UNIVERSIDADE FEDERAL DE MINAS GERAIS
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
Departamento de Botânica
Programa de Pós-Graduação em Biologia Vegetal

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NARA FURTADO DE OLIVEIRA MOTA

FILOGENIA E DIVERSIDADE DE XYRIDACEAE NEOTROPICAIS, COM ÊNFASE NO GÊNERO *XYRIS*

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Departamento de Botânica do Instituto de Ciências Biológicas da Universidade Federal de Minas Gerais, como requisito parcial à obtenção do título de Doutor em Biologia Vegetal.

Área de Concentração Sistemática Vegetal

BELO HORIZONTE – MG

2014

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Área de Concentração Sistemática Vegetal

Orientador: Prof. Dra. Maria das Graças Lapa Wanderley
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ABSTRACT

The family Xyridaceae includes five genera of petaloid monocots, distributed mainly in tropical and subtropical regions. Four of the five genera, *Abolboda* (23 species), *Aratitiyopea* (one species), *Achlyphylla* (one species), and *Orectanthe* (two species) are restricted to South America and the latter three are exclusive to the Guiana Shield, in Northern South America. *Xyris*, the largest genus of the family, with about 400 species, is the most widespread of them, occurring in tropical and subtropical regions of the Americas, Africa, Asia and Australia and, in some temperate areas. Xyridaceae have been poorly sampled in phylogenetic studies, either using morphological and/or molecular data. Therefore the position of the family is controversial within the clade of Commelinids and the infrageneric classification of the largest genus remained obscure. This thesis is divided into two chapters: 1. Phylogeny o *Xyris* with emphasis on South American species; and 2. Xyridaceae of the Viruá National Park, Roraima state, Brazil, with emphasis on the genus *Xyris*. Both studies were based on samples collected during fieldwork between 2008 and 2013 and in the herbarium samples. To better understand the richness, biogeography and evolution of the group, over 30 field trips were conducted throughout the Brazilian territory, in order to sample the largest number of habitats and covering the morphological and taxonomical diversity of the genus. A total of 718 samples were collected, comprising approximately 137 species of Xyridaceae. Samples from Australia, North and Central America, provided by the New York Botanical Garden, were also included in the analyses. For the phylogeny of the genus *Xyris* five markers were investigated: two mitochondrial (*cox3* and *orf25*) and three plastid (*matK*, *ndhF* and *rbcL*) and parsimony, maximum likelihood and Bayesian analyses were performed. As a result within *Xyris*, the Australian species of

Xyris form a clade sister to the American species (Chapter 1). All sections of *Xyris* were recovered – *Xyris* sect. *Pomatoxyris* and *Xyris* sect. *Nematopus* and *Xyirs* sect. *Xyris*. However, *Xyris* sect. *Pomatoxyris* had a small sampling (< 10 %) and, to confirm its monophyly, a wider sampling is required. Within *Xyris* sect. *Nematopus*, seven clades were highlighted and discussed based on at least one of the following three parameters: high to moderate support; species are morphologically similar; and species present similar biogeographic patterns. This study consists of the first phylogenetic approach to the family with an satisfactory sampling; generating new questions to be investigated regarding of the infrageneric classification. In the second chapter, as a result of field work for the phylogeny sampling and a deep herbarium investigation, a flora of the Viruá National Park, in Roraima, Brazil, was elaborated for the species of Xyridaceae. The flora includes detailed morphological descriptions, dichotomous keys, plates and images of scanning electron microscopy of the seeds. Sixteen species of *Xyris*, and four *Abolboda* were recorded in the Park and a new synonym is proposed. These studies represent an advance in understanding the infrageneric classification of *Xyris* in a phylogenetic context, and guiding future actions to find most informative markers and guiding the future field works to areas poorly sampling yet, such as Africa, Asia and Australia.

RESUMO

A família Xyridaceae é formada por cinco gêneros de monocotiledôneas petalóides, distribuídas principalmente nas regiões tropicais e subtropicais. Quatro dos cinco gêneros, *Abolboda* (23 espécies), *Achlyphylla* (uma espécie), *Aratitiyopea* (uma espécie) e *Orectanthe* (duas espécies) são restritos à América do Sul, sendo os três últimos exclusivos do escudo cristalino das guianas ao norte da América do Sul. *Xyris*, o maior dos gêneros com cerca de 400 espécies, ocorre nas regiões tropicais e subtropicais da América, África, Ásia e Austrália e, em algumas áreas temperadas. As Xyridaceae são marcadas pela baixa amostragem em estudo filogenéticos, seja baseado em dados morfológicos ou moleculares. Consequentemente, a posição da família é controversa dentro do clado das Commelinídeas, bem como a classificação infragenérica do maior dos gêneros permanecia obscura. Esta estudo é composto por dois capítulos: 1. Phylogeny o *Xyris* with emphasis on South American species; e 2. Xyridaceae of the Viruá National Park, Roraima state, Brazil, with emphasis on the genus *Xyris*. Para melhor compreender a riqueza, biogeografia e evolução do grupo foram realizadas mais de 30 excursões de campo no território brasileiro para coleta de amostras durante os anos de 2008 e 2013. Também foram analisadas profundamente as principais coleções brasileiras e Norte Americanas com elevada riqueza em Xyridaceae. Foram amostrados o maior número possível de ambientes, cobrindo também a diversidade morfológica e taxonômica do gênero *Xyris*. Foram coletadas 718 amostras, aproximadamente 137 espécies de Xyridaceae. Amostras provenientes da Austrália, América do Norte e Central foram cedidas pelo Jardim Botânico de Nova Iorque para inclusão nas análises filogenéticas. Para a filogenia do gênero *Xyris* cinco marcadores foram investigados: dois mitocondrial (*cox3* e *orf25*) e três

plastidiais (*matK*, *ndhF* e *rbcL*). Foram realizadas as análises de parcimônia, máxima verossimilhança e bayesiana na tentativa de reconstruir a história evolutiva do gênero. Como resultado do primeiro capítulo, as espécies de australianas de *Xyris* são monofiléticas, irmãs das espécies Americanas. Todas as seções do gênero *Xyris* foram recuperadas, *Xyris* seção *Pomatoxyris*, *Xyris* seção *Nematopus* e *Xyris* sect. *Xyris*, no entanto *Xyris* seção *Pomatoxyris* teve uma amostragem pequena (<10%), sendo necessários um acréscimo de amostras para confirmar o seu monofiletismo. Dentro de *Xyris* seção *Nematopus* sete clados foram destacados e discutidos baseado em pelo menos em um dos três seguintes parâmetros: suporte alto a moderado, coesão de caracteres morfológicos e/ou padrões biogeográficos. No segundo capítulo, fruto das viagens de campo para amostragem da filogenia e de profundo estudo dos principais herbários brasileiros, foi confeccionada a flora do Parque Nacional do Viruá. A flora consiste em descrições detalhadas, chaves dicotômicas, pranchas e imagens de microscopia eletrônica de varredura das sementes das espécies. Foram registradas 16 espécies de *Xyris*, e quatro de *Abolboda* no parque e um novo sinônimo é proposto. Este estudo representa um importante avanço na compreensão da classificação infragenérica do gênero *Xyris* num contexto filogenético. Também fornece suporte busca de marcadores mais informativos, além de guiar futuras excursões de campo para áreas ainda pobremente amostradas como África, Ásia e Austrália.

INTRODUÇÃO GERAL

A sistemática tem como alicerce dois grandes segmentos da ciências naturais: a classificação e a evolução. A base da classificação está enraizada nos estudos de Aristóteles, e a da evolução nos estudos de Darwin (Wheeler et al., 2013). Ambos influenciaram o pensamento filosófico em torno das ciências biológicas, criando importantes paradigmas.

A classificação dos organismos vivos passou por quatro grandes períodos, cada um embasado pelo arcabouço teórico disponível historicamente: sistemas artificiais, naturais, fenéticos e filogenéticos (Judd et al., 2008; Wheeler et al., 2013). O pensamento evolucionista consolida-se como paradigma nos sistemas de classificação filogenéticos e, deste ponto, a sistemática emerge como o ramo da ciências biológicas que estuda a diversidade dos organismos, através de sua organização em grupos, com base em relações evolutivas.

O primeiro sistema artificial de classificação das plantas foi proposto por Teofrasto de Ereso (371-287 a.C.), discípulo de Aristóteles. Em sua obra "*De Historia Plantarum*", Teofrasto descreve mais de 500 espécies e variedades de plantas, classificando as mesmas em grupos baseado principalmente em seu hábito.

Na Idade Média, pouco progresso foi feito na classificação vegetal bem como na botânica, muito dos avanços anteriores foram perdidos e, somente no final do século XIV, com o Renascimento europeu, a botânica influenciada pelos herbalistas como Otto Brunfels (1488-1534), Leonard Fuchs (1501-1566), Hieronymus Bock (1498-1554) ressurge como um ramo das Ciências Naturais (Judd et al., 2008). Preocupados com as propriedades medicinais das plantas, os herbalistas forneciam descrições e ilustrações de modo a facilitar a identificação e comunicação entre a comunidade científica.

Após os herbalistas, o conhecimento das plantas passa por um momento de sistematização, inaugurando o período dos sistemas de classificação ditos "naturais", nos quais as espécies eram descritas e classificadas com o maior número de atributos possíveis. Destacam-se os estudos de Adreas Caesalpino (1519-1603) e Gaspar Bauhin (1560-1624).

Karl Linnaeus (1707-1778), em sua obra *Species plantarum* (1753), descreve mais de 7000 espécies vegetais, classificando-as basicamente em relação ao número e posição dos estames. Mesmo não sendo considerado um sistema natural de classificação, "o sistema sexual de Linneus" é considerado um importante marco na história da classificação das plantas. Linnaeus propõe a utilização do sistema binominal para nomeação das espécies, bem como descreve a hierarquia da classificação contemporânea dos seres vivos, incluindo sete níveis: Reino, Filo, Classe, Ordem, Família, Gênero e Espécie (Linnaeus, 1751). Apesar da grande contribuição de Linnaeus para classificação dos seres vivos, foi Antoine-Laurent de Jussieu (1748-1836) que propõe um dos mais importantes sistemas de classificação dos vegetais. Utilizando a hierarquia proposta por Linnaeus, Jussieu descreve os gêneros e famílias das plantas e as classifica em classes (1813). A classificação proposta por Jussieu em 1813 seria a base da classificação atualmente aceita (The Angiosperm Phylogeny Group, 2009, 2003, 1998).

Muitos outros sistemas naturais continuaram sendo propostos (e.g. Bentham and Hooker, 1862-1883; Candolle, 1813). Mesmo sendo chamados de "naturais" os sistemas de classificação continuavam agrupando os organismos de forma arbitrárias, pouco refletindo a relação entre eles.

No final do século XVII e início do século XIX as ideias evolucionistas começam a tomar forma e vão de encontro com os sistemas de classificação vigentes,

iniciando uma revolução na forma de interpretar as classificações biológicas. Comte Buffon (1749-1788) introduz a ideia de que as espécies são mutáveis. Lamarck (1809) relata a existência de um processo de mudança orgânica ordenada pelo tempo, a qual seria responsável pela diversidade biológica. Mas ainda faltavam explicações sobre quais mecanismos seriam responsáveis por esse processo de mudança.

Foi então que Charles Darwin (1809-1882), com a teoria da seleção natural (1859), estremece as bases da ciências biológicas. As classificações não deveriam ser apenas informativas e úteis, mas também deveriam refletir as linhagens evolutivas. Reconstruir a história evolutiva dos seres vivos passa a ser uma premissa e, como consequência as classificações deveriam refleti-la, surgindo então a primeira fase das classificações filogenéticas, também conhecida como escola gradista.

Os primeiros estudiosos a proporem uma classificação filogenética foram Eichler (1883) e Bessey (1915). Nesta primeira fase, pouco se alterou no processo de classificação, mudando apenas a forma de interpreta-los. Os caracteres e estados de caráter continuavam sendo selecionados e descritos como nos sistemas naturais, sendo a interpretação evolutiva e o estabelecimento de estados ancestrais ou derivados totalmente subjetivos (Judd et al., 2008).

A falta de objetividade e instabilidade das classificações filogenéticas vigentes e, sob o argumento da impossibilidade de conhecer a história evolutiva dos organismos, emerge então o método feneticista. Apesar ter se originado já no século XVIII com os estudos de Andanson (1763), foi na década de 1960 que a fenética ganha notoriedade (Sneath and Sokal, 1973; Sokal and Sneath, 1963). Nela o grupamento das espécies ou OTU's (unidades taxonômicas de observação) se dava pela similaridade máxima ou global (maior número de caracteres possível). No entanto, a dificuldade de agregar um grande montante de informações sobre as

espécies e a impossibilidade de fazer inferências evolutivas, faz com que o método feneticista rapidamente perca espaço, sendo suplantado pelos métodos cladísticos e probabilísticos, a segunda fase das classificações filogenéticas.

A cladística, concebida por Henning (1950), introduz novos métodos para interpretação das linhagens, formando a base da sistemática contemporânea. Foi o primeiro método objetivo capaz de diferenciar a semelhança resultante de ancestralidade da semelhança gerada por convergência. Os caracteres para a classificação passam a ser selecionados *a posteriori*, baseado em conceitos e métodos para determinar os padrões de ramificação da evolução (Wheeler et al., 2013), ou seja, é o único método fundamentação teórica evolutiva. Desde então esta é a metodologia mais empregada na reconstrução da história evolutiva dos seres vivos, e consequentemente, na sua classificação.

A maioria dos estudos cladísticos que se seguiram utilizavam dados morfológicos (e.g. Bremer, 1987; Crane, 1985; Dahlgren and Bremer, 1985). No entanto, com a revolução tecnológica, a facilidade na obtenção de dados moleculares, principalmente macromoleculares, como sequências de DNA, associado à melhora nas ciências computacionais, os estudos passam a incorporar essas novas fontes de dados. Estudos como o de Chase *et al.* (1996) e de Doyle e Endress (2000), utilizando dados morfológicos e moleculares iriam se popularizar, e inspirar os atuais sistemas de classificação (Donoghue and Sanderson, 1992).

Não só a classificação se modificou, mas também a forma de trabalhar dos pesquisadores. Com o elevado número de dados e metodologias disponíveis, o espírito colaborativo entre os pesquisadores se fez necessário. A interpretação dos dados e as amplas propostas de classificação seriam possíveis e satisfatórias principalmente se realizadas colaborativamente.

Fruto de esforços amplamente colaborativos, o Grupo de Filogenia de Angiospermas, ou *APG* (The Angiosperm Phylogeny Group, 2009, 2003, 1998), representa um grande avanço na classificação de grandes grupos de plantas floríferas. No entanto, as relações evolutivas entre táxons como gêneros, seções e espécies continua em aberto para muitos grupos. Muitos nunca foram incluídos de maneira representativa em amostragens filogenéticas como no caso do especioso gênero *Xyris* Gronov ex L.

Xyris (Xyridaceae) é um gênero com aproximadamente 400 espécies aceitas, distribuídas principalmente nas regiões tropicais e subtropicais, poucas chegando em áreas temperadas (Mota and Wanderley, 2013a, 2013b; Wanderley, 2011). Apesar de figurar entre os maiores gêneros de monocotiledôneas, sua classificação infragenérica nunca foi testada a luz da filogenética, permanecendo obscura as relações entre as espécies do gênero.

A morfologia do gênero é relativamente uniforme com folhas unifaciais; inflorescência do tipo espiga encimada em um longo pedúnculo; sépalas dimórficas, uma membranácea, cedo caduca, e duas naviculares persistentes; pétalas membranáceas, amarelas, unguiculadas; estames epipétalos, estaminódios geralmente plumosos; sementes numerosas e pequenas, geralmente menores que 1.5 mm. Tal uniformidade morfológica dificulta estudos taxonômicos, principalmente estudos que buscam reconhecer grandes grupos, como as seções, dentro do gênero *Xyris*.

O conhecimento sobre a diversidade e taxonomia do gênero está intimamente associado às floras realizadas em diversas regiões do mundo (Kral, 2005, 1988, 1983; Lock, 1999; Robert and Wanderley, 1995; Seubert, 1855; Silva and Wanderley, 2013; Wanderley, 2011), sendo encontrados poucos estudos revisionais (Conn and Doust, 1997; Doust and Conn, 1994; Malme, 1913a, 1913b). A pobreza de estudos

revisionais observada para o gênero *Xyris* está intimamente associada ao elevado número de espécies (cerca de 400 espécies), à dificuldade de separação das mesmas, à baixa amostragem observada nas coleções científicas e, principalmente, ao fato de a classificação infragenérica vigente estar extremamente desatualizada, englobando poucas seções com um grande número de espécies.

Atualmente o gênero está dividido em três seções fundamentadas basicamente pela distribuição geográfica e tipo de placentação das espécies (Kral, 1988; Smith and Downs, 1968; Wanderley, 2011). *Xyris* seção *Xyris* (ca. 140 espécies) possui distribuição pantropical e placentação pariental; *Xyris* seção *Pomatoxyris* (22 espécies) é restrita à Austrália e possui placentação axilar; e, por fim, *Xyris* seção *Nematopus* (ca. 250 espécies) possui distribuição Neotropical e placentação central ou basal. No entanto, essas seções nunca foram testadas sob ponto de vista filogenético, confirmando ou refutando a monofilia destes grupos.

Como objetivo principal, buscamos testar o monofiletismo das espécies Neotropicais de *Xyris* seção *Nematopus*, a mais especiosa de todas as seções do gênero. A maioria das espécies desta seção (>90%) são restritas a América do Sul e/ou ao Brasil. Os dois maiores centros de diversidade do gênero foram amostrados sistematicamente: as serras do sudeste brasileiro e no escudo cristalino das Guianas, incluindo aqui as terras baixas abertas. Consequentemente, avaliamos as relações evolutivas dentro das espécies americanas de *Xyris* e a relação das mesmas com as espécies Australianas de *Xyris* seção *Pomatoxyris*. Como resultado direto da amostragem Amazônica e do estudo dos principais herbários brasileiros, foi possível concretizar a flora das Xyridaceae do Parque Nacional do Viruá, no estado de Roraima, uma das principais áreas visitadas na Amazônia para a amostragem da filogenia.

Este trabalho compreende a primeira investigação sobre as relações filogenéticas no gênero *Xyris*. Objetiva-se dar o primeiro passo na reconstrução da história evolutiva do grupo, com os seguintes objetivos específicos: testar o monofiletismo de *Xyris* seção *Nematopus* bem como das *Xyris* Neotropicais; reconhecer possíveis grupos naturais dentro de *Xyris* seção *Nematopus*, potenciais para futuras revisões taxonômicas; verificar o quão são informativos os caracteres morfológicos tradicionalmente utilizados para a separação das seções (tipo de placenta) e para separar grupos de espécies (fusão das sépalas laterais); verificar padrões biogeográficos relacionados aos grupos; ampliar o conhecimento sobre o gênero na região Amazônica e enriquecer as coleções científicas nacionais.

A tese está organizada na forma de dois capítulos. O primeiro intitulado "Phylogeny o *Xyris* with emphasis on South American species", teve como objetivo compreender as relações evolutivas das espécies do gênero *Xyris* baseado em dados moleculares, com foco nas espécies de *Xyris* seção *Nematopus*, todas exclusivamente Neotropicais. O segundo capítulo intitulado "Xyridaceae of the Viruá National Park, Roraima state, Brazil, with emphasis on the genus *Xyris*" consiste no tratado taxonômico das espécies ocorrentes no Parque Nacional do Viruá, no estado de Roraima, Brasil.

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Title. Phylogeny of *Xyris* with emphasis on South American species

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Abstract

Xyris (Xyridaceae) is a petaloid genus of monocots comprising about 400 species. The genus is mostly pantropical and subtropical, with some species occurring in temperate areas. Many species have narrow distribution and are restrict to a single continent and there are only two putative amphiatlantic disjunctions. Three sections are recognized in the infrageneric classification of the genus: *Xyris* sect. *Xyris* (ca. 140 spp.) occur throughout the geographic distribution of the genus, *X.* sect. *Nematopus* (ca. 250 spp.) is Neotropical, and species of *X.* sect. *Pomatoxyris*. (18 spp.) occur in southern Australia. These sections are delimited basically by the distribution range and type of placentation. Nevertheless, their monophyly was never

tested. Utilizing five molecular markers, two mitochondrial (*cox3* and *orf25*) and three plastid (*matK*, *ndhF* and *rbcL*), our phylogenetic analysis aimed to test the monophyly of the genus *Xyris* and the currently accepted sections, as well to test two traditionally used important morphological features – connation of the lateral sepals and type of placentation. Secondarily, we searched for smaller well supported clades, in order to facilitate further taxonomic treatment of this diverse genus. As outgroup we included six species of *Abolboda* (Xyridaceae), four species of Rapateaceae, two of Mayacaceae, eigth of Eriocaulaceae. Ingroup includes 117 species of all sections of *Xyris*. Sampling was concentrated in Brazilian species, mainly for *Xyris* sect. *Nematopus*. Samples of *Xyris* sect. *Xyris* were prevenient predominantly from Central, North and South America. Only two species of *Xyris* sect. *Pomatoxyris*, from Australia, were sampled. We performed parsimony, maximum likelihood and Bayesian analyses to reconstruct the evolutionary history of the genus. Our analyses revealed that *Xyris* is monophyletic and the three sections were recovered with high to moderate support. In *Xyris* sect. *Nematopus* seven clades were recognized based at least one of the tree criteria: (1) the group is moderately to strongly supported in the phylogenetic analyses; and (2) the species are morphologically congruent, and (3) the species are biogeographically related. The morphology and biogeography is discussed for each of those clades. The phylogenetic hypothesis here inferred is the first proposed for *Xyris* based on a comprehensive sampling, and it will assist future taxonomic treatments within the genus.

Key words Neotropics, *Xyris sect. Nematopus*, Poales, placentation, *evolution*

1. Introduction

The genus *Xyris* Gronov. ex L. (Xyridaceae C.Agardh) encompasses about 400 species, mostly occurring in tropical and subtropical regions, and within temperate regions (Kral, 1988; Wanderley, 2011). Within the wide distribution of the genus, there are two main centers of highest species concentration: the southeastern Brazilian shield and the Guiana Shield (Kral, 1988; Wanderley, 2011). *Xyris* exhibits a remarkable level of species endemism, exceeding 70% in areas such as the Espinhaço Range in eastern Brazil (Wanderley, in prep.).

Xyris is by far the richest genus of the family, with more than 90% of the species, and its morphology is quite distinct from the other genera of Xyridaceae (Wanderley, 2011). While it is easy to distinguish the genera of Xyridaceae, the highly conservative morphology within *Xyris* makes the distinction among species very difficult. Almost all *Xyris* species present rhizomatous stems with short internodes; leaves with open sheaths and isobilateral blades; a spike inflorescence borne on a long peduncle; flowers with dimorphic sepals (one anterior cucullate and membranous, usually soon deciduous, the other two navicular, firm, sclerotic, and persistent); yellow petals unguiculate; androecium consisting of antesepalous staminodia and three epipetalous stamens; and a capsule loculicidal with numerous seeds, that are usually less than 1.5 mm long. Most of the taxonomically informative morphological characters are those of the leaves, spike bracts, sepals, and ovary (e.g. Kral, 1988; Smith and Downs, 1968, 1960; Wanderley, 2011).

Endlicher (1836) recognized two subgenera in *Xyris* based mainly on geographic distribution and placentation type. *Xyris* subg. *Xyris*, included species occurring

throughout the genus distribution range and characterized by parietal placentation, and *X.* subg. *Pomatoxyris* Endl. included species restricted to either southeastern or southwestern Australia, characterized by axillary placentation. Seubert in 1855, reduced the status of the two subgenera to sections and created another new section: *Xyris* sect. *Nematopus* Seub., composed of Neotropical species with central or basal placentation. In 1913, Malme re-established *X. sect. Pomatoxyris* and *X.* sect. *Xyris* as subgenera and raised *X.* sect. *Nematopus* also to subgenus (Malme, 1913a, 1913b), but later in 1930, he returned to his initial view, reestablishing the three sections (Malme, 1930). Since then, three sections have been recognized based on differences in filament adnation to the corolla, placentation, fruit dehiscence, seed shape, and geographic distribution (Campbell, 2004; Conn and Doust, 1997; Endlicher, 1836; Malme, 1930; Seubert, 1855). A fourth section, *Xyris* sect. *Cipoxyris*, has been suggested but not formally proposed by Wanderley (1992), that included eight species robust, many-flowered inflorescences endemic to the rocky fields (*campos rupestres*) of the Espinhaço Range, in Minas Gerais state, Brazil.

Since then, regional treatments by various authors have been produced, often based solely on herbarium specimens (e.g. Conn and Doust, 1997; Doust and Conn, 1994; Kral, 1988; Smith and Downs, 1968). The absence of a revision on the genus has led to persistent underestimates of species numbers (e.g. Heywood, 2007; Mabberley, 2008; R. F. Thorne, 2000), showing that a modern monograph utilizing a consistent species concept is needed. A necessary step in this way is a revision of the infrageneric classification of the genus *Xyris* in a phylogenetic context that will support a monography of *Xyris* and the recognition of possible synapomorphies. To date, support for the sections has been based primarily on geographic distribution and

type of placentation of their species. Recently, Kral (1988) observed species of *X.* sect. *Nematopus* with ovary distinctly or partially trilocular, challenging the infrageneric classification based on the number of ovarian locus and placentation type. However, these and other characters have not been evaluated in a phylogenetic context. Such analysis could be useful to evaluate the proposed infrageneric classifications and identify additional putative synapomorphies.

Despite being the largest genus of the family Xyridaceae and having a wide distribution, *Xyris* is underrepresented in molecular systematic studies. Probably, this is due to a large number of species of *Xyris* occuring in areas extremely difficult to access; and few species are cultivated (e.g. Johnson et al., 2012; Tamura et al., 2008), hindering the access to genetic material. Less than ten species of *Xyris* have been sequenced in the context of general phylogenetic analyses of families of Poales (de Andrade et al., 2010; Givnish et al., 1999; Michelangeli et al., 2003).

Contrary to the suggestions of Kral (1988), the relatively homogeneous floral and seed morphology within *X.* sect. *Nematopus* suggests that it could be monophyletic. Furthermore, similarities in floral morphology between some American and African species of *X.* sect. *Xyris* suggests relationship between groups of both regions. Nevertheless, the currently available sampling of the genus in molecular studies is insufficient to address these phylogenetic questions. A phylogenetic hypothesis for the American species of the genus, especially the species in *X.* sect. *Nematopus*, which encompasses more than 70% of the genus richness, should also enlighten the infrageneric classification of the genus and enhance stability to the taxonomic system, favoring the necessary taxonomic revisions.

Here, we investigate the phylogeny of *Xyris* with a focus on *X.* sect. *Nematopus*, the richest section of the genus, with the following goals: (1) to establish whether Neotropical species of *X.* sect. *Nematopus* form a monophyletic group; (2) to evaluate the current sectional classification of American species in the light of a phylogenetic hypothesis; (3) test the congruence of diagnostic morphological characters with the retrieved phylogenetic hypothesis, in the search for putative synapomorphies.

2. Materials and methods

2.1 Taxon sampling

A total of 290 terminals was sampled, covering 138 taxa, ca. 30% of the genus *Xyris*. Of these, 118 taxa belong to *X.* sect. *Nematopus* (ca. 50% of the section). The sampling efforts were focused in the Brazilian Southeastern Shield – including the Espinhaço Range, Chapada dos Veadeiros, Chapada dos Guimarães, and mountains of the Atlantic Forest – whereas the highlands of Northern South America, or *tepuys*, remain to be widely sampled. Twenty-one species of *X.* sect. *Xyris* were sampled (ca. 15%), of which 13 were collected in North America, two in Central American and four in South America. Only two species of *X.* sect. *Pomatoxyris* (ca. 12%), from Australia, were sampled. The outgroup includes six species of *Abolboda* (Xyridaceae) as well as representatives of Eriocaulaceae (eight spp.), Mayacaceae (two spp.) and Rapateaceae (four spp.), being rooted in the latter family. Most of the plant material was field-collected and dried in silica gel, but in a few instances, herbarium specimens were used. Multiple individuals were sampled of species with broad geographic distributions or significant morphological variability. Voucher

information, geographic origin, and GenBank accessions numbers are listed in Table 1.

2.2 Herbarium studies

The identification of the collected samples and the morphological characterization of the species were also based on study of specimens of the herbaria BHCB, INPA, MG, MO, NYBG, R and US.

2.3 DNA ex*traction*

Samples of dried leaf tissue (10 mg) were disrupted in a 1.6 mL tube using two stainless steel ball bearings (3 mm) and a TissueLyser (Qiagen) at 30 Hz (2 × 90 s). Samples were incubated for 18 h at 42 °C with 40 rpm horizontal shaking in 600 µL extraction buffer (modified from Alexander et al., 2007; 8 mM NaCl, 16 mM sucrose, 5.8 mM EDTA, 0.5% [w/v] sodium dodecyl sulphate, 12.4 mM tris [pH 9.1], and 200 µg/mL proteinase K). After incubation, 200 µL of 3 M potassium acetate (pH 4.7) was added to each sample. Following 600 s of incubation at 0 °C, samples were centrifuged at 14,000 g for 300 s. 600 µL of each sample's aqueous phase was mixed with 900 µL of 2 M guanidine hydrochloride in 95% (v/v) ethanol. The mixtures were applied to silica spin columns (Epoch Life Science), 500 µL at a time, by centrifugation at 7,000 g for 60 s. Wash buffer (M. S. Elphinstone, 2003; 50% [v/v] ethanol, 10 mM tris [pH 7.4], 0.5 mM EDTA, and 50 mM NaCl) was applied twice, 500 µL at a time, by centrifugation at 7,000 g. Columns were dried by centrifugation at 7,000 g for 120 s. Total DNA was eluted in 200 µL 10 mM tris (pH 8.0) by centrifugation at 7,000 g for 60 s.

2.4 Molecular markers and PCR amplification

Individual PCR amplifications took place in a 15 μL volume containing: 1.5 μL PCR buffer; 0.2 mM dNTPs; 0.025 μg/μL BSA; 10% (w/v) sucrose; 0.05% (w/v) orange G; 0.4 M betain (*matK* and *rbcL* only); 1 μM of each primer; 1 unit of Ex-*Taq* polymerase (Takara Bio Inc, Shiga, Japan); 1 μL genomic DNA.

The amplification and sequencing primers for a portion of the *cox3* (mitochondrial) coding region were F (5'-CCG-TAG-GAG-GTG-TGA-TGT-3'; Duminil et al., 2002) and R (5'-CTC-CCC-ACC-AAT-AGA-TAG-AG-3'; Duminil et al., 2002). Cycling conditions for *cox3* were: 95 °C 150 s; 35 cycles: 95 °C 30 s, 53 °C 30 s, 72 °C 30s; 600 s final extension.

The amplification and sequencing primers for a portion of the *matK* (plastid) coding region were 390F (5'-CGA-TCT-ATT-CAT-TCA-ATA-TTT-C-3'; Cuénoud et al., 2002) and 1326R (5'-TCT-AGC-ACA-CGA-AAG-TCG AAG-T-3'; Cuénoud et al., 2002). If amplification using 390F and 1326R failed, *matK* amplification was generated in two parts using the pairs 390F/1198R (5'-CTG-TGT-TAG-ATA-TAC-GAA-TAC-C-3'; Thiv et al., 1999) and 1326R/H2-1660F (5'-TAA-ATG-GAA-ATA-TTA-CCT-TG-3'; Meimberg et al., 20000). Cycling conditions for *matK* were: 95 °C 150 s; 35 cycles: 95 °C 30 s, 50 °C 30 s, 72 °C 60 s (30 s for amplification of fragments); 600 s final extension.

The amplification primers for a portion of the *ndhF* (plastid) coding region were 274F (5'-CTT-ACT-TCT-ATT-ATG-TCA-ATA-TTA-AT-3'; Olmstead and Sweere, 1994) and 1600R* (5'-CAT-AGT-ATT-GTC-CGA-TTC-GTG-AGG-3'; Terry et al., 1997);

additional primers 972F (5'-GTC-TCA-ATT-GGG-TTA-TAT-GAT-G-3'; Olmstead and Sweere, 1994) and 972R (5'-CAT-CAT-ATA-ACC-CAA-TTG-AGA-C-3'; Olmstead and Sweere, 1994) were used for sequencing. Cycling conditions for *ndhF* were: 95 °C 150 s; 35 cycles: 95 °C 30 s, 48 °C 30 s, 72 °C 60 s; 600 s final extension. If amplification with 274F and 1600R* failed, samples were amplified in two fragments using the pairs 274F/972R and 972F/1600R*. Fragmentary *ndhF* amplifications used the same cycling conditions as the full–length *ndhF* amplifications.

Amplification primers for a portion of the *orf25* (mitochondrial) coding region were F (5'- AAG-ACC-RCC-AAG-CYY-TCT-CG-3'; Duminil et al., 2002) and R (5'- TTG-CTG-CTA-TTC-TAT-CTA-TT-3'; Duminil et al., 2002). Cycling conditions for *orf25* were the same as those used for *matK* amplifications.

Amplification primers for a portion of the *rbcL* (plastid) coding region were F1 (5'-ATG-TCA-CCA-CAA-ACA-GAA-AC-3'; Lledo et al., 1998) and 1379R (5'-TCA-CAA-GCA-GCA-GCT-AGT-TCA-GGA-CTC-3'; Wolf et al., 1999; Zurawski et al., 1984); additional primers 655F (5'-GCG-TTG-GAG-AGA-CCG-TTT-C-3'; Zurawski et al., 1984) and 635R (5'-AAA-CGA-TCA-CTC-CAA-CGC-A-3') were used for sequencing. Cycling conditions for *rbcL* were: 95 °C 150 s; 35 cycles: 95 °C 30 s, 55 °C 30 s, 72 °C 90 s; 600 s final extension. If amplification with F1 and 1379R failed, samples were amplified in two fragments using the pairs F1/635R and 655F/1379R. Fragmentary *rbcL* amplifications used the same cycling conditions as the fragmentary *matK* amplifications.

2.5 DNA sequencing, sequence analysis and alignment

PCR products were treated with ExoSAP-IT and sequenced with BigDye 3.1 chemistry (1 µL treated PCR product in each 5 µL reaction) on an ABI 3730 sequencer (High–Throughput Genomics Unit, University of Washington).

Chromatograms were processed with KB (version 1.4; Life Technologies). Contigs were created and edited with Sequencher (version 4.10; Gene Codes). Nucleotide sequences were aligned as amino acids using translatorX (version 1.1; Abascal et al., 2010) and MUSCLE (version 3.8; Edgar, 2004).

2.6 Phylogenetic analyses

Parsimony, maximum likelihood, and Bayesian analyses were performed to evaluate the evolutionary history of Neotropical *Xyris*, with emphasis on *X.* sect. *Nematopus*. Alignment indel characters were coded using "simple indel coding" (Simmons and Ochoterena, 2000) as implemented in 2matrix (version 1.0; Salinas and Little, 2014). All characters were nonadditive and equally weighted. The *cox3*, *matK*, *ndhF*, *orf25*, and *rbcL* sequences were analyzed separately and in combination.

Parsimony analyses were performed using TNT (version 1.1; Goloboff et al., 2008). For each data set, 1000 200–iteration ratchet (Nixon, 1999) searches were conducted: each search began with a Wagner tree (random addition sequence) followed by full SPR branch–swapping (holding two trees) and full TBR branch–swapping (holding two trees). Ratchet perturbation was applied to 10% of the informative characters (5% up weighted, 5% down weighted). Jackknife support values (Farris et al., 1996) were

calculated from 10,000 replicates. Each replicate was analyzed with five random addition sequences (Wagner tree with SPR followed by TBR branch–swapping) holding up to five trees per search. The strict consensus of each replicate was used to calculate jackknife frequencies.

For the Maximum Likelihood analyses (ML) and Bayesian inferences (BI), evolutionary models for each gene were chosen using MrModeltest 2.3 (Nylander, 2004) with Akaike Information Criterion (AIC).

The maximum likelihood tree searches were conducted using RAxML (version 7.8.4; Stamatakis, 2006) with rapid maximum likelihood bootstrap analysis (Stamatakis et al., 2008). The GTR substitution model was applied to nucleotide characters and the binary model was applied to indel characters. Both models used gamma correction for rate heterogeneity (the alpha parameter was automatically estimated). 10,000 bootstrap replicates were calculated for each dataset.

Bayesian inference was performed by MrBayes (version 3.2.2; Ronquist et al., 2012). The GTR substitution model with gamma–distributed rate variation (eight rate categories) was applied to nucleotide characters and the binary model with gamma–distributed rate variation (eight rate categories) was applied to indel characters. For each dataset, branch length priors were specified following the technique of Brown et al. (2010) using the median branch length of the optimal RAxML tree to estimate $\overline{brl}$. Each dataset was analyzed using 10 independent searches each consisting of 100 million generations. Each search used 10 simultaneous Markov chains with the heating parameter set to 0.2, swap frequency set to 1, and auto parameter tuning. The

cold chain was sampled every 5000th generation. The first half of the sampled trees were discarded as burn–in and the remaining 1,000 trees were used to build a 50% majority–rule tree.

The BI did not converge on a topology after 100 million generations thus the results are not presented here. The parsimony jackknife and likelihood bootstrap were mapped onto the maximum likelihood tree using SumTrees (version 3.12.0; Sukumaran and Holder, 2010). Figures of the resulting trees were prepared in FigTree 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/). Jackknife (JS) and bootstrap (BS) values are described as high (90–100%), moderate (80–89%), and low (<80%).

2.7 Morphological Ancestral State Reconstruction

To investigate the evolution of key characters traditionally used to distinguish sections and groups of species of *Xyris* were optimized onto the onto the maximum likelihood tree (the best phylogenetic hypothesis here presented). Placentation type (parietal, axillar, basal and central placentation) was coded for all samples and the fusion of lateral sepals (free or connate) was coded only for *Xyris* using the literature (Campbell, 2005; Conn and Doust, 1997; Kral and Smith 1980; Kral and Wanderley, 1993, 1988; Kral, 1983, 1982; Mota and Wanderley 2013; Wanderley 2010, 2003) and herbarium specimens. The coding of placentation as "non Xyridaceae" followed the literature (Huber and Kubitzki, 1998; Judd et al., 2008). The character states were optimized with the parsimony criteria using in Mesquite 2.75 (Maddison and Madisson, 2011). All characters were treated as unordered and optimized with accelerated transformations (ACCTRAN).

3. Results

The combined maximum likelihood (ML) tree is presented in Figures 1 and 2. The plastid and mitochondrial maximum likelihood (ML) trees and the combined parsimony (P) are presented in the supplementary (Fig. S1 S2 and S3). Parsimony jackknife and ML bootstrap (in that order) are mapped onto the ML trees (Figs. 1 and 2). The results of P and ML are summarized in the Table 2.

3.1 Parsimony analyses

The *cox3* matrix did not have any indels. The matrix had 606 characters, of which 72 (12%) are parsimony-informative. The P analyses found 20 optimal trees 126 steps long, consistency index (CI) = 0.667 (excluding uninformative characters) and retention index (RI) = 0.955. The *matK* matrix had 849 characters, of which 560 (66%) are parsimony-informative (18 *indels*). The P analyses was terminated after one million shortest trees were found: 1943 steps long, CI = 0.499 (excluding uninformative characters), and RI = 0.909. The *ndhF* matrix consisted of 1318 characters, of which 547 (42%) are parsimony-informative (22 *indels*). The P analyses was terminated after one million shortest trees were found, 1862 steps long, CI = 0.475 (excluding uninformative characters), and RI = 0.866. The *orf25* matrix consisted of 401 characters, of which 115 (29%) are parsimony-informative (two *indels*). The P analyses found two shortest trees 185 steps long, CI = 0.751 (excluding uninformative characters), and RI = 0.966. The *rbcL* matrix did not have any *indels*. It consisted of 1221 characters, of which 363 (30%) are parsimony-informative. The P analyses found 102,120 equally parsimonious trees, 1155 steps long, CI = 0.461 (excluding uninformative characters), and RI = 0.927.

The parsimony analyses of the mitochondrial dataset found 156,600 shortest trees of 318 steps, CI = 0.701 (excluding uninformative characters), and RI = 0.959. For the combined plastid dataset the analysis was terminated after one million shortest trees were found 5517 steps long, CI = 0.432 (excluding uninformative characters), and RI = 0.881. Finally, the combined matrix consisted of 4395 characters, of which 1657 (38%) are parsimony-informative. 829,440 shortest trees were found 5901 steps long, CI = 0.441 (excluding uninformative characters), and RI = 0.885.

The genus *Xyris* is monophyletic sister to *Abolboda* (which also appears monophyletic), strongly supported (100% JS). The Australian section, *X.* sect. *Pomatoxyris*, diverges from the remaining *Xyris* first (Figs. 1 and 2) and is sister of all American *Xyris*, forming a well-supported clade (100% JS). *Xyris* sect. *Xyris* was recovered in parsimony analyses for each marker and for the combined data set. *Xyris* sect. *Nematopus* formes a highly supported clade (90% JS), with the ambiguous position of *X. capensis* Thunb. (a South American sample), as sister group (low support, 51% JS).

3.2 Maximum likelihood

ML results are highly congruent with the P results (Figs. 1 and 2). The branches between genera of Xyridaceae and between families are very long (Fig. 2 – phylogram). *matK* and *ndhF* had the greatest phylogenetic information to the tree topology (Table 1). *Xyris* formed a well-supported clade (100% BS) with *Abolboda* as sister. Also American *Xyris* formed a well-supported clade (100% BS). The two Australian *Xyris* – *X.* sect. *Pomatoxyris* – are sister to all American *Xyris* (100% BS).

As in P analyses, *X.* sect. *Nematopus* was recovered (87% BS), with *X. capensis* as sister (51% BS). Like in the P analyses, *X.* sect. *Xyris* was recovered in the ML analyses, excluding *X. capensis*.

3.3 Morphological Ancestral State Reconstruction

Our results suggest that both characters evaluated are homoplastic in *Xyris* (placentation type CI = 0.3 and the presence of lateral sepal fusion CI = 0.2; Figs. 3 and 4). Nevertheless, these characters can be important to distinguish some clades within *Xyris*. Axial placentation appears to be the general state in *Xyris* sect. *Pomatoxyris*. Parietal placentation occurs in the core *Xyris* sect. *Xyris* and *Xyris capensis*. All sampled species of *Xyris* sect. *Nematopus* have central or basal placentation and both states have originated several times in this clade (Fig. 3).

Connate lateral sepals are found in two distinct clades of *X.* sect. *Nematopus,* clades E and F (Fig. 4). The remaining species of *X.* sect. *Nematopus* have free lateral sepals, as is found in the species of the other sections of the genus.

4. Discussion

4.1 A phylogenetic hypothesis for Xyris

In contrast with previous studies (Bremer, 2002; Davis *et al.*, 2004; Michelangeli *et al.*, 2003, Linder and Rudall, 2005) our phylogeny shows *Abolboda* Bonpl. close related to *Xyris*, as sister group. Bremer et al. (2002) suggest a clade compound by *Abolboda* and *Orectanthe* Maguire as sister group of *Xyris*, whereas other authors (Davis *et al.*, 2004; Michelangeli *et al.*, 2003, Linder and Rudall, 2005) infer Mayacaecae as sister of *Xyris*. However, neither of these studies included the critical

Xyridaceae genera *Achlyphila* Maguire & Wurdack and *Aratitiyopea* (L.B.Sm.) Steyerm. & P.E.Berry. On the other hand, Campbell (2004), in a morphologically based phylogeny for the family (including all genera), suggests *Achlyphila* as sister to *Xyris*, what was not tested in a molecular approach yet.

All recognized sections of *Xyris* (*X.* sect. *Xyris*, *X.* sect. *Nematopus* and *X.* sect. *Pomatoxyris*) were recovered in our phylogeny. The placement of *Xyris capensis* outside of the *X.* sect. *Xyris* clade do not refute the monophyly of this section, once this branch present extreme low support values (45% JS and 50% BS).

4.2 Phylogenetic relationships within Xyris *sect.* Nematopus

Several of the internal nodes of *Xyris* sect. *Nematopus* clade formed monophyletic subgroups (Figs. 1 and 2), seven of which were recovered that fulfill at least one of the following criteria: (1) the group is moderately to strongly supported in the phylogenetic analyses; and (2) the species are morphologically congruent, and (3) the species are biogeographically related. Unfortunately, the relationships between the subgroups are unclear due to poor resolution and/or weak support.

4.2.1 Clade A

Clade A – The *Xyris brachysepala* group (Fig. 7 – red cluster) – has low support (78% JS and 58% BS) and encompasses two Amazonian species included in these analyses, as well as the uncertain species, *Xyris* aff. *shepherdiana*, *X. machrisiana* and *X. savanensis*. The latter species is widespread in South America and it is traditionally suggested as a species related to the complex of *Xyris paraensis* (Kral 1988). Most of the species in this clade have basal placentation, excluding *Xyris* aff. *shepherdiana*,

that has central placentation, and they present free lateral sepals, except for *X. machrisiana*, which has connate lateral sepals at the base.

4.2.2 Clade B

Clade B is well-supported clade (100% JP, 100% BS and 0.7 PP), comprising a single species, *X. eleocharioides* Kral & L.B.Sm. (Fig. 7 – green cluster). *Xyris eleocharioides* is endemic of Espinhaço Range, in Bahia state, and it presents central placentation and free lateral sepals.

4.2.3 Clade C

Clade C is well-supported (100% JP and 100% BS) and formed by the *Xyris bialata* group (Fig. 7 – orange cluster). Three of the four close related species - *X. malanopoda*, *X. kralii* and *X. spinulosa* - are endemic to the Espinhaço Mountain Range and usually occur in sympatry (Wanderley, 2011). *Xyris bialata* has a disjunct distribution, occuring in the *restingas* (Atlantic coastal vegetation) and Espinhaço Range. A similar pattern was also observed for some Eriocaulaceae (Echternacht *et al.*, 2014). All species in the clade present central placentation, free lateral sepals and bracts with conspicuous macula.

4.2.4 Clade D

Clade D - *Xyris teres* group – is a moderate to poorly supported clade (65% JP and 83% BS). In spite of its low statistical support, this clade is highly coherent biogeographically and morphologically. It includes all species endemic of high altitude open formations of Atlantic Rain Forest (*campos de altitude*), as well as two species from the Espinhaço Range, *X. harley* and *X. sparsifolia,* and one from the

mountains of Central-Western Brazil, *Xyris veruina* (Fig. 7 – purple cluster). Those three species are in a basal position in the clade, but support is low. The free lateral sepal is the ancestral state of character in the genus, and it appears as conservative in clade D. The basal placentation occurs in most species, except in *X. harley*, *X. wawrae* and *X. teres*, which present central placentation. Other recurrent feature in this clade is the terete leaves with presence of an evident ligule, putatives synapomorphies that should be investigated.

4.2.5 Clade E

Clade E – *Xyris seubertii* group (Fig. 7 – blue cluster) - is a highly supported clade (97% JP and 99% BS) and composed mainly by endemic species from Espinhaço Range. *Xyris sebeurtii* var. *seubertii* is the only species of the group widespread in South America, but it is also extremely common in the Espinhaço Range, where one variety is endemic to this region, *Xyris seubertii* var. *espinhacae*. *Xyris sparsifolia* has an ambiguous position, with one sample nested in clade D and other in clade E, both with low support (Fig. 1). However, morphological features of the species such as basal placentation, free lateral sepals and terete leaves, suggest it is related to clade D. Nevertheless, only four molecular markers for the sample *Xyris sparsifolia* X0502 were sequenced, placed in clade E. *Xyris velutina*, a basal lineage in this clade, is the only species with free lateral sepals, considering that of *X. sparsifolia* belongs to clade D. Other feature of this clade is the lateral sepal with dense, long trichomes, commonly used to separate species.

4.2.6 Clade F

Clade F – *Xyris trachyphylla* group (Fig. 7 – yellow cluster)- is a well-supported clade (90% JP and 99% BS) that includes morphologically related species with three main distribution patterns: endemic to the Espinhaço Range – *X. anamariae*, *X. archeri*, *X. celiae*, *X. diamantinae*, *X. longiscapa* and *X. pilosa*; endemic to open Atlantic Forest formations – *X. caparaoensis*; and with disjunct distribution between the Espinhaço Range and open Atlantic Forest formations – *X. itatiayensis*, *X. obtusiuscula* and *Xyris trachyphylla*. All species occur in humid habitats, with lower average temperature and high elevations, usually associated with physiognomies of the Atlantic Forest Domain, as are the species of clade D. Nonetheless species in clade F occur in better drained and dryer habitats, if compared with species of the clade D, which occur in regularly soggy habitats, like swamps and ponds. Morphologically, clades E and F share central placentation and connate lateral sepals. However, the species of clade F have leaves and/or peduncles surface rugose to rugulose, while the species of clade E, usually have leaves and/or peduncles with smooth surface.

4.2.7 Clade G

The G clade – Brazilian shield – is large, poorly supported clade (57% JP and 51% BS) (Fig. 8 – pink cluster), with most species widely distributed in mountainous regions of eastern South America (*e.g.* Espinhaço Range, in Bahia and Minas Gerais states, Chapada dos Veadeiros, Goiás state, Chapada dos Guimarães, Mato Grosso state), and some widespread species along the *Cerrado* and in the *campos de altitude*, *X. schizachne*, *X. metallica* and *X. asperula*. Two species, *X. ciliata* and *X. mertensiana*, are shared between the Espinhaço Range (in Bahia state) and the

restingas (Atlantic coastal vegetation), in a disjunct distribution. *Xyris fusca* is the only one species in this clade that is endemic species of the high altitude grasslands in the *campos de altitude* in this clade. However, this species presents morphological features shared with *X. bahiana* and *X. hymenachne*, such as the very broad, pale, scarious bract borders and the absence of a macula in the bracts. Such morphological proximity is corroborated by the molecular data presented here, were these species form a highly supported clade (99 % JP and 98% BS).

The majority of species in Clade G present basal placentation, except for the well-supported clade formed by *X. glochidiata* and related species (98% JP and 98 BS). This clade consists of species endemic to the Espinhaço Range (in Bahia state) and some species shared with this area and with the *restingas*. This biogeography pattern has been observed in other families such as Bonnetiaceae, Droseraceae, Eriocaulaceae and Poaceae (Alves et al., 2007; Echternacht et al., 2014). In clade G, free lateral sepal appears only in a species with doubtful identification.

The clade formed by *Xyris aurea*, *X. cipoensis*, *X. coutensis*, *X. fredericoi*, *X. hystrix*, *X. nigra*, *X. platystachya* and *X. spectabilis* was recovered with high support (99% JP and 99% BS). This clade corresponds to a putative fourth section of *Xyris* – *Xyris* sect. *Cipoxyris* – that has been suggested but not formally proposed (Wanderley, 1992). All these species are endemic to the Espinhaço Range in Brazil, have numerous sterile bracts and inflorescence 40-125-flowered, and are mostly exploited for ornamental proposes (Wanderley, 1992). Despite the high support of the clade, its recognition as a new section at this moment is premature. This clade is deeply nested in *X.* sect. *Nematopus* and its taxonomic status will depend on a revision of the

classification of the whole section. Due to the low support for most of the internal nodes of this large, more inclusive clade, any further characterization and discussion of its subdivision is premature at this moment.

5. Conclusions

The phylogeny presented here is the first reconstruction of the evolutionary history of *Xyris* with a comprehensive – but not complete - sampling. Although no taxonomic changes were proposed here, *X.* sect. *Nematopus* appears monophyletic and clades within this section were discernable. Despite the low support for some nodes, biogeographic and morphological patterns were observed.

However, to obtain a more complete and robust phylogeny of *Xyris*, additional molecular markers and a more comprehensive taxonomic sampling – including a wide sampling of species from Africa, Asia, Australia and the Guayana highlands – are essential.

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Table 1

Voucher information for the sequences analyzed in this study.

Family	Species	Code	Voucher	State/Country
Eriocaulaceae	*Eriocaulon aquaticum* (Hill) Druce	X0249	L. M. Campbell 1053[3]	NY/U.S.A.
	E. aquaticum (Hill) Druce	X0313	D. Atha 8891[3]	ME/U.S.A.
	E. aquaticum (Hill) Druce	X0314	D. Atha 8755[3]	ME/U.S.A.
	E. compressum Lam.	X0312	D. Atha 9393[3]	NC/U.S.A.
	E. parkeri B.L. Rob.	X0016	M. Nee 50916[3]	ME/U.S.A.
	Lachnocaulon anceps (Walter) Morong	X0311	D. Atha 2511[3]	FL/U.S.A.
	Paepalanthus flaccidus (Bong.) Kunth	X0073	F. N. Costa 135[3]	MG/Brazil
	Syngonanthus flavidulus (Michx.) Ruhland	X0310	D. Atha 2497[3]	FL/U.S.A.
	S. humboldtii (Kunth) Ruhland	X0873	N. F. O. Mota 2383[1]	RR/Brazil
	S. tenuis (Kunth) Ruhland	X0872	N. F. O. Mota 2380[1]	RR/Brazil
Mayacaceae	*Mayaca fluviatilis* Aubl.	X0306	L. M. Campbell 1056[3]	NY/U.S.A.
	M. sellowiana Kunth	X0868	N. F. O. Mota 1556[1]	GO/Brazil
Rapateaceae	*Cephalostemon riedleianus* Körn.	X0869	N. F. O. Mota 1725[1]	MG/Brazil
	Monotrema xyridoides Gleason	X0870	N. F. O. Mota 2376[1]	RR/Brazil
	Rapatea paludosa Aubl.	X0068	W. Thomas 14422	BA/Brazil
	Spathanthus bicolor Ducke	X0871	N. F. O. Mota 2373[1]	RR/Brazil
Xyridaceae	*Abolboda americana* (Aubl.) Lanj.	X0337	N. F. O. Mota 2343[1]	RR/Brazil
	A. americana (Aubl.) Lanj.	X0338	N. F. O. Mota 2485[1]	BA/Brazil
	A. americana (Aubl.) Lanj.	X0339	N. F. O. Mota 2488[1]	BA/Brazil
	A. egleri L.B.Sm. & Downs	X0331	N. F. O. Mota 2055[1]	MT/Brazil
	A. egleri L.B.Sm. & Downs	X0332	N. F. O. Mota 2153[1]	MT/Brazil
	A. killipii Lasser	X0336	N. F. O. Mota 2325[1]	RR/Brazil
	A. macrostachya var. *macrostachya* Spruce ex Malme	X0333	N. F. O. Mota 2304[1]	RR/Brazil
	A. macrostachya var. *macrostachya* Spruce ex Malme	X0334	N. F. O. Mota 2319[1]	RR/Brazil
	A. poarchon Seub.	X0245	M. G. L. Wanderley 2846[2]	MG/Brazil
	A. poarchon Seub.	X0328	N. F. O. Mota 1552[1]	GO/Brazil
	A. pulchella Humb.	X0329	N. F. O. Mota 1554[1]	GO/Brazil
	A. pulchella Humb.	X0330	N. F. O. Mota 1743[1]	MG/Brazil
	A. pulchella Humb.	X0335	N. F. O. Mota 2322[1]	RR/Brazil
	Xyris* section *Nematopus			
	X. anamariae Wand. & Kral	X0510	N. F. O. Mota 2188[1]	MG/Brazil
	X. anamariae Wand. & Kral	X0684	M. G. L. Wanderley 2940[2]	MG/Brazil
	X. archeri L.B.Sm. & Downs	X0683	M. G. L. Wanderley 2939[2]	MG/Brazil
	X. archeri L.B.Sm. & Downs	X0760	N. F. O. Mota 2689[1]	MG/Brazil
	X. asperula Mart.	X0577	N. F. O. Mota 2296[1]	MG/Brazil
	X. asperula Mart.	X0751	N. F. O. Mota 2652[1]	MG/Brazil
	X. aff. *asperula* Mart.	X0639	L. F. A. de Paula 418[1]	GO/Brazil
	X. aff. *aurea* L.B.Sm. & Downs	X0429	N. F. O. Mota 1759[1]	MG/Brazil
	X. aurea L.B.Sm. & Downs	X0686	M. G. L. Wanderley 2947[2]	MG/Brazil
	X. bahiana Malme	X0479	N. F. O. Mota 1698[1]	BA/Brazil
	X. bahiana Malme	X0482	N. F. O. Mota 1702[1]	BA/Brazil

Family	Species	Code	Voucher	State/Country
	X. bahiana Malme	X0673	B. L. Lau 080[1]	BA/Brazil
	X. bialata Malme	X0365	N. F. O. Mota 722[1]	MG/Brazil
	X. bialata Malme	X0685	M. G. L. Wanderley 2941[2]	MG/Brazil
	X. blanchetiana Malme	X0501	N. F. O. Mota 1632[1]	MG/Brazil
	X. blanchetiana Malme	X0726	N. F. O. Mota 2623[1]	MG/Brazil
	X. brachysepala Kral	X0767	P. L. Viana 5252[1]	PA/Brazil
	X. calostachys Paulsen ex Warm.	X0364	N. F. O. Mota 710[1]	MG/Brazil
	X. calostachys Paulsen ex Warm.	X0755	N. F. O. Mota 2658[1]	MG/Brazil
	X. caparoensis Wand.	X0624	T. M. Machado 305[1]	MG/Brazil
	X. celiae L.B.Sm. & Downs	X0468	N. F. O. Mota 1668[1]	BA/Brazil
	X. celiae L.B.Sm. & Downs	X0503	N. F. O. Mota 1634[1]	MG/Brazil
	X. ciliata Thunb.	X0474	N. F. O. Mota 1674[1]	BA/Brazil
	X. ciliata Thunb.	X0594	N. F. O. Mota 2484[1]	BA/Brazil
	X. aff. *ciliata* Thunb.	X0484	N. F. O. Mota 1704[1]	BA/Brazil
	X. cipoensis L.B.Sm. & Downs	X0679	M. G. L. Wanderley 2924[2]	MG/Brazil
	X. coutensis Wand. & Cerati	X0643	M. Augsten 85[1]	MG/Brazil
	X. dawsonii L.B.Sm. & Downs	X0347	N. F. O. Mota 1560[1]	GO/Brazil
	X. dawsonii L.B.Sm. & Downs	X0348	N. F. O. Mota 1562[1]	GO/Brazil
	X. dawsonii L.B.Sm. & Downs	X0358	N. F. O. Mota 1576[1]	GO/Brazil
	X. diamantinae Malme	X0480	N. F. O. Mota 1699[1]	BA/Brazil
	X. diamantinae Malme	X0651	E. K. O. Hattori 1388[1]	MG/Brazil
	X. diamantinae Malme	X0664	E. K. O. Hattori 1482[1]	MG/Brazil
	X. diaphanobracteata Kral & Wand.	X0359	N. F. O. Mota 1577[1]	GO/Brazil
	X. diaphanobracteata Kral & Wand.	X0344	N. F. O. Mota 1551[1]	GO/Brazil
	X. disticha L.B.Sm. & Downs	X0518	N. F. O. Mota 2207[1]	MG/Brazil
	X. eleocharioides Kral & Wand.	X0672	B. L. Lau 079[1]	BA/Brazil
	X. eleocharioides Kral & Wand.	X0675	B. L. Lau 082[1]	BA/Brazil
	X. filifolia L.A. Nilsson	X0580	N. F. O. Mota 23331	MG/Brazil
	X. cf. *filifolia* L.A. Nilsson	X0623	T. M. Machado 306[1]	MG/Brazil
	X. aff. *filifolia* L.A. Nilsson	X0489	N. F. O. Mota 1736[1]	MG/Brazil
	X. aff. *filifolia* L.A. Nilsson	X0631	J. A. N. Batista 3056[1]	MG/Brazil
	X. fredericoi Wand.	X0523	N. F. O. Mota 2215[1]	MG/Brazil
	X. fusca L.A. Nilsson	X0589	N. F. O. Mota 2457[1]	MG/Brazil
	X. glaucescens Malme	X0512	N. F. O. Mota 2190[1]	MG/Brazil
	X. glaucescens Malme	X0522	N. F. O. Mota 2214[1]	MG/Brazil
	X. glaucescens Malme	X0738	N. F. O. Mota 2638[1]	MG/Brazil
	X. aff. *glaucescens* Malme	X0758	N. F. O. Mota 2685[1]	MG/Brazil
	X. glochidiata Kral & L.B.Sm.	X0477	N. F. O. Mota 1695[1]	BA/Brazil
	X. aff. *glochidiata* Kral & L.B.Sm.	X0460	N. F. O. Mota 1652[1]	BA/Brazil
	X. aff. *glochidiata* Kral & L.B.Sm.	X0463	N. F. O. Mota 1655[1]	BA/Brazil
	X. graminosa Pohl ex Mart.	X0727	N. F. O. Mota 2624[1]	MG/Brazil
	X. graomogolensis Wand. & Kral	X0567	N. F. O. Mota 2273[1]	MG/Brazil
	X. harleyi Kral & L.B.Sm.	X0770	G. H. S. Freitas 03[1]	BA/Brazil
	X. hilariana Malme	X0450	N. F. O. Mota 1637[1]	MG/Brazil
	X. hilariana Malme	X0507	N. F. O. Mota 1641[1]	MG/Brazil

Family	Species	Code	Voucher	State/Country
	X. hymenachne Mart.	X0478	N. F. O. Mota 1696[1]	BA/Brazil
	X. hymenachne Mart.	X0657	E. K. O. Hattori 1445[1]	BA/Brazil
	X. hymenachne Mart.	X0730	N. F. O. Mota 2629[1]	MG/Brazil
	X. hystrix Seub.	X0681	M. G. L. Wanderley 2932[2]	MG/Brazil
	X. insignis L.A. Nilsson	X0367	N. F. O. Mota 913[1]	MG/Brazil
	X. insignis L.A. Nilsson	X0449	N. F. O. Mota 1636[1]	MG/Brazil
	X. insignis L.A. Nilsson	X0736	N. F. O. Mota 2635[1]	MG/Brazil
	X. itatiayensis (Malme) Wand. & Sajo	X0732	N. F. O. Mota 2631[1]	MG/Brazil
	X. jataiana Kral & Wand.	X0638	L. F. A. de Paula 417[1]	GO/Brazil
	X. jolyi Wand. & Cerati	X0521	N. F. O. Mota 2211[1]	MG/Brazil
	X. jolyi Wand. & Cerati	X0680	M. G. L. Wanderley 2929[2]	MG/Brazil
	X. kralii Wand.	X0693	M. G. L. Wanderley 2963[2]	MG/Brazil
	X. kralii Wand.	X0728	N. F. O. Mota 2625[1]	MG/Brazil
	X. lacerata R.Br.	X0447	N. F. O. Mota 2173[1]	MT/Brazil
	X. lacerata R.Br.	X0448	N. F. O. Mota 2174[1]	MT/Brazil
	X. lanuginosa Seub.	X0444	N. F. O. Mota 2136[1]	MT/Brazil
	X. longiscapa L.A. Nilsson	X0529	N. F. O. Mota 2227[1]	MG/Brazil
	X. longiscapa L.A. Nilsson	X0735	N. F. O. Mota 2634[1]	MG/Brazil
	X. cf. *luetzelburgii* Malme	X0653	E. K. O. Hattori 1393[1]	MG/Brazil
	X. lutescens Kral & Wand.	X0356	N. F. O. Mota 1573[1]	GO/Brazil
	X. machrisiana L.B.Sm. & Downs	X0829	N. F. O. Mota 1550[1]	GO/Brazil
	X. melanopoda L.B.Sm. & Downs	X0663	E. K. O. Hattori 1481[1]	MG/Brazil
	X. mello-barretoi L.B.Sm. & Downs	X0469	N. F. O. Mota 1669[1]	BA/Brazil
	X. mertensiana Körn. ex Malme	X0596	N. F. O. Mota 2487[1]	BA/Brazil
	X. metallica Klotzsch ex Seub.	X0355	N. F. O. Mota 1572[1]	GO/Brazil
	X. metallica Klotzsch ex Seub.	X0361	N. F. O. Mota 1579[1]	GO/Brazil
	X. metallica Klotzsch ex Seub.	X0634	L. F. A. de Paula 406[1]	GO/Brazil
	X. metallica Klotzsch ex Seub.	X0640	L. F. A. de Paula 419[1]	GO/Brazil
	X. aff. *metallica* Klotzsch ex Seub.	X0644	E. K. O. Hattori 1277[1]	MG/Brazil
	X. aff. *metallica* Klotzsch ex Seub.	X0645	E. K. O. Hattori 1279[1]	MG/Brazil
	X. minarum Seub.	X0366	N. F. O. Mota 727[1]	MG/Brazil
	X. minarum Seub.	X0757	N. F. O. Mota 2666[1]	MG/Brazil
	X. morii Kral & L.B.Sm.	X0481	N. F. O. Mota 1700[1]	BA/Brazil
	X. aff. *morii* Kral & L.B.Sm.	X0659	E. K. O. Hattori 1447[1]	BA/Brazil
	X. mucugensis Kral & L.B.Sm.	X0670	B. L. Lau 068[1]	BA/Brazil
	X. aff. *mucugensis* Kral & L.B.Sm.	X0668	B. L. Lau 066[1]	BA/Brazil
	X. nanuzae Wand.	X0729	N. F. O. Mota 2628[1]	MG/Brazil
	X. nigra Mota & Wand.	X0761	N. F. O. Mota 2690[1]	MG/Brazil
	X. nilssonii Malme	X0446	N. F. O. Mota 2172[1]	MT/Brazil
	X. nubigena Kunth	X0485	N. F. O. Mota 1730[1]	MG/Brazil
	X. nubigena Kunth	X0725	N. F. O. Mota 2622[1]	MG/Brazil
	X. nubigena Kunth	X0747	N. F. O. Mota 2648[1]	MG/Brazil
	X. nubigena Kunth	X0753	N. F. O. Mota 2655[1]	MG/Brazil
	X. nubigena Kunth	X0756	N. F. O. Mota 2659[1]	MG/Brazil
	X. obcordata Kral & Wand.	X0570	N. F. O. Mota 2280[1]	MG/Brazil

Family	Species	Code	Voucher	State/Country
	X. obcordata Kral & Wand.	X0578	N. F. O. Mota 2297[1]	MG/Brazil
	X. obtusiuscula L.A. Nilsson	X0517	N. F. O. Mota 2206[1]	MG/Brazil
	X. obtusiuscula L.A. Nilsson	X0592	N. F. O. Mota 2461[1]	MG/Brazil
	X. peregrina Malme	X0363	N. F. O. Mota 708[1]	MG/Brazil
	X. peregrina Malme	X0494	N. F. O. Mota 1744[1]	MG/Brazil
	X. peregrina Malme	X0498	N. F. O. Mota 1750[1]	MG/Brazil
	X. peregrina Malme	X0724	N. F. O. Mota 2621[1]	MG/Brazil
	X. peregrina Malme	X0734	N. F. O. Mota 2633[1]	MG/Brazil
	X. peregrina Malme	X0754	N. F. O. Mota 2657[1]	MG/Brazil
	X. aff. *peregrina* Malme	X0739	N. F. O. Mota 2640[1]	MG/Brazil
	X. phaeocephala Kral & Wand.	X0483	N. F. O. Mota 1703[1]	BA/Brazil
	X. phaeocephala Kral & Wand.	X0654	E. K. O. Hattori 1441[1]	BA/Brazil
	X. picea Kral & Wand.	X0666	B. L. Lau 063[1]	BA/Brazil
	X. aff. *picea* Kral & Wand.	X0655	E. K. O. Hattori 1443[1]	BA/Brazil
	X. pilosa Kunth	X0519	N. F. O. Mota 2209[1]	MG/Brazil
	X. pilosa Kunth	X0688	M. G. L. Wanderley 2949[2]	MG/Brazil
	X. aff. *pilosa1* Kunth	X0374	N. F. O. Mota 2029[1]	MG/Brazil
	X. aff. *pilosa2* Kunth	X0565	N. F. O. Mota 2268[1]	MG/Brazil
	X. aff. *pilosa2* Kunth	X0575	N. F. O. Mota 2294[1]	MG/Brazil
	X. plantaginea Mart.	X0766	P. Burkowski 1312[1]	MG/Brazil
	X. platystachya Nilsson ex Malme	X0520	N. F. O. Mota 2210[1]	MG/Brazil
	X. platystachya Nilsson ex Malme	X0691	M. G. L. Wanderley 2959[2]	MG/Brazil
	X. cf. *pranceana* Kral & Wand.	X0360	N. F. O. Mota 1578[1]	GO/Brazil
	X. pterygoblephara Steud.	X0362	N. F. O. Mota 637[1]	MG/Brazil
	X. pterygoblephara Steud.	X0368	N. F. O. Mota 1287[1]	MG/Brazil
	X. pterygoblephara Steud.	X0514	N. F. O. Mota 2194[1]	MG/Brazil
	X. pterygoblephara Steud.	X0564	N. F. O. Mota 2267[1]	MG/Brazil
	X. pterygoblephara Steud.	X0569	N. F. O. Mota 2278[1]	MG/Brazil
	X. pterygoblephara Steud.	X0737	N. F. O. Mota 2636[1]	MG/Brazil
	X. pterygoblephara Steud.	X0762	N. F. O. Mota 2691[1]	MG/Brazil
	X. pterygoblephara Steud.	X0764	N. F. O. Mota 2693[1]	MG/Brazil
	X. aff. *pterygoblephara1* Steud.	X0499	N. F. O. Mota 1751[1]	MG/Brazil
	X. aff. *pterygoblephara2* Steud.	X0742	N. F. O. Mota 2643[1]	MG/Brazil
	X. aff. *pterygoblephara2* Steud.	X0743	N. F. O. Mota 2644[1]	MG/Brazil
	X. aff. *pterygoblephara2* Steud.	X0746	N. F. O. Mota 2647[1]	MG/Brazil
	X. pterygoblephara var. vernicosa Kral & Wand.	X0662	E. K. O. Hattori 14801	MG/Brazil
	X. pterygoblephara var. vernicosa Kral & Wand.	X0665	E. K. O. Hattori 14831	MG/Brazil
	X. aff. *pterygoblephara* var. *vernicosa* Kral & Wand.	X0574	N. F. O. Mota 2293[1]	MG/Brazil
	X. aff. *regnelii* L.A. Nilsson	X0628	L. L. Giacomin 1641[1]	MG/Brazil
	X. retrorsifimbriata Kral & L.B.Sm.	X0455	N. F. O. Mota 1646[1]	BA/Brazil
	X. retrorsifimbriata Kral & L.B.Sm.	X0571	N. F. O. Mota 2289[1]	MG/Brazil
	X. rigida Kunth	X0708	N. F. O. Mota 2514[1]	SC/Brazil
	X. aff. rigida Kunth	X0579	N. F. O. Mota 2332[1]	MG/Brazil
	X. roraimae Malme	X0346	N. F. O. Mota 1559[1]	GO/Brazil
	X. roraimae Malme	X0504	N. F. O. Mota 1635[1]	MG/Brazil

Family	Species	Code	Voucher	State/Country
	X. roraimae Malme	X0530	N. F. O. Mota 2230[1]	MG/Brazil
	X. roraimae Malme	X0745	N. F. O. Mota 2646[1]	MG/Brazil
	X. rubromarginata Kral & L.B.Sm.	X0456	N. F. O. Mota 1648[1]	BA/Brazil
	Xyris rubromarginata Kral & L.B.Sm.	X0669	B. L. Lau 067[1]	BA/Brazil
	X. rubromarginata Kral & L.B.Sm.	X0465	N. F. O. Mota 1657[1]	BA/Brazil
	X. rubromarginata Kral & L.B.Sm.	X0667	B. L. Lau 065[1]	BA/Brazil
	X. rupicola Kunth	X0375	N. F. O. Mota 2033[1]	MG/Brazil
	X. savanensis Miq.	X0439	N. F. O. Mota 2093[1]	MT/Brazil
	X. savanensis Miq.	X0649	E. K. O. Hattori 1312[1]	MG/Brazil
	X. savanensis Miq.	X0831	N. F. O. Mota 2302[1]	MG/Brazil
	X. savanensis var. *glabrata* Miq.	X0437	N. F. O. Mota 2088[1]	MT/Brazil
	X. schizachne Mart.	X0434	N. F. O. Mota 1787[1]	MG/Brazil
	X. schizachne Mart.	X0583	N. F. O. Mota 2338[1]	MG/Brazil
	X. schizachne Mart.	X0637	L. F. A. de Paula 411[1]	GO/Brazil
	X. schizachne Mart.	X0825	S. Moreira 350[1]	MS/Brazil
	X. scoparia Mota & Wand.	X0373	N. F. O. Mota 2028[1]	MG/Brazil
	X. seubertii L.A. Nilsson	X0370	N. F. O. Mota 1509[1]	MG/Brazil
	X. seubertii L.A.Nilsson	X0752	N. F. O. Mota 2654[1]	MG/Brazil
	X. seubertii L.A. Nilsson	X0495	N. F. O. Mota 1746[1]	MG/Brazil
	X. seubertii L.A. Nilsson	X0525	N. F. O. Mota 2222[1]	MG/Brazil
	X. seubertii L.A. Nilsson	X0591	N. F. O. Mota 2460[1]	MG/Brazil
	X. seubertii L.A. Nilsson	X0660	E. K. O. Hattori 1448[1]	BA/Brazil
	X. seubertii L.A. Nilsson	X0671	B. L. Lau 074[1]	BA/Brazil
	X. seubertii L.A. Nilsson	X0749	N. F. O. Mota 2650[1]	MG/Brazil
	X. seubertii var. *espinhacae* Kral & Wand.	X0656	E. K. O. Hattori 1444[1]	BA/Brazil
	X. seubertii var. *espinhacae* Kral & Wand.	X0658	E. K. O. Hattori 1446[1]	BA/Brazil
	X. shepherdiana Wand. & J.S.Guedes	X0748	N. F. O. Mota 2649[1]	MG/Brazil
	X. aff. *shepherdiana* Wand. & J.S.Guedes	X0497	N. F. O. Mota 1746[1]	MG/Brazil
	X. sincorana Kral & Wand.	X0573	N. F. O. Mota 2291[1]	MG/Brazil
	X. sparsifolia Kral & L.B.Sm.	X0502	N. F. O. Mota 1633[1]	MG/Brazil
	X. sparsifolia Kral & L.B.Sm.	X0568	N. F. O. Mota 2277[1]	MG/Brazil
	X. spectabilis Mart.	X0687	M. G. L. Wanderley 2948[2]	MG/Brazil
	X. spinulosa Kral & L.B.Sm.	X0692	M. G. L. Wanderley 2950[2]	MG/Brazil
	X. stenocephala Malme	X0442	N. F. O. Mota 2099[1]	MT/Brazil
	X. stenophylla L.A. Nilsson	X0585	N. F. O. Mota 2442[1]	MG/Brazil
	X. subsetigera Malme	X0508	N. F. O. Mota 2259[1]	MG/Brazil
	X. subsetigera Malme	X0690	M. G. L. Wanderley 2955[2]	MG/Brazil
	X. subsetigera Malme	X0509	N. F. O. Mota 2185[1]	MG/Brazil
	X. subsetigera Malme	X0731	N. F. O. Mota 2630[1]	MG/Brazil
	X. subsetigera Malme	X0759	N. F. O. Mota 2686[1]	MG/Brazil
	X. subulata Ruiz & Pav.	X0128	M. Sundue 1343	Limon/Costa Rica
	X. tenella Kunth	X0636	L. F. A. de Paula 410[1]	GO/Brazil
	X. tenella Kunth	X0352	N. F. O. Mota 1567a[1]	GO/Brazil
	X. aff. *tenella* Kunth	X0461	N. F. O. Mota 1653[1]	BA/Brazil
	X. teres L.A. Nilsson	X0625	L. L. Giacomin 941[1]	RJ/Brazil

Family	Species	Code	Voucher	State/Country
	X. tortula Mart.	X0431	N. F. O. Mota 1763[1]	MG/Brazil
	X. tortula Mart.	X0467	N. F. O. Mota 1667[1]	BA/Brazil
	X. tortula Mart.	X0584	N. F. O. Mota 2336[1]	MG/Brazil
	X. tortula Mart.	X0769	G. H. S. Freitas 02[1]	BA/Brazil
	X. cf. *tortula* Mart.	X0350	N. F. O. Mota 1564[1]	GO/Brazil
	X. aff. *tortula1* Mart.	X0433	N. F. O. Mota 1783[1]	MG/Brazil
	X. aff. *tortula2* Mart.	X0443	N. F. O. Mota 2106[1]	MT/Brazil
	X. trachyphylla Mart.	X0430	N. F. O. Mota 1761[1]	MG/Brazil
	X. trachyphylla Mart.	X0454	N. F. O. Mota 1645[1]	BA/Brazil
	X. trachyphylla Mart.	X0513	N. F. O. Mota 2192[1]	MG/Brazil
	X. aff. *trachyphylla1* Mart.	X0451	N. F. O. Mota 2262[1]	MG/Brazil
	X. aff. *trachyphylla1* Mart.	X0505	N. F. O. Mota 1639[1]	MG/Brazil
	X. aff. *trachyphylla2* Mart.	X0576	N. F. O. Mota 2295[1]	MG/Brazil
	X. vacillans Malme	X0581	N. F. O. Mota 2334[1]	MG/Brazil
	X. vacillans Malme	X0582	N. F. O. Mota 2335[1]	MG/Brazil
	X. velutina Mota & Wand.	X0372	N. F. O. Mota 2026[1]	MG/Brazil
	X. veruina Malme	X0351	N. F. O. Mota 1565[1]	GO/Brazil
	X. wawrae Heimerl	X0587	N. F. O. Mota 2446[1]	MG/Brazil
	X. wawrae Heimerl	X0590	N. F. O. Mota 2458[1]	MG/Brazil
	Xyris sp.1	X0428	N. F. O. Mota 1758[1]	MG/Brazil
	Xyris sp.2	X0768	G. H. S. Freitas 01[1]	BA/Brazil
	Xyris* section *Pomatoxyris			
	Xyris operculata Labill.	X0282	B. J. Conn 5687[3]	NSW/Australia
	X. ustulata L.A. Nilsson	X0289	B. J. Conn 5702[3]	NSW/Australia
	Xyris* section *Xyris			
	Xyris ambigua Beyr. ex Kunth	X0049	J. Horn 4896[3]	NY/U.S.A.
	X. brevifolia Michx.	X0001	D. Atha 2508[3]	FL/U.S.A.
	X. brevifolia Michx.	X0048	J. Horn 4893[3]	GA/U.S.A.
	X. brevifolia Michx.	X0168	L. M. Campbell 1048[3]	GA/U.S.A.
	X. capensis Thunb.	X0593	N. F. O. Mota 2463[1]	MG/Brazil
	X. difformis Chapm.	X0018	D. Atha 2507[3]	FL/U.S.A.
	X. difformis var. *difformis* Chapm.	X0248	L. M. Campbell 1052[3]	NY/U.S.A.
	X. elliottii Chapm.	X0067	J. Horn 4892[3]	GA/U.S.A.
	X. elliottii Chapm.	X0193	D. Atha 2604[3]	FL/U.S.A.
	X. fallax Malme	X0440	N. F. O. Mota 2095[1]	MT/Brazil
	X. fallax Malme	X0488	N. F. O. Mota 1735[1]	MG/Brazil
	X. fallax Malme	X0650	E. K. O. Hattori 1313[1]	MG/Brazil
	X. fimbriata Elliott	X0054	J. Horn 4907[3]	GA/U.S.A.
	X. fimbriata Elliott	X0227	L. C. Anderson 24687[3]	FL/U.S.A.
	X. floridana (Kral) E.L.Bridges & Orzell	X0194	J. Horn 4883[3]	SC/U.S.A.
	X. iridifolia Chapm.	X0136	J. Horn 4481[3]	SC/U.S.A.
	X. iridifolia Chapm.	X0144	R. D. Thomas 154982[3]	LA/U.S.A.
	X. iridifolia Chapm.	X0163	R. D. Thomas 154982[3]	LA/U.S.A.
	X. jupicai Rich.	X0007	L. M. Campbell 1047[3]	GA/U.S.A.
	X. jupicai Rich.	X0127	R. Kral 25057[3]	VC/Mexico

Family	Species	Code	Voucher	State/Country
	X. jupicai Rich.	X0151	J. Horn 4899[3]	GA/U.S.A.
	X. jupicai Rich.	X0167	L. M. Campbell 1047[3]	GA/U.S.A.
	X. jupicai Rich.	X0476	N. F. O. Mota 1676[1]	BA/Brazil
	X. jupicai Rich.	X0676	B. L. Lau 083[1]	BA/Brazil
	X. macrocephala Vahl	X0172	L. J. Gillespie 4312[3]	P-S/Guyana
	X. macrocephala Vahl	X0438	N. F. O. Mota 2090[1]	MT/Brazil
	X. macrocephala Vahl	X0470	N. F. O. Mota 1670[1]	BA/Brazil
	X. macrocephala Vahl	X0527	N. F. O. Mota 2225[1]	MG/Brazil
	X. macrocephala Vahl	X0531	N. F. O. Mota 2298[1]	RR/Brazil
	X. macrocephala Vahl	X0633	L. F. A. de Paula 404[1]	GO/Brazil
	X. macrocephala Vahl	X0635	L. F. A. de Paula 409[1]	GO/Brazil
	X. macrocephala Vahl	X0646	E. K. O. Hattori 1281[1]	MG/Brazil
	X. macrocephala Vahl	X0652	E. K. O. Hattori 1389[1]	MG/Brazil
	X. macrocephala Vahl	X0750	N. F. O. Mota 2651[1]	MG/Brazil
	X. macrocephala Vahl	X0765	P. Burkowski 1248[1]	PA/Brazil
	X. macrocephala Vahl	X0823	S. Moreira 353[1]	MS/Brazil
	X. macrocephala Vahl	X0824	S. Moreira 352[1]	MS/Brazil
	X. montana Ries	X0142	S. R. Hill 33933[3]	U.S.A.
	X. navicularis Griseb.	X0863	G. Carnevali s.n. [3]	OWD/Belize
	X. navicularis Griseb.	X0864	G. Carnevali s.n. [3]	OWD/Belize
	X. platylepis Chapm.	X0050	J. Horn 4900[3]	NY/U.S.A.
	X. serotina Chapm.	X0053	J. Horn 4904[3]	GA/U.S.A.
	X. smalliana Nash	X0051	J. Horn 4901[3]	GA/U.S.A.
	X. smalliana Nash	X0246	L. M. Campbell 1051[3]	NY/U.S.A.
	X. stricta Chapm.	X0052	J. Horn 4903[3]	GA/U.S.A.
	X. torta Sm.	X0247	L. M. Campbell 1054[3]	NY/U.S.A.
	Xyris sp.3	X0257	NYBG prop; e-vouchered[3]	U.S.A.

Abbreviations for Brazilian states are: BA = Bahia; GO = Goiás; MG = Minas Gerais; MS = Mato Grosso do Sul; MT = Mato Grosso; PA = Pará; RJ = Rio de Janeiro; RR = Roraima; SC = Santa Catarina. Abbreviations for states in the United States of America are: FL = Florida; GA = Georgia; LA = Louisiana; ME = Maine; NC = North Carolina; NY = New York; Orange Walk District, Belize is abbreviated OWD. New South Wales, Australia state is abbreviated NSW. Abbreviation for Guyana: P-S= Potaro-Siparuni. Abbreviation for Mexico: VC = Veracruz. [1] BHCB Herbarium; [2] SP Herbarium; [3] NY Herbarium

Table 2

Taxon sampling, matrix, maximum likelihood, and parsimony statistics for *ndhF*, *matK*, *rbcL*, *cox3*, *orf25* and combined data sets. Tree lengths and consistency index exclude uninformative characters.

	cox3	matK	ndhF	orf25	rbcL	Mitochondrial	Plastid	Combined
taxa	157	157	151	131	159	158	159	159
nº of sequences	281	288	269	213	290	285	290	290
Aligned length+indel	606 + 0	831 + 18	1296 + 22	399 + 2	1221 + 0	1005 + 2	3348 + 40	4353 + 42
uninformative characters	534	289	771	286	858	820	1918	2738
Parsimony-informative characters	72	560	547	115	363	187	1470	1657
Shortest tree length	126	1943	1862	185	1155	318	5517	5901
nº of trees	20	>1000000	>1000000	2	102120	156600	>1000000	829440
Consistency index (CI)	0.667	0.499	0.475	0.751	0.461	0.701	0.432	0.441
Retention index (RI)	0.955	0.909	0.866	0.966	0.927	0.959	0.881	0.885
Log Likelihood	-1944.354047	-12149.48921	-12890.31724	-1651.445938	-8744.72483	-3507.920863	-37906.81167	-42083.30276

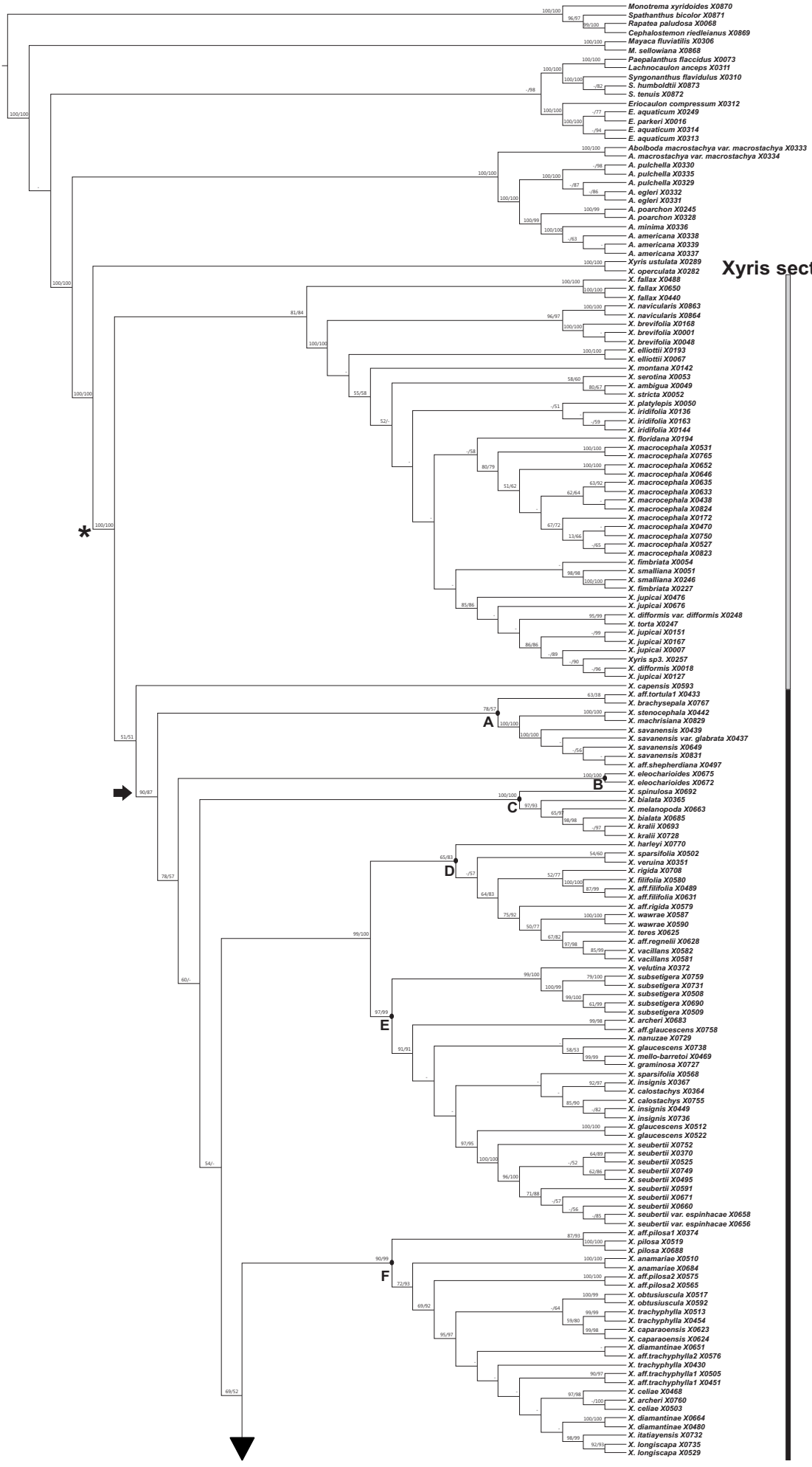
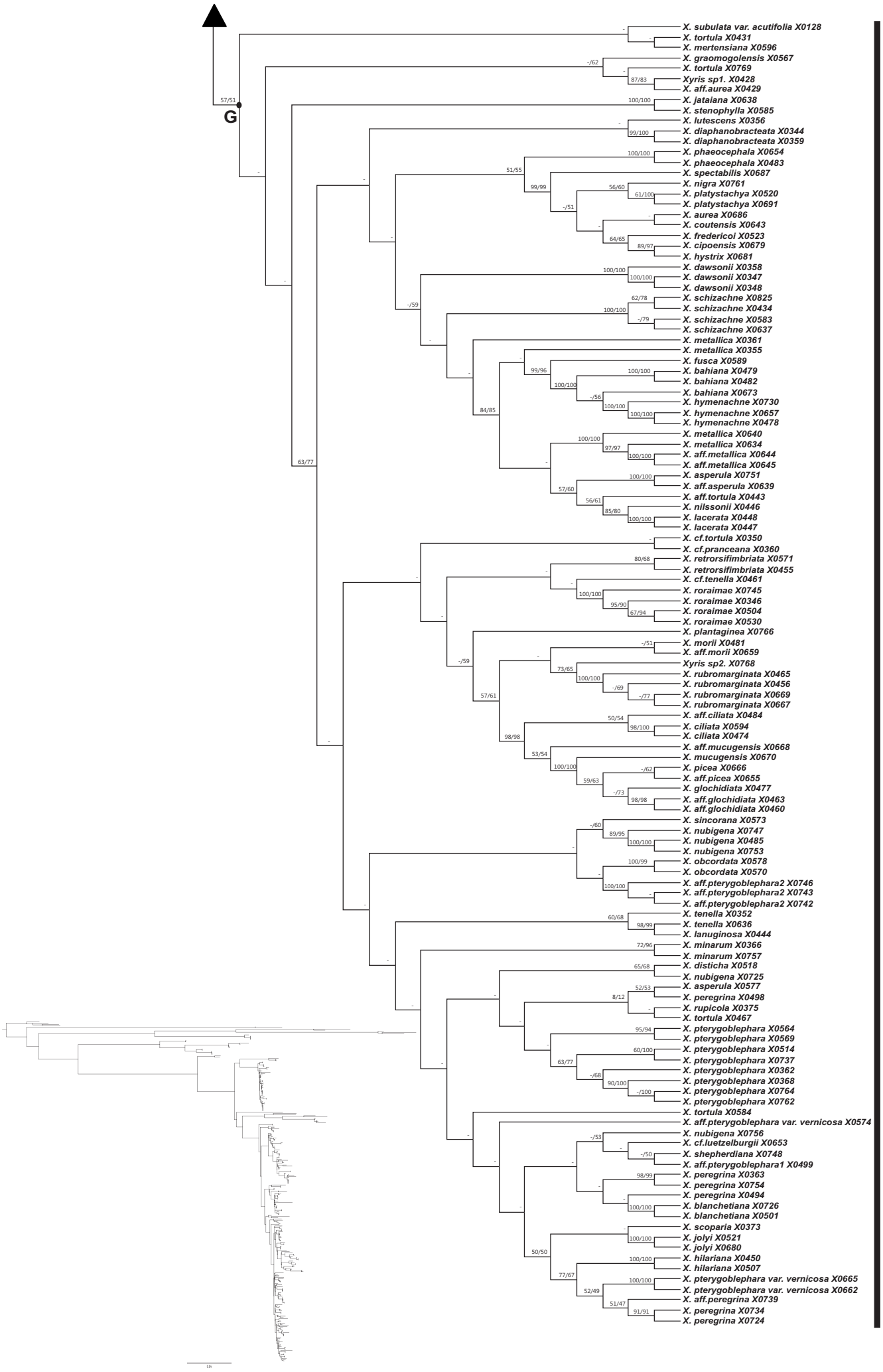
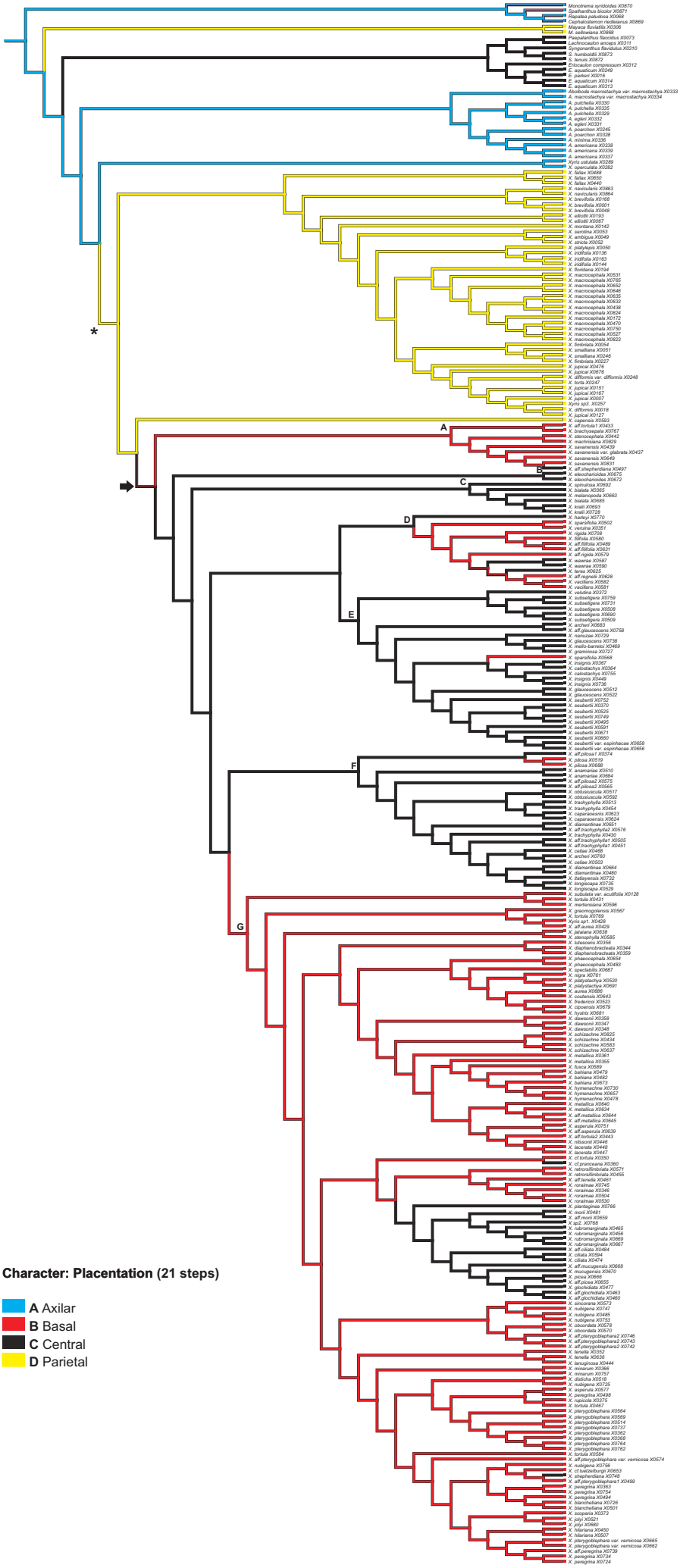

Monotrema xyridoides X0870
Spathanthus bicolor X0871
Rapatea paludosa X0068
Cephalostemon riedleianus X0869
Mayaca fluviatilis X0306
M. sellowiana X0868
Paepalanthus flaccidus X0073
Lachnocaulon anceps X0311
Syngonanthus flavidulus X0310
S. humboldtii X0873
S. tenuis X0872
Eriocaulon compressum X0312
E. aquaticum X0249
E. parkeri X0016
E. aquaticum X0314
E. aquaticum X0313
Abolboda macrostachya var. macrostachya X0333
A. macrostachya var. macrostachya X0334
A. pulchella X0330
A. pulchella X0335
A. pulchella X0329
A. egleri X0332
A. egleri X0331
A. poarchon X0245
A. poarchon X0328
A. minima X0336
A. americana X0338
A. americana X0339
A. americana X0337
Xyris ustulata X0289
X. operculata X0282
X. fallax X0488
X. fallax X0650
X. fallax X0440
X. navicularis X0863
X. navicularis X0864
X. brevifolia X0168
X. brevifolia X0001
X. brevifolia X0048
X. elliottii X0193
X. elliottii X0067
X. montana X0142
X. serotina X0053
X. ambigua X0049
X. stricta X0052
X. platylepis X0050
X. iridifolia X0136
X. iridifolia X0163
X. iridifolia X0144
X. floridana X0194
X. macrocephala X0531
X. macrocephala X0765
X. macrocephala X0652
X. macrocephala X0646
X. macrocephala X0635
X. macrocephala X0633
X. macrocephala X0438
X. macrocephala X0824
X. macrocephala X0172
X. macrocephala X0470
X. macrocephala X0750
X. macrocephala X0527
X. macrocephala X0823
X. fimbriata X0054
X. smalliana X0051
X. smalliana X0246
X. fimbriata X0227
X. jupicai X0476
X. jupicai X0676
X. difformis var. difformis X0248
X. torta X0247
X. jupicai X0151
X. jupicai X0167
X. jupicai X0007
Xyris sp3. X0257
X. difformis X0018
X. jupicai X0127
X. capensis X0593
X. aff.tortula1 X0433
X. brachysepala X0767
X. stenocephala X0442
X. machrisiana X0829
X. savanensis X0439
X. savanensis var. glabrata X0437
X. savanensis X0649
X. savanensis X0831
X. aff.shepherdiana X0497
X. eleocharioides X0675
X. eleocharioides X0672
X. spinulosa X0692
X. bialata X0365
X. melanopoda X0663
X. bialata X0685
X. kralii X0693
X. kralii X0728
X. harleyi X0770
X. sparsifolia X0502
X. veruina X0351
X. rigida X0708
X. filifolia X0580
X. aff.filifolia X0489
X. aff.filifolia X0631
X. aff.rigida X0579
X. wawrae X0587
X. wawrae X0590
X. teres X0625
X. aff.regnelii X0628
X. vacillans X0582
X. vacillans X0581
X. velutina X0372
X. subsetigera X0759
X. subsetigera X0731
X. subsetigera X0508
X. subsetigera X0690
X. subsetigera X0509
X. archeri X0683
X. aff.glaucescens X0758
X. nanuzae X0729
X. glaucescens X0738
X. mello-barretoi X0469
X. graminosa X0727
X. sparsifolia X0568
X. insignis X0367
X. calostachys X0364
X. calostachys X0755
X. insignis X0449
X. insignis X0736
X. glaucescens X0512
X. glaucescens X0522
X. seubertii X0752
X. seubertii X0370
X. seubertii X0525
X. seubertii X0749
X. seubertii X0495
X. seubertii X0591
X. seubertii X0671
X. seubertii X0660
X. seubertii var. espinhacae X0658
X. seubertii var. espinhacae X0656
X. aff.pilosa1 X0374
X. pilosa X0519
X. pilosa X0688
X. anamariae X0510
X. anamariae X0684
X. aff.pilosa2 X0575
X. aff.pilosa2 X0565
X. obtusiuscula X0517
X. obtusiuscula X0592
X. trachyphylla X0513
X. trachyphylla X0454
X. caparaoensis X0623
X. caparaoensis X0624
X. diamantinae X0651
X. aff.trachyphylla2 X0576
X. trachyphylla X0430
X. aff.trachyphylla1 X0505
X. aff.trachyphylla1 X0451
X. celiae X0468
X. archeri X0760
X. celiae X0503
X. diamantinae X0664
X. diamantinae X0480
X. itatiayensis X0732
X. longiscapa X0735
X. longiscapa X0529
A
B
C
D
E
F
*
Xyris section Pomatoxyris
Xyris section Xyris
Xyris section Nematopus

Fig. 1. Maximum likelihood tree from combined *cox3*, *matK*, *ndhF*, *orf25* and *rbcL* datasets. Parsinomy jackknife percentage, bootstrap percentages from the maximum likelihood analysis are shown next to nodes (in this order). The clade of Neotropical *Xyris* is indicated with an asterisk "*". The sectional classification of *Xyris* is shown and an arrow indicates the hypothetical ancestor of *Xyris* section *Nematopus*. Seven internal nodes of *X.* sect. *Nematopus* are named (A to G). The code following each species corresponds to the voucher of the specimen (Table 1).



Xyris section Nematopus

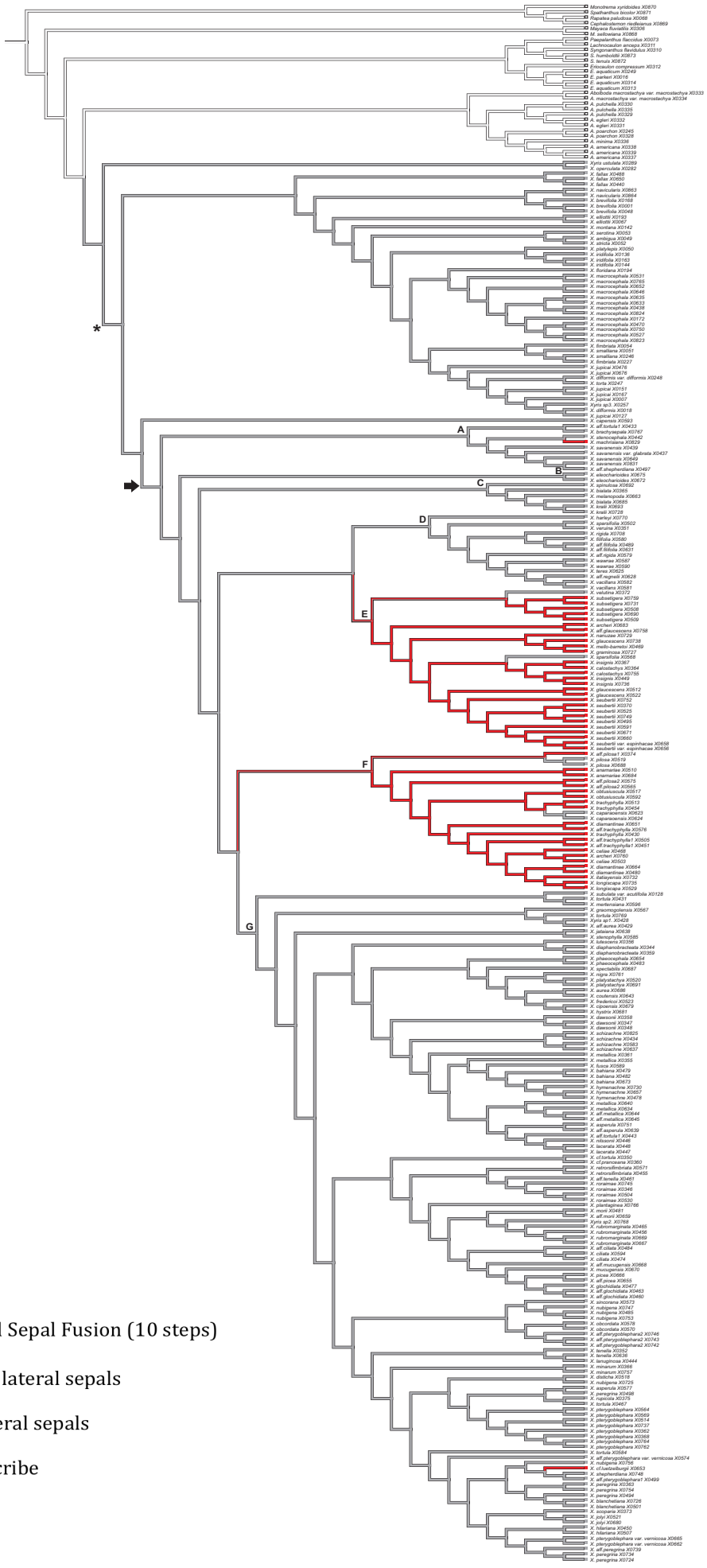
Fig. 2. Continuation of Fig. 1. A phylogram with proportional branch lengths is shown on left (scale bar 0.04 changes).



Character: Placentation (21 steps)

- **A** Axilar
- **B** Basal
- **C** Central
- **D** Parietal

Fig. 3. Parsimony ancestral state reconstruction on the combined maximum likelihood tree for placentation type. Colors: blue = axillar placentation, red = basal placentation, black = central placentation, yellow = parietal placentation. Symbols and notation follow Fig. 1.



Character: Lateral Sepal Fusion (10 steps)

Connate lateral sepals

Free lateral sepals

Not describe

Fig. 4. Parsimony ancestral state reconstruction on the combined maximum likelihood tree for lateral sepal connation. Colors: red = connate lateral sepals, grey= free lateral sepals, white = state unknown. Symbols and notation follow Fig. 1. Illustration by Cecília Tomasi (USP).


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y

Fig. 5. White cluster – *Xyris* sec. *Xyris* – (A) *X. jupicai*, (B) *X. fallax*, (C) *X. capensis*. Red cluster – Clade A – (D) *X. paraensis*[*], (E) *X. brachysepala*[*], (F) *X. savanensis*. Green cluster – Clade B – (G) *X. eleocharioides*. Orange cluster – Clade C – (H) *X. spinulosa*, (I) *X. bialata*[*], (J) *X. melanopoda*. Purple cluster – Clade D – (K) *X. harley*, (L) *X. sparsifolia*, (M) *X. veruina*[*], (N) *X. teres*, (O) *X. wawrae*. Blue cluster – Clade E – (P) *X. velutina*, (Q) *X. subsetigera*, (R) *X. glaucescens*[*], (S) *X. mello-barretoi*, (T) *X. seubertii*[**]. Yellow cluster – Clade F – (U) *X. pilosa*, (V) *X. diamantinae*, (W) *X. longiscapa*[*], (X) *X. obtusiuscula*[**], (Y) *X. trachyphylla*. [*] Photographs provided by Pedro L. Viana; [**] Photographs provided by Lilian M. Costa.

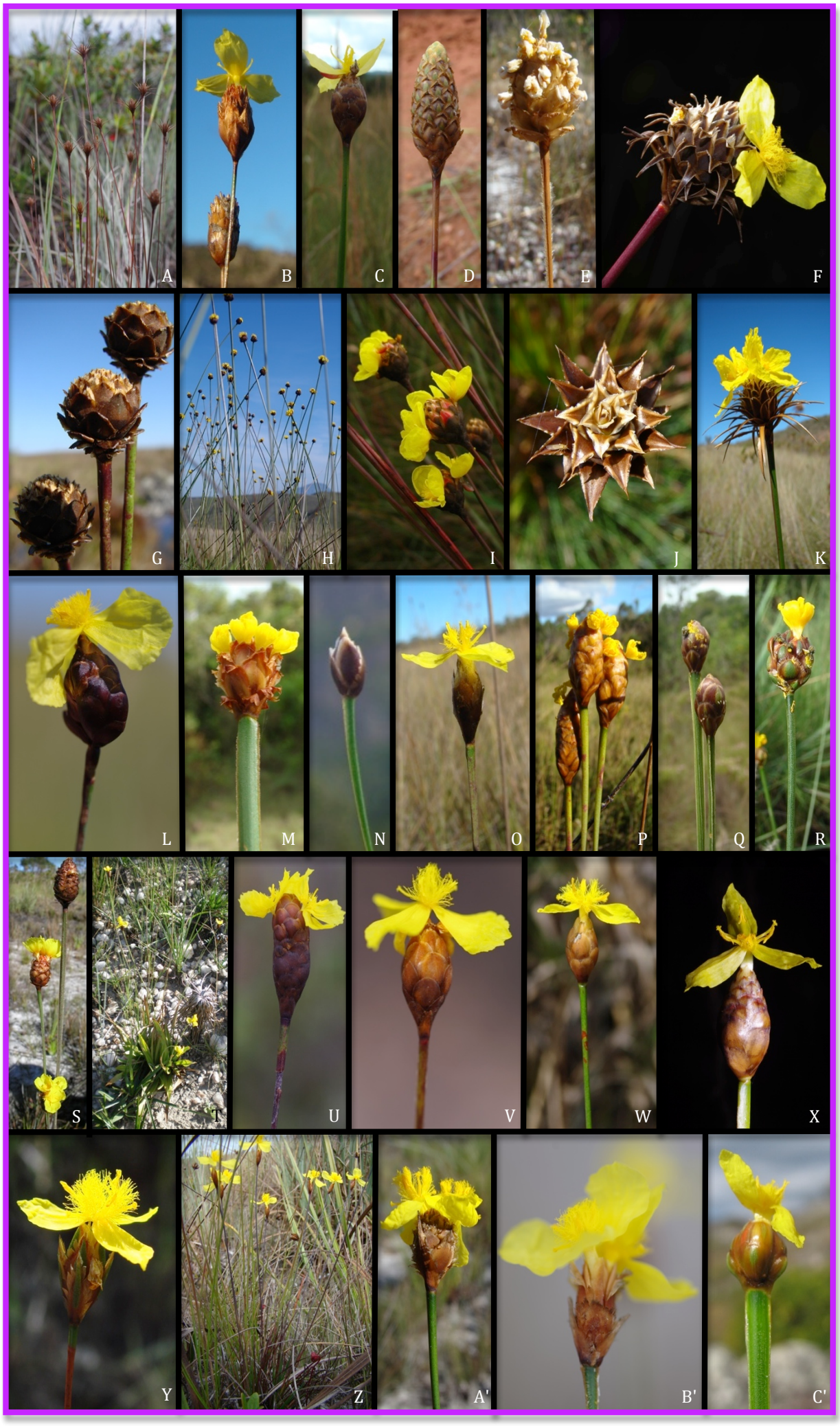

A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
A'
B'
C'

Fig. 6. Pink cluster – Clade G– (A) *X. mertensiana*[*], (B) *X. graomogolensis*, (C) *X. tortula*, (D) *X. aff. aurea*, (E) *X. diaphanobracteata*, (F) *X. nigricans*[*], (G) *X. nigra*[*], (H) *X. platystachya*[*], (I) *X. aurea*, (J) *X. coutensis*, (K) *X. cipoensis*, (L) *X. dawsonii*[*], (M) *X. schizachne*, (N) *X. fusca*, (O) *X. hymenachne*, (P) *X. asperula*, (Q) *X. nilssonii*, (R) *X. lacerate*, (S) *X. roraimae*, (T) *X. plantaginea*[**], (U) *X. ciliata*[*], (V) *X. glochidiata*[*], (W) *X. nubigena*[*], (X) *X. pterygoblepagra*[*], (Y) *X. minarum*[*], (Z) *X. rupicola*, (A') *X. blanchetiana*, (B') *X. hilariana*, (C') *X. pterygoblepahra var. vernicosa*. [*] Photographs provided by Pedro L. Viana; [**] Photograph provided by Pablo Burkowisk.

Appendix A. Supplementary material

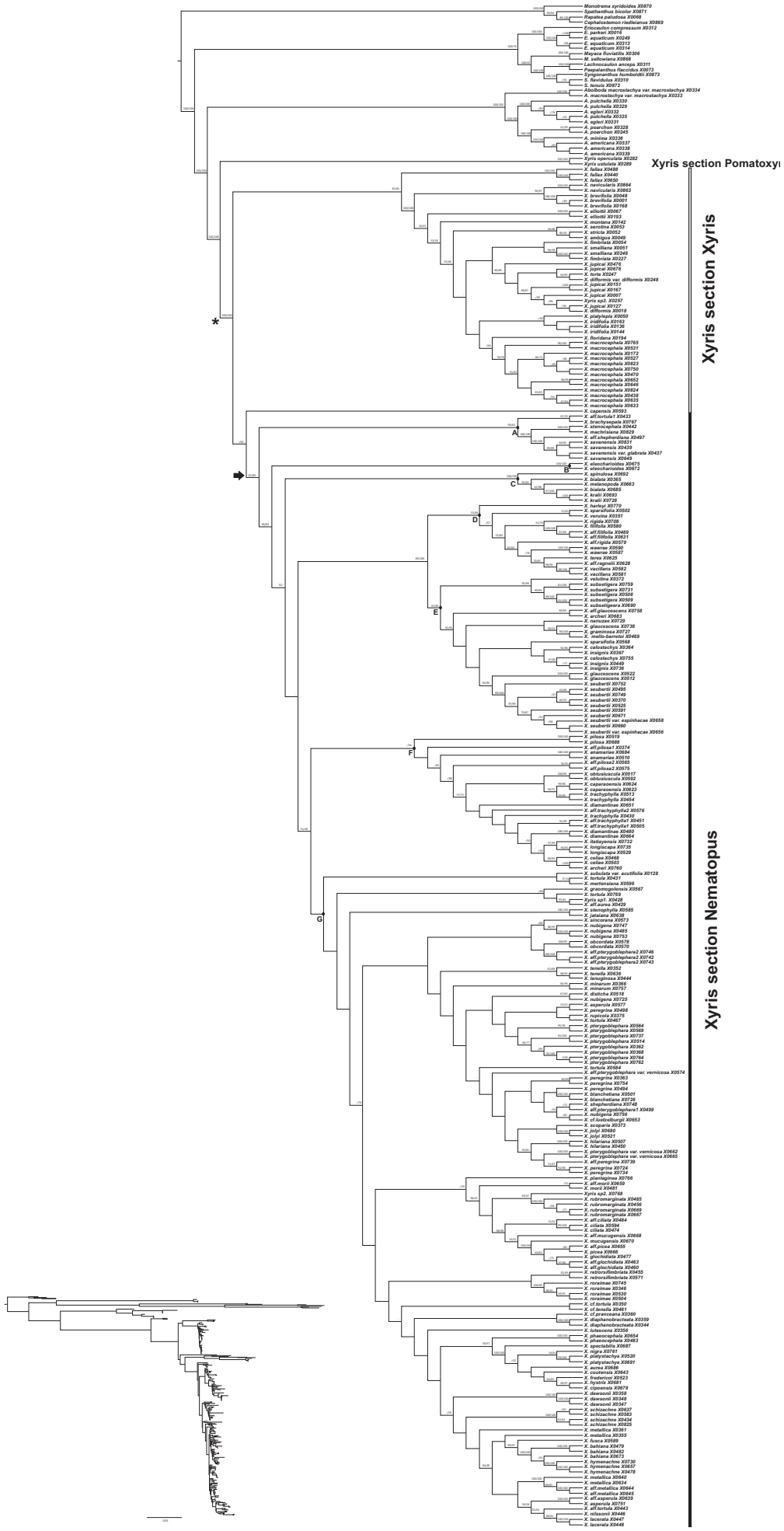


Figure S1. Maximum likelihood tree from the plastid datasets: *matK*, *ndhF,* and *rbcL*. Symbols and notation follow Fig. 1.


Monotrema xyridoides X0870
Rapatea paludosa X0068
Cephalostemon riedlelianus X0869
Spathanthus bicolor X0871
Mayaca fluviatilis X0306
M. sellowiana X0868
Eriocaulon parkeri X0016
E. aquaticum X0313
E. aquaticum X0314
E. compressum X0312
E. aquaticum X0349
Lachnocaulon anceps X0311
Paepalanthus flaccidus X0073
Syngonanthus flavidulus X0310
S. femoris X0872
S. humboldtii X0873
Abolboda macrostachya var. macrostachya X0333
A. macrostachya X0334 var. macrostachya X0334
A. americana X0336
A. americana X0337
A. americana X0339
A. americana X0338
A. poarchon X0228
A. poarchon X0345
A. pulchella X0335
A. egleri X0332
A. egleri X0331
X. ophiolata X0289
X. operculata X0282
X. fallax X0468
X. fallax X0440
X. fallax X0650
X. platylepis X0050
X. jupicai X0127
X. jupicai X0151
X. smalliana X0346
X. torta X0247
X. macrocephala X0635
X. macrocephala X0470
X. iridifolia X0144
X. smalliana X0051
X. fimbriata X0054
X. iridifolia X0163
X. iridifolia X0136
X. difformis X0018
X. brevifolia X0001
X. fimbriata X0221
X. macrocephala X0633
X. macrocephala X0527
X. macrocephala X0765
X. ambigua X0049
X. jupicai X0607
X. jupicai X0676
X. navicularis X0863
X. jupicai X0167
X. elliottii X0067
X. brevifolia X0156
X. brevifolia X0048
X. macrocephala X0172
X. machrisiana X0829
X. brachypapala X0767
X. savanensis X0831
X. seubertii X0525
X. savanensis X0649
X. aff.shepherdiana X0497
X. macrocephala X0750
X. difformis var. difformis X0248
X. macrocephala X0824
X. floridana X0194
X. macrocephala X0652
X. macrocephala X0823
X. elliottii X0193
Xyris sp3. X0357
X. stricta X0052
X. jupicai X0476
X. macrocephala X0531
X. macrocephala X0646
X. navicularis X0864
X. montana X0742
X. serotina X0053
X. macrocephala X0438
X. savanensis var. glabrata X0437
X. savanensis X0439
X. stenocephala X0442
X. aff.pterygoblephara1 X0459
X. mertensiana X0596
X. eleocharioides X0675
X. eleocharioides X0672
X. seubertii X0680
X. harleyi X0770
X. seubertii X0370
X. seubertii X0495
X. seubertii X0678
X. glaucescens X0752
X. seubertii var. aspinhacae X0656
X. seubertii var. aspinhacae X0658
X. seubertii X0749
X. glaucescens X0522
X. glaucescens X0512
X. calostachya X0755
X. glaucescens X0738
X. teres X0635
X. graminosa X0727
X. insignis X0387
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X. rigida X0708
X. sparsifolia X0502
X. nanuzae X0729
X. versina X0251
X. aff.filifolia X0489
X. filifolia X0580
X. aff.rigida X0679
X. wawrae X0590
X. sparsifolia X0568
X. aff.glaucescens X0758
X. insignis X0449
X. insignis X0736
X. arcuei X0683
X. vacillans X0582
X. aff.filifolia X0631
X. mello-barretoi X0690
X. subsetigera X0509
X. subsetigera X0731
X. velutina X0372
X. subsetigera X0759
X. subsetigera X0508
X. vacillans X0581
X. anamariae X0684
X. aff.piloxa1 X0374
X. piloxa X0519
X. piloxa X0511
X. aff.piloxa1 X0575
X. aff.piloxa2 X0565
X. kraliI X0722
X. bialata X0669
X. bialata X0360
X. melanopodo X0663
X. spinulosa X0692
X. kraliI X0693
X. ceilae X0468
X. trachyphylla X0430
X. aff.trachyphylla2 X0576
X. diamantinae X0480
X. diamantinae X0664
X. aff.trachyphylla1 X0505
X. wawrae X0567
X. calostachya X0364
X. anamariae X0510
X. diamantinae X0651
X. trachyphylla X0454
X. trachyphylla X0513
X. aff.trachyphylla1 X0451
X. longicapa X0735
X. caparaoensis X0624
X. caparaoensis X0623
X. ceilae X0502
X. ilatiayensis X0732
X. obtusiuscula X0592
X. obtusiuscula X0517
X. longicapa X0529
X. archeri X0760
X. stenophylla X0585
X. schizachne X0424
X. peregrina X0498
X. nubigena X0725
X. tortula X0467
X. fredericii X0523
X. ismelia X0352
X. bahiana X0479
X. aff.pterygoblephara var. vernicosa X0574
X. metallica X0540
X. peregrina X0754
X. lamiginosa X0444
X. schizachne X0825
Xyris sp4. X0636
X. tortula X0636
X. hymenachne X0657
X. hymenachne X0478
X. hymenachne X0730
X. aff.peregrina X0739
X. aff.metallica X0645
X. aff.metallica X0644
X. nilsaonii X0646
X. pterygoblephara X0564
X. nubigena X0485
X. tortula X0431
X. roraimae X0504
X. disticha X0518
X. minarum X0366
X. aff.asperula X0639
X. jatalana X0630
X. aff.mucogenea X0668
X. bahiana X0673
X. rupicula X0370
X. pterygoblephara X0764
X. lutescens X0356
X. picea X0666
X. blanchetiana X0501
X. spectabilis X0687
X. dawsonii X0358
X. pterygoblephara var. vernicosa X0665
X. retrostriata X0571
X. aff.glochidiata2 X0655
X. pterygoblephara X0362
X. aff.glochidiata1 X0463
X. fusca X0589
X. peregrina X0754
X. aff.pterygoblephara2 X0742
X. pterygoblephara X0737
X. jolyi X0521
X. schizachne X0583
X. coutensis X0643
X. dawsonii X0349
X. minarum X0367
X. pterygoblephara X0743
X. aff.glochidiata1 X0460
X. roraimae X0346
X. shepherdiana X0748
X. nubigena X0753
X. nubigena X0747
X. cf.tortula X0350
Xyris sp1. X0428
X. aff.aurea X0429
X. roraimae X0530
X. nigra X0761
X. nubigena X0756
X. ciliata X0594
X. schizachne X0637
X. asperula X0751
X. peregrina X0734
X. platystachya X0691
X. retrostriata X0455
X. tortula X0760
X. hilariana X0450
X. graomogolensis X0567
X. pterygoblephara X0762
X. morii X0481
X. pterygoblephara X0368
X. diaphanobracteata X0359
X. aff.ciliata X0464
X. cf.lwitzelburgii X0653
X. cf.prancana X0360
X. jolyi X0680
X. pterygoblephara var. vernicosa X0662
X. aff.pterygoblephara2 X0746
X. obcordata X0578
X. metallica X0355
X. pterygoblephara X0514
X. lutescens X0344
X. scoparia X0373
X. platystachya X0573
X. bahiana X0482
X. cf.tenella X0461
X. blanchetiana X0726
X. platystachya X0520
X. plantaginea X0766
X. dawsonii X0347
X. obcordata X0570
X. cipoensis X0679
X. peregrina X0363
X. lacerata X0447
X. hystrix X0681
X. aff.morii X0659
X. ciliata X0474
X. glochidiata X0477
X. metallica X0361
X. aurea X0686
X. peregrina X0494
X. mucogenea X0670
X. hilariana X0507
X. rubromarginata X0456
X. rubromarginata X0465
X. rubromarginata X0667
X. roraimae X0745
X. amorimii X0669
X. metallica X0634
X. aff.tortula1 X0433
X. lacerata X0449
X. asperula X0577
X. pterygoblephara X0569
X. subulata var. acutifolia X0128
X. tortula X0584
X. phaeocephala X0654
X. phaeocephala X0483

Figure S2. Maximum likelihood tree from the mitochondrial datasets: *cox3* and *orf25*.

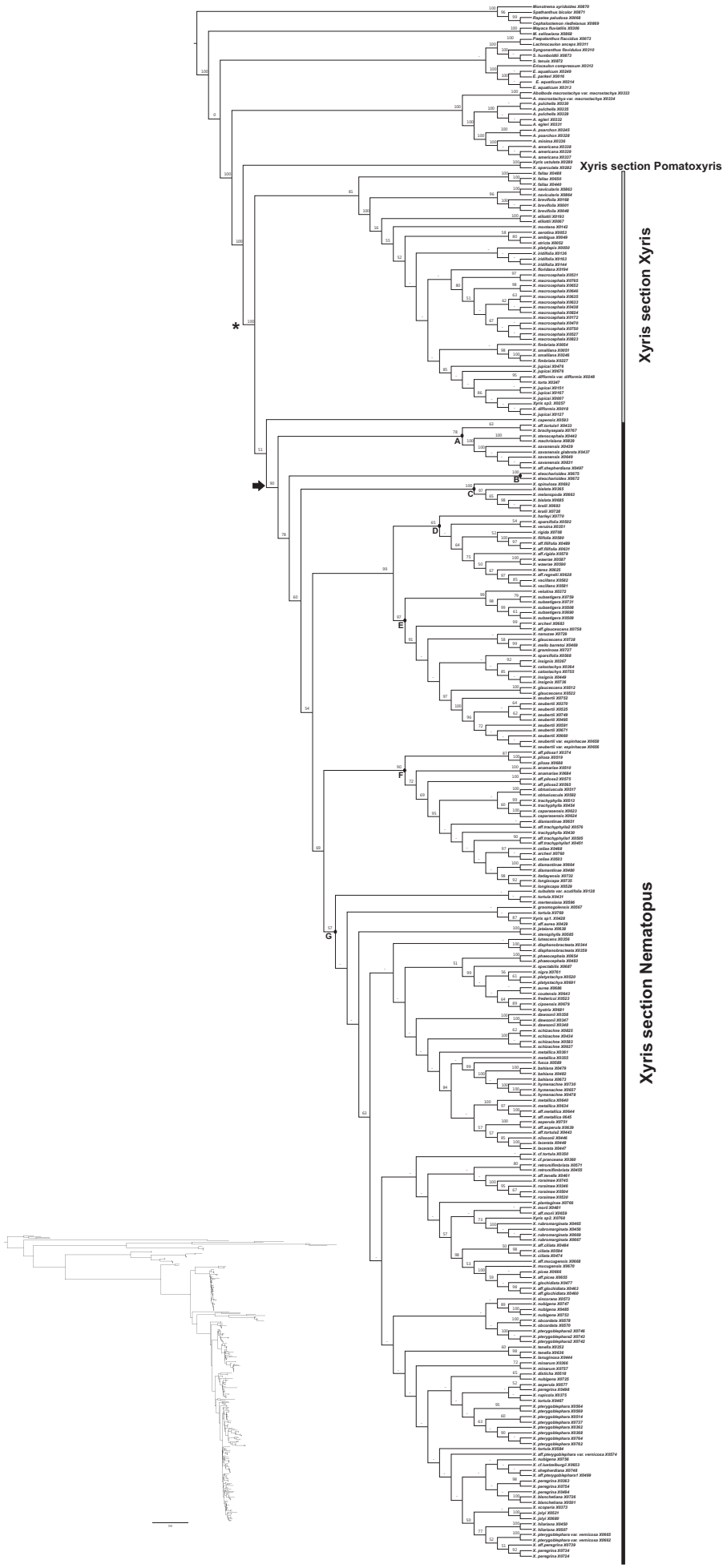

Xyris section Pomatoxyris
Xyris section Xyris
Xyris section Nematopus
A
B
C
D
E
F
G
*

Figure S3. Strict consensus tree from the parsimony analysis of the combined *cox3*, *matK*, *ndhF*, *orf25,* and *rbcL* datasets. Parsinomy jackknife percentage is indicated at the nodes. Phylogram (optimization) with proportional branch lengths is shown on left (scale bar 0.04 steps). Symbols and notation follow Fig. 1.

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Xyridaceae of the Viruá National Park, Roraima state, Brazil, with emphasis on the genus *Xyris*

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Abstract

A taxonomic treatment of the Xyridaceae in the Viruá National Park emphasising the genus *Xyris* is presented. Located in Roraima state, Northern Brazil, the park comprises a mosaic of lowland vegetation types, including forests, wetlands and one of the larger continuous areas of *campinarana* in the Brazilian Amazon basin. Xyridaceae are represented in the park by 20 species in the genera *Xyris* and *Abolboda*. Seven of the 16 *Xyris* species, as well the variety *X. uleana var. angustifolia*, were recorded for the first time in Roraima state based on material

collected in the study area, being *X. dilatatiscapa* the first record in Brazil. Although the four species of *Abolboda* are widespread, most of the *Xyris* species (75%) are endemic to Amazonian open formations, such as *campinaranas* and savannas. This study was based on fieldwork, herbarium and scanning electron microscopy research. The taxonomic treatment includes identification keys for genera and species, morphological descriptions and SEM images of seeds for *Xyris* species, iconography, geographic distribution and comments on ecology of the species. The poorly known *Xyris connosepala* is synonymized in *Xyris guianensis*.

Resumo

É apresentado o tratamento taxonômico de Xyridaceae no Parque Nacional do Viruá, com ênfase no gênero *Xyris*. Localizado no estado de Roraima, ao norte do Brasil, o parque é composto por um mosaico de diferentes tipos de vegetação, incluindo florestas, áreas húmidas e uma das maiores áreas contínuas de *campinarana* na Amazônia brasileira. A família é representada por 20 espécies e dois gêneros, *Xyris* e *Abolboda*. Sete das 16 espécies de *Xyris* inventariadas, bem como a variedade *X. uleana var. angustifolia* foram registradas pela primeira vez no estado de Roraima com base em materiais provenientes da área de estudos, sendo *X. dilatatiscapa* o primeiro registro para o Brasil. Embora as quatro espécies de *Abolboda* sejam de ampla distribuição, a maioria das espécies ocorrentes no parque (75%) é endêmica de formações abertas da Amazônia, como as *campinaranas* e savanas. O tratamento taxonômico inclui chaves de identificação para gêneros e espécies, descrições morfológicas e imagens das sementes em MEV das espécies de *Xyris*, iconografia, comentários ecológicos, bem como, de padrões de distribuição geográfica. *Xyris connosepala* é aqui sinonimizada em *Xyris guianensis*.

Key words

Amazon, *campinarana*, new synonym, seed, micromorphology**,** white sand vegetation

Introduction

Xyridaceae C. Agardh constitute a group of petaloid monocotyledons classified in Poales (APG 2009; Chase et al. 2000; Soltis et al. 2000; Davis et al. 2004). The family includes more than 420 accepted species in five genera: *Xyris* L., with about 400 species, *Abolboda* Humb., with 23 species, *Orectanthe* Maguire, with two species, and *Achlyphila* Maguire & Wurdack and *Aratitiyopea* Steyerm. & P.E. Berry, with one species each (Kral 1988; Campbell 2004a; Campbell 2008; Wanderley 2011; Wanderley et al. 2014). *Achlyphila*, *Aratitiyopea* and *Orectanthe* occur mainly in the highlands of the Guyana Shield, on the remarkable quartzite *tepuys* of the region (Campbell 2004b; 2005; 2008). Most species of *Abolboda* occurs exclusively in Northern South America, especially in the Guayana Shield and lowland open formations of the Amazon Forest, but few species are also found in the Brazilian Cerrado biome, in central Brazil (Kral 1992; Campbell 2005; 2008). *Xyris* has a wider distribution range, mainly in tropical and subtropical regions of the Americas, Africa, Asia and Australia. In the Neotropics, *Xyris* is widely distributed, presenting two main centers of richness: the mountains of Southeastern Brazil and the Guayana Shield (Kral 1988; Campbell 2004b; 2008). This genus is remarkable by its high level of species endemism and the majority of the species have narrow geographic distribution. Most occur in open areas such as bogs, sandy soils, or rock fields that are and acid poor in nutrients (Kral 1988, Campbell and Stevenson 2005).

The first comprehensive taxonomic study of Xyridaceae in Brazil was published in the early nineteenth century by Seubert (1855), in the seminal *Flora Brasiliensis*, where 28 species of *Xyris* and six species of *Abolboda* were treated. Later, Gustav Oskar Andersson Malme, in the late nineteenth and early twentieth centuries,

published a series of treatments on Xyridaceae (Malme 1896; 1898; 1901; 1912; 1913a; 1913b; 1929), contributing substantially to the taxonomy of the family. Subsequent publications by Lyman B. Smith and Robert J. Downs, of the Smithsonian Institution (e.g. Smith & Downs 1954; 1958; 1960; 1965), culminated with a comprehensive monograph of the family in Brazil (Smith & Downs 1968), which included 115 species of *Xyris*, 18 *Abobolda*, one *Achlyphyla* and one *Orectanthe*. In this same decade, botanical exploration orchestrated by the New York Botanical Garden in the Guayana Highlands, particularly in Venezuela, resulted in an important collection of Xyridaceae from that region available in herbaria. Based mainly in this collection, Maguire & Smith (1963; 1964) monographed the family for the Guayana Highlands, which was the main basis of Kral's (1988; 1992) important treatments of Xyridaceae in northern South America.

Robert Kral also collaborated with Lyman B. Smith (Kral & Smith 1980; 1982a, b), and Maria das Graças L. Wanderley (1988a, b; 1992; 1995), who is continuously publishing taxonomic works on the family (e.g. Wanderley 2003; 2010; 2011). Despite the increasing knowledge on Brazilian Xyridaceae, most of the published floras of the family in Brazil were done in the southeastern or southern (e.g. Mota 2009; Silva & Wanderley 2013; Smith & Downs 1965; Wanderley 2003; 2011; Wanderley & Silva 2009). In Brazil, no flora of Xyridaceae has ever been published in the Amazon.

The taxonomic utility of seed morphology characters in Xyridaceae has been noted in the literature as potentially taxonomically useful (Malmanche 1919; Blomquist 1955; Kral 1966; 1988; Ruddal & Sajo 1999). However, few floras and taxonomic treatments around the world present these characters combined with macro-morphology (e.g. Doust & Conn 1994; Lock 1998; Phonsena et al. 2012). In

Eriocaulaceae, sister group of Xyridaceae, seed coat ornamentation has been demonstrated to have taxonomic value at several taxonomic ranks allowing distinguish genera and some subgenera (Zona et al. 2012; Barreto et al. 2013).

Based mainly on macro-morphological and seed ornamentation characters, this work aims a taxonomic treatment of the Xyridaceae – with emphasis on the genus *Xyris* – in the Viruá National Park, Roraima state, Northern Brazil. Detailed morphological descriptions and characterization of seed morphology under SEM are provided for *Xyris* species. An identification key for genera and species, comments on ecology, morphology, and distribution for all species are provided here.

Methods

STUDY SITE

Viruá National Park is situated in Roraima state, northern Brazil, and is delimited by the coordinates: 0°56'N, 61°09'W (south), 1°43'N, 61 08'W (north), 1°17'N, 60°58'W (east), 1 17'N, 61°18'W (west), at the northern border of the Pantanal Setentrional (Santos & Nelsson 1993) – a depressed zone between the Rio Negro and Branco basins. The VNP has a total area of 227,000 hectares and is bounded by the rivers Barauana on the east, Branco on the west, and Anauá, which constitutes its southern limit. According to Rossetti et al. (2012a, b), the topography of VNP is formed by the Viruá Megafan, an uncommon geological feature, the result of alluvial sediment deposition from fluvial channels.

The topography is predominantly low elevation (45–60 m), composed of sandy, nutrient-poor and poorly drained soils, developed on an extensive sedimentary lowland plain, derived from quartzite sands from the Içá geological formation

(ICMBio, in press). The area has scattered elevations that reach altitudes of 350 m, such as the Serra do Preto (1º13'07"N, 61º08'53"W).

The vegetation is an extensive mosaic of complex, seasonally flooded forested and non-forested systems (Mendonça 2011) (Fig. 1 A–E). The phytophysiognomies in the area are classified in *terra firme* forests, *várzea* forests, *igapó* forests, *Mauritia flexuosa* L.f. dominated communities (*buritizais*), arborescent *campinarana*, grassy *campinarana* (or *campina*) and aquatic vegetation in bodies of water (ICMBio, in press). The *campinaranas* in the area grow over white sandy soils, which are seasonally flooded, in a wide system of sandy wetlands (ICMBio, in press). This vegetation type is known to be rich in graminoid monocots, especially the families Cyperaceae, Eriocualaceae, Rapateaceae, and Xyridaceae (Pires & Prance 1985). The *campinaranas* of Viruá National Park are one of the larger continuous areas of this vegetation type in the Brazilian Amazon (ICMBio, in press).

According to Köppen (1948) classification, the climate is monsoon-tropical (Am). The monthly mean temperatures ranges from 20ºC to 38ºC, the annual mean being 24ºC (Rossetti et al. 2012b). The average annual rainfall is about 2000 mm, the same as the annual average of Roraima state.

FIELDWORK

Three field expeditions were conducted in both the dry and wet season (January 2009, September and November 2011). The sampling was concentrated in the open areas of the park, such as *campinaranas* and aquatic vegetation. Herbarium specimens were deposited in BHCB, INPA, NY, and SP. Additionally all specimens from the studied area previously deposited in INPA Herbarium were studied (about 50% of the specimens examined).

TAXONOMIC TREATMENT

Species were identified using protologues and other pertinent literature (Kral 1988; 1992; 2005; Kral & Jansen-Jacobs 1998; Malme 1912; 1913a, b; Nilsson 1892; Seubert 1855; Steudel 1855; Steyermark 1984; Smith & Downs 1968) and through study of specimens at B, BHCB, INPA, K, MG, MO, NY, SP, SPF and US, as well as on-line images from BRG, BRIT (VDB), P, S and U herbaria. At least one type specimen of each species, except *X. dilatatiscapa* Kral & Jans.-Jac., was seen from images and/or exsicates. Descriptions are provided only for the species of *Xyris*, and were based on specimens examined, illustrations and photographs were done for all species of Xyridaceae sampled in the study area.

The morphological characters that have long been used by taxonomists (e.g. Smith & Downs 1968; Kral 1988; 1992; Wanderley 2011) for species recognition in Xyridaceae were used in the descriptions: features of leaves (shape of sheath and lamina, presence or not of a ligule, indumenta, surface texture), inflorescence (peduncle, bracts, number of flowers), flowers (sepals shape and ornamentation, type of placentation, staminodia) and seeds (shape, ornamentation, dimensions).

Morphological terminology follows Kral (1988; 1992), except for the terms “dorsal area” and “scape”, being here adopted “macula” and “peduncle”, respectively. Some changes were made in Kral’s (1988) terminologies for seed ornamentation too: “stria” instead of “rib”, “reticulate” instead of “anastomosing ribs” and “moniliform” instead of “pebbled”. Illustrations are provided for all species and consist at least the apex and base of leaves, spike and lateral sepals. Data on geographic distribution were gathered from Kral (1988; 1992), Campbell (2005) and Wanderley et al. (2014).

SCANNING ELECTRON MICROSCOPY (SEM)

Seeds of *Xyris* species were taken from dried specimens and coated with gold palladium in a Hummer 6.2 sputtering system (Anatech, Union City, CA, U.S.A). Observations were made with a JEOL JSM-5410LV SEM (JEOL, Tokyo, Japan) at 10 kV and digital images were acquired using Orion software (JEOL, Tokyo, Japan). Only seeds that appeared fully formed were measured.

Results and discussion

FLORA

A total of 21 taxa, including four *Abolboda* and 16 *Xyris* species, and one variety *Xyris uleana var. angustifolia* Lanj., were recorded in the study area. These amounts correspond to 64% of Xyridaceae species in the Roraima state flora (Wanderley et al. 2014).

The *Abolboda* species are widely distributed in low to mid elevation species. Two of them, *A. americana* (Aubl.) Lanj. and *A. minima* Maguire, were recorded for the first time in Roraima state in the study area (Wanderley et al. 2014). One expected *Abolboda*, *A. grandis* Griseb. var. *grandis*, reported from Roraima state (Kral 1992; Wanderley et al. 2014), was not detected in this study.

The VNP encloses 30% of *Xyris* species known to occur in the Brazilian Amazon (Wanderley et al. 2014). Ten of these are endemic to this biome: *X. cryptantha* Maguire & L.B.Sm., *X. dilatatiscapa* Kral & Jans.-Jac., *X. guianensis* Steud., *X. involucrata* Nees, *X. malmeana* L.B.Sm., *X. mima* L.B.Sm. & Downs, *X. subglabrata* Malme, *X. subuniflora* Malme, *X. surinamensis* Spreng., *X. uleana* Malme (Kral 1988, Wanderley et al. 2014). Five are widespread in South America: *Xyris fallax* Malme, *X. jupicai* Rich., *X. macrocephala* Vahl., *X. paraensis* Poepp. ex Kunth and

X. savanensis Miq. (Wanderley *et al.* 2010). One *Xyris* species (referred as *Xyris* sp.1), belonging to the *X. paraensis* complex, could not be identified and is probably a new taxon. A comprehensive study of types of all names related to the *X. paraensis* complex is necessary to confirm this hypothesis.

Previously known only from Guyana, *Xyris dilatatiscapa* is recorded for the first time in Brazil, and seven other taxa (*X. cryptantha*, *X. fallax*, *X. malmeana*, *X. mima*, *X. paraenses*, *X. subglabrata* and *X. uleana* var. *angustifolia*) are new records for Roraima state (Wanderley et al. 2014).

All recorded species were documented in open formations (*campinaranas* or *campinas*). During the rainy season, it is common to find plants of *Xyris* and *Abolboda* partially or completely submerged in the lakes and streams (or *igarapés*) thoughout the *campinaranas* of the VNP. None of the species recorded in the VNP is formally considered threatened, acording to the current official list of threatened species of Brazilian flora (MMA 2008). Although habitat loss is increasing rapidly in the Amazon basin, most of Amazonian *Xyris* species are classified as Data Deficient in the aforementioned list.

SHAPE AND ORNAMENTATION OF SEEDS OF *XYRIS* SPECIES AS VIEWED USING SEM

Seeds of *Xyris* species occurring in the VNP are 0.3–1.5 mm long, ovoid, ellipsoid to obovoid, striate, with an apex apiculate (Fig. 4 A–Q). The striae can be thickened (*X. cryptantha*, *X. subuniflora* and *X. uleana var. uleana*, Fig. 4 A, M and O) or not (*X. dilatatiscapa* and *X. fallax*, Fig. 4 C and D), smooth (*X. subglabrata*, Fig. 4 L), sinuous (*X. guianensis*, Fig. 4 D) or moniliform (*X. mima,* Fig. 4 H), and sometimes with more than one kind of stria on the same seed, as is found in *X. paraensis* (Fig. 4 J). The region between the striae can be clearly visible, as in *X. jupicai* and *X.*

macrocephala (Fig. 4 F G), or not, as in *X. fallax* (Fig. 4 C). Some species have cross-lines (transverse striae) frequently forming a reticulate pattern of ornamentation (striae and cross lines evenly distributed), as seen in *X. dilatatiscapa* (Fig. 4 B). The ornamentation of the seed coat has shown to be of high taxonomic utility, being very useful in distinguishing morphologically close species, such as *Xyris mima* and *Xyris paraensis* (see comments under *X. mima*) and was helpful in proposing *X. connosepala* a new synonym of *X. guianensis* (see comments under *X. guianensis*).

The main taxonomic value seed characters of *Xyris* species are summarized comparatively in Table 1.

TAXONOMIC TREATMENT

Key to the genera of Xyridaceae occurring in the Viruá National Park

1 Leaves arranged in rosette; peduncle with at least one pair of bracts, or spikes almost sessile; petals blue or purple; staminodia absent; style with two or three basal appendices ……...……**1. *Abolboda***

– Leaves distichously arranged, less commonly spiralate; peduncle not bracteate, spikes never sessile; petals yellow; staminodia present; style not appendiculate …… **2. *Xyris***

1. *Abolboda* Humb. in Humb. & Bonpl. Pl. Aequinoct. 2: 25, pl. 114. 1809.

Key to the *Abolboda* species in the Viruá National Park

1 Peduncle inconspicuous, the spikes sessile..... **3. *Abolboda minima***

– Spikes borne on a peduncle **2**

2 Plants annual to short living perennial; peduncles 2.5–12 cm long, ebracteate..... **1. *Abolboda americana***

– Plans prennial; peduncle longer that 12 cm, with one or more pairs of bracts **3**

3 Spikes 3.5–8 cm long, over 10-flowered ..... **2. *Abolboda macrostachya***

– Spikes 1–1.5 cm long, 2–5-flowered ..... **4. *Abolboda pulchella***

1. *Abolboda americana* (Aubl.) Malme ex Lanj. Recueil Trav. Bot. Neerl. 34: 492. 1937.

(Figures 2 A, 7 A)

Morphological comments, as in *Abolboda pulchela* and *A. minima* (in the study area), the spikes in *A. americana* are few-flowered (never more than 5 flowers per spike), but it can be distinguished by its mainly patent leaves and annual (or shot living perennial) life cycle. The peduncles are shorter than those of *A. pulchella* (2.5–12 cm long vs. 10–25 cm in *A. puclella*), sometimes shorter than the main leaves, but never inconspicuous, and then spikes are sessile, like in *A. minima*.

Distribution and habitat, Abolboda pulchella occurs in Colombia, French Guiana and Venezuela. In Brazil it is widespread, occurring in Amapá, Amazonas, Bahia, Pará, Rondônia, and Roraima states. In VNP, *Abolboda americana* is widespread throughout the *campinaranas*, being particularly common growing in peaty bogs, where it forms dense mats. During the rainy season, it was observed partially submerse, exposing only the spikes.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, beira da Estrada Perdida, borda de campina arbustiva, 28 Nov 2006, F.A. Carvalho and M. Roache 938 (INPA); Estrada Perdida, 1°26'14”N, 60°58'49”W, 12 Oct 2011, G.O. Silva et al. 98 (INPA, SP); Estrada Perdida, primeira campina após a guarita, margem esquerda, 1°28'24,6”N, 60°58'0,07”W, 76 m, 12 Oct 2011, N.F.O. Mota et al. 2343 (BHCB, INPA); grade PPBio, 1°28'56”N, 61°02'50”W, 17 Oct 2011,

N.F.O. Mota et al. 2406 (BHCB, INPA); PPBio L1/N6, 1°29'18”N, 61°02'82”W, 12 Sept 2010, S.M. Costa and T.D.M. Barbosa 703 (INPA, UEC); 1°24'46”N, 60°59'16”W, 21 March 2011, S.M. Costa and T.D.M. Barbosa 928 (INPA); 0°5730”N, 61°11'32”W, 24 July 2010, S.M. Costa and T.D.M. Barbosa 999 (INPA); 1°24'51”N, 60°59'12”W, 20 Dec 2010, T.D.M. Barbosa and S.M. Costa 1233 (INPA); 1°24'52”N, 60°59'13”W, 21 July 2010, T.D.M. Barbosa and S.M. Costa 1257 (INPA, UEC); grade PPBio, 1°28'06’N, 61°00'25”W, 24 July 2010, T.D.M. Barbosa and S.M. Costa 1305 (INPA); 1°28'5,8’N, 61°00'48”W, 67 m, 24 July 2010, T.D.M. Barbosa and S.M. Costa 1322 (INPA); 1°24'09”N, 60°59'11”W, 25 Dec 2010, T.D.M. Barbosa and S.M. Costa 1337 (INPA, UEC); 1°27'34”N, 61°01'57”W, 27 July 2010, T.D.M. Barbosa and S.M. Costa 1369 (INPA); campinarana arbustivo-arbórea, 1°06'16”N, 61°01'00”W, 27 March 2011, T.D.M. Barbosa and S.M. Costa 1434 (INPA).

2. *Abolboda macrostachya* Spruce ex Malme Bih. Kongl. Svenska Vetensk.-Akad. Handl. 26, Afd. 3(19): 15. 1901.

(Figures 2 B, 7 B–C)

Morphological comments, Abolboda macrostachya is the most conspicuous species of the genus in the VNP, characterized by robust rhizomes, leaves up to 35 cm long, and spikes 3.5–8 cm long, with noticeable bluish flowers. A single specimen with unusual white flowers has been documented (*Mota 2425*). The plants are usually dense cespitose, but some few solitary individuals formed narrows clumps, like observed in the field.

Distribution and habitat, It occurs in Brazil, Colombia and Venezuela. In Brazil, it has been recorded in Amazonas, Mato Grosso, and Roraima states. *Abolboda macrostachya* is probably the most common species of the genus in VNP. Plants of

this species grow in dense graminoid formations in the bogs of *campinaranas* of the study area.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, 1°29'01"N, 61°02'50"W, 12 Sept 2010, A.R. Lourenço et al. 361 (INPA); P116, 22 Jan 2010, F.N. Cabral et al. 173 (INPA); 28 Aug 1987, C.A.C. Ferreira et al. 9252 (INPA); 1°23'68"N, 61°59'5"W, 2 Sept 2002, C.A.C. Ferreira et al. 12420 (INPA); grade PPBio Grid L1, N6, 17 Dec 2011, C.T. Pedrollo et al. 143 (INPA); grade PPBio N2, 1°28'07"N, 61°00'27"W, 18 Sept 2011, E. Pessoa et al. 648 (INPA); Estrada Perdida, 1°16'48"N, 61°00'00"W, 28 Nov 2006, F.A. Carvalho and R. Nascimento 1027 (INPA); Estrada Perdida, 1°16'48"N, 61°00'00"W, 1 Dec 2006, F.A. Carvalho and R. Nascimento 1040 (INPA); 1°48'67"N, 61°1'57"W, 30 May 2005, F.R.C. Costa et al. 1189 (INPA); 1°48'67"N, 61°1'57"W, 15 Jan 2006; F.R.C. Costa et al. 1547 (INPA); PPBio L06 T2500, 1°48'67"N, 61°01'57"W, 2006, F.R.C. Costa 1678 (INPA); grade PPBio NS5, 1°48'67"N, 61°01'57"W, 15 Jan 2006, F.R.C. Costa 1698 (INPA); Estrada Perdida, 1°26'14"N, 60°58'49"W, 10 Dec 2011, G.O. Silva et al. 93 (INPA); grade PPBio L3N4, 1°27'56"N, 61°01'46"W, 17 Dec 2011, J. Lins et al. 36 (INPA); 12 Sept 2010, M.F. Calió and C.M. Siniscalchi 226 (INPA, SPF); campina, 1°15'39,5"N, 60°58'10,5"W, 55 m, 24 Jan 2008, N.F.O Mota and P.L. Viana 1223 (BHCB, SP); campina, 0°27'33,3"N, 61°01'43,5"W, 64 m, 25 Jan 2008, N.F.O Mota and P.L. Viana 1227 (BHCB, SP); Estrada Perdida, campina próxima a guarita do parque, campo úmido, 1°28'24,6"N, 60°58'7,7"W, 76 m, 22 Sept 2011, N.F.O Mota et al. 2304 (BHCB, SP); campina cerca de 1 km depois da segunda bueira na Estrada Perdida, 1°21'91"N, 60°58'46,8"W, 59 m, 23 Sept 2011, N.F.O Mota et al. 2319 (BHCB, SP); Estrada Perdida, campina na margem direita próxima a primeira bueira, 1°25'16,5"N, 60°59'7,9"W, 63 m, 21 Oct 2011, N.F.O Mota et al.

2423 (BHCB, INPA, SP); campina L3 500, 1°28'10'N, 61°00'48"W, 17 Dec 2011, P.A. Pereira et al. 110 (INPA); 1°29'18'N, 61°02'82"W, 12 Sept 2010, S.M. Costa and T.D.M. Barbosa 705 (INPA, UEC); grade PPBio L3/N2, 13 Sept 2010, S.M. Costa and T.D.M. Barbosa 723 (INPA, UEC); Estrada Perdida, próximo a 2ª bueira, 16 Sept 2010, S.M. Costa et al. 758 (INPA, UEC); Estrada Perdida, 19 Jan 2011, S.M. Costa et al. 822 (INPA); 1°27'35"N, 61°01'55"W, 20 March 2011, S.M. Costa and T.D.M. Barbosa 923 (INPA); 1°24'46"N, 60°59'16"W, 21 March 2010, S.M. Costa and T.D.M. Barbosa 929 (INPA); 1°57'30"N, 61°09'36"W, 24 March 2011, S.M. Costa and T.D.M. Barbosa 992 (INPA); 01 March 2010, T.D.M. Barbosa and N. Dávilla 1055 (INPA, UEC); 1°14'31'N, 60°57'56"W, 5 March 2010, T.D.M. Barbosa and S.M. Costa 1083 (INPA, UEC); 1°14'31'N, 60°57'56"W, 5 March 2010, T.D.M. Barbosa and S.M. Costa 1084 (INPA, UEC); 1°24'51"N, 60°59'12"W, 20 July 2010, T.D.M. Barbosa and S.M. Costa 1211 (INPA, UEC); 1°24'59"N, 60°59'11"W, 25 July 2010, T.D.M. Barbosa and S.M. Costa 1332 (INPA, UEC); 1°6'23,1"N, 61°00'47,5"W, 49 m, 25 July 2010, T.D.M. Barbosa and S.M. Costa 1430 (INPA).

3. *Abolboda minima* Maguire Mem. New York Bot. Gard. 10(5): 7. 1964.

(Figures 2 C, 7 D)

Morphological comments, This diminutive plant can be easily distinguished from other congeners in the VNP by its sessile spikes. The other three species of *Abolboda* found in the study area have spikes borne on a peduncle.

Distribution and habitat, Abolboda minima is a rare species, occurring in Venezuela and Brazil. In Brazil, it occurs in Amazonas and Roraima states. In the study area, *A. minima* was found growing on exposed white sand fields, or *campinaranas*, which are seasonally flooded. The leaves are typically densely compacted and gathered at the

soil, forming tiny green pads, growing together with *Xyris subuniflora*, *X. mima*, and some small Rubiaceae, Eriocaulaceae and Lentibulariaceae.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, Estrada Perdida, após a 1ª bueira, 22 July 2010, A. Melo et al. 406 (INPA); Estrada Perdida, 1°25'34"N, 60°59'10"W, 22 July 2010, D. Cavalcanti et al. 200 (INPA); campina cerca de 1 km depois da segunda bueira na Estrada Perdida, 1°20'39,1"N, 60°58'43,2"W, 61 m, 23 Sept 2011, N.F.O Mota and P.L.Viana 2325 (BHCB, SP); 0°57'30"N, 61°11'32"W, 23 March 2011, S.M. Costa and T.D.M. Barbosa 998 (INPA); 1°25'57"N, 60°58'59"W, 07 March 2010, T.D.M. Barbosa et al. 1095 (INPA, UEC).

4. *Abolboda pulchella* Humb. in Humb. & Bonpland Pl. Aequinoct. 2: 110, pl. 114. 1809.

(Figures 2 D, 7 E)

Morphological comments, Abolboda pulchella is a morphologically variable species that superficially resembles *A. americana*, among the species on the VNP, because both species have few-flowered spikes, up to 1,5 cm, with one pair of bracts in the peduncle. *Abolboda pulchella*, however, can be distinguished by longer peduncles and erect leaves, which are never patent, like those in *A. americana*.

Distribution and habitat, Abolboda pulchella is probably the most widespread species of the genus. It occurs in French Guiana, Paraguay, Venezuela, and Brazil. In Brazil it is known from the states of Bahia, Espírito Santo, Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Piauí, Roraima, São Paulo, and Tocantins and Distrito Federal. *Abolboda pulchella* is, nonetheless, a rare species in the study area, and the

few individuals recorded were observed at margins of streams (*igarapés*), in association with dense graminoid vegetation.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, Lavrado da Perdida - São José do Anauá, 1°29'05"N, 60°58'19"W, 26 March 1999, A. Vicentini and A. Carneiro 1460 (INPA); campina cerca de 1 km depois da segunda bueira na Estrada Perdida, 1°21'91"N, 60°58'46,8"W, 59 m, 23 Sept 2011, N.F.O Mota and P.L.Viana 2322 (BHCB, SP); 1°28'06"N, 61°00'25"W, 67 m, 20 Mar 2010, S.M. Costa and T.D.M. Barbosa 921 (INPA); 1°24'09"N, 60°59'11"W, 63 m, 24 July 2010, T.D.M. Barbosa and S.M. Costa 1313 (INPA); 1°24'09"N, 60°59'11"W, 63 m, 24 July 2010, T.D.M. Barbosa and S.M. Costa 1325 (INPA, UEC); 1°27'34"N, 61°01'57"W, 63 m, 25 July 2010, T.D.M. Barbosa and S.M. Costa 1342 (INPA, UEC); 1°27'35"N, 61°01'55"W, 57 m, 25 July 2010, T.D.M. Barbosa and S.M. Costa 1346 (INPA, UEC); 1°28'06"N, 61°00'25"W, 67 m, 27 July 2010, T.D.M. Barbosa and S.M. Costa 1366 (INPA).

2. *Xyris* Gronov. ex L. Species Plantarum 1: 42. 1753.

Description, Annual or perennial herbs, terrestrial, rare aquatics. Plants solitary or clump-forming. Base of the plant flattened, sub-bulbous to bulbous, fibrous or not, sometimes with mucilage. Rhizome usually with short internodes. Leaves isobilateral, distichous to spiral, erect to spreading, twisted or not; sheaths open, dilated or narrow at the base, smooth, papilose, verrucous, or rugose, margins glabrous to long ciliate, ligule present or not; lamina flattened to terete, smooth, papillose, verrucous, or rugose, nerves prominent or not, margins glabrous to ciliate. Spathe larger, smaller to equalling the leaves, sheaths and laminae differentiated. Peduncle terete, triquetrous

to compressed, not bracteate, twisted or not, glabrous to ciliate, smooth, papillose, verrucous or rugose, ecostate to multicostate, rarely winged. Spike 1-multi-flowered, ovoid, obovoid, ellipsoid, oblong, cylindrical, hemispherical to globous. Sterile bracts 2-many, the lower ones different or similar to the inner bracts, keeled or not, sometimes with one macula on the dorsal surface, margins differentiated or not, entire to lacerate, glabrous to ciliate. Fertile bracts generally alike to very distinct of the sterile bracts, keeled or not, macula present or not, margins differentiated or not, entire to lacerate, glabrous to ciliate. Sepals 3; dorsal sepal cucullate, membranous, deciduous; lateral sepals navicular, symmetric to asymmetric, free to connate, shorter or larger than the bracts, keel glabrous to ciliate, entire to lacerate; Petals 3, unguiculate, membranaceous, yellow or white, free to connate; staminodia 3, alternate with the petals, branched, glabrous to pubescent, hairs long-penicillate; stamens 3; filaments flattened; anthers basifixed, extrorse, dehiscing by vertical slits; style filiform, apex 3-branched; ovary usually sessile, 1- or 3-loculed, or imperfectly 3-loculed, placentation parietal, central, basal, suprabasal or axial. Capsule usually with numerous seeds. Seeds ovoid, obovoid, cylindrical to ellipsoid, rarely angular, striate, with or without cross-lines, apex usually apiculate.

Key to the species of *Xyris* in the Viruá National Park

1 Lamina terete or subterete, canaliculate or sulcate ……..……..……..…**2**

– Lamina flattened ….……..…… **4**

2 Spathe longer than the leaves, peduncle dilated in the 1–3.3 cm of the distal portion ……...……..…..…….... **2. *Xyris dilatatiscapa***

– Spathe shorter than the leaves, peduncle not dilated at the apex ……....…. **3**

3 Spike 4–6-flowered; the lower sterile bracts distinctly longer than the fertile bracts; axial placentation ……**1.** ***Xyris cryptantha***

– Spike 10–15-flowered; the lower sterile bracts about 1/2 the length of the fertile bracts; central placentation …..…… **12.** ***Xyris subglabrata***

4 Leaves ligulate ……..… **5**

– Leaves eligulate ……... **11**

5 Peduncle ecostate or 1-costulate ……..…….. **6**

– Peduncle 1- to 2-costate or multi-costulate ……...…… **8**

6 Lamina surface papillose to densely rugose; spike 10–35-flowered ……..…..…… **11.** ***Xyris savanensis***

– Lamina surface smooth; spike 1–3-flowered ……..……**7**

7 Lateral sepals longer than the bracts, exerted, keeled; central placentation ……..... **4.** ***Xyris guianensis***

– Lateral sepals shorter than the bracts, not exerted, not keeled; basal placentation ……..…...…. **13.** ***Xyris subuniflora***

8 Sterile bracts 10–20; basal placentation …… **9**

– Sterile bracts 4; parietal placentation …….. **10**

9 Leaf sheath margins glabrous; seeds 0.5–0.8 mm long……...…… **6.** ***Xyris jupicai***

– Leaf sheath margins ciliate; seeds 1.3–1.5 mm long ……... **3.** ***Xyris fallax***

10 Lamina surface densely transversely rugose; seeds longer than 1 mm, apex acute with a coma of bristles …….…….…….. **9.** ***Xyris mima***

– Lamina surface smooth; seeds 0.3–0.4 mm long, apex apiculate, without a coma of bristles ..…….……...…**15.** ***Xyris uleana var. angustifolia***

11 Peduncle ancipital, two winged ……..……...…….……... **12**

– Peduncle flattened, subterete, terete or triquetrous, not winged ……..….. **13**

12 Lamina margins densely ciliate; peduncles longer than 38 cm …… **5.** ***Xyris involucrata***

– Lamina margins glabrous; peduncles smaller than 26 cm long…….. …….. **16.** ***Xyris uleana var. uleana***

13 Leaf sheath margins ciliate ……..... **14**

– Leaf sheath margins glabrous …….. **15**

14 Peduncle flattened, not filiform, 2-costate; sterile bracts 4 …… **8.** ***Xyris malmeana***

– Peduncle terete to subterete, filiform, 3 or 4-costate; sterile bracts 18–22 ..... ……...……... **14.** ***Xyris surinamensis***

15 Peduncle longer than 100 cm; sterile bracts 16–22; seeds reticulate …… …… **7.** ***Xyris macrocephala***

– Peduncle shorter than 32 cm; sterile bracts 4; seeds not reticulate ……..…….. **16**

16 Spike ovoid; keel of lateral sepals glabrous and slightly lacerate; seed striate monilliform and smooth, twisted ……...……..…... **10.** ***Xyris paraensis***

– Spike cylindrical; keel of lateral sepal evenly ciliate; seed striate smooth, straight ……..…….……**17.** ***Xyris sp.1***

1. ***Xyris cryptantha*** Maguire & L.B.Sm, Mem. New York Bot. Gard. 10(5): 16, fig. 2A–E. 1964.

(Figures 3 A, 4 A–D, 7 F)

Description, Perennial, terrestrial, short living, clump-forming. Base of the plant sub-bulbous, fibrous, without mucilage. Leaves 7.9–19 cm long, spiral, erect, not twisted; sheaths 1/4–1/10 the leaf length, gradually dilating toward the base, smooth, with prominent nerves, castaneous, margins not scarious, floccose-ciliate, eligulate; lamina 5.9–15.2 cm × 0.5–0.7 mm, terete to subterete, smooth and pale-puncticulate, nerves

not evident at the base, margins undifferentiated, glabrous, apex subulate to conic, usually incurved. Spathe shorter than the leaves. Peduncle 11.5–30 cm long, 0.4–0.5 mm wide, filiform, terete, without distal dilatation, not twisted to sligthly twisted, glabrous, smooth, densely pale-puncticulate, ecostate. Spike 4–6-flowered, 6–11 × 2–4 mm, oblanlaceolate to obovoid, reddish castaneous. Sterile bracts 4–6, the lower ones distinctly longer than the fertile bracts; the uppermost oblong to oblong-pandurate, slightly keeled at the apex, maculate, margins scarious, glabrous, apex keeled to cucullate. Fertile bracts 5.4–7.3 × 1.3–1.6 mm, oblong to oblong-lanceolate, navicular, margins glabrous, scarious, entire to lacerate, pale to reddish, apex cucullate; macula along the distal 1/2 of the fertile bract, oval-lanceolate, greenish and becoming castaneuous with age, pale-puncticulate. Lateral sepals 4.5–6 mm, linear-lanceolate, slightly asymmetric, free, shorter than the bracts, keel glabrous to slightly ciliolate at the tip; corolla lobes obovate to broadly obovate; staminodia densely long-penicillate, branches not flat; stamens 2.5 mm long; anther 1.5 mm long, sagittate; style 7.5 mm long, branches 3 mm long; ovary 2.2 mm long, trilocular, placentation axial. Capsule 0.5 mm long, ellipsoid. Seeds 0.4–0.5 × 0.2–0.3 mm, ovoid to ellipsoid, reddish to castaneous, apex apiculate; striae 5–6 per 100 μm of seed width in the midle portion, slightly prominent, straight, slightly sinuous, with thin cross-lines, not reticulate.

Morphological comments, Xyris cryptantha is distinguished by its oblong to obovoid spikes, with sterile bracts erect and conspicuously longer than the fertile bracts, hiding the main axis of the spike. The laminae are terete to sub-terete and the sheaths have long ciliate margins. Its trilocular ovary with axial placentation is unique among the species of *Xyris* occurring in the studied area.

Xyris oxylepis Idobro & L.B.Sm., known from savannas of Colombia and Venezuela is remarkably similar to *X. cryptantha* in its usually solitary habit, leaf shape, and trilocular ovary. However, *X. oxylepis* differs by its ellipsoid to fusiform spikes, with sterile bracts not hiding the axis of spike.

Distribution and habitat, According to Kral (1988), *X. cryptantha* is a common species in sandy lowland savannas of southeastern Colombia and Amazonas state, Venezuela, being recorded as disjunction on Serra do Aracá, Amazonas state, Brazil. These records in the VNP, which is located between Serra do Aracá and Amazonas state in Venezuela, are the firsts in Roraima state, Brazil. In VNP, the species occurs in *campinaranas* with sandy soils, seasonally flooded.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina, estrada para Serra do Preto, brejo, 1°16'28"N, 61°00'33"W, 59 m, 23 Jan 2008, N.F.O. Mota et al. 1229 (BHCB, INPA, SP); campina no final da estrada Perdida, solo arenoso com denso estrato graminoso, 1°15'42"N, 60°58'04"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2316 (BHCB, INPA, NY, SP); campina após a primeira bueira, margem direita, 1°25'17"N, 60°59'08"W, 63 m, 14 Oct 2011, N.F.O. Mota et al. 2377 (BHCB, INPA, NY, SP); grade do PPBio, L1 com N, campina úmida, 1°28'56"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2405 (INPA, SP); na grade da PPBio, L1/N6, 1°29'18"N, 61°02'82"W, 12 Sep 2010, S.M. Costa et al. 704 (INPA, UEC).

2. *Xyris dilatatiscapa* Kral & Jan.-Jac., Novon 8: 399-401. 1998, Figure 1.

(Figures 3 B, 4 E–I, 7 G)

Description, Annual, aquatic, rare terrestrial, clump-forming, rarely solitary. Base of the plant flattened, not fibrous, without mucilage. Leaves 1.2–5 cm long, distichous,

erect to spreading, not twisted; sheaths 1/6–2/3 the leaf length, gradually dilating toward the base, papillose, with prominent nerves, reddish to purple, margins scarious, long ciliate, eligulate; lamina 1–4.5 cm × 0.5–0.8 mm, terete in fresh material, canaliculate and involute when dried, densely papillose to undulate-rugose, nerves evident, margins undifferentiated, glabrous, apex obtuse, straight. Spathe longer than the leaves. Peduncle 7.9–16.7 cm long, 0.1–0.2 mm wide, filiform, subterete, with its apical 1.0–3.3 cm portion abruptly dilated to 0.5 mm wide, not twisted, glabrous, mostly smooth, transversely rugose-scabridulous or rugulose-papillate in dilated region, ecostate. Spike 4–6-flowered, 4–8 × 2–6 mm, ellipsoid, pale to purple. Sterile bracts 4, the lower ones ca. 1/2 of the fertile bracts; the uppermost elliptic to oval-lanceolate, not keeled, maculate, margins scarious, entire to slightly lacerate, glabrous, apex obtuse. Fertile bracts 3–4.2 × 0.1–0.2 mm, elliptic, margins glabrous, scarious, entire to slightly lacerate, pale brown, apex acute; macula along the distal 1/2 of the fertile bract, lanceolate, green, gray or purple. Lateral sepals 2.5–4 mm, elliptic, slightly asymmetric to asymmetric, free, shorter than the bracts, keel glabrous; corolla lobes elliptic; staminodia glabrous, the branches flattened; stamens 1.5 mm long; anther 1 mm long, sagittate; style 3.5 mm long, branches 1.6 mm long; ovary 1.8 mm long, unilocular, central placentation, with column three-branched distally. Capsule 3.0–3.5 mm long, globous. Seeds 0.5–0.7 × 0.2–0.3 mm, cylindric-ellipsoid to obovoid, reddish to castaneous, apex apiculate; striae 3–4 per 100 μm of seed width in the midle portion, strong prominent, straight, smooth, with prominent and evenly distributed cross-lines, reticulate.

Morphological comments, Xyris dilatatiscapa are usually partially submerged plants, occurring at peaty bogs, where they form dense clumps of an unusual bluish to purplish color. This species has some morphological peculiarities, like a noticeable

distal dilation on the peduncle (what gives the name for the epithet) and the leaves cylindrical to canaliculated, strongly papillose to undulate-rugose. *Xyris dilatatiscapa* has glabrous staminodia, as well as in *Xyris savanensis* Miq., which differs by its flattened leaves and peduncle not distally dilated. Other features that distinguish this species among its congeners in the VNP are the central placentation with column three-branched distally, and the seeds with several longitudinal and transversal striae, conspicuously thickened and evenly distributed, which is unique among species of *Xyris* of the VNP (pers. obs.).

Distribution and habitat, Xyris dilatatiscapa was previously known only from the type collection (J. Jansen-Jacobs et al. 2734) in Guayana (Kral & Jansen-Jacobs 1998). In Brazil, it occurs in Roraima, being the collections from the VNP the first record in Brazil. It occurs in periodic lakes throughout the *campinaranas*, growing during the rainy season.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina L3 500, 1°28'10"N, 61°00'48"W, 17 Oct 2011, C.B. Curty et al. 10 (BHCB, INPA, SP); estrada perdida, primeira campina após a guarita, margem esquerda, 1°28'25"N, 60°58'08"W, 76 m, 12 Oct 2011, N.F.O. Mota et al. 2344 (BHCB, INPA, NY, SP); campina L3 500, 1°28'10"N, 61°00'48"W, 17 Oct 2011, P.A. Pereira et al. 112 (INPA, SP).

3. *Xyris fallax* Malme, Bih. Svensk. Vet.-Akad. Handl. 22, Afd. 3, no. 2: 12, pl. 1, f. 5. 1896.

(Figures 3 C, 4 J–N, 7 H)

Description, Perennial, terrestrial or aquatic, densely clump-forming. Base of the plant not flattened, with mucilage. Leaves 17–65 cm long, spiral, erect to spreading,

not twisted; sheaths 1/2–1/5 the leaf length, gradually dilating toward the base, smooth, with prominent nerves, pale to reddish, lustrous, margins scarious, ciliate close to the base, ligulate; lamina 12–52 cm × 2.6–5.2 mm, flattened, smooth, nerves slightly evident, margins undifferentiated or slightly incrassate, glabrous, apex incurved-acute, minutely scabrociliate. Spathe shorter than the leaves. Peduncle 52–101.2 cm long, 1.2–2.0 mm wide, terete, without distal dilatation, twisted, glabrous, smooth, multi-costulate, becoming ecostulate toward the apex. Spike 15–26(–35)-flowered, 8–25 × 5–12 mm, globous, subglobous, ovoid, ellipsoid or cylindric, castaneous. Sterile bracts 10–20, the lower ones scale-like, less than 2 mm long, shorter than the fertile bracts and grading into them; the uppermost oblong to obovate, not keeled, maculate, margins entire to slightly lacerate, glabrous, apex obtuse, round. Fertile bracts 4.2–5.5 × 2.2–3.5 mm, broadly oblong to obovate, margins glabrous, entire to slightly lacerate, pale brown, apex obtuse; macula along the distal 1/3 of the fertile bract, elliptic, seldom triagular, greenish, castaneous or gray, with a distinctive midnerve. Lateral sepals 2–5.1 mm, linear-oblanceolate, symmetric to slightly asymmetric, free, shorter than the bracts, keel lacerociliate; corolla lobes obovate; staminodia long-pennicillate, branches not flat; stamens 2.5 mm long; anther 1.5 mm long, sagittate; style 3.5 mm long, branches 2 mm long; ovary 3 mm long, unilocular, placentation perietal. Capsule 5.0–5.5 mm long, broadly obovoid. Seeds 1.3–1.5 × 0.3–0.4 mm, cylindric-fusiform, angulate, reddish to castaneous and translucent, apex acute; striae 2–3 per 100 μm of seed width in the midle portion, strongly prominent, straight, strongly sinuous, cross-lines absent.

Morphological comments, Xyris fallax is a polymorphic species, with spikes that can vary in length and shape. Two morphotypes can be recognized in the study area: one with ellipsoid to cylindrical spikes longer than 2 cm (e.g. N.F.O. Mota et al. 2341),

and the other with ovoid spikes, shorter than 2 cm (e.g. N.F.O. Mota et al. 2430). The first morphotype grows at margins of perennial lakes, while the second was observed on sandy seasonally flooded fields. *Xyris fallax* is also characterized by the presence of hyaline mucilage on the base of the leaves, as in *X. jupicai* Rich. and *X. macrocephala* Vahl, which also occur in the study area. These three species are classified within *Xyris* sect. *Xyris*, a group characterized by unilocular ovary with parietal placentation (Smith & Downs 1968). *Xyris fallax* can be easily distinguished from its multicostelate peduncles and seeds longer than 1 mm, angulose, with longitudinal striae thickened, sinuous, and strongly prominent. *Xyris jupicai* and *X. macrocephala* have peduncles 2-costate or less and seeds shorter than 1 mm, with longitudinal and transversal striae sparsely and evenly distributed.

Distribution and habitat, Xyris fallax is a pantropical species, recorded in Africa, Central America and South America. In Brazil, it occurs throughout regions North, Midwest, Northeast and Southeast (Wanderley et al. 2014). In VNP and surroundings, this species usually grow in areas affected by humans, like artificial lakes and roadside vegetation.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina, trilha N4 (2500) PPbio, 1°16'48"N, 61°00'00"W, 26 Nov 2006, F.A. Carvalho et al. 877 (INPA); grade do PPBio, L3 500, 1°16'48"N, 61°00'00"W, 17 Oct 2011, G.H. Shimizu 563 (BHCB, INPA, NY, SP); início da estrada Perdida, 1°26'14"N, 60°58'49"W, 61 m, 10 Oct 2011, G.O. Silva et al. 92 (BHCB, INPA, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2303 (BHCB, INPA, NY, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2305 (BHCB, INPA, NY, SP);

estrada Perdida, primeira campina após a guarita, margem esquerda, 1°28'25"N, 60°58'08"W, 76 m, 10 Oct 2011, N.F.O. Mota et al. 2341 (BHCB, INPA, NY); grade do PPBio, campina parcialmente alagada em L3, entre N1 e N2, 1°28'07"N, 61°00'27"W, 62 m, 23 Oct 2011, N.F.O. Mota et al. 2430 (BHCB, INPA, NY, SP); grade do PPBio, entre L1-L2/N2-N3, 1°16'48"N, 61°00'00"W, 15 Sep 2010, S.M. Costa et al. 741 (INPA, NY, UEC).

4. *Xyris guianensis* Steud., Syn. P1. Glum. 2: 285. 1855.

(Figures 3 D, 4 O–R, 7 I)

Type. Guayana: 1848, "Guiana anglica. Schomburghk No. 1058" (Lectotype: K!; Isolectotypes: B!, K!, L) – Designate by Kral 1988.

Xyris gardneri Malme, Bih. Svensk. Vet. Akad. Handl. 26, Afd. 3(19); 8, pl. 1, f. 1. 1901.

Type. Brazil: Ceará: 1838. Gardner, G. 1058. (Lectotype: S [S6574!]; Isolectotype, NY!) , Kral 1988.

Xyris filiscapa Malme, Repert. Spec. Nov. Regni Veg. 3: 112. 1906.

Type. Brazil: Amazonas: "In arenosis humidis. Manaos. Amazonas. Brasil." Ule 6172 (Lectotype: S [S6571!]; Isolectotypes: L, NY!, US!), Kral 1988.

Xyris connosepala Lanj. & Lindeman, **syn. nov.** Bull. Torrey Bot. Club 75: 639. 1948, **syn. nov.**

Type. Surinam: Tafelberg (Table Mountain). Frequent, wet sphagnum-filled cracks in rocks, Savanna No. IV, 16 Aug 1944, B. Maguire 24395[a] (Holotype: NY!; Isotype: U)

Description, Annual, terrestrial, rare aquatic, clump-forming, rarely solitary. Base of the plant flattened, without mucilage. Leaves 0.8–7.6 cm long, distichous, erect,

slightly spreading flabellate, often twisted at the apex; sheaths 1/3–1/5 the leaf length, gradually dilating toward the base, smooth, without prominent nerves, castaneous, margins scarious, glabrous, ligulate; lamina 0.6–5.8 cm × 0.4–1.5 mm, flattened, smooth, nerves slightly evident, margins pale cartilaginous, glabrous, apex incurved acute, slightly cartinlaginous thickened, papillose, with short tricomes. Spathe shorter or equaling the leaves length. Peduncle 1.8–25.5 cm long, 0.1–0.3 mm wide, filiform, terete, without distal dilatation, not twisted to sligthly twisted, glabrous, smooth, ecostate to 1-costulate. Spike 2–3-flowered, 3–8 × 1–4 mm, ellipsoid to obconic, castaneous. Sterile bracts 4, the lower ones 1/2–2/3 of the fertile bracts; the uppermost ovate-triagular, not keeled, maculate, margins indifferenciated, bacoming lacerate with age, glabrous, apex acute. Fertile bracts 2–4 × 0.5–1.5 mm, ovate, margins glabrous, indifferenciated becoming lacerate with age, concolor, apex acute; macula along the distal 1/2 of the fertile bract, oval-lanceolate, green to purple. Lateral sepals 2–3 mm, lanceolate, slightly asymmetric, free to connate on its 1/3 basal portion, exert, keel shortly ciliate; petals connate, corolla lobes broadly obovate; staminodia with sparse penicillate hairs distally, on its typically flattened branches; stamens 1 mm long; anther 0.7 mm long, oblong with prominent connective; style 1.5 mm long, branches 1 mm long; ovary 1.3 mm long, unilocular, central placentation. Capsule 2.5–3.0 mm long, ellipsoid. Seeds 0.3–0.5 × 0.2–0.3 mm, broadly ellipsoid to obovoid, reddish to castaneous, apex apiculate; striae 5–6 per 100 μm of seed width in the midle portion, slightly prominent, straight, sinuous, cross-lines absent.

Morphological comments, The species is characterized by its narrow flabellate and ligulate leaves, with margins thickened, apex incurved and papillate, and spikes ellipsoid to obconic, usually showing strongly exert sepals.

Such set of features is shared with the type material of *Xyris connosepala* Lanj. & Lindeman (B. Maguire 24395a), leading previous authors (Kral 1988) to treat it as close related to *X. guianensis,* differing by the level of sepals connation and seed features (shape and ornamentation). According to Kral (1988), while in *X. guianensis* the sepals are free and the seeds are ovoid to ellipsoid, in *X. connosepala* the sepals are fused on its 1/3 basal portion and the seeds are ellipsoid and strongly striate. Nevertheless, our analyses reveal that these characters do not support the segregation of both species, because they can vary even in the same individual. Some specimens of *X. guianensis* from VNP (e.g. G.O. Silva et al. 96; N.F.O. Mota et al. 2299, 2313) have lateral sepals free to connate at the base, even in the same spike. Despite the level of sepal connation is usually considered to be a useful taxonomic character in the genus, being uniform in the majority of species, it, however, shows plasticity in some species (Kral 1988), as in *X. uleana*, which occurs in the VNP, and *X. thysanolepis* Maguire & L.B.Sm., in Venezuela (Kral 1988).

The study of seed ornamentation under SEM of the type specimen of *X. connosepala* (B. Maguire 24395a) and the material collected at the VNP (Table 1), here treated as *X. guianensis* (N.F.O. Mota et al. 2299, 2313 e 2397), did not reveal any significant distinction among them. All of the sampled seeds are about 0.5 mm long, ellipsoid to ovoid, with longitudinal striae slightly thickened and sinuous.

Given this reasons, *Xyris connosepala* is proposed as a new synonym for *Xyris guianensis*, which has nomenclatural priority (McNeill et al. 2012 - art. 11.3 of Melbourne Code).

Distribution and habitat, Xyris guianensis is common in low to medium elevation savannas in northern Brazil, Colombia and Surinam. In Brazil it occurs in Amazonas, Pará and Roraima states. *Xyris guianensis* is commonly found growing in

campinaranas of VNP, forming dense clumps, often sympatric with *X. subuniflora* and *Abolboda minima*.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campinarana, próximo à estrada Perdida, 1°16'48"N, 61°00'00"W, 22 July 2010, A.N. Conceição et al. 6 (INPA, NY); campina na estrada Perdida, 1°16'48"N, 61°00'00"W, 21 July 2010, E. Pessoa et al. 327 (INPA); beira da estrada Perdida, campina aberta, 1°16'48"N, 61°00'00"W, 28 Nov 2006, F.A. Carvalho et al. 976 (INPA); estrada Perdida, campina aberta, 1°16'48"N, 61°00'00"W, 30 Nov 2006, F.A. Carvalho et al. 1022 (INPA); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2299 (BHCB, INPA, NY, SP); estrada Perdida, campina próxima à primeira buera da estrada Perdida, solo arenoso, 1°25'15"N, 60°59'09"W, 63 m, 23 Sep 2011, N.F.O. Mota et al. 2313 (BHCB, INPA, NY, SP); grade do PPBio, L1 com N6, campina úmida, 1°29'11"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2397 (BHCB, INPA, NY, SP); área alagada, na margem da estrada Perdida, solo argiloso, 1°24'51"N, 60°59'12"W, 63 m, 20 July 2010, T.D.M. Barbosa et al.1210 (INPA, UEC); área alagada, na margem da estrada Perdida (Segunda boeira), solo argiloso, 1°24'09"N, 60°59'11"W, 63 m, 25 July 2010, T.D.M. Barbosa et al. 1333 (INPA, UEC).

5. ***Xyris involucrata*** Nees in Hooker, J. Bot. 2: 397. 1840.

(Figures 3 E, 4 S–W, 7 J)

Description, Perennial, terrestrial, solitary to clump-forming. Base of the plant flattened, with mucilage. Leaves 13–28.5 cm long, distichous, spreading flabellate, not twisted; sheaths 1/2–3/5 the leaf length, gradually to abruptly dilated at the base,

smooth, with prominent nerves, pale to yellowish, castaneous at the very base, margins indiferenciated to slightly scarious, glabrous, eligulate; lamina 8–13 cm × 2.6–6.3 mm, flattened, smooth, with two peripherical evident nerves, margins slightly incrassate, densely ciliate, apex obtuse or incurved-obtuse. Spathe equaling the leaves. Peduncle 38–60 cm long, 3.2–3.6 mm wide, ancipital, strongly flattened distally, not twisted to sligthly twisted, densely ciliate, smooth, 1-costate at the middle portion. Spike 25–50-flowered, 6–10 × 10–18 mm, hemispherical to subglobous, yellowish to pale. Sterile bracts several, the lower ones distinctly longer than the bracts; the uppermost obtrullate, not keeled, maculate, margins indifferenciated, villosulous-ciliate, apex acute. Fertile bracts 5.1–6.5 × 3.2–3.6 mm, obtrullate, margins villosulous-ciliate, indifferenciated, reddish, apex acute; macula along the distal 2/3 of the fertile bract, losangular, castaneous to reddish. Lateral sepals 3.5–5 mm, oblong, curved, slightly asymmetric, free, shorter than the bracts, keel ciliolate, trichomes red; corolla lobes elliptic; staminodia long-penicillate, branches not flat; stamens 2 mm long; anther 1.5 mm long, oblong; style 5.5 mm long, branches 2.3 mm long; ovary 3 mm long, unilocular, basal placentation. Capsule 3.0–4.0 mm long, broadly ellipsoid to obovoid. Seeds 0.5–0.7 × 0.2–0.3 mm, ellipsoid-cylindric, dark amber, apex apiculate; striae 4–5 per 100 μm of seed width in the midle portion, slightly prominent, straight, slightly sinuous, with thin cross-lines, not reticulate.

Morphological comments, Xyris involucrata can be characterized by its multi-flowered spikes with several patent sterile bracts, distinctly longer than the main axis of the spike. Because of these features, it resembles *X. spruceana* Malme, widely distributed in the Amazonian savannas, and *X. pallidula* Kral & Wand., known only from its type locality, in Amazonas state, Brazil. *Xyris spruceana,* however, includes plants shorter than 25 cm, contrasting with plants up to 60 cm of *X. involucrata*. *Xyris*

pallidula, in turn, have overall size similar to *X. involucrata*, but can be differentiated by laminae with margins undifferentiated and glabrous, while the latter has laminae with margins conspicuously thickened and densely ciliate. Aditionally, both *X. pallidula* and *X. spruceana* can be distinguished from *X. involucrata* by fertile bracts with the apex acuminate-subulate (acute in *X. involucrata*). *Xyris involucrata*, together with *X. macrocephala* Vahl, are the only species occurring in VNP that present several flowers in anthesis in a single spike at the same time.

Distribution and habitat, It is a widespread species in low to high elevation savannas and *campinaranas* in Brazil, Colombia, Guayanas, Surinam and Venezuela. In Brazil, it occurs in the states of Amazonas and Roraima.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina próxima a buritizal, 1°15'40"N, 60°58'11"W, 55 m, 24 Jan 2008, N.F.O. Mota et al. 1226 (BHCB, INPA, SP); estrada Perdida, campina no final da estrada Perdida, solo arenoso com denso extrato graminoso, população associada a buritizal, 1°15'42"N, 60°58'04"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2318 (BHCB, INPA, NY, SP).

Additional specimens examined, **BRAZIL: Roraima:** Município Caracaraí, BR174, km 350, North of Rio Brancinho, cerrado on white sand, in shaded areas, 18 Nov 1977, W.C. Steward 75 (INPA).

6. *Xyris jupicai* Rich., Act. Soc. Hist. Nat. Paris I: 100. 1792.

(Figures 3 F, 4 X–A', 7 K)

Description, Annual, terrestrial or aquatic, solitary to clump-forming. Base of the plant flattened, with mucilage. Leaves 13–55.5 cm long, distichous to spiral, erect to spreading flabellate, not twisted; sheaths 1/2–3/5 the leaf length, gradually dilating

toward the base, smooth, with prominent nerves, pale to yellowish, margins scarious, glabrous, ligulate; lamina 7–22.5 cm × 1.4–9.0 mm, flattened, smooth, nerves slightly evident, margins slightly incrassate, glabrous, apex obtuse to incurved-acute. Spathe shorter than the leaves. Peduncle 22.3–94.5 cm long, 1.2–1.4 mm wide, proximally terete, becoming flattened toward the apex, not twisted to sligthly twisted, papillose-tuberculate at the edges, striate, 1–2-costate. Spike 18–40-flowered, 7.4–27.4 × 4.8–8.4 mm, ovoid, obovoid to ellipsoid, green to castaneous. Sterile bracts 10–12, the lower ones scale-like, shorter than the fertile bracts and grading into them; the uppermost oblong to round, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse, round. Fertile bracts 5.5–7.1 × 4–6.2 mm, broadly obovate, margins glabrous, indifferenciated, concolor, apex obtuse to round; macula along the distal 1/3 of the fertile bract, ovate to triangular, green to gray. Lateral sepals 4.2–6 mm, linear, oblong-curved or obovate-curved, symmetric to slightly asymmetric, free, shorter than the bracts, keel lacerate from middle to the apex; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 2 mm long; anther 1.2 mm long, oblong; style 4.8 mm long, branches 1.5 mm long; ovary 3 mm long, unilocular, parietal placentation. Capsule 5.0–6.0 mm long, obovoid. Seeds 0.5–0.8 × 0.2–0.3 mm, ellipsoid, pale, apex apiculate, dark; striae 2 per 100 μm of seed width in the midle portion, strong prominent, straight, slightly sinuous, with prominent and evenly distributed cross-lines, reticulate.

Morphological comments, Xyris jupicai is a widely distributed species with a noticeably morphological plasticity. It is similar to *X. macrocephala*, with which it forms a complex of difficult delimitation of its entities. But in VNP, these species appear to not present individuals of intermediate morphology, being easily distinguished from each other. *Xyris jupicai* are annual plants, shorter than 1 m, while

X. macrocephala are robust, perennial plants, always taller that 1 meter. *Xyris jupicai* has peduncle 1–2-costate, terete and becoming flattened toward the apex, whilst *X. macrocephala* has subterete to trichetous, ecostate to 2-costate peduncle. The seed morphology is also useful for distinguishing these species: *X. macrocephala* seeds have cross-lines less thickened than the longitudinal striae; in *X. jupicai*, cross-lines and longitudinal striae are equally thickened.

Distribution and habitat, It is a widespread species, occurring from North America to South America (Argentina), at low elevations, often in disturbed sites. In Brazil it is known to occur in all states (Wanderley *et al.* 2010). *Xyris jupicai* and *X. macrocephala* occur in disturbed environments, being found in the study area growing in humid areas, close to roads and other anthropic areas.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, estrada perdida, campinarna graminosa aberta, 1°14'53"N, 60°58'07"W, 59 m, 4 Mar 2010, T.D.M. Barbosa et al. 1070 (INPA, UEC); estrada perdida, campinarna graminosa aberta, 1°14'53"N, 60°58'07"W, 59 m, 4 Mar 2010, T.D.M. Barbosa et al. 1071 (INPA, UEC); estrada perdida entre primeira e segunda boeira, 1°16'48"N, 61°00'00"W, 29 Mar 2011, T.D.M. Barbosa et al. 1443 (INPA); próximo a 2ª bueira, 1°23'54"N, 60°59'10"W, 50 m, 25 Jan 2011, S.M. Costa et al. 884 (INPA); mata do Seu Nerí, 1°26'51"N, 60°59'24"W, 49 m, 26 Jan 2011, S.M. Costa et al. 908 (INPA); grade do PPBio, campina parcialmente alagada em L3, entre N1 e N2, 1°28'07"N, 61°00'27"W, 62 m, 23 Oct 2011, N.F.O. Mota et al. 2429 (INPA, NY, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2307 (BHCB, INPA, NY, SP); estrada Perdida, campina próxima à primeira buera da estrada Perdida, solo arenoso, 1°25'15"N, 60°59'09"W, 63 m, 23 Sep 2011, N.F.O. Mota et al. 2311 (BHCB, INPA,

NY, SP); campina arbustiva, úmida L6 (1000), 1°16'48"N, 61°00'00"W, 11 Oct 2011, C.T. Pedrollo et al. 125 (BHCB, INPA, SP).

7. *Xyris macrocephala* Vahl., Enum. Pl. 2: 204. 1805.

(Figures 3 G, 4 B'–E', 7 L)

Description, Perennial, terrestrial or aquatic, solitary to clump-forming. Base flattened, robust, with mucilage. Leaves 38–64 cm long, distichous to spiral, erect or spreading flabellate, not twisted; sheaths more than 1/2 the leaf length, gradually to abruptly dilating toward the base, smooth, with sligthly prominent nerves, castaneous, red to purple at the base, margins scarious to entire, glabrous, eligulate; lamina 36–40 cm × 4.2–8.6 mm, flattened, smooth, striate, nerves not evident, margins slightly incrassate, glabrous, apex incurved-acute to straight-acute. Spathe shorter than the leaves. Peduncle 113–122 cm long, 3.0–4.0 mm wide, subterete to trichetous, without distal dilatation, not twisted, glabrous, smooth to striate, ecostate to 2-costate. Spike 25–35-flowered, 20.8–30.5 × 12–15.4 mm, ovoid to cylindric, green to dark brown. Sterile bracts 16–22, the lower ones bracts much smaller than the fertile bracts and grading into them; the uppermost obovate to ovate or suborbicular, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse, round. Fertile bracts 3.5–5.7 × 3.5–5.5 mm, obovate to ovate or suborbicular, margins glabrous, indifferenciated, concolor, apex obtuse to round; macula along the distal 1/3 of the fertile bract, ovate to round, green to gray. Lateral sepals 4–7 mm, linear to oblong-curved, slightly asymmetric, free, shorter than the bracts, keel lacerate or lacerofimbriate; corolla lobes obovate; staminodia long-pennicillate, branches not flat; stamens 2.2 mm long; anther 1.5 mm long, sagittate; style 8.5 mm long, branches 3 mm long; ovary 3.5 mm long, unilocular, parietal placentation. Capsule 5.0–7.0 mm

long, obovoid. Seeds 0.6–0.7 × 0.2–0.3 mm, ellipsoid, pale, apex apiculate; striae 1–2 per 100 μm of seed width in the midle portion, strong prominent, straight, moniliform, with thin and evenly distributed cross-lines, reticulate.

Morphological comments, Xyris macrocephala are robust plants reaching more than 1 meter tall, and with hyaline mucilage on the plant base. The spikes are multi-flowered (with more than 25 flowers). For observations about its affinities, see comments under *X. fallax* and *X. jupicai*.

Distribution and habitat, It is widespread in South America, occurring in low to medium elevation. In Brazil, it occurs in all states. In VNP is locally rare, known from just one locality, in a disturbed flooded *campinarana* area.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, margem esquerda, próximo à ponte do Rio Barauana, 1°28'34"N, 60°50'30"W, 66 m, 19 Oct 2011, N.F.O. Mota et al. 2416 (BHCB, INPA, NY, SP)

Additional specimen examined. BRAZIL: Roraima: Município Boa Vista, BR-174 Boa Vista - Caracaraí, savanas adajcentes à estrada, campo úmido, 2°34'42"N, 60°52'36"W, 22 Sep 2011, N.F.O. Mota et al. 2298 (BHCB, INPA).

8. *Xyris malmeana* L.B.Sm., Bol. Inspet. Fed. Obras Contra Secas, Rio 10: 126. 1939.

(Figures 3 H, 4 F'–I', 7 M)

Description, Perennial, terrestrial, solitary, rarely clump-forming. Base of the plant sub-bulbous, without mucilage. Leaves 5.5–28.2 cm long, distichous, erect, twisted or not; sheaths 1/3–2/5 the leaf length, abruptly dilated at the base, smooth, with prominent nerves, pale to reddish, lustrous, castaneous at very base, margins scarious,

long ciliate, eligulate; lamina 3.3–20 cm × 0.8–2.0 mm, flattened, finely rugose, nerves slightly evident, margins slightly incrassate, glabrous, apex acute, acuminate to subulate. Spathe shorter than the leaves. Peduncle 22–51.2 cm long, 0.7–0.8 mm wide, terete to sub-terete, filiform, without distal dilatation, twisted, glabrous, smooth to finely rugose, 3–4-costate. Spike 8–12-flowered, 5.3–7.5 × 2–6.1 mm, broadly ellipsoid or ovoid, reddish to castaneous. Sterile bracts 4, the lower ones ca. 1/2–1/3 of the fertile bracts; the uppermost elliptic to obovate, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse, round. Fertile bracts 3–6.2 × 2.2–3.1 mm, broadly elliptic to obovate, margins glabrous, indifferenciated, concolor, apex obtuse to round; macula along the distal 1/3 to 2/3 of the fertile bract, oval-lanceolate, green to gray. Lateral sepals 4–5.5 mm, obovate, incurved, oblong-curved to elliptic-curved, asymmetric, free, shorter than the bracts, keel entire to lacero-ciliolate; corolla lobes obovate; staminodia long-pennicillate, branches not flat; stamens 2 mm long; anther 1.2 mm long, oblong; style 4 mm long, branches 1.5 mm long; ovary 3.2 mm long, unilocular, basal placentation. Capsule 4.5–5.0 mm long, broadly ellipsoid. Seeds 0.4 × 0.1–0.2 mm, ellipsoid, castaneous, apex apiculate; striae 5–7 per 100 μm of seed width in the midle portion, prominent, straight, smooth, with thin cross-lines, not reticulate.

Morphological comments, Xyris malmeana is characterized by solitary individuals, which are erect, with a bulbous stem, and peduncle clearly 3–4-costate. The spikes are small (never larger than 8 mm long), with fertile bracts with a narrow macula, and margins entire to slightly lacerate when senescent. *Xyris malmeana* resembles *X. lacerata* Pohl ex Seub., a widely distributed species in South America, by the shape of spikes (ellipsoid to ovoid), the peduncle 3 or more costate, and for a solitary and erect habit. *Xyris lacerata* differs by a more robust and strongly bulbous stems, and fertile

bracts with a broad macula and margins lacerate. The lateral sepals of *X. lacerata* are lacerate-ciliate, whereas in *X. malmeana,* they are ciliolate.

Distribution and habitat, A Neotropical species, known from sandy savannas in low to medium elevations of Brazil, Guayana, and Venezuela in South American, and Trinidad in Central American. In Brazil, it occurs in the states of Amapá, Amazonas, Mato Grosso, Pará and Roraima.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2310 (BHCB, INPA, NY, SP); grade do PPBio, campina da L3/N2, 1°16'48"N, 61°00'00"W, 13 Sep 2010, S.M. Costa et al. 725 (INPA, UEC); estrada Perdida, após a 3ª bueira, 1°19'51"N, 60°59'00"W, 20 Sep 2010, S.M. Costa et al. 778 (INPA, NY, UEC); rio Anauá, 0°57'30"N, 61°11'32"W, 49 m, 24 Mar 2011, S.M. Costa et al. 997 (INPA).

9. *Xyris mima* L.B.Sm. & Downs, Proc. Biol. Soc. Wash. 73: 250, fig. 4. 1960.

(Figures 3 I, 5 A–F, 7 N)

Description, Annual, terrestrial, rare aquatic, solitary to clump-forming. Base of the plant flattened, without mucilage. Leaves 3–24 cm long, distichous, erect or spreading flabellate, twisted or not; sheaths less than 1/2 the leaf length, gradually dilating toward the base, papillate to densely rugose, with strongly prominet nerves, castaneous to reddish, margins scarious, glabrous, ligulate; lamina 2–18 cm × 2.0–5.0 mm, flattened, densely transversely undulate-rugose, nerves evident, margins turbeculate-scabrid, glabrous, apex incurved-acute. Spathe shorter than the leaves. Peduncle 8–52 cm long, 2.0–4.0 mm wide, subterete, without distal dilatation, often becoming flattened toward the apex, not twisted to sligthly twisted, strong

tuberculate-scabrid, rugose, 2–costate. Spike 15–35-flowered, 4–25 × 2–5 mm, ovoid to cylindric, castaneous. Sterile bracts 4, the lower ones 1/2 of the fertile bracts; the uppermost obovate, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse, round. Fertile bracts 3–5 × 3–5 mm, obovate to round, margins glabrous, indifferenciated, concolor, apex broadly round; macula along the distal 1/3 of the fertile bract, not reaching the margin, broadly ovate, green to gray. Lateral sepals 3–3.5 mm, oblong-curved to elliptic-curved, strongly asymmetric, free, shorter than the bracts, keel ciliate; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 1 mm long; anther 0.5 mm long, sagittate; style 3.5 mm long, branches 1.3 mm long; ovary 1.8 mm long, unilocular, basal placentation. Capsule 2.5–3.0 mm long, obovoid. Seeds 1.0–1.1 × 0.3 mm, ellipsoid to obovoid, castaneous, apex acute with a coma of bristles; striae 4–5 per 100 μm of seed width in the midle portion, prominent, straight, moniliform, cross-lines absent.

Morphological comments, Xyris mima is recognized by the surface of leaves and peduncle densely rugose, presence of ligule, scarious sheaths, and spikes usually cylindrical. These characters suggest superficial affinity with *X. savanensis* Miq. However, *X. mima* has 2-costate peduncle, pilose staminodia, and seeds around 1 mm long, ellipsoid to obovoid, with monilliform striae and apex with a coma of bristles, while *X. savanensis* has ecostate peduncle, glabrous staminodia, and smaller seeds (~0.5 mm long), narrow ellipsoid, striae in alternate groups of monilliform and sinuous, with a typical truncate base and apex acute and glabrous. Both species become reddish ferruginous (the whole plant) when senescent, composing beautiful colored fields in VNP.

Distribution and habitat, Xyris mima is known for Brazil and Venezuela. In Brazil, it occurs in the states of Amazonas, Pará and Roraima, being this is the first record in

the latter state. *Xyris mima* is commonly found growing in wet, sometimes flooded, sandy *campinaranas*, in the VNP.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, estrada Perdida, campina aberta, 1°16'48"N, 61°00'00"W, 29 Nov 2006, F.A. Carvalho et al. 933 (INPA); início da estrada Perdida, 1°26'14"N, 60°58'49"W, 52 m, 13 Oct 2011, G.O. Silva et al. 95 (BHCB, INPA, SP); estrada Perdida, lago na margem, após a segunda bueira, 1°22'02"N, 60°58'54"W, 17 Jan 2011, M.C.E. Amaral et al. 28 (INPA); campina, 1°16'17"N, 60°58'07"W, 50 m, 22 Jan 2008, N.F.O. Mota et al. 1235 (BHCB, INPA, SP); estrada Perdida, campina próxima à primeira buera, solo arenoso, 1°25'15"N, 60°59'09"W, 63 m, 23 Sep 2011, N.F.O. Mota et al. 2312 (BHCB, INPA, NY, SP); estrada Perdida, campina cerca de 1km depois da segunda bueira, solo arenoso exposto, 1°20'39"N, 60°58'43"W, 61 m, 23 Sep 2011, N.F.O. Mota et al. 2320 (BHCB, INPA, NY, SP); grade do PPBio, L1 com N6, campina úmida, 1°28'56"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2400 (BHCB, INPA, NY, SP); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 801 (INPA, UEC); estrada perdida entre primeira e segunda boeira, 1°16'48"N, 61°00'00"W, 29 Mar 2011, T.D.M. Barbosa et al. 1442 (INPA).

10. *Xyris paraensis* Poepp. ex Kunth, Enum. P1.4: 9. 1843.

(Figures 4 J, 6 G–K)

Description, Annual, terrestrial, solitary to clump-forming. Base of the plant flattened, without mucilage. Leaves 2–13 cm long, distichous, erect or spreading flabellate, usually not twisted; sheaths 1/3–1/2 the leaf length, gradually dilating toward the base, smooth, with sligthly prominent nerves, castaneous to reddish, margins scarious,

glabrous, eligulate; lamina 1.5–8 cm × 1.0–3.0 mm, flattened, smooth, nerves evident, margins undifferentiated, glabrous, apex acute. Spathe shorter or equaling the leaves length. Peduncle 8–31 cm long, 0.3–0.7 mm wide, terete, without distal dilatation, not twisted to sligthly twisted, glabrous, smooth, ecostate. Spike 10–15-flowered, 3.2–7.4 × 2–4.5 mm, ovoid, castaneous. Sterile bracts 4, the lower ones 1/2 of the fertile bracts; the uppermost obovate, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse. Fertile bracts 2–4 × 1.5–3.5 mm, obovate, margins glabrous, indifferenciated, concolor, apex obtuse; macula along the distal 1/3 of the fertile bract, broadly ovate, green to gray. Lateral sepals 0.8–3.5 mm, elliptic to obovate-curved, strongly asymmetric, free, shorter than the bracts, keel glabrous, ciliate to slightly lacerate; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 1.4 mm long; anther 1.1 mm long, oblong; style 3.5 mm long, branches 1.3 mm long; ovary 2.7 mm long, unilocular, basal placentation. Capsule 1.0–2.2 mm long, ellipsoid. Seeds 0.7–0.8 × 0.2–0.3 mm, ellipsoid, castaneous, apex strongly apiculate; striae 4–5 per 100 μm of seed width in the midle portion, prominent, straight, forming groups of moniliform and smooth striae, cross-lines absent.

Morphological comments, Xyris paraensis can be distinguished from other congeners in the study area by the following set of characteristics: lamina surface smooth with prominent nerves, sheaths with margins scarious and glabrous, absence of a ligule, and peduncle smooth and ecostate. *Xyris paraensis* has seeds about 0.8 mm long, with apex strongly apiculate, and striae distributed in alternate groups of moniliform and smooth striae.

Several specimens previously named as *Xyris paraensis* in the studied herbaria were erroneously identified and consist, in fact, of *X. mima* or *X. savanensis*. These two species closely resemble *X. paraensis* by their usually caespitose habit, with

distichous leaves, erect to spreading flabellate, and sheaths scarious and glabous. Additionally, the spikes of these three species can be ovoid and their bracts present a visible macula that can be narrow ovate to triangular in shape. Both *X. mima* and *X. savanensis*, differ from *X. paraensis* by their laminae and peduncle strongly rugose and seed shape. In *X. mima*, the seeds are longer than 1 mm, with a coma of bristles at the apex, and the striae are all moliniform. *Xyris savanensis*' seeds are smaller (shorter than 0.5 mm long), with a truncate base, acute apex and striae sinuous and moniliform.

Xyris paraensis comprises a nomenclatural and morphological complex of difficult delimitation of sub-taxa, a subject that deserves further detailed investigation.

Distribution and habitat, Xyris paraensis is known from Brazil, Guayana, French Guayana and Venezuela in South American and in Belize, in Central American. In Brazil it occurs in the states of Amazonas, Ceará, Mato Grosso, Pará, Pernambuco Piauí and Roraima. Few populations with scattered individuals of this annual species were found in the study area.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina L3 500, 1°28'10"N, 61°00'48"W, 17 Oct 2011, C.B. Curty et al. 8 (INPA); grade PPBio L03 T500, 1°48'67" S, 61°01'57"W, 15 Jan 2006, F.R.C. Costa et al.1530 (INPA); estrada perdida, campina na margem esquerda próximo à primeira bueira, 1°25'17"N, 60°59'08"W, 63 m, 21 Oct 2011, N.F.O. Mota et al. 2422 (BHCB, INPA, NY, SP); campina L3 500, 1°28'10"N, 61°00'48"W, 17 Oct 2011, P.A. Pereira et al. 113 (INPA, SP); mata do Seu Nerí, 1°26'51"N, 60°59'24"W, 49 m, 26 Jan 2011, S.M. Costa et al. 909 (INPA).

11. *Xyris savanensis* Miq., Linn. 18: 605. 1844.

(Figures 3 K, 5 L–P, 7 O)

Description, Annual, terrestrial or aquatic, solitary to clump-forming. Base of the plant flattened, soft, without mucilage. Leaves 3.2–23.8 cm long, distichous, erect to spreading flabellate, not twisted; sheaths less than 1/2 the leaf length, gradually dilating toward the base, papillose, papillate to densely rugose, castaneous to reddish, margins scarious, glabrous, ligulate; lamina 2–19 cm × 1.2–2.6 mm, flattened, papillose to densely rugose, nerves evident, margins incrassate, glabrous to papillose, apex acute to incurved-acute. Spathe shorter than the leaves. Peduncle 12–54.5 cm long, 0.6–1.3 mm wide, terete to sub-terete, without distal dilatation, not twisted to sligthly twisted, glabrous, smooth, papillose to densely rugose, ecostate. Spike 10–35-flowered, 3.7–21.2 × 2.4–8.5 mm, ovoid to cylindric, ellipsoid or subglobous, reddish to castaneous. Sterile bracts 4, the lower ones 1/2 of the fertile bracts; the uppermost orbicular, not keeled, maculate, margins indifferenciated, glabrous, apex round. Fertile bracts 3–5.2 × 2.9–5 mm, obovate, suborbicular to orbicular, margins glabrous, indifferenciated, concolor, apex round; macula along the distal 1/2 of the fertile bract, triangular, green to gray. Lateral sepals 3–4 mm, elliptic-curved, strongly asymmetric, free, shorter than the bracts, keel ciliate to ciliolate; corolla lobes obovate; staminodia glabrous, branches not flat; stamens 1.2 mm long; anther 0.6 mm long, oblong; style 3.3 mm long, branches 1 mm long; ovary 1 mm long, unilocular, basal placentation. Capsule 2.0–2.5 mm long, broadly obovoid. Seeds 0.4–0.5 × 0.3 mm, broadly ellipsoid to ovoid, reddish to castaneous, apex acute; striae 5–6 per 100 μm of seed width in the midle portion, prominent, straight, mixing moniliforms and sinuous striae, cross-lines absent.

Morphological comments, Xyris savanensis is a species with high morphological plasticity and broad geographic distribution. It is distinguished by its glabrous

staminodia, seeds smaller than 0.5 mm long with monilliform longitudinal striae, and leaves and peduncle strongly rugose (except for *X. savanensis* var. *glabrata*, that does not occur in the study area, with its leaves and peduncle smooth). For notes about affinities between these species, see comments under *X. mima*.

Distribution and habitat, Xyris savanensis is widely distributed throughout tropical South America. In Brazil, it is known to occur in all states. In VNP, *X. savanensis* is found on sandy *campinaranas* sympatric with *X. mima*, often being confounded with it.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campina, estrada para Serra do Preto, brejo, 1°16'28"N, 61°00'33"W, 59 m, 23 Jan 2008, N.F.O. Mota et al. 1228 (BHCB, INPA, NY, SP); campo arenoso, borda de trilha, campina, 1°16'17"N, 60°58'07"W, 50 m, 22 Jan 2008, N.F.O. Mota et al. 1233 (BHCB, INPA, NY, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2302 (BHCB, INPA, NY, SP); estrada perdida, primeira campina após a guarita, margem esquerda, 1°28'25"N, 60°58'08"W, 76 m, 10 Oct 2011, N.F.O. Mota et al. 2340 (INPA); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°19'51"N, 60°59'00"W, 20 Sep 2010, S.M. Costa et al. 784 (INPA, NY, UEC); área alagada, na margem da estrada perdida (segunda boeira), solo argiloso, 1°24'09"N, 60°59'11"W, 63 m, 25 July 2010, T.D.M. Barbosa et al. 1336 (INPA, UEC).

12. *Xyris subglabrata* Malme, Bull. Torrey Bot. Club 48: 322. 1931.

(Figures 3 L, 5 Q–U, 7 P)

Description, Perennial, terrestrial, clump-forming. Base of the plant sub-bulbous, without mucilage. Leaves 5–23.4 cm long, spiral, erect, not twisted; sheaths 1/3–1/10

the leaf length, abruptly dilated at the base, rugose, rarely smooth, with strongly prominet nerves, reddish to brown, margins indiferenciated to slightly scarious, densely long ciliate, eligulate; lamina 3–17 cm × 0.4–1.2 mm, terete, subterete, often sulcate, papillose to smooth, nerves slightly evident, margins undifferentiated, glabrous, apex conic, some times pilose-tufted. Spathe shorter than the leaves. Peduncle 10–34.5 cm long, 0.7–1.0 mm wide, terete, becoming subterete toward the apex, slightly twisted, glabrous, smooth to papillose, ecostate. Spike 10–15-flowered, 5–8 × 3–7 mm, ovoid, ellipsoid, subglobous, globous to obovoid, dark brown. Sterile bracts 6–8, the lower ones 1/2 of the fertile bracts; the uppermost obovate to orbicular, not keeled, maculate, margins lacerate, glabrous, apex obtuse. Fertile bracts 5–7 × 2–2.5 mm, obovate to oblong, margins glabrous, lacerate, concolor, apex obtuse; macula along the distal 1/3 to 1/2 of the fertile bract, triangular, green to gray, becoming dark with age. Lateral sepals 5–6 mm, linear to lanceolate, curved, asymmetric, free, shorter than the bracts, keel ciliolate above de middle; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 3 mm long; anther 1.5 mm long, sagittate; style 6.5 mm long, branches 3 mm long; ovary 3 mm long, unilocular, central placentation. Capsule 2.8–4.0 mm long, obovoid to cilindric. Seeds 0.6–0.7 × 0.2–0.3 mm, cylindric-fusiform, reddish to castaneous, apex apiculate; striae 6–8 per 100 μm of seed width in the midle portion, prominent, straight, smooth to slightly sinuous, with thin cross-lines, not reticulate.

Morphological comments, Xyris subglabrata are small plants, rarely taller than 15 cm. The leaves and peduncle are terete to sub-terete, the spikes are blackish and small (around 8 mm long), 10–15-flowered. Because of the nigrescence of its bracts, the macula, although present, is hardly visible, especially in dried specimens. In the study area, *X. subglabrata* and *X. surinamensis* are often sympatric that can be misidentified

if not carefully examined. *Xyris surinamensis* can be distinguished from *X. subglabrata* by its leaves and peduncle clearly flattened, spikes up to 23 mm long, brownish, 12–20-flowered and macula clearly visible.

Distribution and habitat, Common in lowland sandy savannas and *campinaranas* in northern Brazil (Amazonas and Roraima), Colombia and Venezuela. In the study area, it occurs in *campinaranas* with white sandy soils.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, grade PPbio/ L1, 1°28'07"N, 61°00'27"W, 23 Sep 2011, E. Pessoa et al. 736 (INPA); início da estrada Perdida, 1°26'14"N, 60°58'49"W, 52 m, 13 Oct 2011, G.O. Silva et al. 97 (INPA, SP); campina no final da estrada Perdida, solo arenoso com denso extrato graminoso, 1°15'42"N, 60°58'04"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2315 (BHCB, INPA, NY, SP); estrada perdida, primeira campina após a guarita, margem esquerda, 1°28'25"N, 60°58'08"W, 76 m, 10 Oct 2011, N.F.O. Mota et al. 2339 (INPA); campina após a primeira bueira, margem direita, 1°25'17"N, 60°59'08"W, 63 m, 14 Oct 2011, N.F.O. Mota et al. 2378 (BHCB, INPA, NY, SP); grade do PPBio, L1 com N6, campina úmida, 1°29'11"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2398 (BHCB, INPA, NY, SP); na grade da PPBio, L1/N6, 1°29'18"N, 61°02'82"W, 12 Sep 2010, S.M. Costa et al. 708 (INPA, UEC); estrada Perdida, próximo a 2ª bueira, 1°16'48"N, 61°00'00"W, 16 Sep 2010, S.M. Costa et al. 757 (INPA, UEC); área alagada, na margem da estrada Perdida, solo argiloso, 1°24'44"N, 60°13'00"W, 63 m, 20 July 2010, T.D.M. Barbosa et al. 1217 (INPA, UEC).

13. ***Xyris subuniflora*** Malme, Rec. Trav. Bot. Neerl. 9: 129. 1912.

(Figures 3 M, 6 A–D, 7 R)

Description, Annual, terrestrial or aquatic, clump-forming. Base of the plant flattened, soft, without mucilage. Leaves 1–5.5 cm long, distichous, erect to spreading flabellate, not twisted; sheaths 1/2 or less than the leaf length, gradually dilating toward the base, smooth, without prominet nerves, pale, reddish to pink, margins scarious, glabrous, ligulate; lamina 0.5–3.8 cm × 0.2–0.5 mm, flattened, filiform, smooth, nerves not evident, margins undifferentiated, glabrous, apex incurved-acute. Spathe equaling the leaves length. Peduncle 1–12 cm long, 0.1–0.3 mm wide, terete, filiform, without distal dilatation, not twisted, glabrous, smooth to papillose, ecostate. Spike 1–2-flowered, 3–4 × 1–2 mm, narrowly ellipsoid, castaneous to dark brown. Sterile bracts 4, the lower ones smaller than the bracts; the uppermost lanceolate, slightly keeled, maculate, margins indifferenciated, glabrous, apex acute. Fertile bracts 3–4 × 0.6–0.8 mm, lanceolate, naviculate, margins glabrous, indifferenciated, concolor, apex acute; macula along the distal 1/2 of the fertile bract, lanceolate, green, castaneous, becoming reddiish wih age. Lateral sepals 2.5–3 mm, narrowly triangular, connate on more than its half portion, lobes asymmetric, incluse, not keelte; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 1.5 mm long; anther 1 mm long, onlong; style 2.8 mm long, branches 0.7 mm long; ovary 2 mm long, unilocular, basal placentation. Capsule 1.8–2.0 mm long, broadly ellipsoid. Seeds 0.4–0.5 × 0.1–0.2 mm, broadly ellipsoid, castaneous, apex apiculate; striae 5–7 per 100 μm of seed width in the midle portion, prominent, twisted toward the apex, sinuous, cross-lines absent.

Morphological comments, Xyris subuniflora is one of the smallest species of the genus known so far, ranging from 1–12 cm high in the study area. It can be distinguished by its leaves and peduncles are filiform, spikes 1–2-flowered and the

sepals connate. Its tiny size and morphological peculiarities cited above makes *X. subuniflora* easily distinguished from the other species of the genus in the study area.

Distribution and habitat, Xyris subuniflora is common in lowland *compinaranas* in northern Brazil, Colombia and Surinam. In Brazil, it is known to occur in the states of Amazonas, Pará and Roraima. Plants of this species form dense clumps and are commonly observed in sympatry with *Abolboda minima* and *X. guianensis*, being frequently mixed with the latter in herbarium specimens.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, campinho, campina baixa no Rio Anauá, 0°34'57"N, 61°12'59"W, 31 July 2011, C.E. Zartman 8522 (INPA); início da estrada Perdida, 1°26'14"N, 60°58'49"W, 52 m, 13 Oct 2011, G.O. Silva et al. 96 (BHCB, INPA, SP); campina, estrada para Serra do Preto, brejo, 1°16'28"N, 61°00'33"W, 59 m, 23 Jan 2008, N.F.O. Mota et al. 1230 (BHCB, INPA, NY, SP); campina, estrada para Serra do Preto, brejo, 1°16'28"N, 61°00'33"W, 59 m, 23 Jan 2008, N.F.O. Mota et al. 1232 (BHCB, INPA, NY, SP); estrada Perdida, campina no final da estrada Perdida, solo arenoso com denso extrato graminoso, 1°15'42"N, 60°58'04"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2317 (BHCB, INPA, NY, SP); campina cerca de 1km depois da segunda bueira na estrada Perdida, solo arenoso exposto, 1°20'39"N, 60°58'43"W, 61 m, 23 Sep 2011, N.F.O. Mota et al. 2326 (BHCB, INPA, NY, SP); grade do PPBiodo PARNA Viruá. L1 com N6, campina úmida, 1°28'56"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2399 (BHCB, INPA, NY, SP); campina próxima ao galpão, próxima à primeira bueira, 1°25'34"N, 60°59'04"W, 57 m, 24 Oct 2011, N.F.O. Mota et al. 2438 (BHCB, INPA, NY, SP); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 798 (INPA, UEC); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N,

60°59'20"W, 21 Sep 2010, S.M. Costa et al. 799 (INPA, UEC); campinarana gramino-lenhosa, grade PPBIO (L4N4), 1°27'34"N, 61°01'57"W, 63 m, 27 July 2010, T.D.M. Barbosa et al. 1367 (INPA).

14. ***Xyris surinamensis*** Spreng., Tent. Suppl. Syst. Veg. Linn. 2. 1828.

(Figures 3 N, 6 E–I, 7 S)

Description, Perennial, terrestrial, clump-forming. Base of the plant bulbous, hard-fibrous, without mucilage. Leaves 9.5–38 cm long, spiral, erect to spreading, often twisted; sheaths 1/3–1/2 the leaf length, abruptly dilated at the base, verrucous to rugose, rare smooth, with sligthly prominet nerves, castaneous to reddish, margins reddish, densely rugose, long ciliate, eligulate; lamina 6–25.5 cm × 1.0–3.5 mm, flattened, smooth to rugose, pale-puncticulate, nerves strongly evident, margins incrassate, glabrous, apex incurved-acute to incurved-round. Spathe shorter or longer than the leaves length. Peduncle 15–42.5 cm long, 2.0–5.0 mm wide, flattened, without distal dilatation, twisted or not, glabrous, smooth to strongly rugose, 2-costate. Spike 12–20-flowered, 5–23 × 5–15 mm, ellipsoid, subglobous to broadly turbinate when dried, ovoid in fresh material, golden castaneous. Sterile bracts 18–22, the lower ones 1/3 of the fertile bracts; the uppermost obovate to oblong, not keeled, maculate, margins indifferenciated, glabrous, apex obtuse. Fertile bracts 9–10 × 4–5 mm, oblong to obovate, margins glabrous, indifferenciated, concolor, apex obtuse; macula along the distal 1/3 to 1/2 of the fertile bract, triangular, green to gray. Lateral sepals 5–7 mm, linear to linear-oblanceolate, asymmetric, free, shorter than the bracts, keel glabrous to villosulous; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 5 mm long; anther 2.5 mm long, oblong; style 12 mm long, branches 5 mm long; ovary 3.5 mm long, unilocar, with strong vestigial

septa, central placentation. Capsule 0.4–0.6 mm long, obovoid. Seeds 0.8–1.0 × 0.3–0.4 mm, cylindric-fusiform, pale to castaneous, apex acute to apiculate; striae 6–7 per 100 μm of seed width in the midle portion, prominent, straight, smooth, with thin cross-lines, not reticulate.

Morphological comments, Xyris surinamensis is easily recognized by leaves and peduncles distinctly flattened, strongly rugose and leaf sheaths margins long-ciliate. For further notes about morphological affinities, see comments under *X. subglabrata*.

Distribution and habitat, Xyris surinamensis is probably one of the most widespread species in northern South American, occurring in Brazil, Colombia, Guayanas and Venezuela. In Brazil, it occurs in the states of Amazonas, Pará and Roraima. In VNP it is widespread throughout the *campinaranas*.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, grade PPbio/ L1, 1°28'07"N, 61°00'27"W, 23 Sep 2011, E. Pessoa et al. 737 (INPA); estrada Perdida, campina aberta, 1°16'48"N, 61°00'00"W, 29 Nov 2006, F.A. Carvalho et al. 997 (INPA); estrada Perdida, campina arbustiva, 1°16'48"N, 61°00'00"W, 30 Nov 2006, F.A. Carvalho et al. 1016 (INPA); campinarana arbustiva, 1°21'59"N, 60°59'12"W, 55 m, 4 Dec 2009, F.N. Cabral 93 (INPA, NY); grade PPBio L03 T500, 1°48'67" S, 61°01'57"W, 15 Jan 2006, F.R.C. Costa et al.1527 (INPA); grade PPBio L04 T4500, 1°48'67" S, 61°01'57"W, 15 Jan 2006, F.R.C. Costa et al.1642 (INPA); grade PPBio L06, campina, 1°48'67" S, 61°01'57"W, 15 Jan 2006, F.R.C. Costa et al.1672 (INPA); grade PPBio L06 T2500, 1°48'67" S, 61°01'57"W, 15 Jan 2006, F.R.C. Costa et al.1677 (INPA); início da estrada Perdida, 1°26'14"N, 60°58'49"W, 52 m, 13 Oct 2011, G.O. Silva et al. 94 (BHCB, INPA, SP); campina aberta ao lado da estrada perdida, 1°24'49"N, 60°59'16"W, 14 Jan 2011, M.C.E. Amaral et al. 4 (INPA, NY); campina, 1°24'11"N, 60°59'09"W, 49 m, 22 Jan 2008,

N.F.O. Mota et al. 1234 (BHCB, INPA, NY, SP); campina, 1°24'11"N, 60°59'09"W, 49 m, 22 Jan 2008, N.F.O. Mota et al. 1237 (BHCB, INPA, NY, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2300 (BHCB, INPA, NY); campina no final da estrada Perdida, solo arenoso com denso extrato graminoso, 1°15'42"N, 60°58'04"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2314 (BHCB, INPA, NY); campina cerca de 1km depois da segunda bueira na estrada Perdida, solo arenoso coberto por denso extrato graminoso, 1°21'91"N, 60°58'47"W, 59 m, 23 Sep 2011, N.F.O. Mota et al. 2323 (BHCB, INPA, NY); campina após a primeira bueira, margem direita, 1°25'17"N, 60°59'08"W, 63 m, 14 Oct 2011, N.F.O. Mota et al. 2383 (BHCB, INPA, NY, SP); grade do PPBiodo PARNA Viruá. L1 com N6, Campina úmida, 1°28'56"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2401 (BHCB, INPA, SP); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 812 (INPA, UEC); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 814 (INPA, NY, UEC); estrada perdida, campinarna graminosa aberta, 1°16'48"N, 61°00'00"W, 1 Mar 2010, T.D.M. Barbosa et al. 1053 (INPA, UEC); área alagada, na margem da estrada Perdida, solo argiloso, 1°25'41"N, 60°58'58"W, 63 m, 18 July 2010, T.D.M. Barbosa et al. 1163 (INPA, NY, UEC); campinarana arbustiva, grade PPBIO, solo encharcado, 1°28'06"N, 61°00'25"W, 67 m, 24 July 2010, T.D.M. Barbosa et al. 1306 (INPA, UEC).

15. ***Xyris uleana var. angustifolia*** Lanj., Kew Bull. 1939: 562. 1939.

(Figures 3 O, 6 J–M, 7 T)

Description, Annual, terrestrial, solitary, rarely clump-forming. Base of the plant flattened, thin, without mucilage. Leaves 2.7–5.2 cm long, distichous, erect, not twisted; sheaths less than 1/2 the leaf length, gradually dilating toward the base, sparsely papillose to smooth, with strongly prominet nerves, pale to gold, margins scarious, glabrous, ligulate; lamina 1.3–5.5 cm × 0.3–0.5 mm, flattened, smooth, nerves evident, margins thin, glabrous, apex acute to incurved-acute. Spathe shorter than the leaves. Peduncle 3–13 cm long, 0.3–0.8 mm wide, terete, without distal dilatation, not twisted, glabrous, smooth, 2-costate. Spike 6–8-flowered, 3–5 × 1.8–4 mm, ovoid to subglobous, castaneous. Sterile bracts 4, the lower ones equal or longer than the fertile bracts, with excurrent apex; the uppermost ovate to elliptic, keeled, maculate, margins scarious, ciliate, apex obtuse. Fertile bracts 2.5–3 × 1.5–1.8 mm, oblong to obovate, margins ciliate, scarious, reddish, apex obtuse; macula along the distal 1/3 of the fertile bract, ovate to triangular, green to gray. Lateral sepals 2.2–3 mm, elliptic, strongly asymmetric, free to connate close to the base, shorter than the bracts, keel sparsely ciliate; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 0.8 mm long; anther 0.5 mm long, oblong; style 3.7 mm long, branches 1 mm long; ovary 1.2 mm long, unilocular, basal placentation. Capsule 1.0–1.5 mm long, obovoid. Seeds 0.3–0.4 × 0.2 mm, broadly ellipsoid, reddish to castaneous, apex apiculate; striae 6–7 per 100 μm of seed width in the midle portion, prominent, twisted, smooth to slightly sinuous, with thin cross-lines, not reticulate.

Morphological comments, Xyris uleana var. *angustifolia* are small plants, never larger than 13 cm long. If differs from *X. uleana* var. *uleana* by its narrower leaves, almost filiform (< 0.5 mm vs. 0.6–2.5 mm wide), and terete peduncle (vs. anciptal). These features approaches *X. uleana* var. *angustifolia* and *X. calderonii* Kral, L.B.Sm. &

Wand., known only from its type locality in Amazonas state, Brazil. *Xyris calderonii*, however, has shorter sepals (2–2.5 cm vs. 2.5–3.0 cm) and reticulate seeds (vs. not reticulate).

Distribution and habitat, This taxon is known from northern Brazil, Guayana and Venezuela. In Brazil, it occurs in the states of Amazonas, Pará and Roraima, occurring savannas with densely graminoid topping. It the VNP, it is rarely observed in sympatry with *Xyris uleana var. uleana*.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, estrada Perdida, lago na margem, após a segunda bueira, 1°22'02"N, 60°58'54"W, 17 Jan 2011, M.C.E. Amaral et al. 39 (INPA); campina próxima à primeira bueira na estrada Perdida, solo arenoso coberto por extrato graminoso, 1°25'15"N, 60°59'09"W, 63 m, 23 Sep 2011, N.F.O. Mota et al. 2327 (BHCB, INPA, NY); estrada Perdida, próximo a 2ª bueira, 1°16'48"N, 61°00'00"W, 16 Sep 2010, S.M. Costa et al. 753 (INPA, UEC).

16. ***Xyris uleana var. uleana*** Malme, Repert. Spec. Nov. Regni Veg. 3: 113. 1906.

(Figures 3 P, 6 N–Q, 7 U)

Description, Annual, terrestrial or aquatic, clump-forming, rarely solitary. Base of the plant flattened, soft, without mucilage. Leaves 2-11.4 cm long, distichous, erect or spreading flabellate, not twisted; sheaths 1/2 or a little bit more the leaf length, gradually dilating toward the base, sparsely papillose to smooth, with strongly prominet nerves, reddish to brown, margins scarious, glabrous, eligulate; lamina 1–4.2 cm × 0.6–2.5 mm, strongly flattened, smooth, nerves evident, margins thin, glabrous, apex acute to incurved-acute. Spathe mostly shorter than the leaves. Peduncle (1.2–)3.5–26.2 cm long, 1.0–2.0 mm wide, ancipital, becoming flattened

towars the apex, not twisted to sligthly twisted, glabrous to scaberolous-ciliate, smooth, ecostate or with two lateral costae in each wing. Spike (5–)10–25-flowered, 2.6–10 × 1.1–3.6 mm, broadly to narrowly ovoid, castaneous. Sterile bracts 4, the lower ones distinctly longer than the fertile bracts, with excurrent apex; the uppermost ovate to elliptic, keeled, maculate, margins scarious, ciliate, apex obtuse. Fertile bracts 1.5–3.5 × 0.7–3 mm, broadly obovate to suborbicular, margins ciliate, scarious, reddish, apex obtuse; macula along the distal 1/3 of the fertile bract, ovate to triangular, green to gray. Lateral sepals 1.4–3 mm, elliptic-curved to obovate-curved, strongly asymmetric, free to connate close to the base, shorter than the bracts, keel ciliate to ciliolate; corolla lobes broadly obovate; staminodia long-pennicillate, branches not flat; stamens 0.8 mm long; anther 0.5 mm long, oblong; style 3 mm long, branches 0.6 mm long; ovary 1.5 mm long, unilocular, basal placentation. Capsule 1.5–3.0 mm long, broadly obovoid. Seeds 0.5–0.7 × 0.3 mm, broadly ellipsoid, reddish to castaneous, apex apiculate; striae 4–5 per 100 μm of seed width in the midle portion, prominent, twisted at the apex, forming groups of moniliform and smooth striae, with few thin cross-lines, not reticulate.

Morphological comments, Xyris uleana var. *uleana* are delicate plants that rarely exceed 15 cm long. It has sterile bracts longer than the main axis of the spike, like in *X. cryptantha* and *X. involucrata*, that also occur in the study area. However, it differs from *X. cryptantha* by its anciptal peduncle (terete in *X. cryptantha*). *Xyris involucrata*, that also has anciptal peduncles, is easily differentiated from *X. uleana* var. *uleana* by its larger size (38–60 cm long vs. plants smaller that 15 cm in *X. uleana* var. *uleana*) and patent sterile bracts (erect in *X. uleana* var. *uleana*).

Distribution and habitat, X. uleana var. uleana occurs in open formations at low to high elevations in Brazil, Colombia, Guiana and Venezuela. In Brazil, this subspecies

occurs in the states of Amazonas, Goiás, Mato Grosso, Pará and Roraima. It is widespread in the *campinaranas* VNP.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, trilha de acesso à Grade do PPBio, L1 5000-N6, 1°29'12"N, 61°02'50"W, 47 m, 23 Sep 2011, A. Melo 917 (INPA, NY); campina próxima a buritizal, 1°15'40"N, 60°58'11"W, 55 m, 24 Jan 2008, N.F.O. Mota et al. 1224 (BHCB, INPA, SP); campina, estrada para Serra do Preto, brejo, 1°16'28"N, 61°00'33"W, 59 m, 23 Jan 2008, N.F.O. Mota et al. 1231 (BHCB, INPA, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2306 (BHCB, INPA, NY, SP); grade do PPBiodo PARNA Viruá. L1 com N6, campina alagada, 1°28'56"N, 61°02'50"W, 57 m, 17 Oct 2011, N.F.O. Mota et al. 2402 (BHCB, INPA, NY, SP); grade do PPBio do PARNA do Viruá, campina parcialmente alagada em L3, entre N1 e N2, 1°28'07"N, 61°00'27"W, 62 m, 23 Oct 2011, N.F.O. Mota et al. 2433 (INPA, SP); campina arbustiva, úmida L6 (1000), 1°26'30"N, 61°00'57"W, 71 m, 24 Oct 2011, N.F.O. Mota et al. 2440 (BHCB, INPA, NY); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 800 (INPA, UEC).

17. *Xyris sp. 1*

(Figures 3 Q, 6 R–V, 7 Q)

Description, Annual, terrestrial or aquatic, solitary, rarely clump-forming. Base of the plant flattened, without mucilage. Leaves 1.5–7 cm long, distichous, erect to spreading, usually not twisted; sheaths 1/3–1/2 the leaf length, gradually dilating toward the base, smooth, with prominent nerves, gold, pale to reddish, margins scarious, glabrous, eligulate; lamina 0.8–4.2 cm × 0.2–1.0 mm, flattened, smooth,

nerves evident, margins slightly incrassate, glabrous, apex acute. Spathe shorter or equaling the leaves length. Peduncle 7.5–32 cm long, 0.1–0.7 mm wide, terete to filiform, without distal dilatation, not twisted, glabrous, smooth, ecostate to 1-costulate. Spike 4–20-flowered, 3–30 × 1–4 mm, cylindric, golden castaneous. Sterile bracts 4, the lower ones smaller to equal than the bracts; the uppermost oblong to obovate, slightly keeled, maculate, margins indifferenciated, glabrous, apex obtuse. Fertile bracts 2.5–4 × 1.5–2 mm, obovate, margins glabrous, indifferenciated, concolor, apex obtuse to round; macula along the distal 1/2 to 2/3 of the fertile bract, ovate, green to gray. Lateral sepals 2–3 mm, elliptic-curved, asymmetric, free, shorter than the bracts, keel evenly ciliolate; corolla lobes obovate; staminodia long-pennicillate, branches not flat; stamens 1.2 mm long; anther 0.5 mm long, oblong; style 3.5 mm long, branches 1.3 mm long; ovary 1.2 mm long, unilocular, basal placentation. Capsule 2.0–3.0 mm long, broadly obovoid. Seeds 0.4–0.6 × 0.2 mm, ellipsoid, reddish to castaneous, apex apiculate; striae 6–7 per 100 μm of seed width in the midle portion, slightly prominent, twisted, smooth, with thin cross-lines, not reticulate.

Morphological comments, Plants of this species are usually solitary, seldom clump-forming, and are characterized by their golden hue, filiform peduncles, cylindrical spikes 3–7 times longer than wide, lateral sepals free with keel regularly ciliolate. It is probably a new taxon belonging to the *Xyris paraensis* complex, but further studies and a detailed inspection of the types of all varieties of this complex are necessary to confirm this hypothesis.

Distribution and habitat, After analyzing the samples from the herbaria studied, this morphotype apparently occurs in the states of Amazonas, Pará and Roraima, in Brazil, and Amazonas state, in Venezuela. *Xyris sp.1* is widespread in the *campinaranas* of

the study area, usually growing together with *Abolboda minima, Xyris subuniflora* and *X. mima*.

Specimens examined, **BRAZIL: Roraima:** Município Caracaraí, Parque Nacional do Viruá, estrada Perdida, campina aberta denominada localmente por "Duninhas", 1°16'48"N, 61°00'00"W, 1 Dec 2006, F.A. Carvalho et al. 2 (INPA); estrada Perdida, campina aberta, 1°16'48"N, 61°00'00"W, 1 Dec 2006, F.A. Carvalho et al. 1058 (INPA); campina na região das dunas, 1°15'40"N, 60°58'11"W, 55 m, 24 Jan 2008, N.F.O. Mota et al. 1225 (BHCB, INPA, SP); estrada Perdida, campina próxima à guarita do parque, campo úmido, 1°28'25"N, 60°58'08"W, 76 m, 22 Sep 2011, N.F.O. Mota et al. 2308 (BHCB, INPA, NY, SP); estrada Perdida, campina cerca de 1km depois da segunda bueira na estrada Perdida, solo arenoso exposto, 1°20'39"N, 60°58'43"W, 61 m, 23 Sep 2011, N.F.O. Mota et al. 2324 (BHCB, INPA, NY, SP); campina próxima ao galpão, próxima à primeira bueira, 1°25'34"N, 60°59'04"W, 57 m, 24 Oct 2011, N.F.O. Mota et al. 2434 (BHCB, INPA, NY, SP); campina próxima ao galpão, próxima à primeira bueira, 1°25'34"N, 60°59'04"W, 57 m, 24 Oct 2011, N.F.O. Mota et al. 2436 (BHCB, INPA, NY, SP); estrada Perdida, entre a 1ª e 2ª bueiras, 1°16'48"N, 61°00'00"W, 14 Sep 2010, S.M. Costa et al. 730 (INPA, NY, UEC); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°19'51"N, 60°59'00"W, 20 Sep 2010, S.M. Costa et al. 782 (INPA, UEC); estrada Perdida, após a 3ª bueira próximo ao segundo igarapé, 1°16'46"N, 60°59'20"W, 21 Sep 2010, S.M. Costa et al. 796 (INPA, UEC).

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TABLE 1. Comparative characters of the seeds of *Xyris* species occurring in the Viruá National Park. Acronyms: F - with thin cross-lines, not reticulate; PR - with prominent and evenly distributed cross-lines, reticulate; FR – with thin and evenly distributed cross-lines, reticulate; A – cross-lines absent.

Species	Length (mm)	Shape	Apex	Type of striae	Cross-line
Xyris cryptantha	0.4–0.5	ovoid to ellipsoid	apiculate	sinuous	F
X. dilatatiscapa	0.5–0.7	cylindric-ellipsoid to obovoid	apiculate	smooth	PR
X. fallax	1.3–1.5	cylindric-fusiform, angulate	acute	sinuous	A
X. guianensis	0.3–0.5	broadly ellipsoid to obovoid	apiculate	sinuous	A
X. involucrata	0.5–0.7	ellipsoid-cylindric	apiculate	sinuous	F
X. jupicai	0.5–0.8	ellipsoid	apiculate	sinuous	PR
X. macrocephala	0.6–0.7	ellipsoid	apiculate	moniliform	FR

X. malmeana	0.4	ellipsoid	apiculate	smooth	F
X. mima	1.0–1.1	ellipsoid to obovoid	acute with coma of bristles	moniliform	A
X. paraensis	0.7–0.8	ellipsoid	strongly apiculate	moniliform and smooth	A
X. savanensis	0.4–0.5	broadly ellipsoid to ovoid	acute	moniliform and sinuous	A
X. subglabrata	0.6–0.7	cylindric-fusiform	apiculate	smooth to sinuous	F
X. subuniflora	0.4–0.5	broadly ellipsoid	apiculate	sinuous	A
X. surinamensis	0.8–1.0	cylindric-fusiform	acute to apiculate	smooth	F
X. uleana var. angustifolia	0.3–0.4	broadly ellipsoid	apiculate	smooth to sinous	F
X. uleana var. uleana	0.5–0.7	broadly ellipsoid	apiculate	moniliform and smooth	F
Xyris sp.1	0.4–0.6	ellipsoid	apiculate	smooth	F

TABLE 2. Comparative characters of the seeds of *Xyris connosepala* Lanj. & Lindeman and *Xyris guianensis* Steud.

Species	Length	Shape	Apex	Type of striae	Cross-lines	Color
Xyris connosepala	≤ 0.5	ellipsoid	apiculate	sinuous	absent	castaneous
X. guianensis	≤ 0.5	broadly ellipsoid to obovoid	apiculate	sinuous	absent	castaneous


A
B
C
D
E

FIGURE 1 Aerial photographs of vegetation types in Viruá National Park **A** Open vegetation, white sand savanna – mosaic of *campinaranas* - covering the Viruá Megafan **B** *Mauritia flexuosa* dominated communities ("buritizal"), tributary Anauá, southern sector of the VNP **C** Paleochannel inserted into a mosaic of *campinaranas* in Viruá Megafan. In the background, view of Serra do Preto **D** "Várzea" forests with small sandy beaches in Anauá river, southern limit of VNP **E** Aquatic vegetation in the small tributary "igarapé Preto". Photographs by: **A** Bruno Mendonça **B–D** Antônio Iaccovazo **E** Rogário Gribel. Courtesy of ICMBio.



Figure 2.

FIGURE 2 Species of Abolboda recorded in the Viruá National Park **A** *Abolboda americana* (N.F.O. Mota et al. 2343) **B** *A. macrostachya* (C.T. Pedrollo et al. 143) **C** *A. minima* (N.F.O Mota and P.L. Viana 2325) **D** *A. pulchella* (S.M. Costa and T.D.M. Barbosa 921)

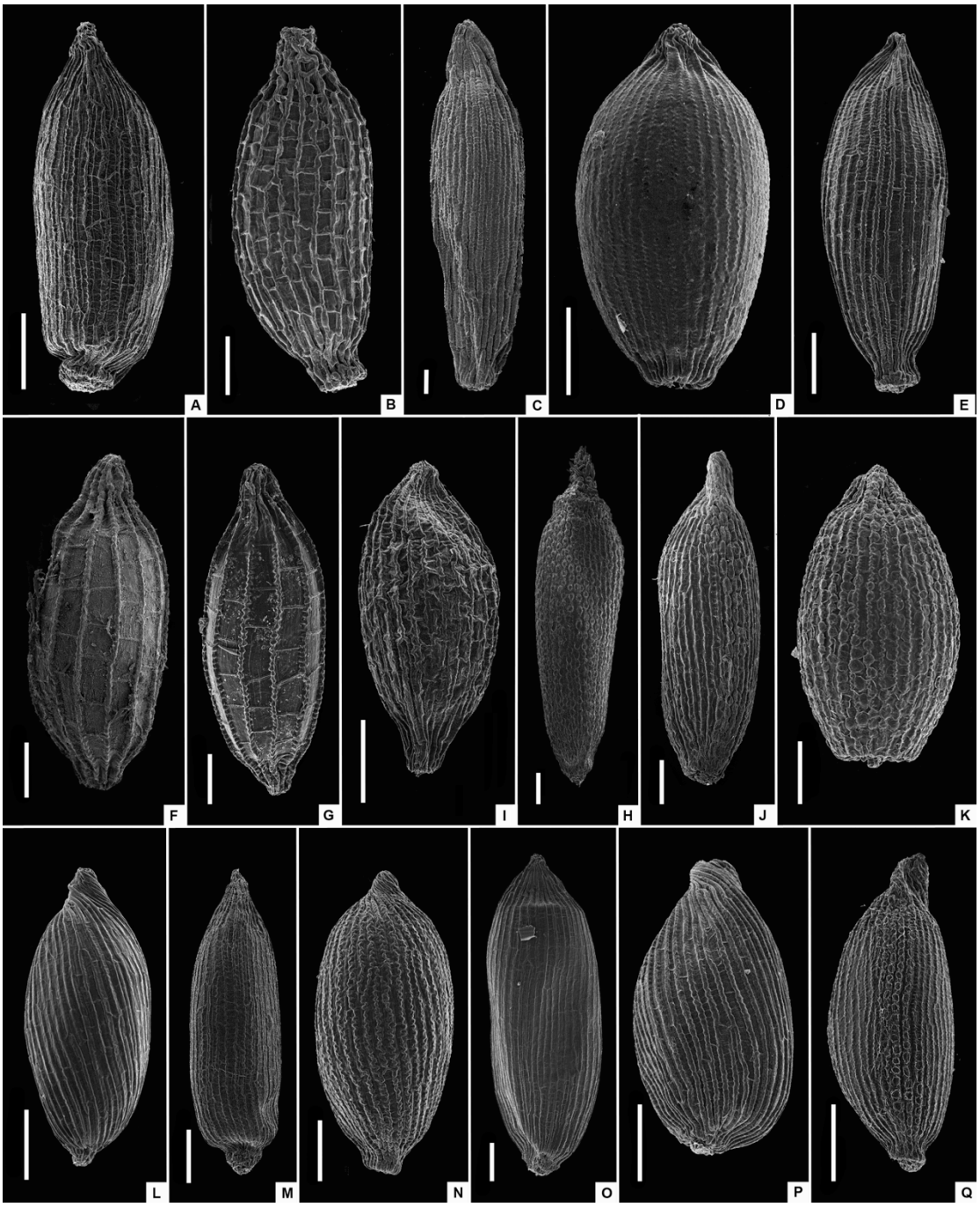


Figure 3.

FIGURE 3 SEM images of *Xyris'* seeds from Viruá National Park, scale bars 100 μm **A** *Xyris cryptantha* (N.F.O. Mota et al. 2316) **B** *X. dilatatiscapa* (N.F.O. Mota et al. 2344) **C** *X. fallax* (N.F.O. Mota et al. 2305) **D** *X. guianensis* (N.F.O. Mota et al. 2397) **E** *X. involucrata* (N.F.O. Mota et al. 2318) **F** *X. jupicai* (N.F.O. Mota et al. 2311) **G** *X. macrocephala* (N.F.O. Mota et al. 2441) **H** *X. malmeana* (N.F.O. Mota et al. 2310) **I** *X. mima* (N.F.O. Mota et al. 2400) **J** *X. paraensis* (N.F.O. Mota et al. 2308) **K** *X. savanensis* (N.F.O. Mota et al. 2320) **L** *X. subglabrata* (N.F.O. Mota et al. 2315) **M** *X. subuniflora* (N.F.O. Mota et al. 2399) **N** *X. surinamensis* (N.F.O. Mota et al. 2323) **O** *X. uleana var. angustifolia* (N.F.O. Mota et al. 2327) **P** *X. uleana var. uleana* (N.F.O. Mota et al. 2402) **Q** *Xyris sp.1* (N.F.O. Mota et al. 2324)

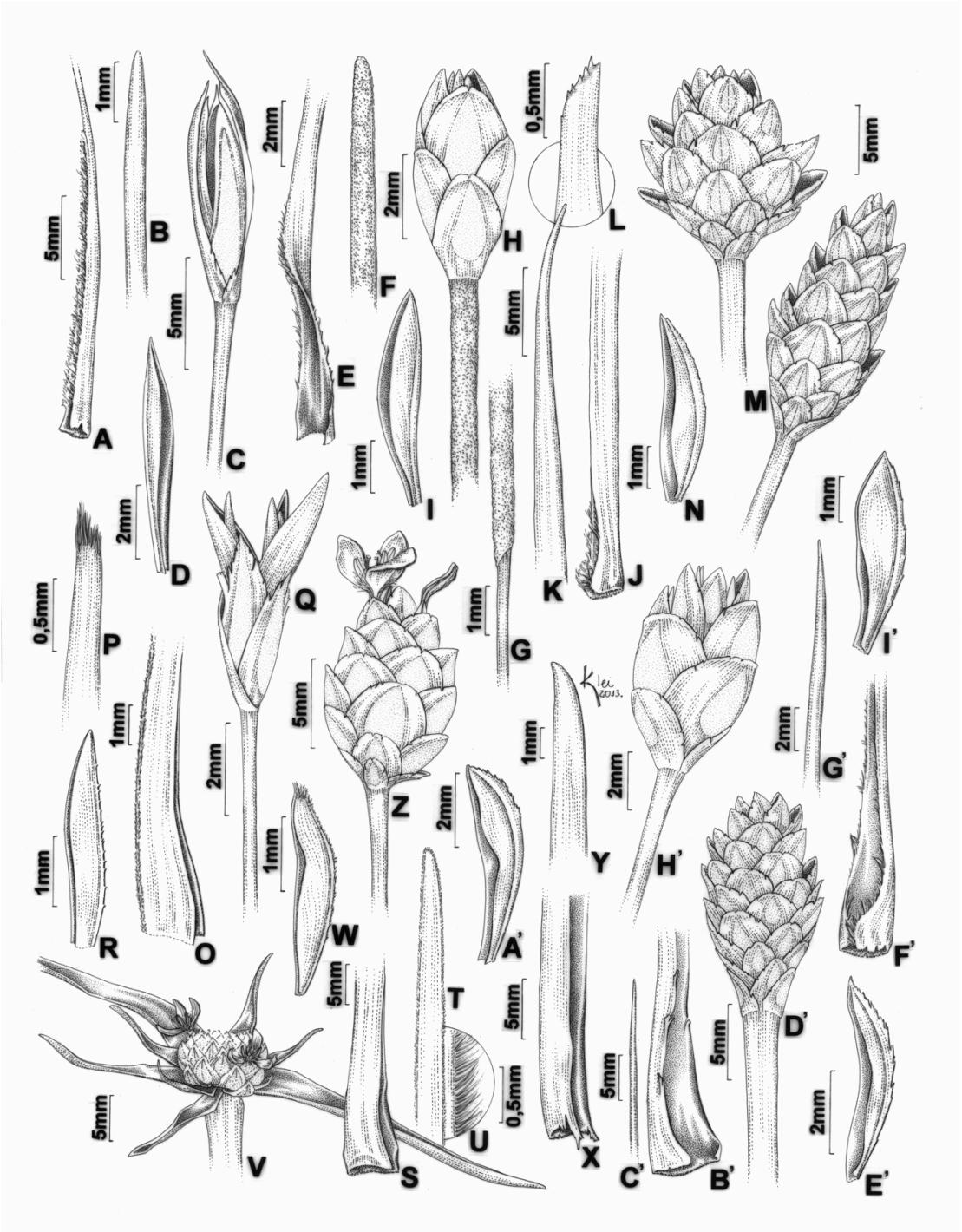

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Klen 2013.

Figure 4.

FIGURE 4 **A–D** *Xyris cryptantha* **A** Leaf sheath **B** Leaf apex **C** Spike **D** Lateral sepal (N.F.O. Mota et al. 2316) **E–I** *X. dilatatiscapa* **E** Leaf sheath **F** Leaf apex **G** Detail of the distal dilatation of the peduncle (with papillose to undulate-rugose surface) **H** Spike **I** Lateral sepal (N.F.O. Mota et al. 2344) **J–N** *X. fallax* **J** Leaf sheath **K** Leaf apex **L** Leaf apex, minutely scabrociliate at the tip **M** Spikes, the upper, morphotype ovoid, shorter than 2 cm (N.F.O. Mota et al. 2430), the lower, morphotype ellipsoid to cylindrical, longer than 2 cm (N.F.O. Mota et al. 2341) **N** Lateral sepal (other details from N.F.O. Mota et al. 2341) **O–R** *X. guianensis* **O** Leaf sheath **P** Leaf apex with short tricomes **Q** Spike showing exert lateral sepals **R** Lateral sepal (N.F.O. Mota et al. 2397) **S–W** *X. involucrata* **S** Leaf sheath **T** Leaf apex **U** detail of margins densely ciliate **V** Multi-flowered spike with long patent sterile bracts **W** Lateral sepal (N.F.O. Mota et al. 2318) **X–A'** *X. jupicai* **X** Leaf sheath **Y** Leaf apex **Z** Spike **A'** Lateral sepal (N.F.O. Mota et al. 2311) **B'–E'** *X. macrocephala* **B'** Leaf sheath **C'** Leaf apex **D'** Spike **E'** Lateral sepal (N.F.O. Mota et al. 2416) **F'–I'** *X. malmeana* **F'** Leaf sheath **G'** Leaf apex **H'** Spike **I'** Lateral sepal (N.F.O. Mota et al. 2310)

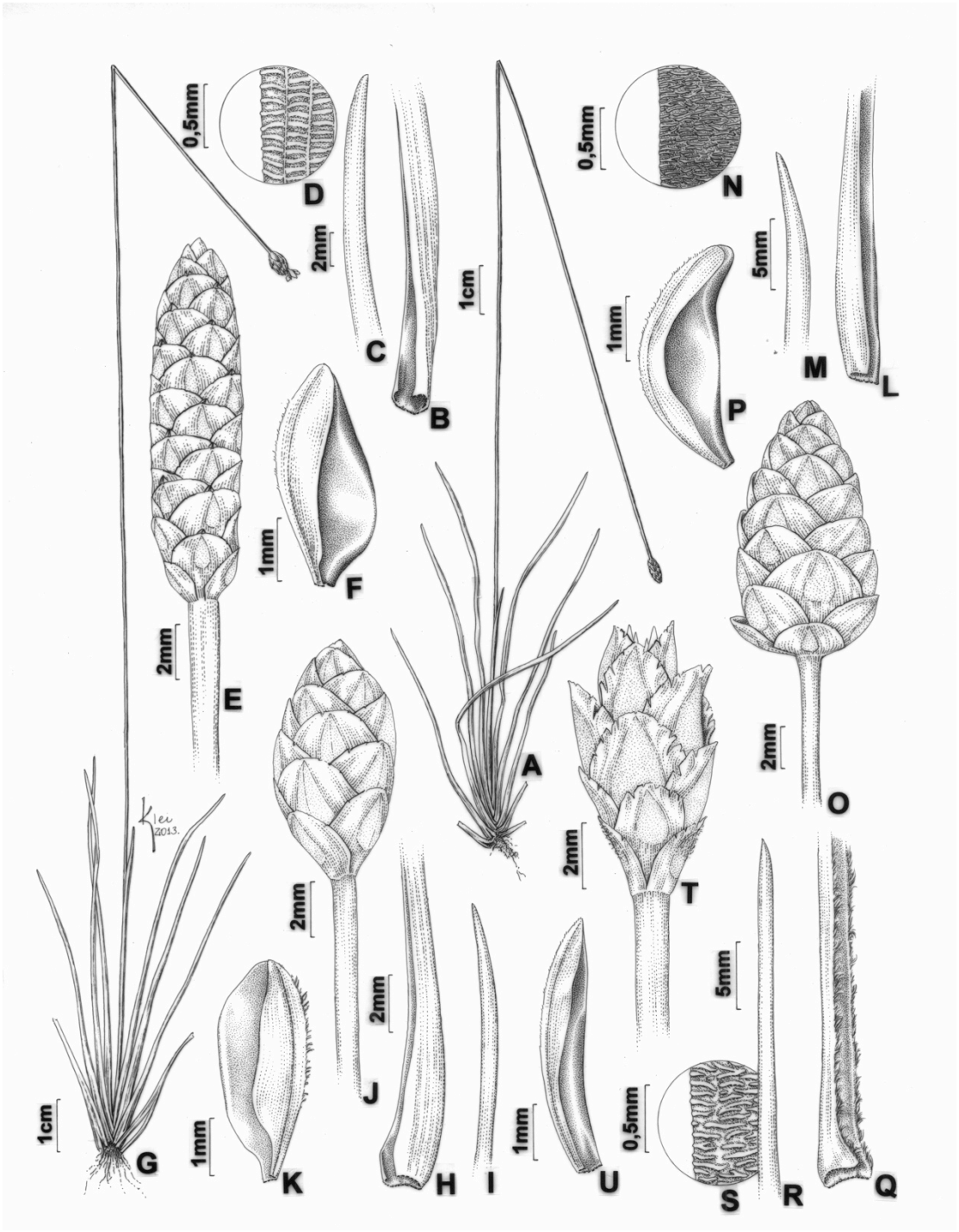

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Figure 5.

FIGURE 5 **A–F** *Xyris mima* **A** Habit **B** Leaf sheath **C** Leaf apex **D** Detail of undulate-rugose leaf surface **E** Spike **F** Lateral sepal (N.F.O. Mota et al. 2312) **G–K** *X. paraensis* **G** Habit **H** Leaf sheath **I** Leaf apex **J** Spike **K** Lateral sepal (N.F.O. Mota et al. 2422) **L–P** *X. savanensis* **L** Leaf sheath **M** Leaf apex **N** Detail of rugose leaf surface **O** Spike **P** Lateral sepal (N.F.O. Mota et al. 2302) **Q–U** *X. subglabrata* **Q** Leaf sheath **R** Leaf apex **S** Detail of rugose leaf surface **T** Spike **U** Lateral sepal (G.O. Silva et al. 97)

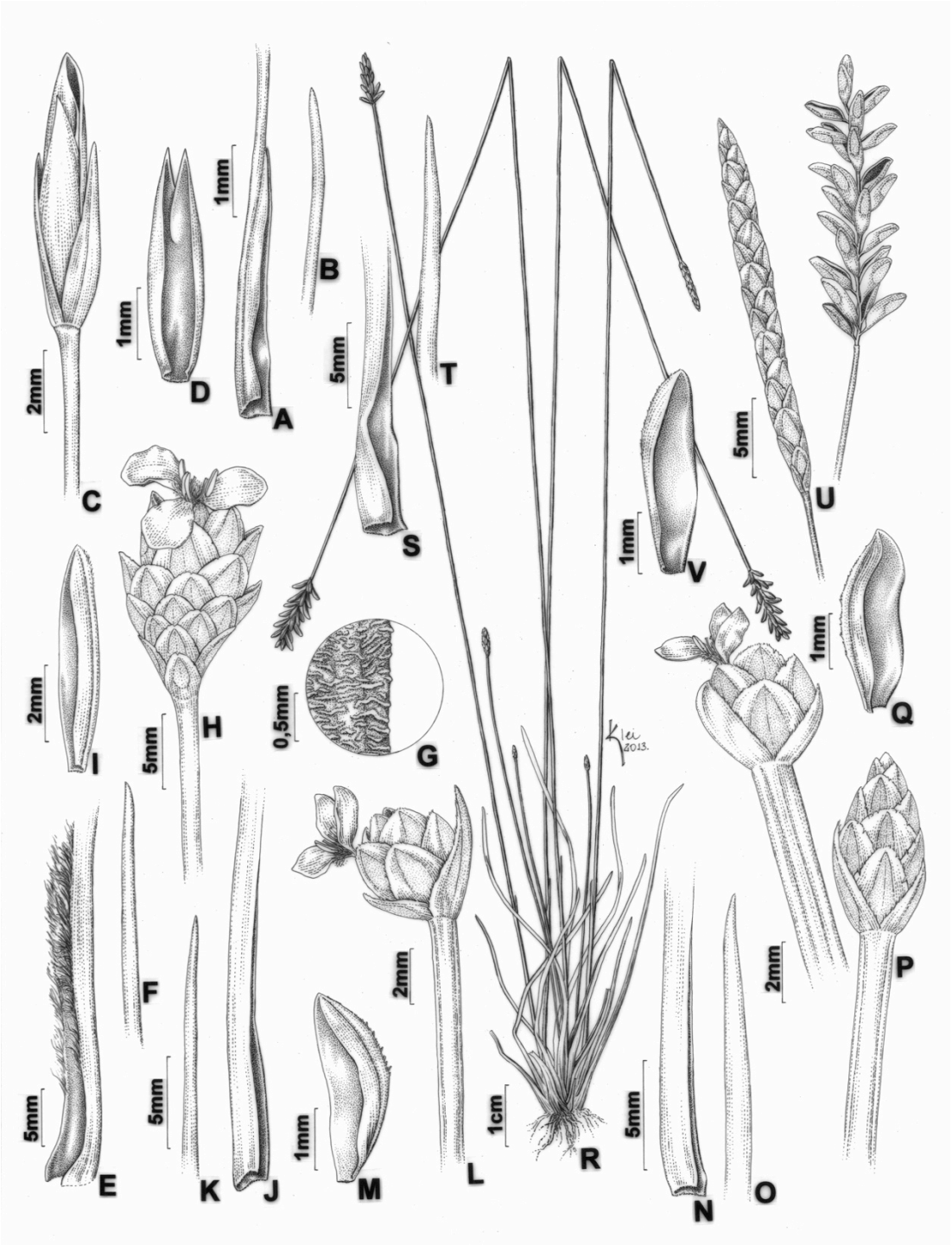

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Klei 2013.

Figure 6.

FIGURE 6 **A–D** *Xyris subuniflora* **A** Leaf sheath **B** Leaf apex **C** Spike **D** Lateral sepals connate at the base (N.F.O. Mota et al. 2399) **E–I** *X. surinamensis* **E** Leaf sheath **F** Leaf apex **G** Detail of rugose leaf surface **H** Spike **I** Lateral sepal (N.F.O. Mota et al. 2300) **J–M** X. *uleana* var. *angustifolia* **J** Leaf sheath **K** Leaf apex **L** Spike **M** Lateral sepal (N.F.O. Mota et al. 2327) **N–Q** *X. uleana* var. *uleana* **N** Leaf sheath **O** Leaf apex **P** Different shapes of spikes, the upper globous (N.F.O. Mota et al. 2306), the lowest ovoid (N.F.O. Mota et al. 2440) **Q** Lateral sepal (leaves details from N.F.O. Mota et al. 2440 and sepal details from N.F.O. Mota et al. 2306) **R–V** *Xyris sp.1* **R** Habit **S** Leaf sheath **T** Leaf apex **U** Spikes, the upper a senescent spike with persistent bracts, the lowest a flowering spike **V** Lateral sepal (N.F.O. Mota et al. 2324)

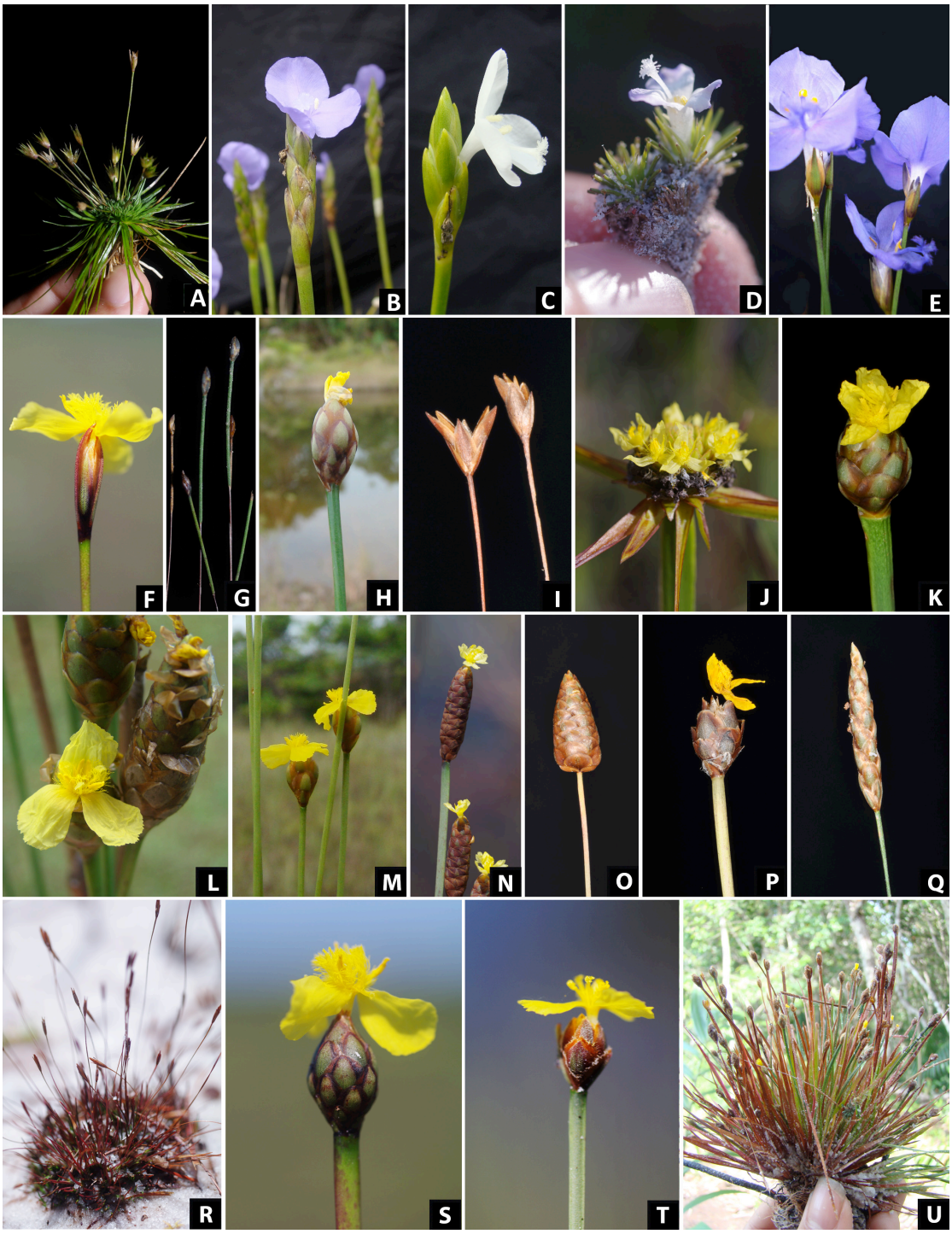


Figure 7.

FIGURE 7 Photograph of Xyridaceae species in Viruá National Park, Brazil **A** *Abolboda americana* **B–C** *A. macrostachya* **D** *A. minima* **E** *A. pulchella* **F** *Xyris cryptantha* **G** *X. dilatatiscapa* **H** *X. fallax* **I** *X. guianensis* **J** *X. involucrata* **K** *X. jupicai* **L** *X. macrocephala* **M** *X. malmeana* **N** *X. mima* **O** *X. savanensis* **P** *X. subglabrata* **Q** *Xyris sp.1* **R** *X. subuniflora* **S** *X. surinamensis* **T** *X. uleana var. angustifolia* **U** *X. uleana var. uleana*. Photographs by P.L.Viana (A, D, F, G, J, N, R, T) and N.F.O. Mota (B–C, H–I, K–M, O–Q, S, U) S.M. Costa and T.D.M. Barbosa (E)

CONSIDERAÇÕES FINAIS

A lacuna sobre o conhecimento da filogenia em Xyridaceae e da classificação infragenérica do gênero *Xyris*, proposta há um século, serviu como ponto inicial desta investigação científica. A evolução das Xyridaceae, bem como das Comelinídeas, sempre representou um ponto obscuro no entendimento da evolução das monocotiledôneas. Apesar do crescente número de trabalhos envolvendo a família, como estudos de biologia floral, germinação, ontogenia, anatomia, sistemática e estudos florísticos, a classificação da família, bem como a classificação infragenérica do gênero *Xyris* se apresentavam desatualizadas, requerendo o estudo da filogenia da família para melhor delimitação e classificação infragenérica deste gênero .

Este estudo representa um grande avanço no entendimento das relações evolutivas dentro do gênero *Xyris*, o maior da família, e lança questões para futuros estudos em Xyridaceae e nas famílias relacionadas. A tentativa de reconhecimento de linhagens e a busca de sinapomorfias trouxe um novo olhar para o gênero, bem como para as demais Xyridaceae. No entanto, para compreender a evolução de qualquer grupo de planta ou ser vivo, seja usando dados morfológicos, moleculares ou ecológicos é de suma importância o conhecimento destes organismos em seu ambiente natural.

Uma árvore filogenética sem o conhecimento prévio das espécies e de toda sua história é apenas um conjunto de ramos interligados entre si. O reconhecimento de padrões naturais e sua interpretação num contexto evolutivo só faz sentido se contextualizado com uma bagagem de informações gerais sobre os táxons envolvidos (morfologia, anatomia, ecologia, distribuição geográfica), proporcionadas por

observações *in loco*, extensa busca em literatura e estudo profundo de coleções em herbários.

Desta maneira, o esforço amostral apresentado para a filogenia do gênero *Xyris* foi o ponto crucial deste trabalho. Vários padrões morfológicos e geográficos inferidos a partir de observações em campo, foram confirmados pela filogenia baseada em dados moleculares. Mesmo com baixos suportes de muitos clados, a hipótese filogenética apresentada representa um importante avanço na interpretação da evolução do gênero.

As três secções do gênero foram amostradas nesta primeira filogenia, com ênfase nas *Xyris* Neotropicais, principalmente *Xyris* seção *Nematopus*. O gênero é monofilético, sendo as espécies Neotropicais um clado com elevado suporte, irmão das *Xyris* Australianas. *Xyris* seção *Pomatoxyris* foi recuperada, porém apenas duas amostras desta seção foram incluídas nesta filogenia, sendo necessária uma melhor amostragem para confirmar tal resultado. A natureza de *Xyris* seção *Xyris* encontrado no presente estudo requer maior investigação, sendo necessária a inclusão de mais espécies da África, Ásia e Austrália. *Xyris* seção *Nematopus* se mostrou monofilética. Nesta seção, destacaram-se sete clados, para os quais foram reconhecidos padrões morfológicos e/ou geográficos. Caracteres morfológicos historicamente utilizados na circunscrição da seção (tipo de placenta) e também no reconhecimento de alguns grupos de espécies (conação das sépalas laterais) foram avaliados e se mostraram homoplásicos, no entanto foram úteis para o reconhecimento de alguns clados.

Como consequência indireta da riqueza de amostragem, marcado por intenso trabalho de campo, floras encontram-se em andamento e algumas já foram concluídas, como a

flora do Parque Nacional do Viruá, apresentada no capítulo 2. Neste estudo foram encontradas 17 espécies de *Xyris* e quatro de *Abolboda*, sendo muitos registros novos para o estado de Roraima e um novo registro para o Brasil. Esta flora, apesar de restrita a uma pequena área do domínio Amazônico, trata-se do primeiro tratamento das Xyridaceae para a Amazônia brasileira, o segundo centro de diversidade da família.

Como ações futuras, devemos destacar a busca de mais marcadores moleculares informativos (nucleares), a finalização da matriz morfológica que encontra-se em andamento, bem como a expansão da área amostral com foco nas espécies amazônicas, africanas, asiáticas e australianas.

Espera-se que, a partir deste ponto, as lacunas de amostragem e diretrizes para filogenias futuras possam ser avaliadas de forma mais objetiva, fornecendo suporte para uma filogenia mais abrangente do gênero *Xyris*. Este é apenas o primeiro passo na classificação da família, bem como seus gêneros a luz da filogenética.