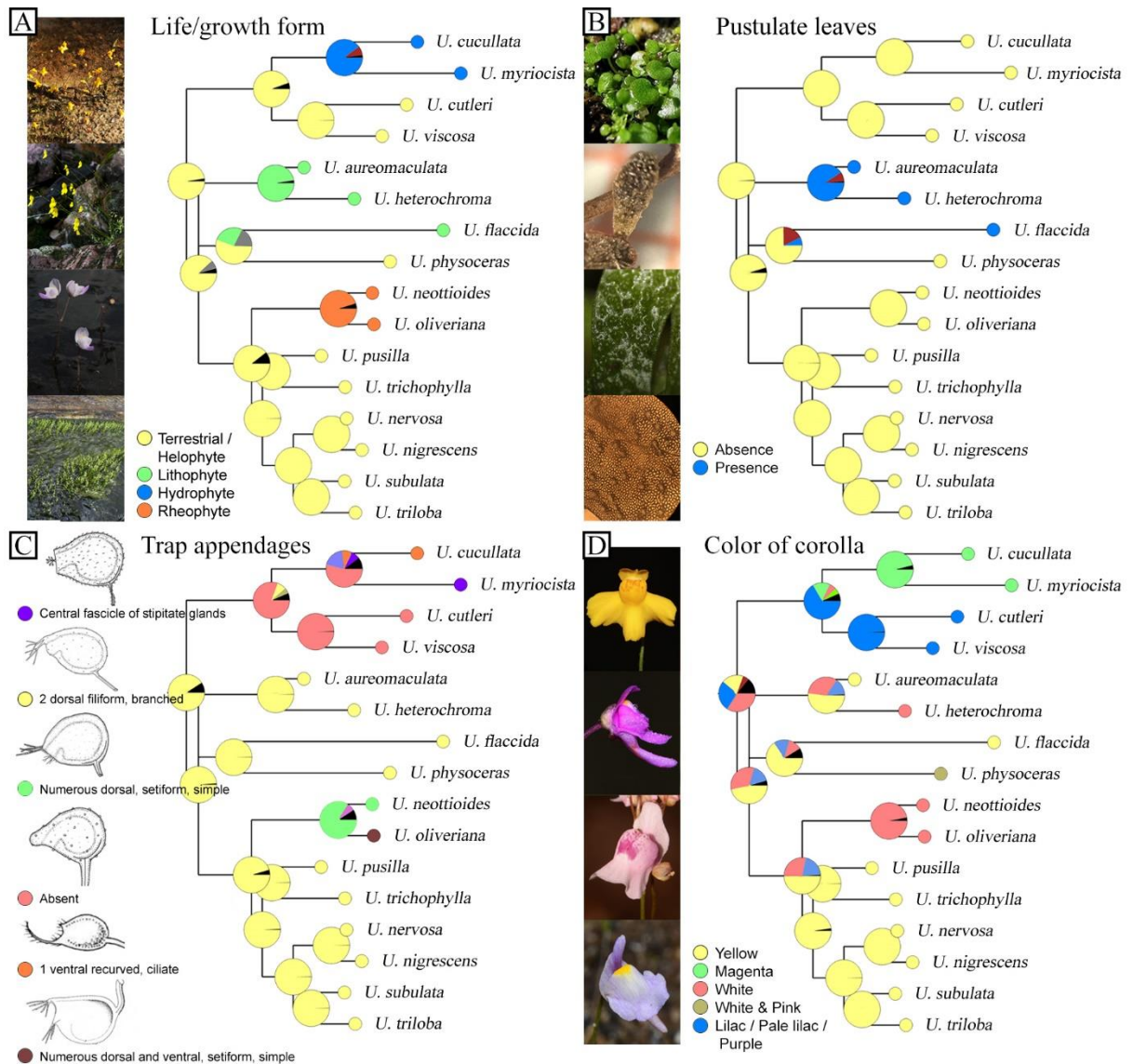


Figure 3. Character tracing history mapped onto the simplified Bayesian Inference (BI) consensus tree, using Bayesian Binary MCMC (BBM) in RASP, including only *U. sect. Vesiculina*, *U. sect. Sprucea*, *U. sect. Steyermarkia*, *U. sect. Mirabiles*, *U. sect. Setiscapella* and *U. sect. Avesicaria*. A. Character 1: life/growth form; B. Character 2: pustulate leaves; C. Character 3: trap appendages; D. Character 4: color of corolla. Photos A by Felipe M. Guedes, Sergio Guzman and Pedro Gabriel, B by Nicole Rebbert and Felipe M. Guedes, C drawings by Felipe M. Guedes and Taylor (1989), and D by Nicole Rebbert, Pedro Lage Viana, Zenilton Miranda and Felipe M. Guedes.

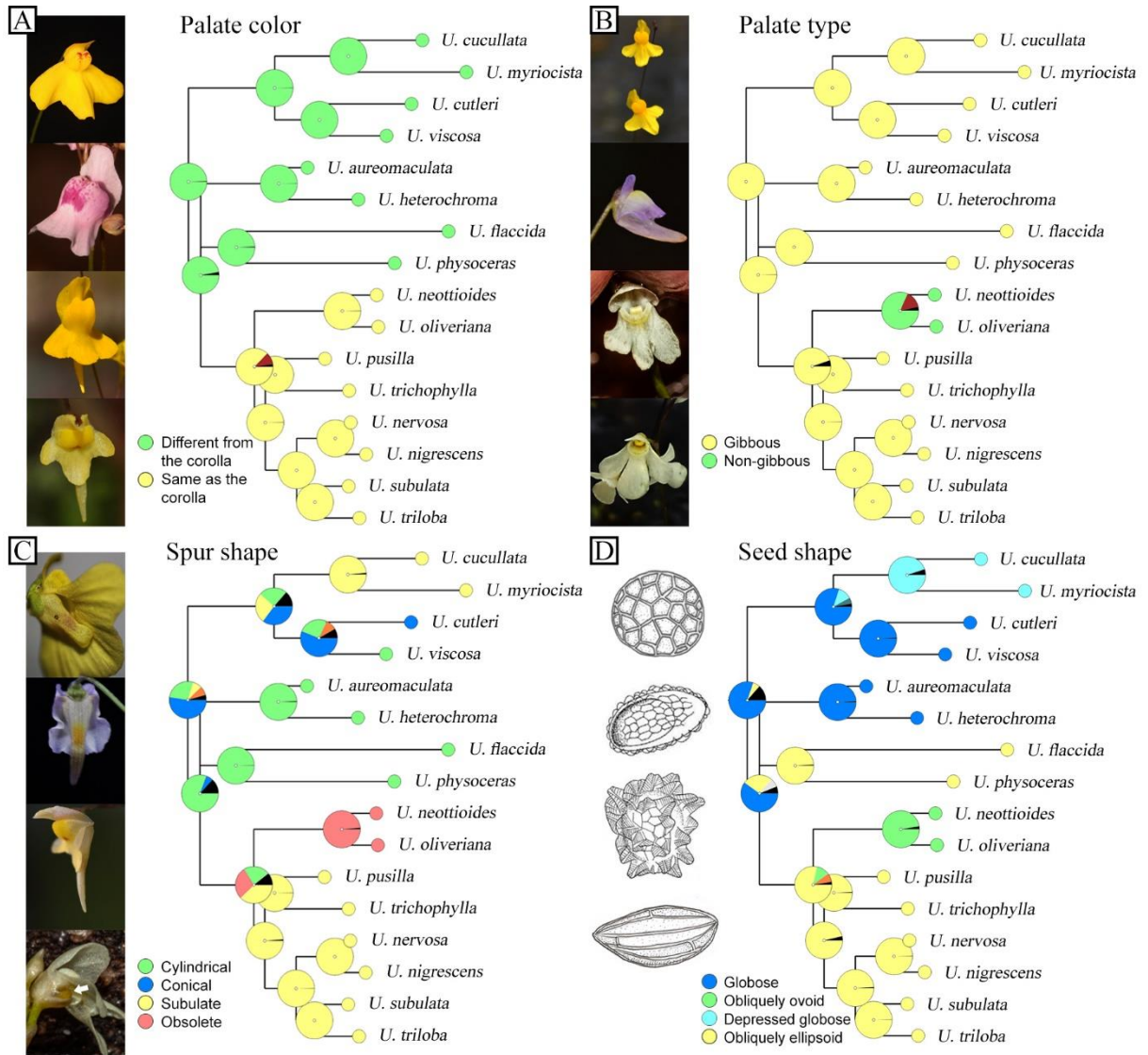


Figure 4. Character tracing history mapped onto the simplified Bayesian Inference (BI) consensus tree, using Bayesian Binary MCMC (BBM) in RASP, including only *U. sect. Vesiculina*, *U. sect. Sprucea*, *U. sect. Steyermarkia*, *U. sect. Mirabiles*, *U. sect. Setiscapella* and *U. sect. Avesicaria*. A. Character 5: palate color; B. Character 6: palate; C. Character 7: spur shape; D. Character 8: seed shape. Photos A by Richard Grows, Caroline Andrino, Gabriel Garcia and Juliano Fabricante, B by Felipe. M Guedes, Gabriel Garcia, Hugo Dolsan and Ricardo Pereira, C by Felipe M. Guedes, Juliano Fabricante and Hugo Dolsan, and D drawings by Felipe M. Guedes and Taylor (1989).

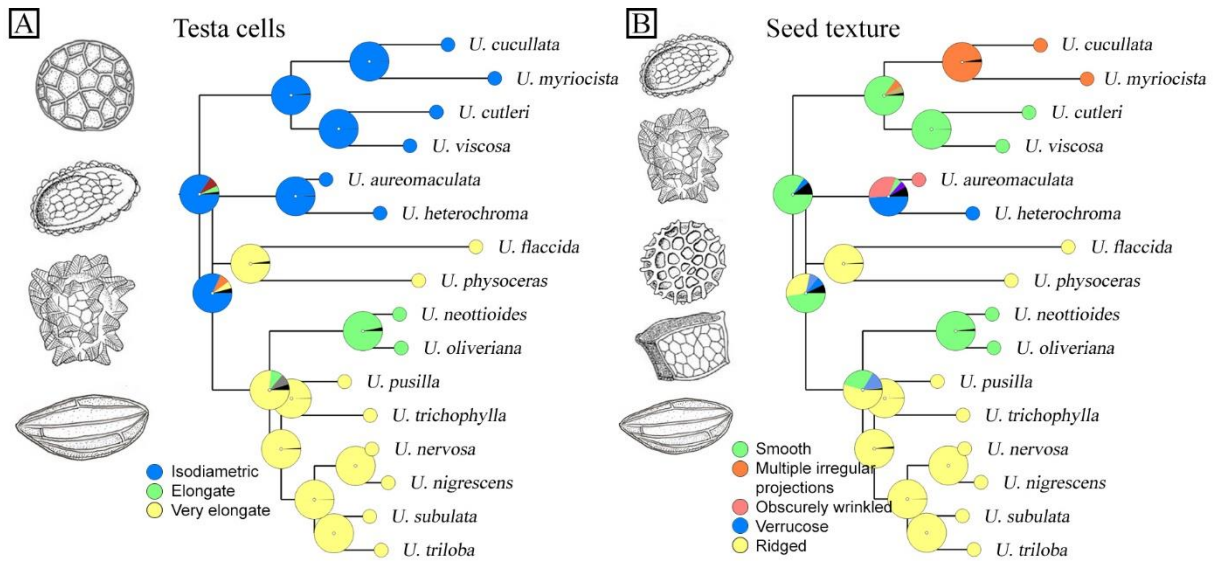


Figure 5. Character tracing history mapped onto the simplified Bayesian Inference (BI) consensus tree, using Bayesian Binary MCMC (BBM) in RASP, including only *U.* sect. *Vesiculina*, *U.* sect. *Sprucea*, *U.* sect. *Steyermarkia*, *U.* sect. *Mirabiles*, *U.* sect. *Setiscapella* and *U.* sect. *Avesicaria*. A. Character 9: seed testa cells; B. Character 10: seed texture. Drawings by Felipe M. Guedes and Taylor (1989).

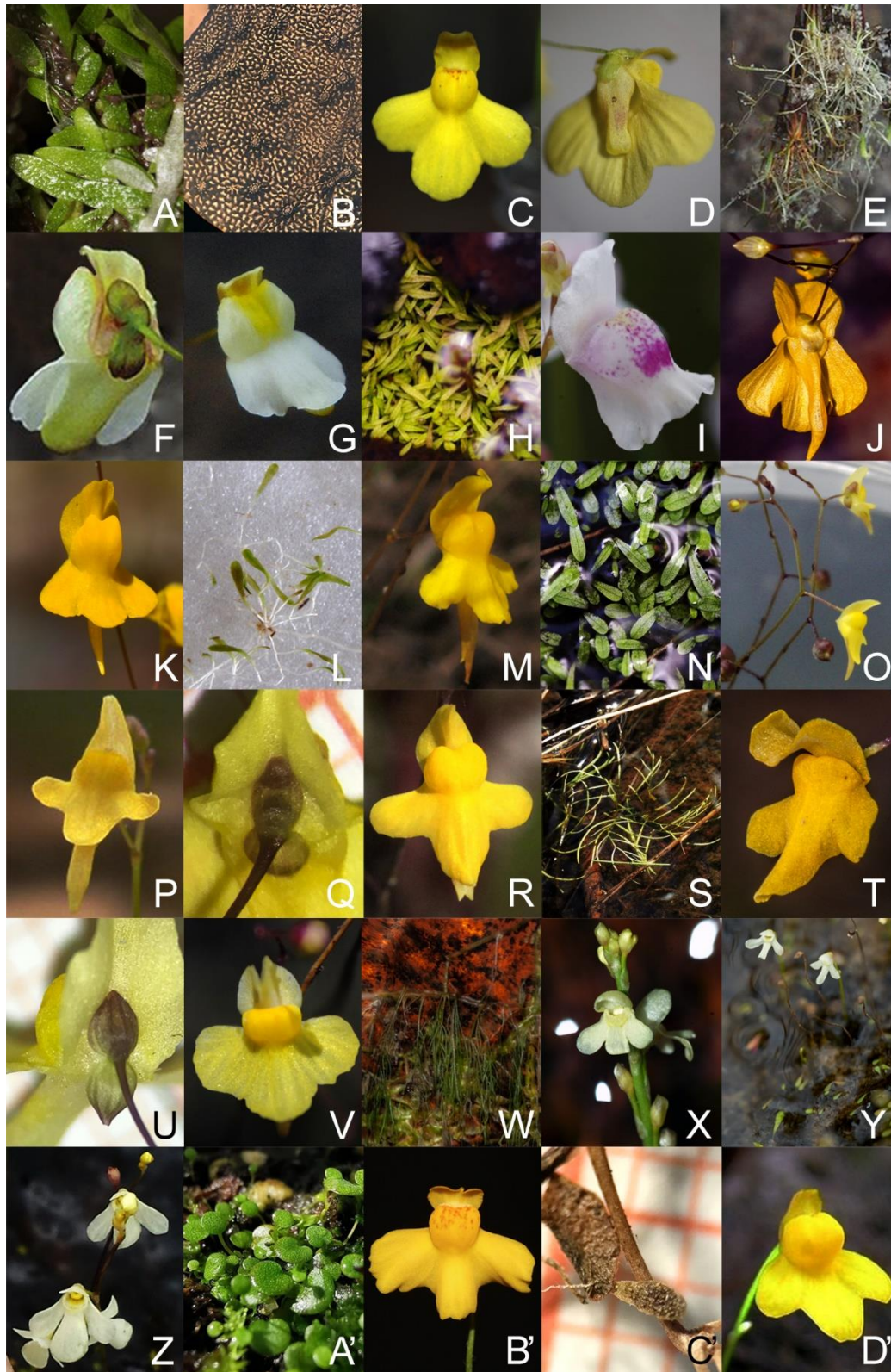


Figure 6. A-K. *Utricularia* section *Diversicolor*; A-D. *U. flaccida*; E-G. *U. jaramacaru*; H-I. *U. physoceras*. J-V. *Utricularia* section *Setiscopella*; J-K. *U. nervosa*; L-M. *U. nigrescens*; N-P. *U. pusilla*; Q-R. *U. subulata*; S-T. *U. trichophylla*; U-V. *U. triloba*. W-Z. *Utricularia* section *Avesicaria*; W-X. *U. neottioides*; Y-Z. *U. oliveriana*. A'-D'. *Utricularia* section *Steyermarkia*; A'-B'. *U. aureomaculata*; C'-D'. *U. steyermarkii*. Photos A-D, O-R, U, V, C' – F.M. Guedes; E-G – C.O. Andrino; H, I – P.L. Viana; J, T, W, X – H. Dolsan; K – G.S. Garcia; L, M – M.F. Cardoso; N – J. Fabricante; S – S. Guzmán; Y, Z – M. Wrazidlo; A' – D.A. Piccione; B' – N. Rebbert; D' – F. Rivadavia.

SUPPLEMENTARY MATERIAL

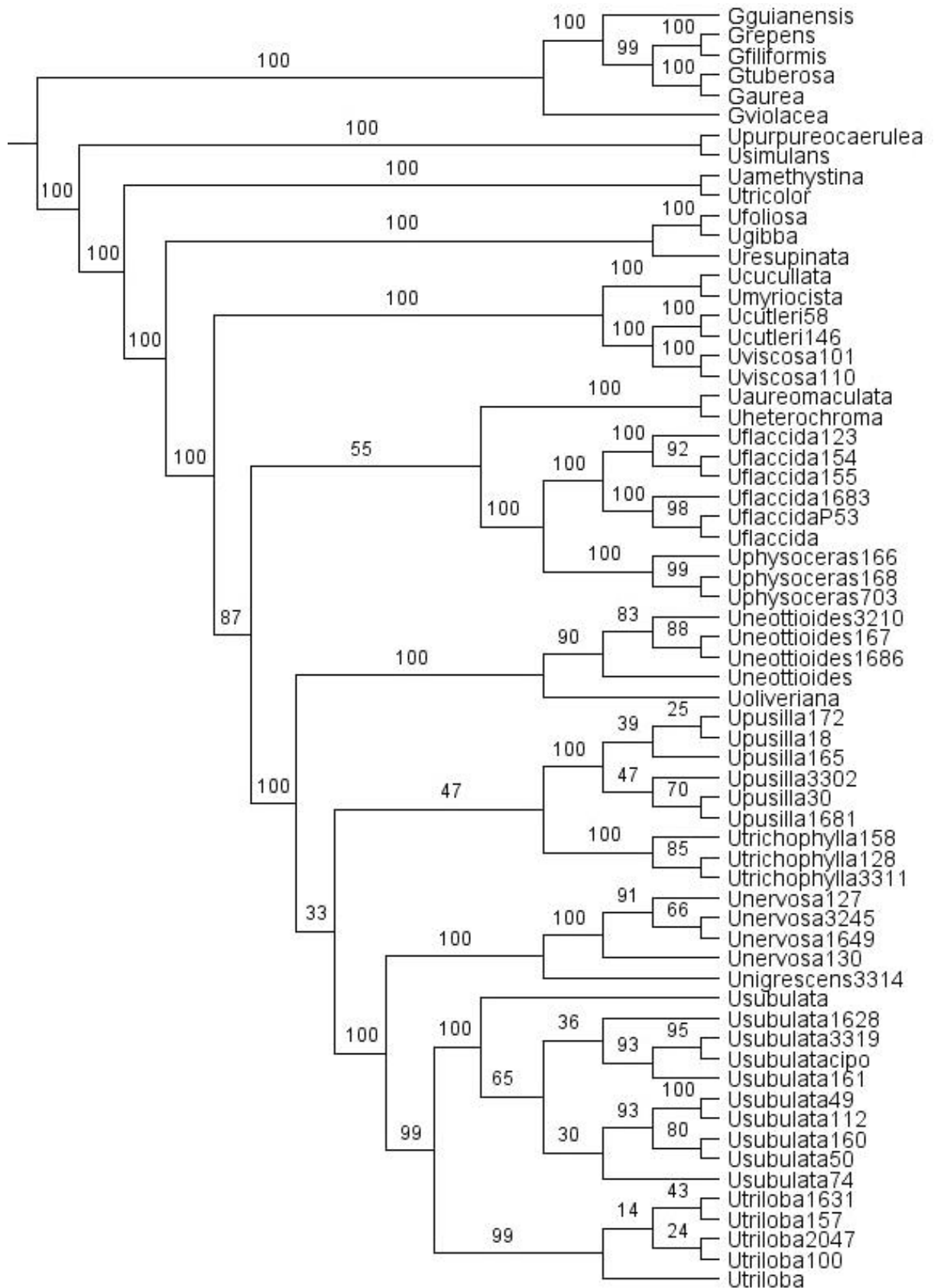


Figure S1. Maximum Likelihood (ML) tree obtained from the complete dataset based on sequences of ITS, *matK*, *rpl20-rps12* spacer, *rps16* intron and *trnL-F* spacer. Support values above branches indicate likelihood rapid bootstrap (RBS).

Table 1. Lentibulariaceae species included in this study and accessions data from GenBank (NCBI), infrageneric classification according to Fleischmann (2012), Taylor (1989), Müller and Borsch (2005) and Guedes et al. (2023). “-” indicate unavailability of sequence in GenBank or it was not possible to be generated in this study.

Species	Infrageneric classification	Voucher	<i>rps16</i> intron	<i>trnL-F</i> spacer	<i>rpl20-rps12</i> spacer	<i>matK</i> region	ITS region
<i>Genlisea aurea</i> A.St.-Hil.	<i>G.</i> subgen. <i>G.</i> sect. <i>Genlisea</i>	F. Rivadavia 1182 (SPF); W. Thomas 4862 (NY)	FN641746.1	AF482614.1	MF593121.1	AF531814.1	-
<i>Genlisea filiformis</i> A.St.-Hil.	<i>G.</i> subgen. <i>G.</i> sect. <i>Genlisea</i>	F. Rivadavia 2106 (SPF); V.F.O. Miranda 1962 (JABU)	FN641749.1	MF593122.1	MF593122.1	MF593122.1	-
<i>Genlisea guianensis</i> N.E.Br.	<i>G.</i> subgen. <i>G.</i> sect. <i>Genlisea</i>	F. Rivadavia 2655 (SPF); F. Rivadavia 971 (SPF)	FN641742.1	AF482615.1	-	FN641696.1	-
<i>Genlisea repens</i> Benj.	<i>G.</i> subgen. <i>G.</i> sect. <i>Genlisea</i>	F. Rivadavia 1876 (SPF); V.F.O. Miranda 1965 (JABU)	FN641751.1	MF593124.1	MF593124.1	MF593124.1	AB212115.1
<i>Genlisea tuberosa</i> Rivadavia, Gonella & A.Fleischm.	<i>G.</i> subgen. <i>G.</i> sect. <i>Genlisea</i>	F. Rivadavia 2611 (SPF); V.F.O. Miranda 2001 (JABU)	KF952604.1	MF593125.1	MF593125.1	MF593125.1	-
<i>Genlisea violacea</i> A.St.-Hil.	<i>G.</i> subgen. <i>Tayloria</i>	F. Rivadavia 2560 (SPF); R.W. Jobson 294 (BRI)	FN641728.1	AF482616.1	MG027790.1	MF593126.1	MG027715.1
<i>Utricularia amethystina</i> Salzm. ex A.St.-Hil. & Girard	<i>U.</i> subgen. <i>U.</i> sect. <i>Foliosa</i>	F. Rivadavia 2109B (SPF); V.F.O. Miranda 1644 (JABU)	MH030266.1	MH030174.1	MG027793.1	-	MH754710.1
<i>Utricularia aureomaculata</i> Steyerm.	<i>U.</i> subgen. <i>U.</i> sect. <i>Steyermarkia</i>	cult. A. Fleischmann,	-	MF765558.1	-	MF765532.1	-
<i>Utricularia cucullata</i> A.St.- Hil. & Girard	<i>U.</i> subgen. <i>U.</i> sect. <i>Vesiculina</i>	F. Rivadavia 941 (SPF); V.F.O. Miranda 1651 (JABU)	AF482566.1	AF482640.1	MG027832.1	-	MG027772.1
<i>Utricularia cutleri</i> Steyerm.	<i>U.</i> subgen. <i>U.</i> sect. <i>Sprucea</i>	F.M. Guedes 58, 146 (UFP, UFRN)	Generated in this study	Generated in this study	Generated in this study	-	Generated in this study
<i>Utricularia flaccida</i> A.DC.	<i>U.</i> subgen. <i>U.</i> sect. <i>Setiscopella</i>	F.M. Guedes 123, 154, 155 (UFP); V.F.O. Miranda 1683, P53 (JABU); R.W. Jobson 169 (BRI)	AF482569.1; Generated in this study	AF482644.1; Generated in this study	Generated in this study	Generated in this study	Generated in this study
<i>Utricularia foliosa</i> L.	<i>U.</i> subgen. <i>U.</i> sect. <i>Utricularia</i>	S.R. Silva 04 (JABU); F. Rivadavia & A. Fleischmann Z68 (M)	MG027706.1	MF765564.1	MG027826.1	MF765538.1	MG027754.1
<i>Utricularia gibba</i> L.	<i>U.</i> subgen. <i>U.</i> sect. <i>Utricularia</i>	F. Rivadavia 974 (SPF); R.W. Jobson 1861 (NSW)	AF482572.1	AF482648.1	MH937553.1	KC997777.1	MT248957.1

<i>Utricularia heterochroma</i> Steyerl.	<i>U. subgen. U. sect. Mirabiles</i>	cult. A. Fleischmann,	-	-	-	MF765533.1	-
<i>Utricularia myriocista</i> A.St.-Hil. & Girard	<i>U. subgen. U. sect. Vesiculina</i>	M. Jansen-Jacobs 4717 (NY)	AF482584.1	AF482660.1	-	-	-
<i>Utricularia neottiioides</i> A.St.-Hil. & Girard	<i>U. subgen. U. sect. Avesicaria</i>	V.F.O. Miranda 1307, 1628, 1629, 3210 (JABU); F. Rivadavia 870 (SPF)	AF482587.1; Generated in this study	AF482663.1; Generated in this study	Generated in this study	KX604194.1	MG027759.1; Generated in this study
<i>Utricularia nervosa</i> G.Weber ex Griseb.	<i>U. subgen. U. sect. Setiscapella</i>	F.M. Guedes 127, 130 (UFP); V.F.O. Miranda 1649, 3245 (JABU); cult. A. Fleischmann	Generated in this study	Generated in this study	Generated in this study	Generated in this study	Generated in this study
<i>Utricularia nigrescens</i> Sylven	<i>U. subgen. U. sect. Setiscapella</i>	V.F.O. Miranda 3314 (JABU); cult. A. Fleischmann	Generated in this study	Generated in this study	-	Generated in this study	Generated in this study
<i>Utricularia oliveriana</i> Steyerl.	<i>U. subgen. U. sect. Avesicaria</i>	R. Kral 71731 (NY); cult. A. Fleischmann	AF482590.1	AF482666.1	-	MF765530.1	-
<i>Utricularia physoceras</i> P. Taylor	<i>U. subgen. U. sect. Setiscapella</i>	F.M. Guedes 166, 168 (UFP)	Generated in this study	Generated in this study	-	-	Generated in this study
<i>Utricularia purpureocaerulea</i> A.St.-Hil. & Girard	<i>U. subgen. Bivalvaria sect. Aranella</i>	F. Rivadavia 663 (SPF)	AF482594.1	AF482670.1	-	MF765511.1	-
<i>Utricularia pusilla</i> Vahl	<i>U. subgen. U. sect. Setiscapella</i>	F.M. Guedes 18, 30 (UFP), 165 (JABU); V.F.O. Miranda 1681, 3302 (JABU); C. Alcantara 172 (UFP)	Generated in this study	Generated in this study	Generated in this study	Generated in this study	Generated in this study
<i>Utricularia resupinata</i> B.D.Greene ex Bigelow	<i>U. subgen. U. sect. Lenticula</i>	B.R. Keener 1948 (UNA); cult. A. Fleischmann	AF488527.1	AF488533.1	MG027828.1	MF765542.1	MT248965.1
<i>Utricularia simulans</i> Pilg.	<i>U. subgen. Bivalvaria sect. Aranella</i>	F. Rivadavia 914 (SPF); cult. A. Fleischmann	AF482597.1	AF482674.1	-	MF765513.1	-
<i>Utricularia subulata</i> L.	<i>U. subgen. U. sect. Setiscapella</i>	F.M. Guedes 49, 50, 74, 112, 160, 161, 706 (UFP); V.F.O. Miranda s.n., 1628, 3319 (JABU); S. Orzell 16213 (NY)	Generated in this study	AF482676.1; Generated in this study	MG027843.1; Generated in this study	AF482676.1; Generated in this study	Generated in this study
<i>Utricularia trichophylla</i> Spruce ex Oliv.	<i>U. subgen. U. sect. Setiscapella</i>	F.M. Guedes 128, 158 (UFP); V.F.O. Miranda 3311 (JABU)	Generated in this study	Generated in this study	Generated in this study	-	Generated in this study

<i>Utricularia tricolor</i> A.St.-Hil.	<i>U.</i> subgen. <i>U.</i> sect. <i>Foliosa</i>	G. Heiden 1764 (SPF); V.F.O. Miranda 2043 (JABU)	MH030251.1	MH030161.1	-	KX604209.1	KY689720.1
<i>Utricularia triloba</i> Benj.	<i>U.</i> subgen. <i>U.</i> sect. <i>Setiscapella</i>	S.R. Silva 100 (JABU); F.M. Guedes 157 (UFP); V.F.O. Miranda 1631, 2047 (JABU); F.Rivadavia 1001 (SPF)	AF482601.1; Generated in this study	AF482678.1; Generated in this study	Generated in this study	KX604206.1	Generated in this study
<i>Utricularia viscosa</i> Spruce ex Oliv.	<i>U.</i> subgen. <i>U.</i> sect. <i>Sprucea</i>	F.M. Guedes 100, 110 (UFP)	Generated in this study	Generated in this study	-	-	Generated in this study

Table 2. *Utricularia* specimens used for DNA extraction to generate sequences in this study.

Species	Section	Voucher	Locality (municipality, state in Brazil)
<i>U. cutleri</i> Steyererm.	<i>Sprucea</i>	F.M. Guedes 58	Maxaranguape, Rio Grande do Norte
		F.M. Guedes 146	Nísia Floresta, Rio Grande do Norte
<i>U. flaccida</i> A.DC.	<i>Setiscapella</i>	F.M. Guedes 123	Areia Branca, Sergipe
		F.M. Guedes 154	Ubajara, Ceará
		F.M. Guedes 155	Ibiapina, Ceará
		V.F.O. Miranda 1683	Ibicoara, Bahia
		V.F.O. Miranda P53	Andaraí, Bahia
<i>U. neottiioides</i> A.St.-Hil. & Girard	<i>Avesicaria</i>	F.M. Guedes 167	Carajás, Pará
		V.F.O. Miranda 1686	Rio de Contas, Bahia
		V.F.O. Miranda 3210	Santana do Riacho, Minas Gerais
<i>U. nervosa</i> G.Weber ex Benj.	<i>Setiscapella</i>	F.M. Guedes 127	Araraquara, São Paulo
		F.M. Guedes 130	Cajuru, São Paulo
		V.F.O. Miranda 1649	Itirapina, São Paulo
		V.F.O. Miranda 3245	Ibitipoca, Minas Gerais
<i>U. nigrescens</i> Sylvén	<i>Setiscapella</i>	V.F.O. Miranda 3314	Sonora, Mato Grosso do Sul
<i>U. physoceras</i> P.Taylor	<i>Setiscapella</i>	F.M. Guedes 166	Carajás, Pará
		F.M. Guedes 168	Carajás, Pará
		C.O. Andrino 703	Carajás, Pará
<i>U. pusilla</i> Vahl	<i>Setiscapella</i>	F.M. Guedes 18	Igarassu, Pernambuco
		F.M. Guedes 30	Gravatá, Pernambuco
		F.M. Guedes 165	Torrinha, São Paulo
		C. Alcantara 172	Alto Paraíso de Goiás, Goiás
		V.F.O. Miranda 1681	Ibicoara, Bahia
		V.F.O. Miranda 3302	Cassilândia, Mato Grosso do Sul
<i>U. subulata</i> L.	<i>Setiscapella</i>	F.M. Guedes 49	Buíque, Pernambuco
		F.M. Guedes 50	Rio do Fogo, Rio Grande do Norte
		F.M. Guedes 74	Mamanguape, Paraíba
		F.M. Guedes 112	Bonito, Pernambuco
		F.M. Guedes 160	Mamanguape, Paraíba
		F.M. Guedes 161	Mamanguape, Paraíba
		V.F.O. Miranda sn.	Santana do Riacho, Minas Gerais
		V.F.O. Miranda 1628	Delfinópolis, Minas Gerais
		V.F.O. Miranda 3319	Sonora, Mato Grosso do Sul
<i>U. trichophylla</i> Spruce ex Oliv.	<i>Setiscapella</i>	F.M. Guedes 128	Araraquara, São Paulo
		F.M. Guedes 158	Mamanguape, Paraíba
		V.F.O. Miranda 3311	Sonora, Mato Grosso do Sul
<i>U. triloba</i> Benj.	<i>Setiscapella</i>	S.R. Silva 100	Cássia dos Coqueiros, São Paulo
		F.M. Guedes 157	Mamanguape, Paraíba
		V.F.O. Miranda 1631	Santana do Riacho, Minas Gerais

		V.F.O. Miranda 2047	Capitólio, Minas Gerais
<i>U. viscosa</i> Spruce ex Oliv.	<i>Sprucea</i>	F.M. Guedes 101	Maracajaú, Rio Grande do Norte
		F.M. Guedes 110	Rio do Fogo, Rio Grande do Norte

Table S1. Protocols for each amplified DNA region used in this study, PCR using 25 μ L reactions. Adapted from White et al. (1990), Hillis and Dixon (1991), Taberlet et al. (1991), Oxelman et al. (1997), Hamilton (1999), Miranda et al. (2010) and Li et al. (2011).

<i>matK</i> gene		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	16,9 μ L	Step 1	94°C	1 min
Buffer	2,5 μ L	Step 2	94°C	40 sec
dntp	0,2 μ L	Step 3	52°C	20 sec
primer 3F_KIM	2,0 μ L	Step 4	72°C	50 sec
primer 1R_KIM	2,0 μ L	Step 5	go back to step 2	34 x
<i>Taq</i>	0,4 μ L	Step 6	72°C	5 min
DNA template	1,0 μ L	Step 7	4°C	∞
<i>rpl20-rps12</i> spacer		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	16,7 μ L	Step 1	94°C	3 min
Buffer	2,5 μ L	Step 2	92°C	40 sec
dntp	0,4 μ L	Step 3	50°C	50 sec
primer <i>rpl20</i>	2,0 μ L	Step 4	72°C	1 min
primer 5'- <i>rps12</i>	2,0 μ L	Step 5	go back to step 2	28 x
<i>Taq</i>	0,4 μ L	Step 6	72°C	10 min
DNA template	1,0 μ L	Step 7	4°C	∞
<i>rps16</i> intron		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	16,7 μ L	Step 1	95°C	5 min
Buffer	2,5 μ L	Step 2	95°C	50 sec
dntp	0,4 μ L	Step 3	52°C	30 sec
primer RPSF	2,0 μ L	Step 4	72°C	2 min
primer RPSR2	2,0 μ L	Step 5	go back to step 2	28 x
<i>Taq</i>	0,4 μ L	Step 6	72°C	5 min
DNA template	1,0 μ L	Step 7	4°C	∞
<i>trnL-F</i> spacer		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	20,6 μ L	Step 1	95°C	3 min
Buffer	2,5 μ L	Step 2	95°C	30 sec

dntp	0,2 µL	Step 3	52°C	45 sec
primer <i>trnL</i> -fwd	0,25 µL	Step 4	72°C	1 min
primer <i>trnF</i> -rev	0,25 µL	Step 5	go back to step 2	34 x
<i>Taq</i>	0,2 µL	Step 6	72°C	5 min
DNA template	1,0 µL	Step 7	4°C	∞
ITS1-5.8S-2		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	19,85 µL	Step 1	95°C	3 min
Buffer	2,5 µL	Step 2	95°C	30 sec
dntp	0,2 µL	Step 3	54°C	30 sec
primer ITS18d	0,25 µL	Step 4	72°C	1 min
primer ITS28cc	0,25 µL	Step 5	go back to step 2	29 x
DMSO	0,75 µL	Step 6	72°C	5 min
<i>Taq</i>	0,2 µL	Step 7	4°C	∞
DNA template	1,0 µL			
ITS1-5.8S-2		Thermocycler profile		
Ultra-filtered autoclaved H ₂ O	14,9 µL	Step 1	95°C	1 min
Buffer	2,5 µL	Step 2	92°C	30 sec
dntp	0,2 µL	Step 3	50°C	50 sec
primer ITS5	2,0 µL	Step 4	70°C	1 min
primer ITS4	2,0 µL	Step 5	go back to step 2	34 x
DMSO	2,0 µL	Step 6	70°C	10 min
<i>Taq</i>	0,4 µL	Step 7	4°C	∞
DNA template	1,0 µL			

6 CONSIDERAÇÕES FINAIS

Em meio às adversidades do cenário de pandemia nos últimos três anos, essa tese sofreu diversos ajustes e mudanças culminando em um compilado de estudos taxonômicos e sistemáticos envolvendo espécies de Lentibulariaceae que ocorrem no Brasil.

Desde a última revisão taxonômica para *Utricularia*, publicada há três décadas, mais de 50 espécies foram descobertas ao redor do globo, diversos estudos florísticos, taxonômicos e filogenéticos foram desenvolvidos. Apesar disso, muitas lacunas sistemáticas e incongruências topológicas vem sendo evidenciadas, mas uma nova revisão do gênero vem sendo evitada, possivelmente, por se tratar de um número copioso de espécies e uma ampla distribuição mundial. Nesse contexto, esforços pontuais e em menor escala geográfica ou nível taxonômico vem sendo desenvolvidos e apresentados afim de trazer resoluções sistemáticas para alguns grupos de *Utricularia* e contribuir para o conhecimento biológico e sistemático do táxon.

Com base nos dados apresentados nos capítulos anteriores, podemos concluir que o estado do Espírito Santo abriga 16 espécies, sendo quatro novas ocorrências. Um desses novos registros é *U. tridentata*, uma espécie considerada ‘Vulnerável’ nos critérios da IUCN, teve confirmada a população mais ao norte conhecida para o táxon. Além disso, esse estudo contou com um levantamento de quantas e quais espécies estão em áreas de proteção, contribuindo para o conhecimento de distribuição e conservação da família em áreas de Mata Atlântica e no País.

Concluímos também que o estado da Bahia concentra a segunda maior riqueza de espécies de Lentibulariaceae no Brasil, com 42 táxons com ocorrências confirmadas, o que representa 46% das espécies da família em território nacional. Os padrões de distribuição encontrados corroboram com hipóteses de conexões vegetacionais durante condições climáticas mais úmidas do passado. As diferenças em composição de espécies de Lentibulariaceae entre diferentes áreas de restinga na costa atlântica do País são consistentes com estudos biogeográficos e de paleomodelagem apontando que o Rio São Francisco age como uma barreira geográfica influenciando processos de especiação e diversidade genética. Ademais, enfatizamos a situação de

abandono de algumas áreas de proteção no estado, com resultados insuficientes para a conservação efetiva dos ambientes e espécies que ali ocorrem.

Por fim, concluímos também que *Utricularia* sect. *Setiscapella* sensu Taylor (1989) não é um grupo monofilético, com base em análises filogenéticas, utilizando sequências plastidiais (gene *matK*, espaçadores *rpl20-rps12* e *trnL-F*, íntron *rps16*) e nucleares (ITS1-5.8-2), e morfológicas. Assim, propusemos uma nova seção, *U.* sect. *Diversicolor*, para acomodar *U. flaccida*, *U. jaramacaru* e *U. physoceras*, originalmente incluídas na seção *Setiscapella*, a qual é aqui reconhecida por sete espécies: *U. nervosa*, *U. nigrescens*, *U. pusilla*, *U. stanfieldii*, *U. subulata*, *U. trichophylla* e *U. triloba*.

Desse modo, o presente trabalho trouxe mudanças sistemáticas e taxonômicas para o gênero *Utricularia*, bem como contribuiu para o conhecimento da flora, distribuição geográfica e conservação de Lentibulariaceae no País.

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