UNIVERSIDADE DE BRASÍLIA
Instituto de Ciências Biológicas
Programa de Pós-Graduação em Botânica

Sistemática e Filogenia da subtribo Praxelinae R.M.King & H.Rob. (Asteraceae, Eupatorieae)

Rogério Neves Ribeiro

Orientadora: **Dra. Carolyn Elinore Barnes Proença**

Co-orientadora: **Dra. Vanessa Lopes Rivera**

Praxelis scaturicola Neves Ribeiro & V.L.Rivera

Brasília

Novembro, 2023

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Rogério Neves Ribeiro

Sistemática e Filogenia da subtribo Praxelinae R.M. King & H. Rob. (Asteraceae, Eupatorieae)

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UNB **(Suplente)**

Brasília, Novembro - 2023

Foi o tempo que dedicaste a tua rosa que a fez tão importante .....

Antoine de Saint – Exupéry

***Chromolaena pseudinsignis* R.M.King & H.Rob.**

“Dedico esta tese ao meu pai Antônio Neves Ribeiro (em memória) e à minha mãe Alcides Bicudo da Rocha Ribeiro”

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RESUMO GERAL: Eupatorieae possui 2200 espécies agrupadas em 182 gêneros pertencentes a 20 subtribos. Dentre as 20 subtribos, *Praxelinae* configura-se como a segunda maior em número de espécies, com cerca de 193 espécies agrupadas em sete gêneros: *Praxelis, Chromolaena, Eupatoriopsis, Lomatozona, Praxeliopsis, Eitenia* e *Osmiopsis.* Exceto por *Osmiopsis*, os demais gêneros possuem representantes no Brasil, principalmente no Cerrado. A subtribo Praxelinae é considerada monofilética, entretanto, as relações evolutivas entre os gêneros ainda são incertas. Tendo em vista, que num estudo publicado em 2016, foram amostrados somente 57 % dos gêneros e 19 % das espécies de Praxelinae, há necessidade de mais estudos por meio de uma maior amostragem das espécies da subtribo. Desta forma, buscamos: i) Reconstruir a filogenia da subtribo Praxelinae com todos os gêneros circunscritos; ii) Apresentar novidades nomenclaturais em *Praxelis*; iii) Confirmar a inclusão dos gêneros circuncritos em Praxelinae baseado em morfologia utilizando ferramentas moleculares. Como resultados, apresentamos três manuscritos em forma de capítulo, os quais estão de acordo com as normas dos periódicos em que serão ou foram publicados. O primeiro capítulo corresponde à filogenia da subtribo Praxelinae. Um total de 32 espécies foram analisadas, sendo que foram obtidas dez novas sequências nucleares e/ou plastidiais (ITS e *ndh*F), amostrando assim todos os gêneros, bem como as suas espécies tipos. Apresentamos no segundo capítulo um manuscrito já publicado que inclui a descrição de uma espécie nova de *Praxelis* e uma nova sinonimização em *P. capillaris*, bem como o reconhecimento da sinonimização prévia de *P. grandiflora* em *P. kleinioides* desconsiderada pela Flora e Funga do Brasil. Por fim, o terceiro capítulo, buscamos investigar a origem de *Osmiopsis plumieri*, discutir a incongruência encontrada entre a topologia da árvore nuclear e de cloroplasto e revisar sua posição taxonômica.

Palavras-Chave: Cerrado, Chromolaena, Compositae, Endemismo, Eupatorium.

INTRODUÇÃO GERAL

Asteraceae (Compositae) Bercht. & J. Presl é a maior família entre as angiospermas; dividida em 16 subfamílias, conta com cerca de 1.600 gêneros e 25.000 espécies, agrupadas em 50 tribos, e distribuídas amplamente em todos continentes, exceto o Antártico (Funk et al., 2009; Panero et al., 2014; Panero & Crozier, 2016; Mandel et al., 2019; Susanna et al., 2020). A família pode ser reconhecida por apresentar inflorescência do tipo capítulo, cálice modificado em pápus, androceu sinântero, estilete bífido, e ovário ínfero, bicarpelar, unilocular, com um único óvulo de placentação basal (Roque & Bautista, 2008; Roque et al., 2017). Além de ser uma das maiores famílias entre as angiospermas, em número de espécies, Asteraceae destaca-se economicamente (Funk et al., 2009), dado que muitas espécies são cultivadas como apícolas, aromáticas, medicinais (arnica, carqueja), ornamentais, oleaginosas (girassol), inseticidas e comestíveis (alface, alcachofra) (Beretta et al., 2008). Além disso, temos a *Stevia rebaudiana* (Bertoni) Bertoni usada como adoçante, a *Lomatozona artemisiifolia* Baker com potencial inseticida.

A família Asteraceae é monofilética, e situa-se no clado das Asterideas, na ordem Asterales, tendo como sinapormofias: corola com prefloração valvar; apresentação secundária do pólen; e substância de reserva inulina APG IV (2016); entretanto, grande parte de suas infracategorias precisam ser redelimitadas (Funk *et al.* 2009; Mandel *et al*. 2019 e Sussana *et al*. 2020). A classificação proposta por Funk *et al.* (2009) e atualizada por Susanna *et al*. (2020) para Asteraceae, há dois clados, um denominado de não Asteroideae e outro de Asteroideae os quais englobam 16 subfamílias e 50 tribos. As não-Asteroideae circunscrevem 15 subfamílias e 30 tribos, as quais possuem folhas geralmente alternas, maiores variação de formas da corola com lóbulos geralmente mais longos do que largos e apresentam ramos com áreas estigmáticas ocupando toda a face interna dos ramos, e com número básico cromossômico X= 9 ou 10 (Funk *et al.* 2009; Susanna *et al.*, 2020). Já a subfamília Asteroideae compreende 20 tribos reconhecidas pelas folhas geralmente opostas, flores do disco comumente actinomórficas com lóbulos tão longos quanto largos, superfície estigmática distribuída em duas linhas na face interna dos ramos do estilete, e com número básico cromossômico X= 9, 10 ou X= 19 (Funk *et al.* 2009, Susanna *et al*. 2020).

Das 20 tribos reportadas para a subfamília Asteroideae, 13 pertencem à aliança Heliantheae (Susanna *et al*. 2020), tendo como sinapomorfia as cipselas enegrecidas graças à presença de uma camada de fitomelanina (Panero 2007). Dentre essas 13 tribos, Eupatorieae Cass. é uma das mais derivadas e a mais rica em número de espécies, conta com cerca de 2.200 espécies reunidas em 182 gêneros (Robinson *et al.* 2009; Susanna *et al*. 2020), distribuídas principalmente no hemisfério

ocidental, com alguns gêneros pantropicais, muitos representantes na América do Norte, e poucas espécies nativas no velho mundo (King & Robinson 1987; Bremer 1994; Funk *et al.* 2009). A tribo Eupatorieae foi descrita por Cassini (1819), e dentro de 12 anos surgiu o primeiro sistema de classificação subtribal, sendo a tribo subdividida em quatro subtribos: Alomieae, Agerateae, Eupatorieae, e Tussilaginae (Lessing 1831). Em seguida, veio outra mudança (de Candolle 1836) que dividiu Eupatorieaceae (a tribo era assim denominada na época), em duas subtribos: Eupatorieae e Tussilagineae. O sistema de classificação atualmente aceito para a tribo foi proposto por King & Robinson (1987), no qual os gêneros da tribo Eupatorieae estão reunidos em 20 subtribos (Rivera *et al*. 2016; Susanna *et al*. 2020). As espécies circunscritas em Eupatorieae incluem plantas usualmente herbáceas ou arbustivas, eretas, ou lianescentes, de folhas opostas, capítulos discoides, corola branca ou lilás, nunca amarelas, ramos do estilete longos, geralmente clavados e com apêndices frequentemente coloridos (Bremer 1994, Roque *et al*. 2017).

Dentre as subtribos circunscritas em Eupatorieae, a subtribo Praxelinae, com cerca de 193 espécies, é a segunda mais rica (sendo superada por Mikaniinae com cerca de 400 espécies), e circuncreve os gêneros *Praxelis* Cass., *Chromolaena* DC., *Eupatoriopsis* Hieron., *Lomatozona* Baker, *Praxeliopsis* G.M. Barroso, *Eitenia* R. M. King & H. Robinson e *Osmiopsis* R.M. King & H.Robinson (Hind & Robinson, 2007; Susanna *et al*. 2020). *Chromolaena* foi inicialmente descrita por de Candolle (1836), com base em *C. horminoides* DC.; o nome do gênero se origina do grego *chroma (= color) e laina (= cloak)*, fazendo alusão às brácteas involucrais coloridas (Fig. 1A – F) (King & Robinson 1987). As espécies circunscritas no gênero são distintas dentro de Praxelineae por apresentarem: pápus com numerosas cerdas, invólucro multisseriado e imbricado (brácteas involucrais fortemente sobrepostas e de tamanhos gradualmente maiores), geralmente colorido (branco, rosado ou lilás); eixo da inflorescência plano a convexo, raramente cônico; e lóbulo da corola mais longo do que largo (King & Robinson, 1987; Ribeiro, 2017). *Chromolaena* é o gênero mais rico em número de espécies na subtribo, com 166 espécies de distribuição neotropical (Hind & Robinson 2007; Susanna *et al*., 2020; Salgado *et al*,. 2023), tendo como maior centro de diversidade o Brasil. Há espécies de *Chromolaena* com ampla distribuição, como por exemplo *C. odorata*, potencialmente invasora enquanto que outras são microendêmicas como *C. pseudinsignis* que ocorre apenas em afloramentos rochosos da Chapada dos Veadeiros Goiás, Brasil (Ribeiro, 2017). Algumas espécies de *Chromolaena* são facilmente confundidas nos herbários com *Praxelis* devido à sua semelhança morfológica. Entretanto, de um modo geral, receptáculo cônico e colar da ântera balustriforme são características diagnósticas de *Praxelis* diferenciando-a assim de *Chromolaena* que tem o eixo da inflorescência plano ou convexo e o colar da ântera cilíndrico (Ribeiro, 2017).

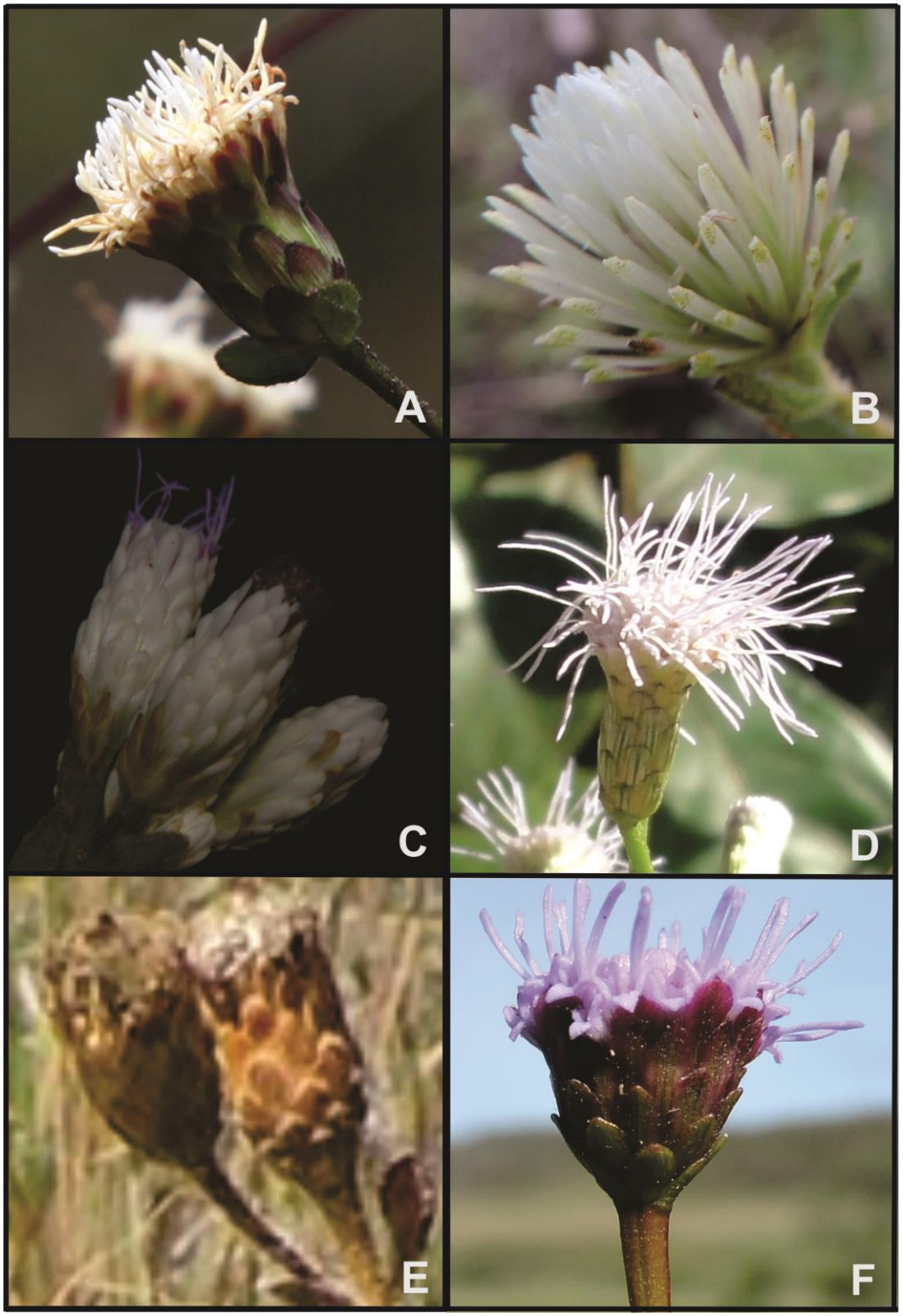

Figura 1. Diversidade de invólucro em espécies de *Chromolaena.* A. *C. arrayana* (esverdeado com ápice lilás). B. *C. candolleana* (esbranquiçado com ápice amarelo). C. *C. leucocephala* (esquanquiçado). D. *C. maximilianii* (creme com estrias esverdeadas. E. *C. myriadenia* (ferruginoso). F. *C. pseudinsignis* (lilás). (Fotografias: A: Henrique J. C. Moreira, C: J. Bringel, B, D − F: *R.N. Ribeiro*).

Praxelis foi proposta por Cassini (1826), com base na espécie tipo *Praxelis diffusa*, sem fazer alusão à etimologia do nome (King & Robinson 1987). Entretanto, só mais tarde no status de gênero, que foi reestabelecido por King & Robinson (1970) a partir de *Eupatorium* sect. *Praxelis* (Cassini) Bentham ex Baker (1753). O gênero abriga espécies com os seguintes caracteres: receptáculo sem páleas, cônico (Fig 2. A) a quase cilíndrico; brácteas involucrais caducas; cipselas obcomprimidas com carpopódio assimétrico; lóbulos da corola internamente densamente papiloso; colar da antera balustriforme (Fig 2. B) (King & Robinson 1987; Hind 2014; Grossi *et al*. 2020). *Praxelis*, configura-se o segundo maior gênero dentro da subtribo Praxelinae, e conta com 18 espécies (Ribeiro *et al*., 2021; Salgado *et al*., 2022). A maioria das espécies é originária da América do Sul, tendo como centro de diversidade o Brasil, sendo reportadas 15 espécies (Ribeiro *et al*. 2021) e duas espécies adventícias na Ásia e na Austrália. Assim como *Chromolaena*, há espécies com ampla distribuição e grande potencial invasor, podendo ser citados *P. clematidea* e *P. diffusa* (King & Robinson 1987; Salgado *et al*., 2022). Por outro lado, são reportadas microendêmicas como *P. spletii* (Fig. 2 C) registrada somente em afloramentos rochosos da Chapada dos Veadeiros, Goiás, Brasil (Ribeiro, 2017), assim como *P. minima* registrada somente no Parque Estadual da Serra do Papagaio, localizado na Serra da Mantiqueira, um remanescente de Mata Atlântica (Teles *et al*. 2016). Como foi citado anteriormente, são observadas nos herbários espécies de *Chromolaena* erroneamente identificadas como *Praxelis*, como, por exemplo, *Chromolaena pseudinsignis* (Fig. 2 D) identificada como *Praxelis insignis*. Embora os epítetos se assemelhem, são plantas distintas quanto a sua morfologia. Contudo, *Praxelis* também se assemelha bastante com o gênero *Eitenia*, compartilhando o eixo da inflorescência cônico, cipselas obcomprimidas, carporpodio assimétrico. Tanto é que *Eitenia polyseta* é frequentemente encontrada nos herbários dentro de *Praxelis*. O número de costas na cipsela é uma característica forte para separá-las sendo 2–(3) para *Eitenia* e 3 – 5 para *Praxelis* (Salgado *et al*., 2023).

O gênero *Lomatozona* foi descrito por Baker (1876), com base em *Lomatozona artemisiifolia* (King & Robinson 1987). O nome do gênero é derivado do grego, *lomatos = fringe or border e zone = belt or girdle*, refere-se ao pápus curtos em forma de coroa, com cerdas desiguais confluentes na base (King & Robinson, 1987). Por quase um século o gênero ficou conhecido apenas pela espécie tipo tendo como características pápus com cerdas curtas, invólucro imbricado, páleas entre as flores, e folhas dissectas (Fig. 2 E) (King & Robinson 1987). Posteriormente, com a descrição de outras espécies notou-se que apenas a espécie tipo apresentava páleas no eixo da inflorescência (King & Robinson 1987). São reportadas quatro espécies para *Lomatozona*, endêmicas do Brasil, registradas em afloramentos rochosos (King & Robinson 1987;

Ribeiro & Teles, 2015; Pacheco, 2014; Ribeiro, 2017). *Lomatozona* é o gênero mais morfologicamente distinto das Praxelineae, com suas folhas pouco a fortemente lobadas e o pápus com cerdas curtas.

Eitenia foi proposto por King & Robinson (1974), tendo como espécie tipo *Eitenia praxelioides*, o nome do gênero foi uma homenagem a George Eiten, co-coletor da espécie tipo (King & Robinson 1987). Eiten foi um grande coletor de plantas, tendo contribuído muito com o herbário da Universidade de Brasília (UB), um grande estudioso em vegetação do Cerrado e do Brasil, tendo atuado nas áreas de Ecologia vegetal, Taxonomia e Fitogeografia (Gomes *et al*., 2012). *Eitenia* abriga duas espécies, endêmicas do Brasil (Hind & Robinson 2007, e BFG 2018), ambas as espécies com receptáculo cônico, cipselas obcomprimidas com 2 (3) costadas, costas denso longo-cerdosas, e lóbulos da corola de tamanhos diferentes (King & Robinson 1987). Dentre os gêneros de Praxelineae, *Eitenia* se aproxima morfologicamente de *Praxelis* devido ao receptáculo cônico e as cipselas obcomprimidas. No entanto, diferem quanto ao número de costas das cipselas sendo 2 a 3 em *Eitenia* e 3 a 5 em *Praxelis*, e ao número de cerdas no papus sendo 2 a 8 em *Eitenia* e 20 a 40 em *Praxelis* (Fig. 2 F) (Ribeiro *et al*., 2021 e Salgado *et al*., 2023). Assim como *Eitenia*, *Eupatoriopsis* também apresenta cipsela obcomprimida com duas costas. Porém, as brácteas involucrais são imbricadas e o colar da antera é espessado em *Eitenia*, enquanto que em *Eupatoriopsis* as brácteas são subimbricadas e o colar da antera não é espessado (King & Robinson 1987, Salgado *et al*., 2023). O gênero *Praxeliopsis* também é próximo morfologicamente de *Eitenia*, por compartilharem número similar de séries de brácteas, o eixo da inflorescência cônico, os ramos do estilete filiformes e os lóbulos da corola desiguais (King & Robinson 1987, Salgado 2023). Por outro lado, *Eitenia* se distingue por apresentar filotaxia oposta, cipsela obcomprimida, e base do estilete não alargada, enquanto *Praxeliopsis* possui folhas opostas, cipsela prismática, e base do estilete alagada (Barroso 1949 e King & Robinson 1987).

O gênero *Praxeliopsis*, monotípico, foi descrito pela pesquisadora Graziela Maciel Barroso em 1949, com base na espécie *Praxeliopsis matogrossensis*, o nome do gênero é derivado do *Praxeli = Praxelis e opsis = similis*, indica a similaridade morfológica com o gênero *Praxelis* (Barroso 1949). *Praxeliopsis* é endêmico do Brasil reportado para os estado de Mato Grosso, e se distingue dos demais gêneros de Praxelinae por apresentar o papus com cinco cerdas, a base do estilete alargada e o apêndice da antera ausente (Barroso 1949). Além disso, *Praxeliopsis* compartilha o receptáculo cônico, com gêneros *Eupatoriopsis*, *Eitenia* e *Praxelis* e *Chromolaena* porém se diferencia por seu carpopódio simétrico, enquanto nos demais é assimétrico (King & Robinson 1987; Salgado *et al*., 2023).

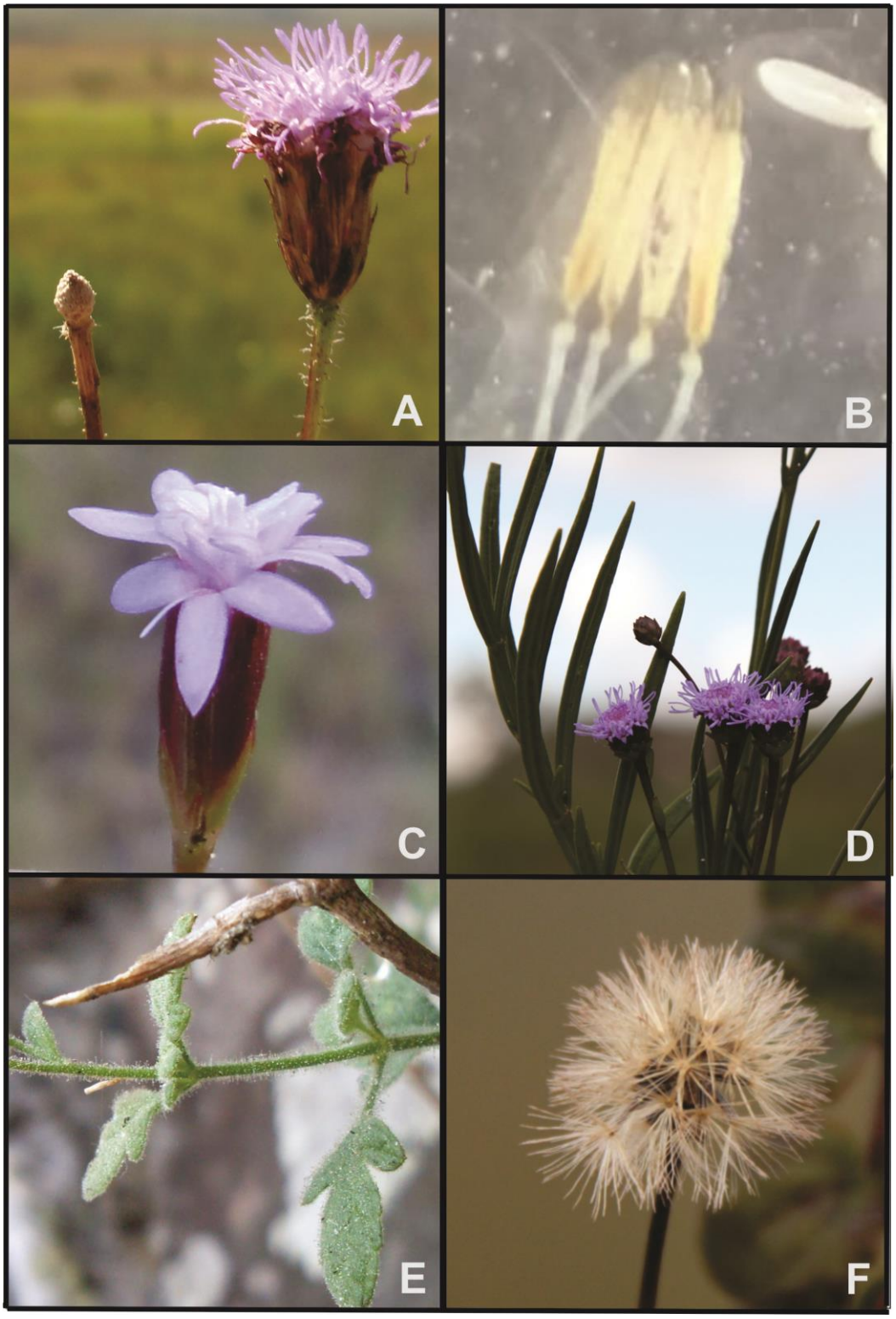

Figura 2. A. *Praxelis kleinioides* (eixo da inflorrência cônico). B. *Praxelis scaturicola* (côlar da ântera balustriforme. C. *Praxelis splettii* (capítulo). D. *Chromolaena pseudoinsignis* (habito). E. *Lomatozona artemisiifolia* (lâmina foliar lobada). F. *Praxelis decumbens* (papus com cerdas numerosas). (Fotografias: A– C: *R.N. Ribeiro*, D, F: *Henrique J. C. Moreira*, E: *A.M. Teles*).

Eupatoriopsis foi proposto por Hieronymos (1893), tendo como espécie tipo *Eupatoriopsis hoffmanniana,* e o nome do gênero faz alusão à similaridade com o gênero *Eupatorium* (King & Robinson 1987). O genêro é endêmico do Brasil, registrado na região Sul de Minas Gerais na cidade de Poços de Caldas, caracterizado por apresentar eixo da inflorescência fortemente cônico, pápus reduzido, e cipsela obcomprimida (King & Robison 1987 e Hind & Hobinson 2007). Além disso, é único gênero de Praxelineae que possui o invólucro com brácteas involucrais subimbricadas, e com 1 – 2 séries de brácteas.

O gênero *Osmiopsis* foi descrito inicialmente com base na espécie *Eupatorium plumieri,* e posteriormente, com a fragmentação de *Eupatorium*, foi feita a nova combinação em *Chromolaena plumieri* (King & Robinson 1987). Cinco anos após a publicação da nova combinação, os mesmos autores perceberam que se tratava de uma espécie que mesclava características do gênero *Chromolaena* (Subtribo Praxelinae) quanto ao hábito e ao invólucro, e do gênero *Koanophyllon* (Subtribo Critoniinae*)* quanto ao lóbulo da corola glandulosa, o apêndice da antera curto e largo, e pontas largas sobre os ramos do estilete (King & Robinson, 1975). Tendo em vista essa sobreposição de características morfológicas entre os gêneros supracitados, foi proposta a criação um novo gênero monotípico, *Osmiopsis* King & Robinson (1975:251). O nome *Osmiopsis* é derivado do nome *Osmia = sinônimo de Chromolaena e opsis = similar* (King & Robinson 1987). *Osmiopsis* é endêmico do Haiti, e se distingue dos demais gêneros de Praxelineae, por apresentar os lóbulos da corola triangulares bem como o apêndice do conectivo (King Robinson 1987 e Hind & Robinson 2007).

Os sete gêneros que circunscrevem a subtribo Praxelineae compartilham brácteas involucrais totalmente decíduas na maturidade dos frutos, sendo considerada sua principal caraterística diagnóstica (King & Robinson 1987). Além disso, as espécies de Praxelinae são facilmente reconhecidas pelas brácteas involucrais imbricadas ou subimbricadas, receptáculo plano, convexo, ou cônico, lóbulo da corola geralmente denso papiloso na face interna, e folhas geralmente opostas, raramente alternas ou verticiladas (King & Robinson 1987 e Hind & Hobinson 2007). Contudo, o baixo número de caracteres com grande plasticididade que definem os gêneros de Praxelinae culminou em um número alto de espécimes identificados de forma errônea ou não determinados nas coleções botânicas, em especial, dos gêneros *Chromolaena* e *Praxelis*. Há, inclusive, um número grande de espécies de difícil identificação e de complexos específicos (*e.g. Chromolaena leucocephala*/*C. horminoides*).

Tendo em vista que quase todas as espécies que compõe Praxelinae ocorrem no Brasil, especialmente no Bioma Cerrado (exceto *Osmiopsis,* que ocorre no Haiti), a falta de características exclusivas dos gêneros, e a necessidade de maior amostragem de gêneros e espécies em estudos filogenéticos, buscamos aqui: i) realizar um estudo filogenético baseado em caracteres moleculares da subtribo Praxelinae ii) apresentar novidades nomenclaturais para o gênero *Praxelis* iii) confirmar a inclusão de *Osmiopsis* na subtribo Praxelinae baseado em morfologia e utilizando ferramentas moleculares.

ORGANIZAÇÃO GERAL DA TESE

A tese compreende três capítulos:

1) Filogenia da subtribo Praxelinae R.M.King & H.Rob. (Asteraceae, Eupatorieae)

   Esse capítulo aborda a filogenia para todos os gêneros atualmente circunscritos em Praxelinae e suas respectivas espécies tipo, baseada em dados moleculares. É apresentada uma árvore filogenética baseada em marcador nuclear (ITS) e de cloroplasto (*ndh*F) e dos marcadores combinados, e são discutidas as relações de parentesco entre os gêneros.

2) Re-evaluation of *Praxelis* (Asteraceae, Eupatorieae) in Brazil and description of *Praxelis scaturicola*, an unsual riverine species

   Nesse capítulo apresentamos a descrição de uma nova espécie, *Praxelis sacturicola* Neves Ribeiro & V.L. Rivera, bem como, descrições morfológicas, comentários taxonômicos, prancha de imagens, ilustrações científicas, mapa de distribuição, status de conservação e uma chave de identificação paras todas as espécies de *Praxelis* do Cerrado. Além disso, propomos a sinonimização de *Praxelis macrocarpa,* espécie recém-descrita para o Cerrado, em *Praxelis capilaris*.

3) x *Koanoxelis*: a substitute nothogeneric name for *Osmiopsis* (Asteraceae) in view of molecular confirmation of its inter-generic and inter-subtribal hybrid status

   No último capítulo discutimos a origem híbrida de *Osmiopsis plumieri*, a incongruência entre a topologia das árvores baseadas em marcador nuclear (ITS) e cloroplasto (*ndh*F) e revisamos sua posição taxonômica.

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Capítulo I

Filogenia da subtribo Praxelinae R.M.King & H.Rob. (Asteraceae, Eupatorieae)

A ser enviado ao periódico: American Journal of Botany

RESUMO Eupatorieae possui 2200 espécies agrupadas em 182 gêneros pertencentes a 20 subtribos. Dentre as subtribos, Praxelinae configura-se como a segunda maior em números de espécies, com cerca de 193 espécies agrupadas em sete gêneros. O gênero mais diverso é *Chromolaena* com 166 espécies seguido de *Praxelis* (18), *Lomatozona* (4), *Eitenia* (2), e *Eupatoriopsis, Praxeliopsis* e *Osmiopsis* com uma espécie. *Osmiopsis* ocorre apenas no Haiti, e os demais gêneros tem ocorrência na América do Sul. A subtribo Praxelinae é monofilética, entretanto as relações evolutivas entre os gêneros ainda são incertas. Tendo em vista que haviam sido amostrados somente 57% dos gêneros e apenas uma das espécies tipo de Praxelinae, verificou-se a necessidade de uma amostragem dos demais gêneros e de suas respectivas espécies tipo. Desta forma, a tese buscou responder as seguintes questões: i) A subtribo Praxelinae e seus gêneros são monofiléticos? ii) Qual é a relação de parentesco entre os gêneros pertencentes a Praxelinae? Foram analisadas 202 espécies de Eupatorieae. Destas, 32 são espécies de Praxelinae, foram geradas dez novas sequências nucleares e/ou plastidiais (ITS e *ndh*F), amostrando assim todos os gêneros, bem como as suas espécies tipos. Para o grupo externo foi incluída a espécie *Galeana pratensis.* Para extração do DNA total foram utilizadas folhas frescas e material de herbário, mediante a autorização dos curadores. As sequências de Eupatorieae, especialmente Praxelinae, disponíveis foram obtidas no GenBank para os seguintes marcadores: (ITS; ETS; *ndh*F; *ndh*I; ndhI-ndhG). As reações de amplificação do marcador nuclear ITS e *ndh*F foram feitas no laboratório de Biologia Molecular de plantas do Departamento de Botânica da UnB. A escolha destes marcadores foi a partir de estudos já publicados. Os produtos da PCR foram enviados a BPI Biotecnologia para limpeza e sequenciamento. As sequências obtidas foram alinhadas por meio do algoritmo do Muscle implementado no programa Geneious Prime e ajustados manualmente quando necessário. Foi feita uma matriz final com todos os marcadores combinados. Os alinhamentos foram submetidos à análise de bayesiana no programa MrBayes, através do portal CIPRES. A subtribo permanece monofilética com a exclusão do notogênero *Koanoxelis*, nome substituto a ser publicado para *Osmiopsis* (Capítulo III). Além disso, os gêneros circunscritos em Praxelinae não são monofileticos, e os resultados sugerem ou que todos os gêneros deveriam ser ou transferidos para *Praxelis* ou uma nova circumscrição genérica que aumentaria o número de gêneros

INTRODUÇÃO

Asteraceae possui mais de 1.700 gêneros, e cerca de 25.000 espécies, agrupadas em 50 tribos, e estão distribuídas amplamente em todo mundo (Funk et al., 2009; Panero & Crozier 2016; Mandel et al., 2019; Susanna et al., 2020). Eupatorieae é a tribo mais rica em número de espécies, e compreende 2.200 espécies reunidas em 182 gêneros e agrupadas em 20 subtribos (Hind & Robinson, 2007; Robinson et al., 2009), distribuídas no hemisfério ocidental, com alguns gêneros pantropicais, com muitos representantes na América do Norte e Sul, e poucas espécies nativas no velho mundo (King & Robinson, 1987; Bremer, 1994; Funk et al., 2009).

Dentre as subtribos, Praxelinae, com 193 espécies, configura-se como a segunda maior subtribo circunscrita na tribo Eupatorieae, sendo superado apenas por Mikaniinae, com 400 espécies. Praxelinae foi estabelecido por King & Robinson em 1980, agrupando sete gêneros, sendo: *Chromolaena* DC.; *Eitenia* R.M. King & H. Rob; *Eupatoriopsis* Hieron.; *Lomatozona*; *Osmiopsis* R.M. King & H. Rob.; *Praxeliopsis* G.M. Barroso e *Praxelis* Cass.. As espécies de Praxelinae podem ser reconhecidas entre as subtribos de Eupatorieae, pelas suas brácteas involucrais totalmente decíduas, receptáculo plano a convexo ou cônico, capítulos com 5 a 65 flores, geralmente liláses ou brancas, e folhas geralmente opostas, raramente alternas (Hind & Hobinson, 2007; Roque et al., 2017).

Dentre os gêneros circunscritos em Praxelinae, *Chromolaena* é o mais rico em número de espécies, com 166 espécies de distribuição neotropical (Hind & Robinson, 2007 Salgado et al., 2023), seguido de *Praxelis* com 18 espécies originárias da América do Sul, e uma espécie adventícia na Ásia e na Austrália (Hind, 2014; Teles et al., 2016; Ribeiro et al., 2021; Salgado et al., 2022). Os demais gêneros são *Lomatozona* com quatro e *Eitenia* com duas espécies, ambos, com distribuição restrita ao Brasil (Hind & Robinson, 2007; Ribeiro & Teles 2015). Por fim, os gêneros monoespécificos, *Eupatoriopsis*, *Praxeliopsis*, ocorrem no Brasil e *Osmiopsis* no Haiti (Hind & Robinson, 2007).

Em termos filogenéticos, quatro gêneros de Praxelinae foram amostrados por Rivera *et al.* (2016), em que usaram os marcadores ITS, ETS, *ndh*F, *ndh*I, e *ndh*I-*ndh*G IGS, os quais apontaram o monofiletismo da subtribo, sustentado pelos gêneros *Chromolaena*, *Lomatozona*, *Praxelis* e *Eitenia* (Figura 1). Porém, *Chromolaena* e *Praxelis* não surgiram como monofiléticos. As espécies de *Chromolaena* brasileiras aparecem em uma gradação e são irmãs da norte-americana *C. sagittata* (A.Gray.) R.M.King & H.Rob. Já as espécies de *Praxelis* (polifilético) aparecem em um clado com suporte máximo que inclui duas espécies de *Lomatozona*, *Eitenia polyseta* R.M.King & H.Rob. e

Chromolaena decumbens Gardner. Segundo Rivera et al., (2016), para se manter o monofiletismo, todos os gêneros da subtribo Praxelinae deveriam ser reunidos em um mesmo gênero.

Tendo em vista que o estudo realizado por Rivera et al, (2016) abordou 57% dos gêneros e apenas um dos tipos de seus gêneros (*Lomatozona artemisiifolia* Baker) ficou claro que há necessidade de mais estudos, com uma maior amostragem que inclua as demais espécies tipo e os gêneros monotipicos *Eupatoriopsis*, *Praxeliopsis* e *Osmiopsis.* Outra meta seria expandir o número de espécies de Praxelinae, para uma melhor compreensão evolutiva e sistemática dos gêneros circunscritos na subtribo e das relações intragenéricas. Em suma, com base na carência de estudos filogenéticos na subtribo Praxelinae, e na falta de características exclusivas dos gêneros, buscamos compreender as relações filogenéticas entre os gêneros de Praxelinae por meio de dados moleculares. Portanto, buscamos responder as seguintes questões: i) A subtribo Praxelinae e seus gêneros são monofiléticos? ii) Qual é a relação de parentesco entre os gêneros e espécies pertencentes a Praxelinae?

MATERIAL E METÓDOS

Um total de 202 espécies de Eupatorieae foram incluídas na análise filogenética, tendo como grupo externo *Galeana pratensis* (Kunth) Rydb (Asteraceae, Perityleae) utilizados na filogenia de Rivera et al., (2016). O alvo deste estudo foi a subtribo Praxelinae, representada por 32 espécies, incluindo todos os gêneros e as espécies tipo não amostrados por Rivera et al., (2016) (Tabela 1). Além destas, foram análisadas todas as espécies do clado C (subtribo Critoniinae) (Tabela 1), da filogenia de Rivera e colaboradores (2016). As espécies do clado C foram incluídas devido ao fato de que *Osmiopsis plumieri* R.M.King & H.Rob. apresentar algumas características morfológicas das espécies circunscritas em Critoniinae e a possibilidade de ser um híbrido (King & Robinson, 1975).

As expedições para coleta do material botânico (*vouchers* e folhas frescas fixadas em sílica gel para extração do DNA) foram realizadas a partir dos registros de ocorrência, por meio de coordenadas geográficas presentes nas exsicatas e em *site* especializado (e.g. *Species Link*). Foram realizadas coletas no município de Paraúna, na Chapada dos Veadeiros, na Serra dos Pireneus e em uma Área de Preservação da Universidade Estadual de Goiás no Campus Henrique Santillo em Anápolis, Goiás. As coletas seguiram as técnicas usuais em taxonomia vegetal (Mori et al., 2011). O material coletado foi incorporado ao acervo do herbário UB e duplicatas serão enviadas a outras instituições nacionais (e.g. HUFU) e estrangeiras (e.g. K, NY). Para complementar as coletas foi

examinado o material do UB, que tem uma grande coleção de Asteraceae, foi realizada uma visita ao herbário UFG, e foram solicitados empréstimos aos herbários AFR e HUFU. Estes herbários foram escolhidos a partir de uma lista de espécies de Praxelinae gerada por meio do *Species Link* (https://specieslink.net/). As amostras das exsicatas para extração de DNA provenientes dos herbários foram retiradas mediante a autorização dos curadores.

Para extração do DNA total foram utilizadas folhas frescas, coletadas em campo e armazenadas em sílica gel ou de material herborizado e seguindo o protocolo do CTAB (Doyle & Doyle, 1987). Foram utilizados dois marcadores moleculares, um nuclear (ITS) e outro de cloroplasto (*ndh*F). Ambos os marcadores foram escolhidos por serem amplamente utilizados em estudos filogenéticos que abordaram a tribo Eupatorieae e apresentaram resultados significativos (Hattori, 2013; Fernandes, 2014; Rivera et al., 2016; Christ, 2022). As reações de amplificação do marcador nuclear ITS foram feitas no laboratório de Biologia Molecular de plantas do Departamento de Botânica da UnB. Foram utilizados os *primers* ITS-4 (TCCTCCGCTTATTGATATGC) e ITS-5 (GGAAGTAAAAGTCGTAACAAGG) (White *et al.* (1990). e *ndh*F 52 (AGGTAAGATCCGGTGAATCGGAAA) *ndh*F 1212 (GGTGGAATACCACAAAGA). Para cada amostra de PCR foram utilizados os reagentes e o protocolo de amplificação da PCR descritos na Tabela 2. Foram realizados inúmeros testes sem sucesso antes de chegar neste protocolo. Quando a extração do DNA e a amplificação foram feitas dentro de um mês os resultados foram melhores. No final do ano de 2019, fizemos a extração do DNA de todo material que tínhamos. Porém, com a chegada da pandemia de COVID-19, as amplificações tiveram que ser adiadas para o segundo semestre de 2021, quando foi possível retornarmos ao laboratório. A grande maioria das extrações não funcionou, inclusive de *Praxelis scaturicola*, espécie nova descrita durante esse estudo do qual tínhamos material coletado há poucos dias. Desta forma, focamos apenas nas espécies tipos e nos gêneros não amostrados por Rivera *et al.* (2016).

Para avaliar a qualidade da amplificação, as amostras resultantes de PCR foram avaliadas em gel agarose a 2% corados com UniSafe Dye 0,03% (v/v) e visualizados sob luz UV. O sequenciamento das amostras em que a amplificação foi avaliada como bem sucedida foi feito em Botucatu-SP pela empresa BPI Biotecnologia. Para o sequenciamento foram utilizados os mesmos primers usados na amplificação seguido de: i) reação de Sequenciamento BigDye® Terminator v3.1 Cycle Sequencing Kit (fabricado pela Applied Biosystems) e reação de precipitação por Etanol/EDTA/Acetato de Sódio de acordo com protocolo sugerido pelo fabricante; e ii) sequenciamento automático por eletroforese capilar no equipamento ABI3730xl Genetic Analyzer

(Applied Biosystems). Recebidas as sequências, foi realizada a análise dos eletroferogramas utilizando os programas Chromas Lite e Geneious 4.8.3 ou Geneious Prime.

As sequências obtidas foram alinhadas por meio do algoritmo do Muscle implementado no Geneious e depois checado manualmente. As ausências (*gaps*) foram tratadas como dados faltantes. Foram produzidas três matrizes: uma apenas com ITS, outra apenas de *ndh*F e a matriz final com todos os marcadores combinados ITS, ETS, *ndh*F, *ndh*I, *ndh*I-*ndh*G (Tabela 3).

Os alinhamentos foram analisados no programa jModeltest 2.1.6 (Darriba et al., 2012) para buscarmos o melhor modelo de evolução sob o Akaike Information Criteria (AIC). A árvore filogenética foi obtida a partir dos critérios de inferência bayesiana (IB) usando os dados moleculares no programa MrBayes on XSEDE 3.2.7 A (Ronquist & Huelsenbeck, 2003), utilizando o modelo GTR + I + G, por meio da plataforma CIPRES (Miller et al., 2010). A análise de IB consistiu em duas corridas independentes e simultâneas, cada uma com quatro cadeias (três cadeias quentes e uma fria) de Monte Carlo de Markov (MCMC), para 10 milhões de gerações, amostrando as árvores a cada 10000 gerações. A estacionaridade das cadeias foi verificada pelo programa Tracer v1.7.2 (Rambaut et al., 2014). Os valores de suporte para os clados foram obtidos por probabilidades posteriores para a análise bayesiana. A árvore filogenética foi visualizada e editada no Figtree v 1.4.4 (Rambaut, 2010).

RESULTADOS

Um total de quatro gêneros e dez espécies tiveram seu DNA extraído, amplificado e sequenciado (ITS e *ndh*F) pela primeira vez. A subtribo Praxelinae se apresentou como monofilética devido à comprovação de status de espécie híbrida de *Osmiopsis* (vide capitulo 3) que foi retirada da tribo.

A primeira espécie a divergir é *Chromolaena sagittata* (A. Gray) R.M.King & H.Rob., espécie restrita ao oeste do México, que é irmã das demais espécies da subtribo, que tratamos como clado A. Em seguida divergiu o clado B, que reúne três espécies: *C. odorata* (L.) R.M.King & H.Rob., espécie Neotropical de ampla distribuição e duas espécies da América do Sul, *Chromolaena maximiliani* (Schrad. Ex DC.) R.M.King & H.Rob. e *C. christieana* (Baker) R.M.King & H.Rob. (Figura 2), grupo irmão do restante das Praxelinae. Posteriormente, divergiu *Chromolaena arrayana* (Gardner) R.M. King & H. Rob., endêmica dos campos rupestres do Cerrado brasileiro, que tratamos como clado C. As demais espécies não mostraram boa resolução, formando-se uma politomia de seis elementos, em que apenas dois clados apresentaram um bom suporte. Esses dois clados bem suportados foram: o clado D (PP=0.9), constituído por

Chromolaena morii R.M.King & H.Rob., + *C. pseudinsignis* R.M.King & H.Rob., reportadas para afloramentos rochosos, respectivamente no estado da Bahia e Goiás, e o clado D (PP=0.95) que reúne todas as espécies tipo dos demais gêneros das Praxelinae: *Eitenia*, *Eupatoriopsis*, *Lomatozona* e *Praxelis*. Dentro da politomia, clado E, é constituído por cinco espécies que possuem afinidade morfológica e representam um complexo denominado "complexo *Chromolaena*. Para o clado F existem três possibilidades: a primeira seria reconhecer o clado todo como um único gênero, denominado de "*Chromolaena* sensu stricto"; a segunda possibilidade seria dividir o clado em dois gêneros: *Chromolaena* e *Eupatoriopsis*; e a última opção dividir o clado em três gêneros: *Chromolaena*, *Eitenia* e *Eupatoriopsis.*

No clado G também há três possibidades. A primeira opção tratar esse clado como o gênero *Praxelis*. A segunda opção, dividir o clado em dois gêneros. E a terceira opção seria o reconhecimento de três gêneros. Por fim, formou-se um clado com algumas espécies de *Koanophyllon*, *Chromolaena colina* (DC.) R.M.King & H.Rob. e *Idiothamnus lilloi* (B.L.Rob.) R.M.King & H.Rob. com alto suporte, no qual também se posicionou *Osmiopsis plumieri*, espécie híbrida, o que foi influenciado pelo marcador ITS (Figura 3).

DISCUSSÃO

A análise filogenética realizada nesse estudo, com base em dados moleculares disponíveis pelo GenBank e obtidos pelos autores, corrobora o estudo de Rivera et al. (2016). Sendo assim, Praxelineae é composto por seis gêneros (Figura 4) e é monofilética. Porém, os gêneros circunscritos em Praxelinae não são monofileticos, e os resultados sugerem que ou todos os gêneros deveriam ser transferidos para *Praxelis,* ou que seja feita uma nova circumscrição genérica que aumentaria o número de gêneros. A primeira opção é reconhecer a subtribo Praxelineae como tendo um único gênero, transferindo *Chromolaena*, *Eupatoriopsis*, *Eitenia*, *Lomatozona* e *Praxeliopsis* para *Praxelis* (sensu lato). Com relação à morfologia do gênero *Praxelis sensu lato* a circumscrição morfológica seria expandida e algumas características seriam incluídas, elencadas a seguir: i) folhas alternas (raras em *Chromolaena*/*Praxeliopsis*) ii) invólucro subimbricado (*Eupatoriopsis/Eitenia praxelioides*); iii) brácteas involucrais externas persistentes (*Eupatoriopsis*) iv) eixo da inflorescência plano ou convexo (*Chromolaena*/*Lomatozona*); v) carpopódio simétrico (*Chromolaena*/*Lomatozona*/*Praxeliopsis*); vi) cipselas biconvexas (*Eitenia*/*Eupatoriopsis*); vii) cipcelas 2-3 costadas (*Eitenia*/*Eupatoriopsis*); viii) apêndice da antera ausente (*Praxeliopsis*); ix) base do estilete alargada (*Praxeliopsis*); e x) pápus com cerdas curtas e irregulares (*Lomatozona*). Desta forma, *Praxelis sensu lato* pode ser reconhecido pelos seguintes caracteres: invólucro com

brácteas involucrais totalmente ou parcialmente decíduas após a maturação do fruto; pápus unisseriado; e ramos do estilete densamente a pouco papilosos.

A segunda opção, com base nesta árvore filogenética, é apresentar uma nova circumscrição genérica, porém, a árvore não se mostrou totalmente resolvida, com uma politomia de seis elementos. Acreditamos que, possívemente, essa politomia nas *Chromolaena* pode ser explicada pelo fato dessas espécies terem apenas um marcador, ITS. De um modo geral foi observado uma correlação entre os clados bem suportados com a distribuição geográfica, e, até certo ponto com a morfologia. Contudo, existe ainda uma dificuldade em elencar conjuntos de características morfológicas diagnósticas nos clados identificados na análise filogenética. A seguir, discutimos as características morfológicas dos clados, que poderiam a vir no futuro a ser reconhecidos como novos gêneros, com os valores de probabilidade posterior da Inferência Bayesiana e sua distribuição geográfica.

1) Clado A: *Chromolaena sagittata* (PP=1) – México (áreas montanhosas). *C. sagittata* é a única espécie mexicana aqui amostrada e a mesma se posicionou como irmã das demais espécies de Praxelineae, corroborando os estudos de Rivera et al., (2016) e Christ (2023). *C. sagittata* é bem distinta das demais Praxelineae amostradas por apresentar as lâminas foliares triangulares e o ápice das brácteas involucrais revolutas e triangulares (King & Robinson, 1987). Outras espécies de *Chromolaena* mexicanas também apresentam as brácteas similares as de *C. sagittata* (por exemplo, *C. bigelovii*, e *C. glaberrima*), e acreditamos ser bem provável que viriam a se posicionar neste clado. Ocorrem no México 17 espécies de *Chromolaena*, das quais 14 se distribuem exclusivamente entre o Texas (EUA) e o Panamá. Seria desejável sua inclusão numa filogenia mais abrangente.

2) Clado B: *Chromolaena maximiliani, C. odorata* e *C. christieana* (PP=1) – América do Sul, América do Norte (áreas de Mata). *C. maximiliani* e *C. odorata* possuem ampla distribuição na América do Sul e Norte, já *C. christieana* é reportada para Argentina, Brasil e Paraguai (King & Robinson, 1987). Estas espécies emergiram como grupo-irmão do restante das espécies em Praxelinae (Figura 5). Essa mesma topologia foi encontrada por Rivera *et al.* (2016) e Christ (2023). A diferença entre as árvores é que no primeiro estudo tinha somente uma espécie amostrada desse clado (*C. odorata*) e já no segundo tinham duas (*C. odorata* e *C. maximiliani*). Nosso estudo agregou *C. christiena* a esse clado. As três espécies de *Chromolaena* supracitadas são morfologicamente semelhantes quanto ao hábito arbustivo, as lâminas foliares lanceoladas, trinervadas, e são as únicas aqui amostradas que possuem invólucro cilíndrico, com brácteas involucrais com estrias esverdeadas (Ribeiro & Teles, 2015; Christ & Ritter, 2019).

3) Clado C: *Chromolaena arrayana* (PP= 1) Brasil (campos rupestres). *C. arrayana* é endêmica do Cerrado brasileiro, ocorrendo em áreas de afloramentos rochosos de arenito, e

encontra-se em risco de extinção (Martinelli & Moraes, 2013; Ribeiro, 2017). É bem distinta das demais Praxelineae por suas brácteas involucrais com o ápice castanho – vináceas.

4) Clado D: *Chromolaena morii* e *C. pseudinsignis* (PP=0.9) – Brasil (campos rupestres). *Chromolaena morii* e *C. pseudinsignis* são reportadas em afloramentos rochosos com solos arenosos, respectivamente no estado da Bahia e Goiás (Riberio, 2017; BFG, 2018). Essas duas espécies são morfologicamente muito distintas. *C. morii* apresenta folhas pecioladas, lâminas foliares lanceoladas ou ovadas, invólucro com brácteas involucrais esverdeadas, receptáculo plano, e cipselas obcônicas. *C. pseudinsignis* apresenta folhas sésseis, lâminas foliares lineares, invólucro com brácteas involucrais lilases, receptáculo cônico, e cipselas fusiformes. Tendo em vista as grandes diferenças morfológicas, uma explicação possível para este posicionamento é que foi um artefato ocasionado pelo fato de que ambas as espécies foram amostradas pelos cinco marcadores. Caso a mesma configuração se mantenha, aponta para fortes pressões evolutivas para adaptação aos campos rupestres, que tem uma grande riqueza de diferentes microhabitas (Chaves et al., 2019a, 2019b).

5) Clado E: *Chromolaena cf. ascendens, C. congesta, C. hirsuta, C. latisquamulosa* e *C. rhinanthacea* (PP=0.56) – Argentina, Bolivia, Brasil, Paraguai e Uruguai (campos de altitude). As cinco espécies desse clado tem registros em todos os estados da região sul do Brasil e algumas delas também em países limítrofes, conforme discriminado a seguir (Flora e Funga do Brasil 2023, POWO, 2023; King & Robinson, 1987). *Chromolaena ascendens* ocorre de MG até RS, Brasil. *C. congesta* ocorre de MG até RS, Brasil, e Argentina, Paraguai e Uruguai. *C. hirsuta* ocorre do RJ até RS, Brasil, mas não em MG, e na Argentina, Bolivia, Paraguai e Uruguai. *C. latisquamulosa* ocorre de SP até RS segundo Flora e Funga e POWO e na Argentina. *C. rhinanthacea* ocorre de MG até RS, e no Paraguai. O clado possui baixo suporte, provavelmente devido à ausência do marcador ITS. Por outro lado, estas espécies tem forte afinidade morfológica e representam um complexo denominado "complexo *Chromolaena congesta*" (Christ & Ritter, 2019), É bem provável que a inclusão do ITS irá melhorar o suporte do clado e possivelmente alinhar as espécies *C. alvimii, C. laevigata, C. stachyophylla*, nos clados C ou D (por compartilharem características morfológicas e habitat) e *C. gentianoides* no clado E (por fazer parte do "complexo *Chromolaena congesta*") ou podem se unir formando um ou mais gêneros.

6) Clado F: há três possibilidades a seguir:

i) O clado F seria formado apenas por: Chromolaena *sensu stricto* (PP=1) – Brasil, Peru, Venezuela e Porto Rico

Nessa transcrição da filogenia para a taxonomia, o gênero *Chromolaena* assumiria uma circunscrição muito mais restrita do que a atual, necessitando a criação de novos gêneros para o clados A, B, C, D e E. Aqui se posicionou a espécie tipo do gênero, *C. horminoides* DC., e mais três espécies de *Chromolaena*, sendo *C. horminoides* DC. e *C. leucocephala* Gardner endêmicas do cerrado brasileiro, *C. squalida* (DC.) R.M.King & H.Rob. com ampla distribuição no Brasil, Peru e Venezuela, e *C. borinquensis* (Britton) R.M.King & H.Rob. endêmica de Porto Rico. Nesse clado também se posicionaram *Eitenia praxelioides* R.M.King & H.Rob., endêmica do Brasil, ocorrendo no estado de Goiás, Pará e Maranhão, e *Eupatoriopsis hoffmanniana* microendêmica do Brasil, numa região de Mata Atlântica do sul de Minas Gerais (BFG, 2018; King & Robinson 1987). Nessa transcrição, seria necessário tranferir *Eitenia praxelioides* e *Eupatoriopsis hoffmanniana* para o gênero *Chromolaena sensu stricto.* Portanto, outras características seriam incluídas em ***Chromolaena sensu stricto***, tais como: i) involucro subimbricado (*Eupatoriopsis* e *Eitenia praxelioides*); ii) brácteas involucrais externas persistentes (*Eupatoriopsis*); iii) cipselas biconvexas (*Eupatoriopsis* e *Eitenia praxelioides*); e iv) cipselas 2-3 costadas (*Eupatoriopsis* e *Eitenia praxelioides*). Entretanto, as características morfológicas que sustentariam esta transcrição taxonômica são muito tênues, porque as espécies dos demais clados também apresentam a maioria delas (excetuando a deciduidade das brácteas), sendo que no clado G, todas estão presentes.

ii) O clado F seria formado por dois gêneros: *Chromolaena* (PP=1) e *Eupatoriopsis* (PP= 0.73)

A segunda opção seria dividir o clado F em dois gêneros. O gênero *Chromolaena* circunscrito por *C. borinquensis, C. horminoides (espécie tipo de Chromolaena), C. leucocephala* e *C. squalida*. Todas essas espécies compartilham do invólucro cilíndrico, receptáculo plano ou convexo, e cipselas prismáticas 5-costadas. O segundo gênero, *Eupatoriopsis*, seria formado por *E. hoffmanniana* (espécie tipo de *Eupatoriopsis*) e *Eitenia praxelioides* que seria transferida para *Eupatoriopsis* e, consequentemente, o gênero *Eitenia* se tornaria um sinônimo de *Eupatoriopsis*). Essas duas espécies compartilham do invólucro campanulado, receptáculo cônico, e cipselas biconvexas 2(3) -costadas (King & Robinson, 1987; Salgado et al., 2023). É esperado que a inclusão de mais marcadores, além de ITS e *ndh*F, poderia melhorar o suporte de *Praxeliopsis*.

iii) O clado F seria formado por três gêneros *Chromolaena* (PP=1), *Eitenia* (PP=0.73) e *Eupatoriopsis* (PP=0.73)

A terceira opção seria dividir o clado em três gêneros, *Chromolaena* com as quatro espécies já citadas anteriormente, sendo distinta dos outros gêneros por seu receptáculo plano a convexo e a cipcela prismática. Já *Eitenia* passaria a ser um gênero monotípico com a exclusão de *E. polyseta* R.M. King & H.Rob., tendo com característica diagnostica o pápus cerdoso com seis cerdas e a

presença de tricomas sobre a nervuras do limbo da corola na face interna (King & Robinson 1987, Pacheco 2014). Por fim, *Eupatoriopsis* distinta dos outros dois gêneros com suas brácteas involucrais externas persisntentes (King & Robinson 1987).

7) Clado G: há três possibilidades a seguir:

i) Clado G: *Praxelis sensu stricto* (PP=0.87) – Centro de origem no Brasil

Composto por oito espécies com distribuição majoritariamente no Cerrado brasileiro, sendo *Praxelis clematidea* R.M.King & H.Rob. e *P. diffusa* (Rich) Pruski, consideradas plantas ruderais, com ampla distribuição no mundo. *Praxelis kleinioides* com registro na Argentina, Bolívia, Brasil e Paraguai, e *P. decumbens* endêmica do Brasil (BFG 2018, Salgado et al 2022). Também temos *Lomatozona artemisiifolia*, *L. huntii* e *Eitenia polyseta*, endêmicos no Brasil e *Praxeliopsis mattogrossensis* G. Barroso., reportada para o estado do Mato Grosso, no Brasil (Barroso 1949, King & Robinson 1987) e provavelmente com registros na Bolívia. A primeira possibilidade é tranferir as espécies de *Lomatozona* e *Praxeliopsis mattogrossensis* para o gênero *Praxelis.* Dessa forma, outras características seriam incluídas em ***Praxelis sensu stricto***, como: 1) lâmina foliar pinatisecta (*Lomatozona*); 2) receptáculo convexo (*Lomatozona*); 3) carpopódio indistinto (*Lomatozona*); 4) cipselas biconvexas (*Eitenia polyseta*); 5) cipselas 2-3 costadas (*Eitenia polyseta*). Com a inclusão de mais marcadores, é provável que *E. hoffmanniana* e *Eitenia Praxelioides* se posicionem neste clado.

ii) Clado G: *Praxelis* (PP=1) e *Lomatozona* (PP=0.71)

Uma segunda opção é dividir este clado em dois gêneros. Sendo, *Praxelis*, com *P. clematidea P. diffusa***,** as quais são semelhantes morfologicamente e frequentemente confundidas. Não há um caracter morfológico forte que separe estas duas espécies, e sendo assim sugerimos mais estudos para que possa ser confirmado se devem ser mantidas como espécies separadas ou se devem ser sinonimizadas. O outro gênero seria *Lomatozona*, com *Praxelis kleinioides* e *P. decumbens* sendo sinonimizados a *Lomatozona*, mas o suporte é ruim, assim como o suporte morfológico. Dessa forma, o clado G2 não seria uma boa opção.

iii) Clado G: *Praxelis* (PP=1) *Lomatozona* (PP=0.99) *Praxeliopsis* (PP=0.96)

Por fim, uma terceira opção seria o reconhecimento de três gêneros. O gênero *Praxelis*, com *P. clematidea* e *P. diffusa*, que são espécies ruderais e com ampla distribuição. *Lomatozona* com *L. artemisiifolia* e *L. huntii*, reportadas apenas em afloramentos rochosos (King & Robinson, 1987; Ribeiro & Teles, 2015). *Praxeliopsis*, com *P. kleinioides*, *P. decumbens* e *Praxeliopsis mattogrossensis*. De certa forma, existe uma correlação com a distribuição geográfica. Porém, morfologicamente apenas *Lomatozona* se sustenta como gênero, por apresentar os seguintes

caracteres: lâmina foliar pinatisecta, glandulosa, carpopódio indistinto e pápus com poucas cerdas, curtas e irregulares (King & Robinson, 1987; Ribeiro & Teles, 2015). Já os outros dois gêneros, *Praxelis* e *Praxeliopsis*, compartilham caracteres morfológicos como brácteas involucrais decíduas e receptáculo cônico (Pacheco, 2014; Ribeiro et al., 2021).

Osmiopsis plumieri foi descrita como um gênero monotípico de Praxelinae. É endêmica do Haiti na ilha de Hispaniola, e possui características do gênero *Chromolaena* e de *Koanophyllon*, pertecente a subtribo Critoniinae, sendo que os dados moleculares obtidos confirmam seu status de espécie hibrida inter-tribal (Capítulo 3).

CONSIDERAÇÕES FINAIS

Tendo em vista dados da morfologia e moleculares, podemos tomar algumas decisões acerca dos gêneros de Praxelineae. De fato, a opção mais simples é transferir todos os gêneros para *Praxelis*, e atualizar a descrição morfológica de *Praxelis sensu lato*. A politomia existente entre os clados A, B, C, D e E, reforçados pela baixa amostragem no gênero *Chromolaena* levantam algumas dúvidas e seria desejável uma melhor amostragem. O clado G, embora com o suporte ligeiramente abaixo do ideal na árvore filogenética (PP=0,87), se sustenta morfologicamente. Acreditamos ser bastante provável que, a inclusão de mais espécies de *Praxelis*, e do maracador ETS, *ndh*I e *ndh*I-*ndh*G, irá melhorar o seu suporte filogenético. Além disso, possivelmente, o clado *Eitenia* + *Eupatoriopsis* (PP=0,73) que se encontra fora do mesmo, e associado a *Chromolaena* sensu stricto no clado F, poderá se posicionar dentro do Clado G. Já uma maior amostragem dentro de *Chromolaena* possivelmente nos revelará uma segregação em diversos gêneros com uma correlação fortemente geográfica.

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Tabela 1: Grupo externo e espécies alvo que foram usados na reconstrução filogenética da Subtribo Praxelinae. x = espécies com sequências disponíveis no GenBank; + = espécies sequenciadas nesse estudo. As espécies tipos estão destacadas em negrito**.**

Táxons		
Gêneros	**Praxelinae**	**Amostradas**
Chromolaena	**1.** *Chromolaena alvimii* R.M.King & H.Rob.	x
	2. *C. arrayana* (Gardner) R.M.King & H.Rob.	x
	3. *C. cf. ascendens* (Sch. Bip. ex Baker) R.M.King & H.Rob.	x
	4. *C. borinquensis* (Britton) R.M.King & H.Rob.	x
	5. *C. collina* (DC.) R.M.King & H.Rob.	x
	6. *C. congesta* (Hook & Ar n.) R.M.King &H.Rob.	x
	7. *C. christieana* (Baker) R.M.King & H.Rob.	+
	8. *C. gentianoides* (B.L. Rob.) R.M.King & H.Rob.	x
	9. *C. hirsuta* (Hook & Arn.) R.M.King &H.Rob.	x
	10. *C. horminoides* DC.	x
	11. *C. laevigata* (Lam.) R.M.King & H.Rob.	x
	12. *C. latisquamulosa* (Hieron) R.M.King & H.Rob.	x
	13. *C. leucocephala* Gardner	+
	14. *C. maximiliani* (Schrad. ex DC.) R.M.King & H.Rob.	+
	15. *C. morii* R.M.King & H.Rob.	x
	16. *C. odorata* (L.) R.M.King & H.Rob.	x
	17. *C. pseudinsignis* R.M.King & H.Rob.	x
	18. *C. rhinanthacea* (DC.) R.M.King & H.Rob.	x
	19. *C. sagittata* (A. Gray) R.M.King & H.Rob.	x
	20. *C. squalida* (DC.) R.M.King & H.Rob.	+
	21. *C. stachyophylla* (Spreng.) R.M.King & H.Rob.	x
Eitenia	**22.** *Eitenia polyseta* R.M.King & H.Rob.	x
Eupatoriospis	**23. *E. praxelioides* R.M.King & H.Rob.**	+
Lomatozona	**24. *Eupatoriopsis hoffmanniana* Hieron**	+
	25. *L. artemisiifolia* Baker	x
Praxeliopsis	**26.** *L. huntii* R.M.King & H.Rob.	x
Praxelis	**27. *Praxeliopsis mattogrossensis*** G.M.Barroso	+
	28. *P. clematidea* (Griseb.) R.M.King & H.Rob.	x
	29. *P. decumbens* (Gardner) A.Teles & R.Esteves	x
	30. *P. diffusa* (Rich.) Pruski	+
Osmiopsis	**31.** *P. kleinioides* (Kunth) Sch.Bip.	+
	32. *Osmiopsis plumieri* (Urb. & Ekman) R.M.King &H.Rob.	+
Galeana	**Grupo externo**	
	1. *Galeana pratensis* (Kunth) Rydb	
Ageratum	**Clado C**	
	1. *Ageratum conyzoides* L.	
Chacoa	**2.** *Ageratum houstonianum* Mill.	
Critonia	**3.** *Chacoa pseudoprasiifolia* (Hassl.) R.M.King & H.Rob.	x
	4.*Critonia hebebotrya* DC.	x
	5. *C. quadrangularis* (DC.) R.M. King & H.Rob.	x
	6. *C. morifolia* (Mill.) R.M. King & H.Rob.	x
Fleischmannia	**7. *C. sexangularis*** (Klatt) R.M.King & H.Rob.	x
	8. *Fleischmannia capillipes* (Benth) R.M.King & H.Rob.	x
	9. *F. incarnata* (Walter) R.M.King & H.Rob.	x
	10. *F. laxa* (Gardner) R.M.King & H.Rob.	x
	11. *F. sonorae* (A. Gray) R.M.King & H.Rob.	x
Idiothamnus	**12**. *F. remotifolia* (DC.) R.M.King & H.Rob.	x
Imeria	**13.** *Idiothamnus lilloi* (B.L. Rob.) R.M.King & H.Rob.	x
	14. *Imeria memorabilis* (Maguire & Wurdack) R.M.King & H.Rob.	x
Koanophyllon	**15.** *Koanophyllon ayapanoides* (Griseb.) R.M.King & H.Rob.	x
	16. *K. polystictum* (Urb.) R.M.King & H.Rob.	x
	17. *K. tinctorium* Arruda	x
	18. *K. villosum* (Sw.) R.M.King & H.Rob.	x
Steyermarkina		x
	19. *Steyermarkina pyrifolia* (DC.) R.M.King & H.Rob.	x
		x

Tabela 2: Quantidade de reagentes utilizados para o marcador nuclear ITS e de cloroplasto *ndh*F, e o protocolo de reações PCR.

Reagente	**ITS**	***ndh*F**
H_2O	8µl	11.5µl
Tampão 10x	2µl	2.5µl
DMSO	1,75µl	0
BSA	0	1.25µl
ITS-4 e ITS-5	2.5 µl	0
ndhF1212 e ndhF52	0	2.5 µl
$MgCl_2$	1µl	1µl
Taq	0,25µl	0,25µl
dNTP	2µl	2µl
DNA	1µl	1µl
Total:	**20µl**	**25µl**
Protocolo de Reações PCR		
Estágio/ ciclos	**ITS**	***ndh*F**
1 (1 x)	94 °C / 5:00 m	95 °C /3:00 m
2 (35 x)	94 °C / 00:45 s 50 °C / 0:45 s 72 °C / 1:00 m	95 °C / 0:30 s 54 °C / 0:40 s 72 °C / 1:00 m
3 (1x)	72 °C / 10:00 m 4°C (∞)	72 °C / 5:00 m 4°C (∞)

Tabela 3: Relação das espécies de Praxelinae e os marcadores moleculares que foram utilizados na análise bayesiana e os dados faltantes para cada marcador. x = marcador molecular incluído na reconstrução filogenética; - = marcador molecular não incluído.

Subtribo Praxelineae	**ITS**	**ETS**	**ndhF** 52-1212	**ndhF** 972-1587	**ndhI**	**ndhI ndhG**
1. *Chromolaena alvimii* R.M.King & H.Rob.	x	x	x	x	x	x
2. *C. arrayana* (Gardner) R.M.King & H.Rob.	x	x	x	x	x	x
3. *C. cf. ascendens* (Sch. Bip. ex Baker) R.M.King & H.Rob.	-	x	x	-	x	x
4. *C. borinquensis* (Britton) R.M.King & H.Rob.	x	-	-	-	-	-
5. *C. collina* (DC.) R.M.King & H.Rob.	x	-	-	-	-	-
6. *C. congesta* (Hook & Ar n.) R.M.King &H.Rob.	-	x	x	x	x	x
7. *C. christieana* (Baker) R.M.King & H.Rob.	x	-	-	-	-	-
8. *C. gentianoides* (B.L. Rob.) R.M.King & H.Rob.	-	x	x	-	x	x
9. *C. hirsuta* (Hook & Arn.) R.M.King &H.Rob.	-	x	x	-	x	x
10. *C. horminoides* DC.	x	-	-	-	-	-
11. *C. laevigata* (Lam.) R.M.King & H.Rob.	x	x	x	x	x	x
12. *C. latisquamulosa* (Hieron) R.M.King & H.Rob.	-	x	x	x	x	x
13. *C. leucocephala* Gardner	x	-	-	-	-	-
14. *C. maximiliani* (Schrad. ex DC.) R.M.King & H.Rob.	x	-	-	-	-	-
15. *C. morii* R.M.King & H.Rob.	x	x	x	x	x	x
16. *C. odorata* (L.) R.M.King & H.Rob.	x	x	x	x	x	x
17. *C. pseudinsignis* R.M.King & H.Rob.	x	x	x	x	x	x
18. *C. rhinanthacea* (DC.) R.M.King & H.Rob.	-	x	x	-	x	x
19. *C. sagittata* (A. Gray) R.M.King & H.Rob.	x	x	x	x	x	x
20. *C. squalida* (DC.) R.M.King & H.Rob.	x	-	-	-	-	-
21. *C. stachyophylla* (Spreng.) R.M.King & H.Rob.	x	x	x	x	x	x
22. *Eitenia polyseta* R.M.King & H.Rob.	x	-	-	-	-	-
23. *E. praxelioides* R.M.King & H.Rob.	x	-	x	-	-	-
24. *Eupatoriopsis hoffmanniana* Hieron	x	-	x	-	-	-
25. *Lomatozona artemisiifolia* Baker	x	-	-	-	-	-
26. *L. huntii* R.M.King & H.Rob.	x	-	-	-	x	x
27. *Praxeliopsis mattogrossensis* G.M.Barroso	x	-	x	-	-	-
28. *P. clematidea* (Griseb.) R.M.King & H.Rob.	x	-	x	x	x	x
29. *P. decumbens* (Gardner) A.Teles & R.Esteves	x	x	x	x	x	x
30. *P. diffusa* (Rich.) Pruski	x	-	x	-	-	-
31. *P. kleinioides* (Kunth) Sch.Bip.	x	-	x	x	x	x
32. *Osmiopsis plumieri* (Urb. & Ekman) R.M.King &H.Rob.	x	-	x	-	-	-
Dados Faltantes (%) por marcador	**18**	**53**	**31**	**65**	**43**	**43**
Dados faltantes (gaps) totais 41%						

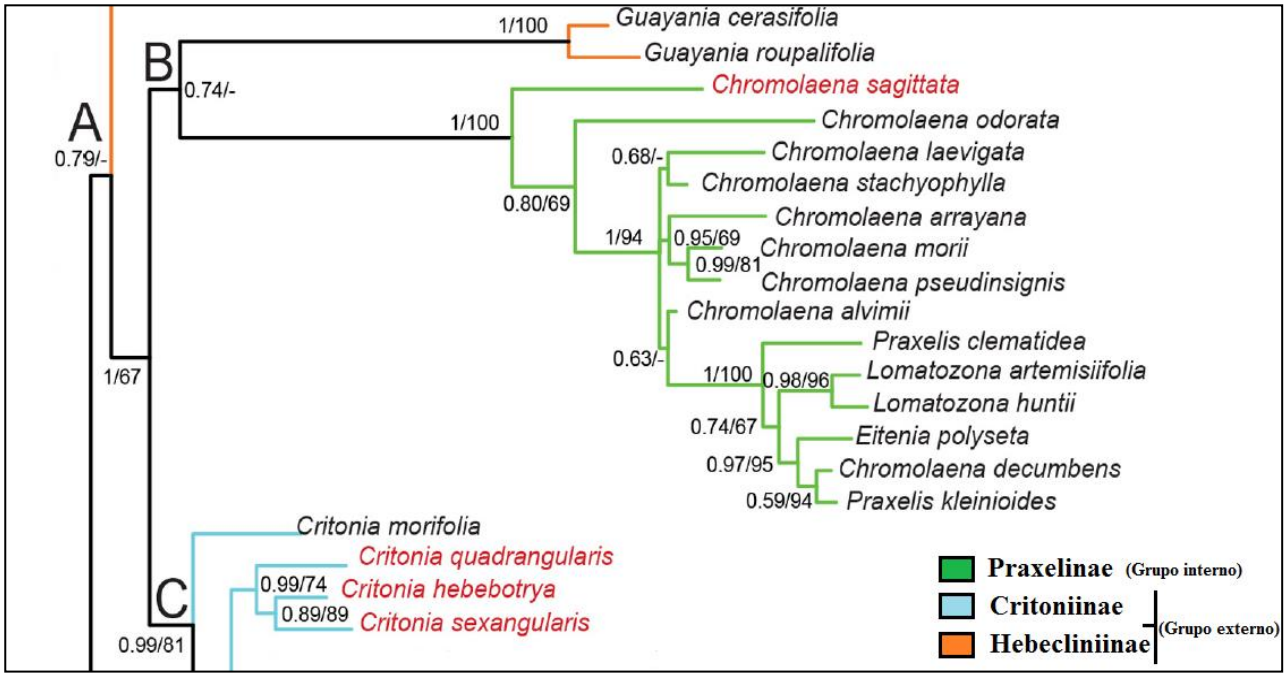


Figura 1. Árvore de consenso de regra majoritária representando as relações das espécies de Praxelinae. Probabilidades posteriores estão indicadasnos nós, seguida dos valores de máxima verossimilhança, quando os clados da análise bayesiana e ML coincidem. (**Fonte:** Rivera *et al.* 2016).

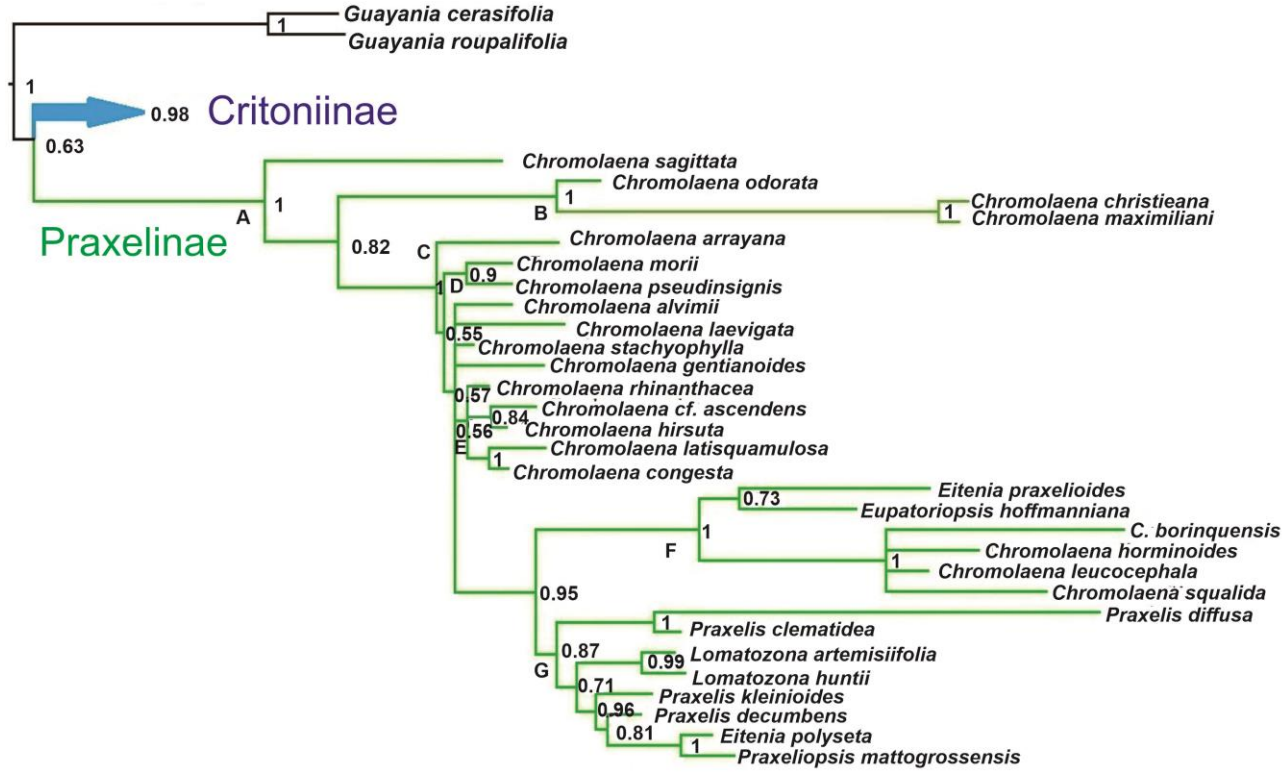


Figura 2. Árvore de consenso de análise Bayesiana dos marcadores (ITS, ETS, *ndh*F, *ndh*I, *ndh*I-*ndh*G, combinados). Probabilidades posteriores são indicadas nas ramificações.

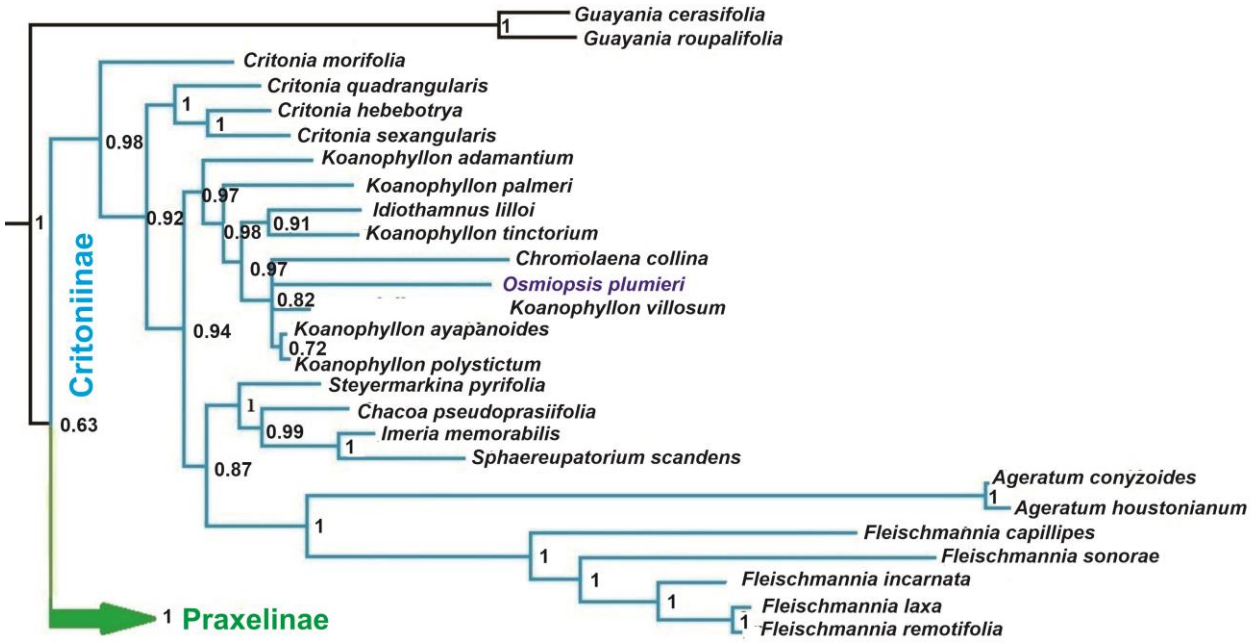


Figura 3. Árvore de consenso de análise Bayesiana dos marcadores (ITS, ETS, *ndh*F, *ndh*I, *ndh*I-*ndh*G, combinados). Probabilidades posteriores são indicadas nas ramificações. *Osmiopsis plumieri* está destacada em azul entre os *Koanophyllon* com suporte 0.97.

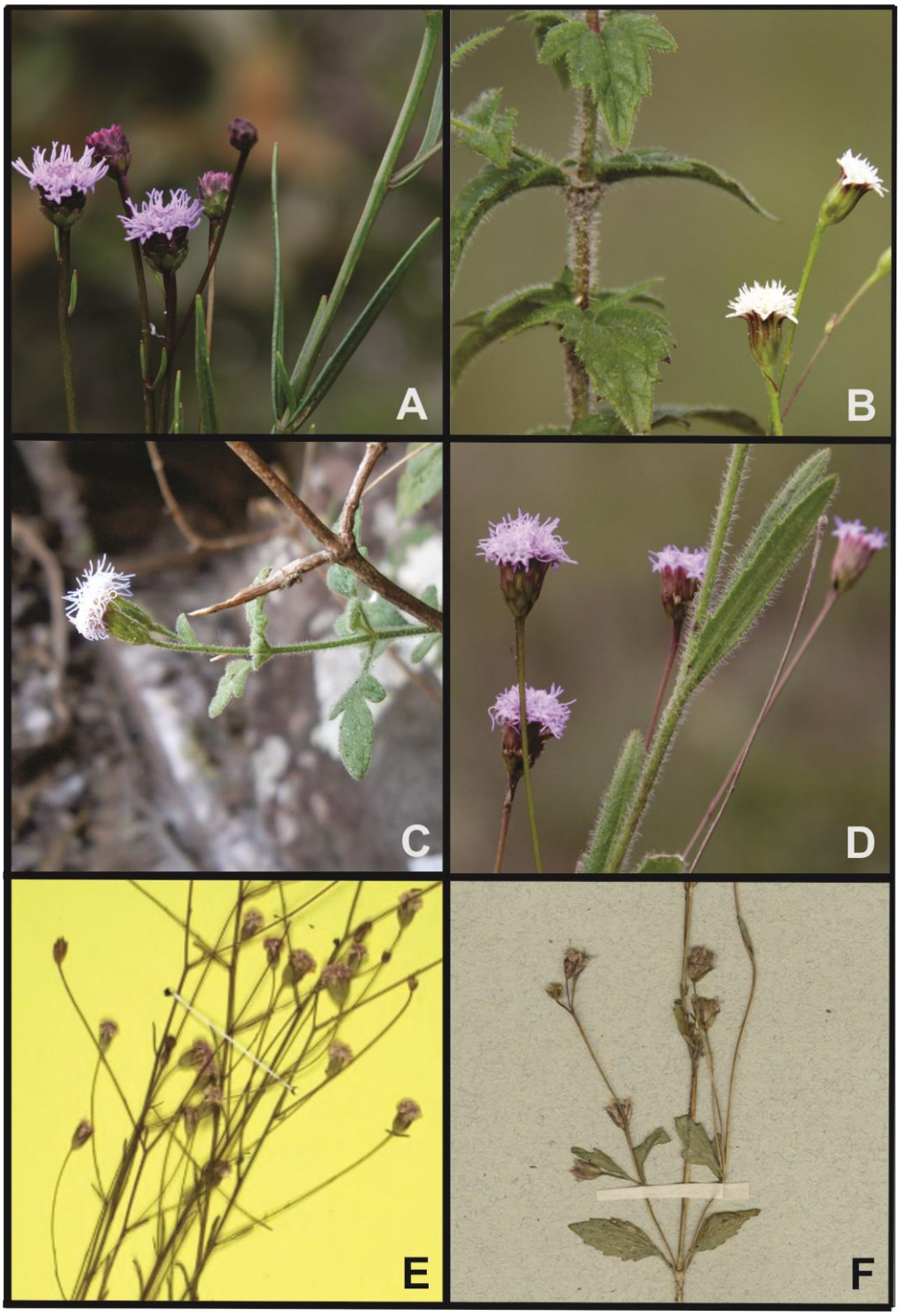


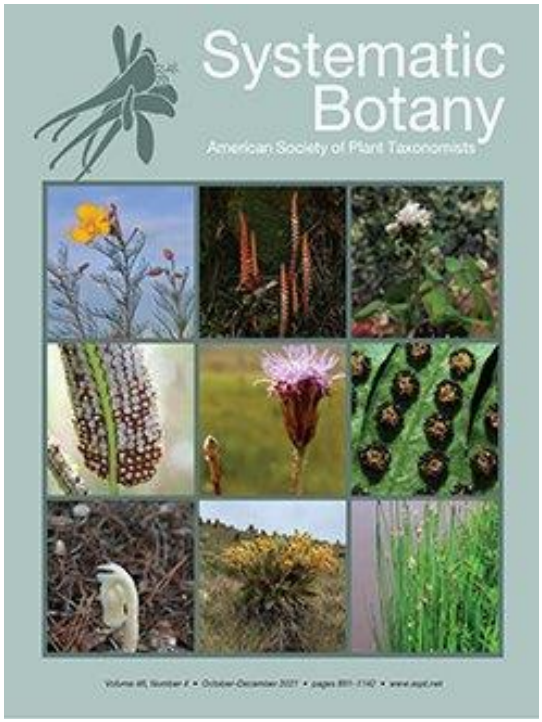
Figura 4. Representantes de todos os gêneros de Praxelineae. A *Chromolaena pseudinsignis.* B *Eitenia polyseta.* C *Lomatozona artemisiifolia*. D *Praxelis kleinioides.* E *Praxeliopsis matogrossensis*. F *Eupatoriopsis hoffmanniana.* (Fotos: A, B, D: Henrique J. C, C: A.M. Teles).

Figura 5. A. *Chromolaena christieana* (inflorescência). B. *Chromolaena maximiliani* (inflorescência). C. *Chromolaena odorata* (inflorescência). (Fotografias: A: A.L. Christ, B: R.N. Ribeiro, C: S. Bordignon).

Capítulo II

Re-evaluation of *Praxelis* (Asteraceae, Eupatorieae) in Brazil and description of *Praxelis scaturicola*, an unsual riverine species

Publicado em 2021 no periódico:



Re-evaluation of *Praxelis* (Asteraceae, Eupatorieae) in Brazil and description of *Praxelis scaturicola*, an unsual riverine species

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Abstract — ***Praxelis scaturicola***, a new *cerrado* species, is described and illustrated. The main morphological features of this new species are: (i) capitula usually isolated; (ii) vinaceous involucral bracts; (iii) reduced, glabrous, leaves well-spaced on the stem. This study also presents information on aspects of the new species' habitat, as well as field images and illustrations. *Praxelis scaturicola* is known only from the Paraúna municipality in Goiás state, Brazil. A key and comments on the Brazilian species of *Praxelis* are also presented with a special note on the status of *P. grandiflora*. Additionally, the synonymy of *P. macrocarpa* under *P. capillaris* is proposed.

Resumo — ***Praxelis scaturicola*** é aqui descrita e ilustrada como uma nova espécie do Cerrado. As principais características morfológicas da espécie nova são: (i) capítulos geralmente isolados; (ii) brácteas involucrais vináceas e (iii) folhas glabras reduzidas e bem espaçadas no caule. O presente estudo apresenta também informações sobre aspectos do habitat da nova espécie bem como fotos no campo e ilustrações. *Praxelis scaturicola* é conhecida apenas do município de Paraúna, Goiás, Brasil. Uma chave de identificação para as espécies circunscritas em *Praxelis* para o Brasil, assim como comentários sobre estas também são aqui apresentados, com destaque para o status de *P. grandiflora*. Adicionalmente, é proposta a sinonimia de *P. macrocarpa* em *P. capillaris*.

Keywords –Compositae, Endemism, Praxelinae, Riparian forest

Praxelis Cassini (1826) can be recognized by the combination of the following characters: caducous involucral bracts, conical epaleate receptacle, corolla lobes densely papillose on the inner surface, balusterform anther collars, obcompressed cypselas with asymmetrical carpopodia, and pappus of numerous capillary bristles (King and Robinson 1970, 1987, Hind 2014, Abreu 2015, Grossi et al. 2020). This genus was reduced to *Eupatorium* sect. *Praxelis* (Cass.) Benth. ex Baker (1876: 341), but later was re-established at generic level by King and Robinson (1970) concept that is currently widely accepted (Freire and Ariza Espinar 2014, Ribeiro and Teles 2015, Rivera et al. 2016, Abreu and Esteves 2017, Contro and Nakajima 2017, Abreu 2020 *Praxelis* in Flora do Brasil 2020).

With ca. 18 South American species, *Praxelis* is the second largest genus in subtribe Praxelinae (King and Robinson 1987), surpassed only by *Chromolaena* DC. (1836: 133). Sixteen *Praxelis* species have been reported from Brazil (Abreu 2020 *Praxelis* in Flora do Brasil 2020), of

which 15 have been described from or recorded in the Brazilian Cerrado and one only from the Atlantic Forest.

Based on recent taxonomic studies that included species of *Praxelis* (Hind 2014, Pacheco 2014, Ribeiro and Teles 2015, Teles et al. 2016, Contro and Nakajima 2017; Ribeiro 2017) and an ongoing study focused on the systematics and phylogeny of the Praxelinae, in production by the first author, we recognize a new species from the Paraúna municipality in the southern region of the state of Goiás, Brazil. We also propose that *Praxelis macrocarpa* V. Abreu & R. Esteves (2017) be synonymized to *P. capillaris* Candolle (1836), and a key and comments on the Brazilian species are also presented.

MATERIALS AND METHODS

The new species was initially identified in the UB herbarium and later recollected and analyzed in its natural habitat by the first author. Field images were processed with CorelDRAW software. The species was morphologically described with terminology that follows Roque and Bautista (2008) and Beentje (2012), and the line art illustration produced with the aid of a Carl Zeiss stereomicroscope. The map was made using ArcGIS 10.8 software. The evaluation of the conservation status of the new species was done using the GeoCAT tool (2020), as described by Bachman et al. (2011), using a 2 km grid (4 km^2 area) for IUCN (2012) occupancy analysis (AOO). The identification key was produced consulting specialized literature cited in the Introduction and our own samples. Synonymization and notes on the species were based on the literature, herbarium material, particularly from LP, UFG and UB, and analysis of types deposited in the UB and RB herbaria.

TAXONOMIC TREATMENT

Praxelis scaturicola Neves Ribeiro & V.L. Rivera, sp. nov. TYPE: BRAZIL. Goiás:

Mun. Paraúna, ca. 2 km do Bar Restaurante Ponte de Pedra, Mata Ciliar, −17.179723°, −50.836857°, 25 May 2020, *Rogério N. Ribeiro* & *Rodrigo N. Ribeiro 610* (holotype: UB!, isotypes: K!, UFG!, HUEG!, ALCB!).

Herbs, erect or decumbent, 17–50 cm tall. **Stems** cylindrical, glabrous. **Leaves** opposite, petiolate; petioles 1 mm long; blades linear or elliptical, 3–30 × 1–20 mm, apex acute, base acute, margins entire or sparsely dentate, revolute, trinervate, glabrous on both sides. **Inflorescences** terminal, capitula usually solitary or in 2-capitulate cyme. **Capitula** homogamous, discoid, pedunculate; peduncles 0.5–5 cm long, glabrous; involucre campanulate, 0.4–0.5 × 0.2–0.4 cm, involucral bracts 9–10, imbricate, vinaceous, 3–seriate, margins slightly ciliate, outer bracts 2 × 0.8 mm, oval, apex apiculate, intermediate bracts 5 × 1.8 mm, linear, apex obtuse, inner bracts 8 × 3 mm, linear, apex obtuse; receptacle conical, epaleate. **Florets** 30–42; corolla white, tubular, actinomorphic, tube ca. 4.5 mm long, externally and internally glabrous, lobes 0.5–0.8 mm long, papillose externally; anthers ca. 1.5 mm long, collar balusterform, connective appendix oval, 0.3 × 0.2 mm; style ca. 2 mm long, base cylindrical, glabrous, style branches ca. 1.5 mm long, clavate, long papillose. **Cypsela** prismatic, 4–ribbed, 1.5–2 ×0.5–0.48 mm, sparsely pilose, carpopodium asymmetrical; pappus persistent, 1.5–4 mm long, bristles free, 1-seriate, barbellate, mainly whitish, vinaceous at apex. Figures 1. A–J, 2.A–D

Distribution and Habitat—This species was collected in the core region of the Cerrado domain and is currently known only from the Ponte de Pedra River banks, in Paraúna, Goiás, Brazil. Plants were found growing on and in crevices between rocks along the river (Fig. 2C), rooted in clumps of

mosses of the genus *Sematophyllum* Mitten (1864), one of which was identified as *S. subsimplex* (Hedw.) Mitt. (widely distributed in Brazil) and the other as *S.* aff. *beyrichii* (Hornsch.) Broth.

Phenology—The species was collected bearing flowers and fruits in May and June.

Etymology—the specific epithet refers to its habitat, unusual in the Eupatorieae, rooted amongst the rocks on the banks of river rapids.

Conservation status—Following IUCN guidelines (2016), the new species here described can be classified as Critically Endangered (CR) due to having a range size smaller than 10 km^2 [B2b(i, iv) criteria]. Furthermore, the plants were found in an area disturbed by tourism and agriculture.

Notes— The new species presented here is described in the genus *Praxelis* due to the following morphological characteristics: conical receptacle (Fig. 1D); caducous involucral bracts; internally densely papillose corolla lobes (Fig. 1F); balusterform anther collar (Fig. 1G); papillose style branches (Fig. 1H) and the cypsela with an asymmetric carpopodium (Fig. 1I).

Of the 16 *Praxelis* species reported for Brazil, 15 occur in the Cerrado biome, the exception being *P. minima* A. Teles & P.L. Viana, recently described from the Atlantic Forest (Teles et al. 2016, Abreu 2020 *Praxelis* in Flora do Brasil 2020). Among these species, some are weedy, including *P. clematidea* (Griseb.) R.M. King & H. Rob., *P. kleinioides* (Kunth) Sch.Bip. (Fig. 3D), and *P. diffusa* (Rich.) Pruski (Fig. 3C), broadly distributed across South America. Some species, on the other hand, are quite restricted, such as *P. splettii* H.Rob. (Fig. 3F), which occurs only on rocky outcrops in the *Chapada dos Veadeiros* mountain chain, in the state of Goiás, Brazil. Likewise, the species described here is restricted to riparian forests with rocky outcrops along the banks of the Ponte de Pedra River (Fig. 4).

In the field *Praxelis scaturicola* can be differentiated from the remaining species of its genus due to the following combination of characters: leaves with linear to elliptic blades with entire

margins (or sparsely dentate) that are glabrous on both surfaces, generally isolated capitula, vinaceous involucral bracts and vinaceous or lilac tips of the pappus bristles and white corollas. It is contrasted with its most similar species in Table 1.

It would be of ecological interest to investigate if the fact that *P. scaturicola* is always rooted in clumps of mosses of family Sematophyllaceae is merely due to this being a favorable microhabitat (seeds are presumably trapped in the moist clumps), or if any additional form of interaction is operating. There are reports of Angiosperms whose seeds will only germinate in the presence of mosses (Bodenberg 1954). There is also evidence that enhanced germination and seedling establishment of Angiosperms in bryophyte carpets are due to lower wind speeds and higher moisture and nitrogen content in terricolous, arctic conditions (Sohlberg and Bliss 1984). However, the possibility that this could be due to mycorrhizal associations should not be, in our opinion, discarded. Asteraceae (including Eupatorieae) are 84% mycorrhizal with arbuscular mycorrhiza being dominant (Wang and Qiu 2006) while a saxicolous Sematophyllaceae (*Brotherella falcatula* Broth.) showed one of the highest incidences of arbuscular mycorrhiza in a sample of 12 families and 24 moss species analyzed by Zhang and Guo (2007). Recently described *P. minima* was also collected among mosses on rocky mountain tops (Teles et al. 2016).

Additional Material Examined (Paratypes)—BRAZIL. — GOIÁS: Paraúna, Ponte de Pedra, *Parque Estadual de Paraúna,* borda do Rio, 16° 09'56" S, 50° 38' 08" W, 1 June 2013, *J.E.Q. Faria et al.* 3769 (HUEG, UB!, RB!); *ibidem,* ca de 2 km do Bar e Restaurante Ponte de Pedra, Mata ciliar, 17°.179723 S, 50°.836857 W, 25 May 2020, *R.N. Ribeiro* & *R.N. Ribeiro 605, 606, 607, 608, 609* (UB!); *ibidem,* 20 June 2020, *R.N. Ribeiro* & *R.N. Ribeiro 615, 616* (UB!).

PRAXELIS CAPILLARIS (DC.) Sch.Bip., Jahresber. Pollichia 22-24: 254. 1866. *Ooclinium capillare* DC. (1836: 134). *Eupatorium capillare* (DC.) Baker, Fl. Bras. (Martius) 6(2): 341. 1876. nom. illeg., not *Eupatorium capillare* Ham. Prodr. Pl. Ind. Occid. (Hamilton) 51. 1825. TYPE: BRAZIL. Minas Gerais, [Serro], Serra do Frio, *Vauthier 311* (holotype G 00464701 [G00464701, photo!]; isotype P [P02476410, photo!]).

Haberle asperguloides Pohl ex Baker, Fl. Bras. (Martius) 6(2): 341. 1876. nom. nud., pro syn.

Ooclinium quinquepartitum Gardner ex Baker, Fl. Bras. (Martius) 6(2): 341. 1876. nom. nud., pro syn.

Praxelis macrocarpa V. Abreu & R. Esteves, syn. nov. Phytotaxa 303(1): 78. 2017. TYPE: BRAZIL. Federal District, Brasília, 16 Apr 1963, *J.M. Pires et al. 9123* (holotype UB!, isotype RB [00427089, photo !]).

Praxelis macrocarpa was described by Abreu and Esteves (2017) as a typical *Cerrado* species. Being based in Goiás, and studying *Praxelis* for his Ph. D., the first author first endeavored to find additional populations of this species for his study. Failure to find any, after repeated field trips, led to a closer examination of the description, illustration and type material of *P. macrocarpa*, as well as the variability of *P. capillaris*.

Abreu and Esteves (2017) recognized *P. macrocarpa* as closely related to *P. capillaris*, but differentiated it basically by the size of the flowers and fruits. However, analyzing the type and paratype collections in the UB herbarium and images of paratypes in specialized websites (e.g., Herbário Virtual Reflora and INCT virtual Flora & Fungos), we saw an overlap between the characters of the two species. The characters used by the authors in the description of the new species are very variable and therefore do not justify the recognition of two distinct species. The overlapping characters are presented in Table 2. Furthermore, the two species show a sympatric distribution in the *Cerrado* biome.

Since the characters used by Abreu and Esteves (2017) to differentiate *P. macrocarpa* from *P. capillaris* are variable, since this variation was found to be uncorrelated between the characters, and as no other characters were found that might differentiate the two species, we are forced to conclude that the recognition of *P. macrocarpa* as a new synonym of *P. capillaris* is in order. The present authors' new collections of *Praxelis capillaris*, the search for *P. macrocarpa* in the field, as well as two publications that appeared almost simultaneously with the description of *P. macrocarpa* (Contro and Nakajima 2017, Ribeiro 2017), have in fact revealed that *P. capillaris* is a very morphologically plastic species, much more so than suggested by the earlier literature. It would be of interest to investigate if this morphological plasticity is associated to the existence of different levels of ploidy, as seen in *Praxelis clematidea* (Turner et al. 1979, Robinson et al. 1989, Wulff et al. 1996) and *Praxelis kleinioides* (Turner and Irwin 1960, Robinson et al. 1989).

PRAXELIS KLEINIOIDES (Kunth) Sch.Bip., Jahresber. Pollichia 22-24: 254. 1866. *Eupatorium kleinioides* Kunth, Nov. Gen. Sp. [H.B.K.] 4(15): 94 (ed. fol.). 1818. TYPE: VENEZUELA. Crescit in aridis montium Cocollar et Tumiriquiri, alt. 600 hex. (Nova Andalusia.). *A.J.A. Bonpland & F.W.H.A. von Humboldt 271* (P [P00320078, photo!])

Praxelis grandiflora (DC.) Sch. Bip. Jahresber. Pollichia 22–24: 254. 1866. *Ooclinium grandiflorum* DC., Prodr. 5: 134. 1836. TYPE: BRAZIL. prov. Sancti-Pauli. *434* (G-DC [G00464699, photo!], P [02476807, photo!])

We follow Baker (1876) in not accepting this species (treated by him as *Ooclinium grandiflorum* DC. and synonymized under *Eupatorium kleinioides* Kunth, the basionym of *Praxelis kleinioides*). This is in disagreement with the recent treatments of *Praxelis* for Brazil by Abreu (2015, 2020) that recognize *P. grandiflora* as a good species. The name *P. grandiflora* is in current use and has been adopted by such Asteraceae specialists as H. Robinson, J.N. Nakajima, E.K.O.

Hattori and one of us (J.B. Bringel) to identify specimens akin to *P. kleinioides* but with narrow, elliptic leaves. The main characters used by Abreu to differentiate the two species (after analyzing her key and the descriptions) are the following: (1) *P. grandiflora* has xylopodiferous roots, pubescent stems, elliptic leaves, and involucral bracts non-caducous to rarely caducous; while (2) *P. kleinioides*: shows simple roots, hirsute stems, ovate leaves, and involucral bracts very caducous.

We have analyzed several specimens of both species and were unable to detect xylopodia in any of them, while the differences in stem indumentum, leaf shape and the caducity of the involucral bracts appear to be uncorrelated and follow a gradient. The distribution in the states of Minas Gerais, São Paulo and Paraná, Brazil also overlaps. Other authors (Nakajima 2000, Esteves 2001, Pacheco 2014) have also reported a close morphological affinity between these two species, listing as distinctive characters the leaf shape, the involucre length and shape, and the number of florets per capitulum, that we consider as extremely variable and not supportive of a clear and precise distinction between the two taxa.

This morphological plasticity could be associated to the different levels of ploidy known to occur in *Praxelis kleinioides* (Turner and Irwin 1960, Robinson et al. 1989). After analyzing type specimens and protologues, literature (Nakajima 2000, Esteves 2001, Abreu 2015, Pacheco 2014), and other specimens (cited in Abreu 2015) we are unable to clearly recognize *P. grandiflora* as separate from *P. kleinioides*. For this reason, we are provisionally following Baker (1876) until additional molecular and cytogenetic studies can clarify if *P. grandiflora* should be recognized as a separate taxon.

KEY TO BRAZILIAN PRAXELIS

1. Leaves all opposite …….....2

2. Leaves petiolate…….....3

3. Capitula in corymbiform inflorescences 4

4. Leaf blade ovate, margin incised-crenate ..... *P. clematidea*

4. Leaf blade elliptic, margin serrate..... *P. ostenii*

3. Capitula solitary, in simple dichasia or dichasial cymes…….....…….…….5

5. Capitula in simple dichasia or dichasial cymes; involucral bracts greenish…….....……*P. diffusa*

5. Capitula solitary; involucral bracts vinaceous.....6

6. Leaf blade linear to elliptic; corolla white..... *P. scaturicola*

6. Leaf blade ovate; ovate to lanceolate; corolla lilac.....7

7. Stem decumbent; leaf blade subcoriaceous…….....……...……... *P. decumbens*

7. Stem erect; leaf blade membranous …….....……..…….. *P. minima*

2. Leaves sessile 8

8. Leaf blade pinnately dissected..... *P. odontodactyla*

8. Leaf blade entire (linear, oblanceolate, lanceolate, oblong or elliptic) 9

9. Leaf blade linear to narrow-elliptic, uninervate…….....……10

10. Inflorescence corymbiform, involucral bracts non-caducous..... …*P. sanctopaulensis*

10. Inflorescence cymose, involucral bracts caducous..... *P. asperulacea*

9. Leaf blade elliptic, lanceolate, oblanceolate or oblong, trinervate.....11

11. Capitula in simple dichasia or dichasial cymes……..….....…..…*P. kleinioides*

11. Capitula solitary……..……12

12. Habit virgate, single stem suberect or procumbent, sometimes apically branched; leaf blade lanceolate; style branches linear …….....……. *P. insignis*

12. Habit cespitose, stems erect; leaf blade elliptic; style branches clavate….....……...*P. missionum*

1. Leaves whorled at the base, alternate or opposite at base and alternatedistally……..…..…….. 13

13. Leaves opposite at base and alternate at apex; leaf blade linear..... *P. splettii*

13. Leaves whorled or in a basal rosette; leaf blade filiform or elliptic.....14

14. Leaves in a basal rosette; leaf blade elliptic, margin serrate..... *P. basifolia*

14. Leaves whorled; leaf blade filiform, margin entire..... *P. capillaris*

COMMENTS ON PRAXELIS IN BRAZIL

1. PRAXELIS ASPERULACEA (Baker) R.M.King & H.Rob., Phytologia 20: 194. 1970.

   This species is endemic to northern Brazil, in the states of Amazonas, Pará and Roraima (Abreu, 2020). It is a predominantly Amazonian species with some collections from the *Pantanal/Cerrado* interface. In Serra dos Carajás, Pará it was reported as growing in swampy and grassland vegetation on ironstone (*canga*) soil (Cruz et al. 2016). It also occurs along sandy riverbanks (Species Link 2021).

2. PRAXELIS BASIFOLIA (Malme) R.M.King & H.Rob., Phytologia 20: 194. 1970.

   This species is endemic to Central Western Brazil in the states of Goiás, Mato Grosso and Mato Grosso do Sul and Distrito Federal (Abreu 2020). A typical *Cerrado* domain species, not very commonly collected, it occurs in seasonally inundated fields (*campos úmidos*) and swampy grassy areas (*veredas*) dominated by *Mauritia flexuosa* L.f. palms (Species Link 2021).

3. PRAXELIS CAPILLARIS (DC.) Sch.Bip., Jahresber. Pollichia 22-24: 254. 1866. Fig. 3 A.

This Brazilian endemic species occurs in the Distrito Federal, and in the state of Goiás and southeastern Minas Gerais (Abreu 2020). A typical *Cerrado* domain species, very commonly collected in southern and highland *Cerrado* areas.

4. PRAXELIS CLEMATIDEA (Griseb.) R.M.King & H.Rob., Phytologia 20: 194. 1970.

This widespread species can be found in Brazil in the North, in the states of Acre, Pará, Roraima and Tocantins; in the Northeast, in the states of Alagoas, Bahia, Ceará, Paraíba, Pernambuco, Piauí, Rio Grande do Norte and Sergipe; in the Central West, in the states if Distrito Federal, Goiás, Mato Grosso do Sul and Mato Grosso; in the Southeast, in the states of Espírito Santo, Minas Gerais, Rio de Janeiro and São Paulo and in the south, in the states of Paraná, Rio Grande do Sul and Santa Catarina (Abreu 2020). It is common in disturbed areas throughout the country and is often misidentified as *Ageratum conyzoides* (L.) L. However, it is easily distinguished by its bristly pappus (paleaceous in *A. conyzoides*). Outside Brazil, it grows in Argentina, Bolivia and Paraguay (Cabrera et al. 1996; King and Robinson 1987; Freire 2008; Robinson 2014) and was recently found in Uruguay (Salgado et al. 2020).

5. PRAXELIS DECUMBENS (Gardner) A. Teles & R. Esteves, Phytotaxa. 278: 49. 2016. Fig. 3 B.

This Brazilian endemic species is distributed in the Southeast, in the states of Minas Gerais and São Paulo. It occurs in the Cerrado biome (Abreu 2020) and on grass-dominated habitats on mountain tops in the Atlantic Forest biome. *P. decumbens* has only recently been recognized as a *Praxelis*, being traditionally included in *Chromolaena* (King and Robinson 1987).

6. PRAXELIS DIFFUSA (Rich.) Pruski, Brittonia 50: 475. 1998. Fig. 3 C.

This species is widely distributed in Brazil, it occurs in the North, in the states of Amazonas and Pará; in the Northeast, in the states of Bahia, Maranhão and Paraíba; in the Central-West in the states of Distrito Federal, Goiás and Mato Grosso do Sul; in the Southeast, in the states of Minas Gerais, Rio de Janeiro and São Paulo and the South in the states of Paraná, Rio Grande

do Sul and Santa Catarina (Abreu 2020). It is common in disturbed areas throughout the country, and it is often misidentified as *Ageratum conyzoides* or as *Praxelis clematidea*. It is also distributed in Bolivia, Colombia, French, Guyana, Peru, Suriname and Venezuela (Avila et al. 2019, Badillo 2001, King and Robinson 1987, Pruski 1998, Robinson 2014).

7. PRAXELIS INSIGNIS R.M.King & H.Rob., Phytologia 20: 194. 1970.

   This Brazilian endemic species is rare, with a few collections from Goiás and Minas Gerais, from the Cerrado biome (Abreu 2020) and vegetation type cited as savanna.

8. PRAXELIS KLEINIOIDES (Kunth) Sch.Bip., Jahresber. Pollichia 22-24: 254. 1866. Fig. 3 D & 3 E.

   This species is widely distributed. In Brazil there are confirmed populations in the Northeast in the state of Bahia; in the Central West in Distrito Federal, Goiás, Mato Grosso and Mato Grosso do Sul; in the Southeast in the states of Minas Gerais and São Paulo and in the South in the state of Paraná. It is commonly collected in the Cerrado biome, including in disturbed areas. Outside of Brazil, it is found in Argentina, Colombia, Peru and Venezuela (Avila et al. 2019, Freire and Ariza Espinar 2014, King and Robinson 1987).

9. PRAXELIS MINIMA A.M.Teles & P.L.Viana. Phytotaxa 278: 49 (2016)

   A Brazilian endemic known only from the type; it is reported as growing in mossy vegetation pockets on top of the Pico do Papagaio mountain at 1900 m above sea level. It is the only *Praxelis* recorded exclusively from the Atlantic Forest domain (Teles et al. 2016).

10. PRAXELIS MISSIONUM *(Malme)* R.M.King & H.Rob., Phytologia 20: 195. 1970.

    In Brazil, this species is found in the South in the states of Paraná and Rio Grande do Sul, with records from the *Pampa, Atlantic Forest* and *Cerrado* biomes in grass-dominated habitats such as *campos limpos*. It also occurs in neighboring regions of Argentina (Freire and Ariza Espinar 2014). This species apparently presents extreme, and very variable numbers of flowers per

capitulum. The original description simply stated numerous flowers (Malme 1932), as did the older literature (Cabrera et al. 1996, Freire 2008). Christ & Ritter (2019) recently reported c. 60 flowers for *P. missionum* in Rio Grande do Sul, Brazil, while Abreu (2020) found between 137 and 208 flowers for the Brazilian flora, observing that this number was high for *Praxelis*. We analyzed specimens from Northern Argentina (the type locality) and found between 85 and 119 flowers, which reinforces the idea that this character is variable in *P. missionum.*

11. PRAXELIS ODONTODACTYLA (B.L.Rob.) R.M.King & H.Rob. Phytologia 20: 195. 1970.

This Brazilian endemic species is reported for the Central West region in the Distrito Federal and state of Goiás and in the Southeast, in the state of São Paulo (Abreu 2020). It dwells in the Atlantic Forest and *Cerrado* biomes (Species Link 2021), associated with Southern latitudes or higher elevations.

12. PRAXELIS OSTENII (B.L.Rob.) R.M.King & H.Rob., Phytologia 20: 195. 1970.

In Brazil, this species occurs mostly in the Central West in the Distrito Federal, and states of Goiás, Mato Grosso and Mato Grosso do Sul, and in the South in the state of Paraná (Abreu 2020). It is a typical Cerrado species but not very common. It has also been reported from Argentina and Paraguay (Cabrera et al. 1996, Freire 2008) and there is a single collection from the Brazilian Northeast in the state of Sergipe, a surprising disjunction.

13. PRAXELIS SANCTOPAULENSIS (B.L.Rob.) R.M.King & H.Rob., Phytologia 65: 488. 1989.

This species is endemic to Brazil where it is found in the Central West in the states of Goiás and Mato Grosso, in the Southeast in the state of São Paulo and in the South in the states of Paraná and Santa Catarina. It occurs in the Atlantic Forest and the Southern *Cerrado*, in highland fields, grassy fields (*campos limpos*) and savannas (c*errado sensu stricto*) (Abreu 2020).

14. ***Praxelis scaturicola*** Neves Ribeiro & V.L. Rivera, sp. nov.

Described here, this species is endemic to the *Cerrado* biome with an apparently narrow-endemic distribution. It has been recorded only from Goiás, from gallery forest riverine habitats with rocky outcrops in a single locality.

15. PRAXELIS SPLETTII H.Rob., Phytologia 88: 148. 2006. Fig. 3 F.

This species is endemic to the *Cerrado* biome. It is rare and has been reported only from the *Chapada dos Veadeiros*, in central Goiás (Ribeiro 2017), recorded as growing in seasonally waterlogged fields (*campos úmidos*) and rocky seasonally waterlogged fields (*campos úmidos rupestres*).

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AUTHOR CONTRIBUTIONS

RNR produced the key, the colored plates and the map, re-collected and photographed the new species in the field, produced the description of the new species and wrote the first draft of the manuscript. VLR contributed significantly to the discussion, made suggestions that improved the key and the description of the new species, and commented on the final version of manuscript. JBAB analyzed additional specimens, made suggestions that improved the description and

commented on the final version of manuscript. VGS analyzed additional specimens and contributed to the final version of the manuscript. CEBP supervised, suggested the specific epithet and made significant contributions to the final version of the manuscript.

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TABLE 1. Comparisons of *Praxelis scaturicola* with similar *Cerrado* species.

Character	*P. asperulacea*	*P. basifolia*	*P. decumbens*	*P. scaturicola*
Habitat	River banks	Wet grasslands	Grasslands, rocky outcrops	River Banks
Habit	Erect herb	Erect herb	Decumbent	Decumbent
Leaf blades	Linear to narrow-elliptic, membranous, pubescent	Ovate, elliptic, or lanceolate membranous, pubescent	Ovate, subcoriaceous, glabrescent	Linear to elliptic, membranous, glabrous
Capitulescence	Triple cyme	Isolated capitula	Isolated capitula	Isolated capitula
Flower color	Lilac	Lilac	Lilac	White
Anther collar	Balusterform	Balusterform	Non differentiated	Balusterform

TABLE 2. Main diagnostic characters used by Abreu and Esteves (2017) and re-analyzed by us to distinguish *P. macrocarpa* and *P. capillaris*, based on Esteves 2001; Pacheco 2014; Ribeiro & Teles 2015; Abreu & Esteves 2017; Contro & Nakajima 2017; Ribeiro 2017.

	P. macrocarpa (fide Abreu & Esteves 2017)	*P. macrocarpa* (our analysis of type material)	*P.capillaris*
Number of series of Involucral bracts	3–4	3–6	4–7
Involucre (length in mm)	8–10	5–9	5–9
Involucral bracts	Persistent	Caducous	Caducous
Fruit (length in mm)	3–3.5	1.7–2	1.2–2
Flower (length in mm)	6–7	4.5–6.5	3.5–5.7
Anther apical appendage	Obtuse	Obtuse	Apiculate/oblong/cuspidate

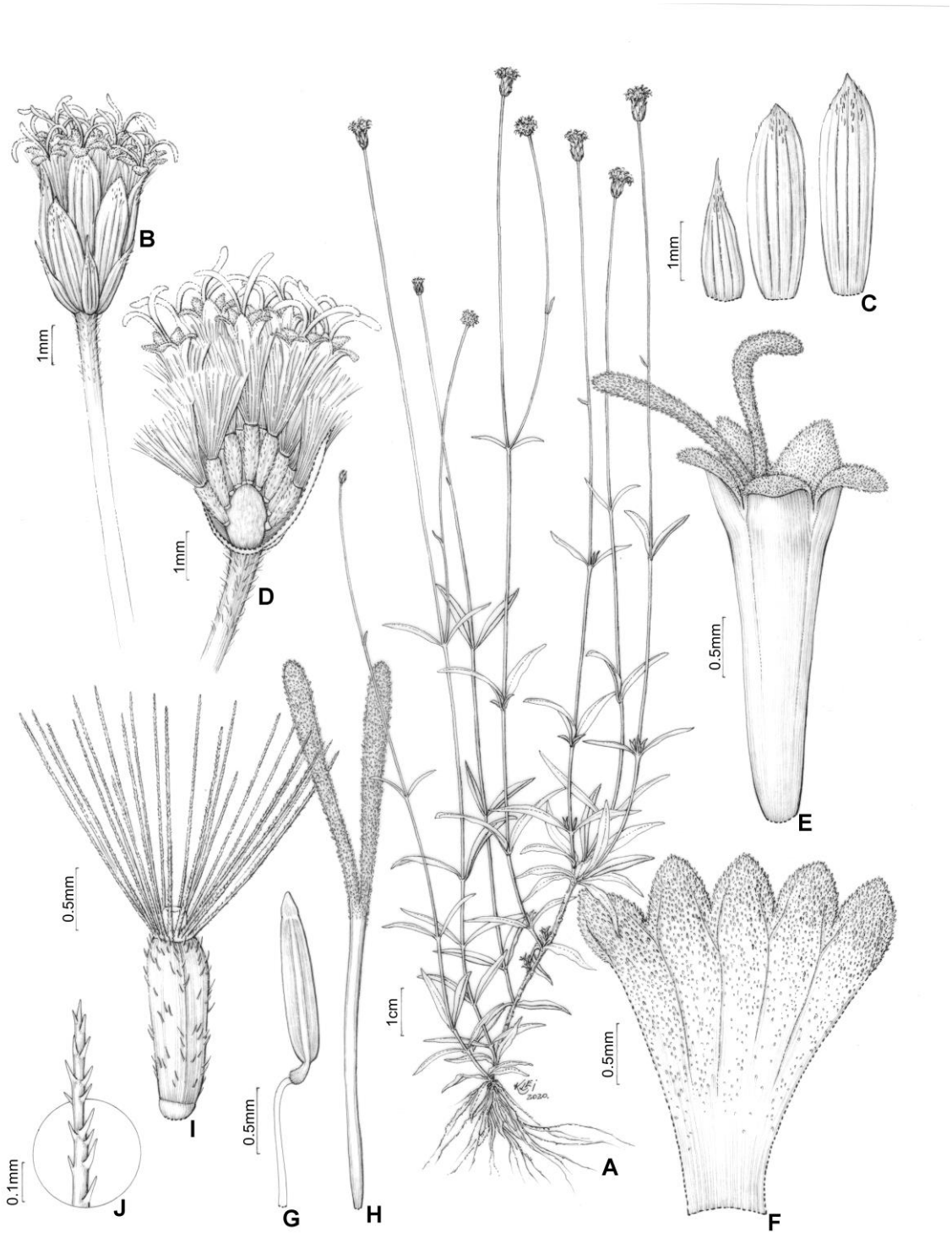

FIG. 1. *Praxelis scaturicola* Neves Ribeiro & V.L. Rivera. A. Habit. B. Capitulum. C. Involucral bracts. D. Conical receptacle. E. Corolla. F. Internally papillose corolla lobe. G. Filament with balusterform anther collar. H. Glabrous style, with papillose appendages. I. Prismatic cypsela, uniseriate pappus. J. Pappus. (Drawings from the holotype by Klei Souza).

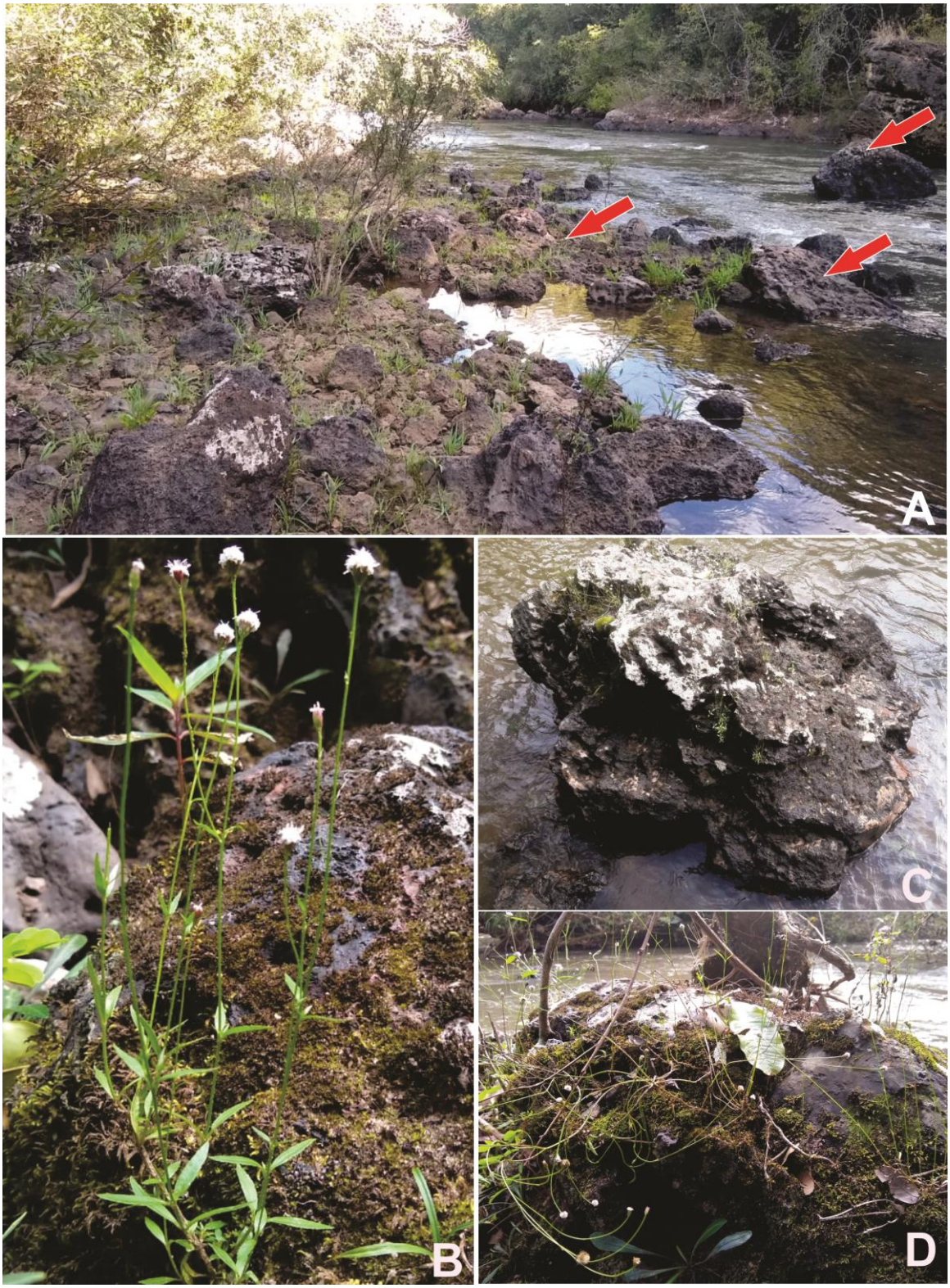

FIG. 2. *Praxelis scaturicola* Neves Ribeiro & V.L. Rivera in the field. A. Habitat (Riparian forest with rocky outcrops). B. Habit. C. Population fixed on a rock. D. Population with decumbent growth. Images: A–D: *R.N. Ribeiro*).

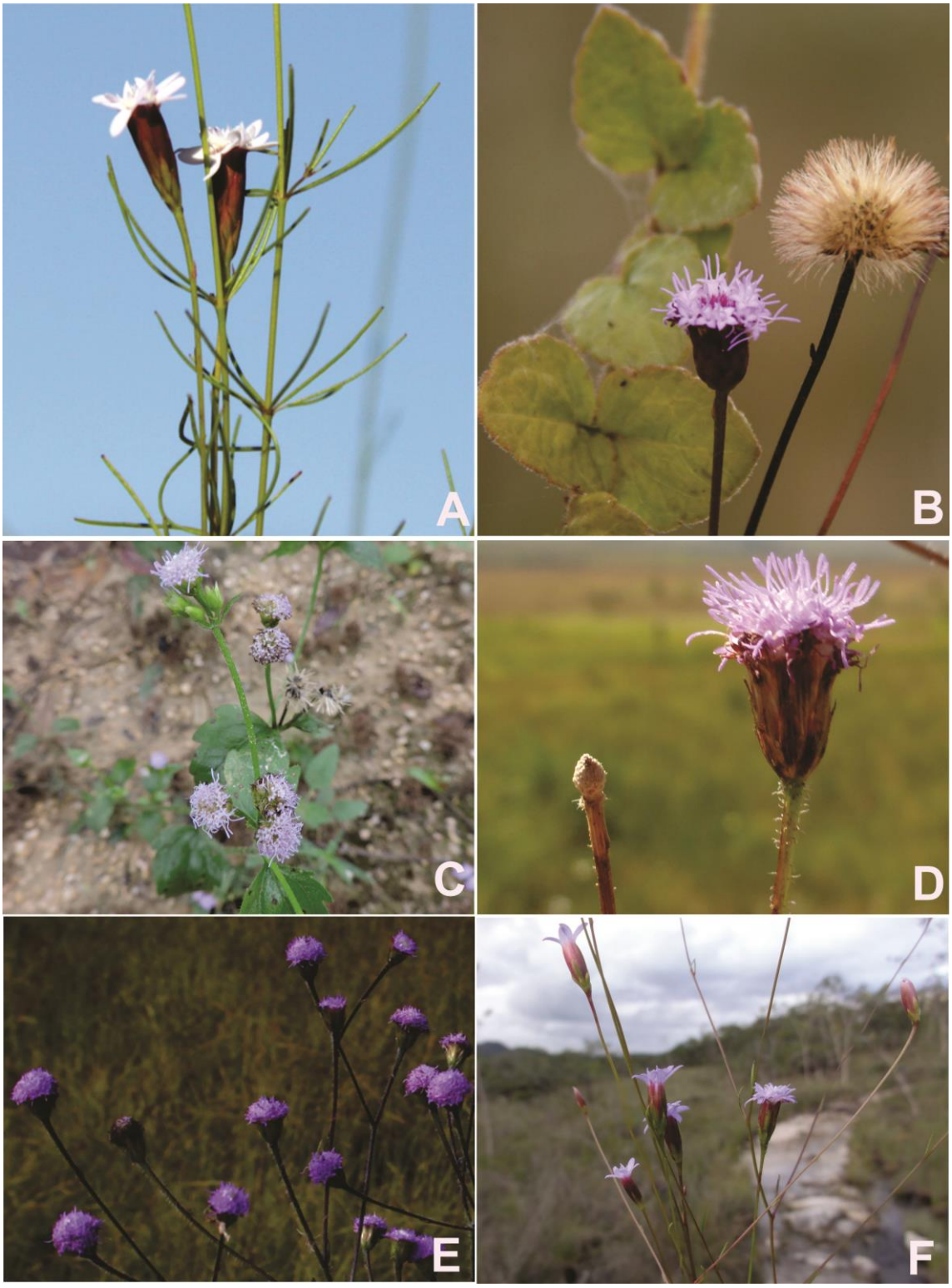

FIG. 3. Selected Brazilian species of *Praxelis.* A. *P. capillaris*. B. *P. decumbens*. C. *P. diffusa*. D. *P. kleinioides*. E. *P. kleinioides*. F. *P. splettii*. (Photographs: A–B, E Henrique J. C. Moreira, C–D, F: *R.N. Ribeiro*).

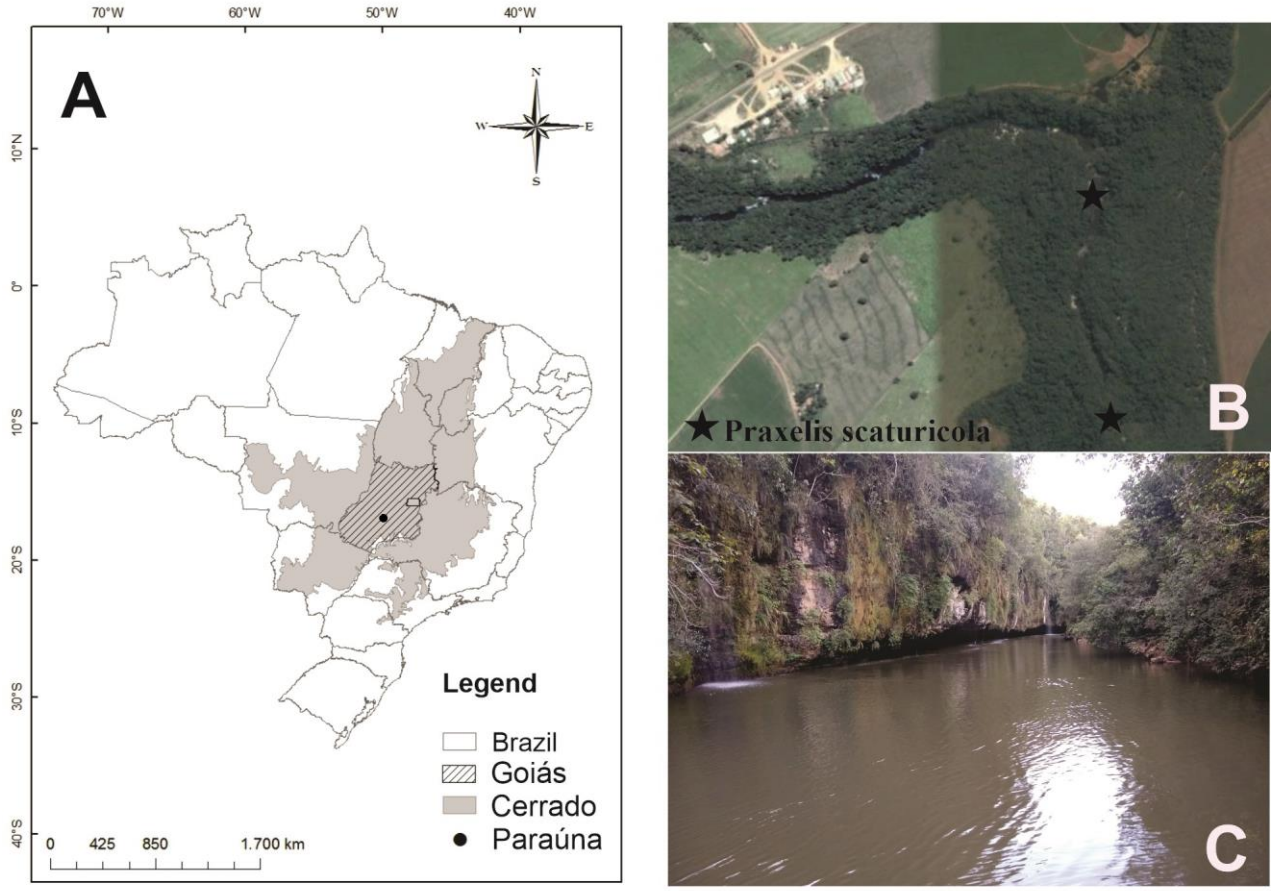

Fig.4. Location of the collections of *Praxelis scaturicola* Neves Ribeiro & V.L. Rivera. A. Municipality of Paraúna, in the southern region of the *Cerrado*, Goiás, Brazil. B. Habitat of two collections along the Ponte de Pedra River. C. River Ponte de Pedra. (Photographs: A–C. *R.N. Ribeiro*).

Capítulo III

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x *Koanoxelis*: a substitute nothogeneric name for *Osmiopsis* (Asteraceae) in view of molecular confirmation of its inter-generic and inter-subtribal hybrid status

A ser enviado ao periódico: TAXON

x *Koanoxelis*: a substitute nothogeneric name for *Osmiopsis* (Asteraceae) in view of molecular confirmation of its inter-generic and inter-subtribal hybrid status

Running title: *Koanoxelis* (Asteraceae) a new nothogenus

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Summary

Osmiopsis is a monotypic genus of Asteraceae (Tribe Eupatorieae) endemic to the Caribbean Island of Hispaniola. It is one of the seven genera that jointly comprise the subtribe Praxelinae. Its only species was originally described as *Eupatorium plumieri* in 1931. *Osmiopsis* was elevated to generic status in 1975; the authors of the genus believed it to be of hybrid origin and proposed as putative parents *Chromolaena* (subtribe Praxelinae) and *Koanophyllon* (subtribe Critoniinae). As a result of our phylogenetic study of the Subtribe Praxelinae, we were able to gather further evidence on the origin of this genus, reconstructed within a matrix of 202 species of Tribe Eupatorieae. DNA was extracted from a paratype (Ekman 6490) of *O. plumieri*, and the ITS nuclear region and *ndh*F chloroplast region were amplified. The ILD test revealed significant incongruity between the nuclear and chloroplast trees. Based on the ITS data, *O. plumieri* emerged in a strongly supported clade (posterior probability=0.98) of 23 species of Critoniinae, closely allied to six species of *Koanophyllon*. Based on the *ndh*F data, *O. plumieri* emerged in a strongly supported clade

(posterior probability=1) of 20 species of Praxelinae that included ten species of *Chromolaena*, four species of *Praxelis* and three other genera; it was closely allied to *Praxelis*. *Osmiopsis plumieri* shares the following characteristics with *Koanophyllon:* (i) funellform corolla with a cylindrical base; (ii) triangular corolla lobes; and (iii) anther appendages wider than longer. *O. plumieri* also shares the following morphological characters with *Chromolaena* and *Praxelis*: (i) semi-scandent habit; and (ii) deciduous involucral bracts. King and Robinson´s hypothesis of *Osmiopsis* as a hybrid taxon between *Chromolaena* and *Koanophyllon*, based on its morphology, is hereby confirmed by molecular evidence. As far as we are aware, this is the first case of molecular confirmation of a nothogenus in the Asteraceae across subtribes. *Osmiopsis* is to be henceforward recognized as a nothogenus at intergeneric and intersubtribal level under the name *Koanoxelis* following Article 6 of the Internationational Code of Nomenclature for algae, fungi and plants.

Key words: Compositae, Critoniinae, Praxelinae

Introduction

Subtribe Praxelinae is one of the 17 subtribes of the Tribe Eupatorieae in the Asteraceae and has been considered monophyletic (Rivera & al., 2016). *Osmiopsis* R.M. King & H. Robinson was described as a monotypic genus endemic to the Caribbean Island of Hispaniola. It is one of the seven genera that comprise subtribe Praxelinae King & Robinson (1980a) and the only genus that does not grow in South America. . *Osmiopsis plumieri*, the single species of the genus, was originally described as *Eupatorium plumieri* Urban & Ekman (1931) based on several Ekman collections from Haiti in the early 20th century. The epithet that appears in the original publication was spelled *plumerii* but this has been corrected following Article 60.4 of the Interntional Code for the Nomenclature of Plants and Fungii, as it is highly likely that it is a reference to French monk and botanist Charles Plumier (1646-1704), one of the first Europeans to collect plants in Haiti.

The new combination *Chromolaena plumieri* (Urban & Ekman) R.M. King & H. Robinson was published (King & Robinson, 1970) based on *Eupatorium plumieri* Urban & Ekm. However, five years later, King and Robinson recanted on the taxonomic position of this species and erected the new genus *Osmiopsis* King & H.Rob. to accommodate it (King & Robinson, 1975). The publication of *Osmiopsis* was rather unusual in that the authors stated that the genus was of probable intergeneric hybrid origin. They argued that the scandent habit and the 4–5-seriate, imbricate, deciduous, involucral bracts were characteristic of *Chromolaena* DC. (Subtribe

Praxelinae), while the wide, glandulose corolla lobes, the short anther appendages and the enlarged tips of the stylar branches were typical of *Koanophyllon* Arruda (Subtribe Critoniinae). They further stated that the hybrid origin was: "based on circumstantial evidence of character distribution" and that "evidence would indicate further that such hybrids were totally viable and capable of further evolution, but that the hybridizations all apparently date from some earlier period and are not continuing at this time" (King & Robinson, 1975, pg. 250). These statements were not supported by any further discussion, nor by any numerical analysis or molecular data. The putative parent in *Koanophyllon* proposed by King and Robinson were either *K. selleanum* (Urb.) King & Robinson or *K. phanioides* (Krug & Urb.) King & Robinson; both these species are endemic to Hispaniola (POWO, 2023). Robinson did not propose a putative parent in *Chromolaena*, merely stating that *O. plumieri* had the characteristic involucre (deciduous) and habit (scandent and weakly branched) of a *Chromolaena*.

Osmiopsis plumieri is known from at least 12 collections made between 1924 and 1929 in Haiti. King & Robinson (1975) observed that *Osmiopsis plumieri* is frequently misidentified in herbaria as *Koanophyllon selleana* King & Robinson (which differs in having 8 to 12 flowers per head) or as *Koanophyllon phanioides* King & Robinson (which differs in having persistent involucral bracts at the base), a fact that presumably led him to propose either one of these species as putative parents in *Koanophyllon*.

During our study of the phylogeny of subtribe Praxelinae (Cap 1), strong incongruence was found between the inferred *ndh*F tree and the inferred ITS tree was detected. The purpose of this paper is to further investigate the origin of this species, to present the first DNA sequences of the genus, and to review its taxonomic position.

Material and Methods

Sequence generation

DNA was extracted from a paratype of *Osmiopsis plumieri* (Ekman 6490 (Figure 1) (S herbarium); see Suppl. Table 1 (appendix) for vouchers. Molecular analysis was performed in the Plant Molecular Biology Laboratory, University of Brasilia. The extraction of total genomic DNA was performed from silica-dried leaf material using a protocol from Riahi & al. (2010). The ITS region of the 18S-26S ribosomal RNA genes, including the 5.8S gene (nuclear region), and the *ndh*F (chloroplast region) were amplified using standard PCR protocols and primers ITS-4 (TCCTCCGCTTATTGATATGC) and ITS-5 (GGAAGTAAAAGTCGTAACAAGG), *ndh*F 52

(AGGTAAGATCCGGTGAATCGGAAA) and *ndh*F 1212 (GGTGGAATACCACAAAGA), respectively. The PCRs were carried out in a final volume of 20 μL as specified in the protocol on Table 1, adapted from Rivera et al. (2016). Amplicons were sequenced using the DNA sequencing services of BPI Biotecnologia in Botucatu, Brazil.

Both sequences from *Osmiopsis* were then added to a matrix containing 202 Eupatorieae species (Supplementary, appendix). The new matrix contained the following molecular data from nuclear and chloroplast markers: ITS, ETS, *ndh*F, *ndh*I and *ndh*I-*ndh*G intergenic spacer for Eupatorieae species and is available in GenBank (Clark & al. 2016). The sequences were then aligned for all the molecular markers individually in Geneious v.11 using its Muscle alignment followed by visual inspection and manual alignment, when needed. Each genetic marker was run on jModeltest 2.1.10 (Guindon & Gascuel, 2003; Darriba & al. 2012) and the model GTR (with gamma-distributed rate variation across sites) was selected as the best model of evolution under the Akaike Information Criteria (AIC) that fits the data. Bayesian inference analysis was then performed on the entire dataset in which each genetic marker was treated as one partition with the specified chosen model of evolution, as well as for individual inferences for ITS and *ndh*F separately, which were performed using MrBayes 3.2.7a (Ronquist & Huelsenbeck 2012) on the CIPRES science gateway (Miller & al. 2010).

Evidence of possible hybrid origin

We evaluated incongruence between the nuclear (ITS) and chloroplast *(ndhF*) regions using the incongruence length difference test (ILD test; Farris & al. 1995). The ILD test has been criticized because of a high false positive rate (Cunningham, 1997; Darlu and Lecointre, 2002; Hipp & al., 2004), therefore, to reduce the chances of false positives we used the recommendations of Cunningham (1997) and Pelser & al. (2010), and only considered ILD *p-values* below 0.01 as evidence of significant incongruence. We implemented the ILD test in PAUP (Swofford 2002) on the CIPRES platform (Miller & al. 2010) as a Partition-homogeneity test with heuristic search with 1000 replicates and random addition of sequences.

We analyzed *Osmiopsis plumieri* morphologically and compared its habit, leaf shape and floral characters to all possible parental species that grow on Hispaniola according to the literature (Acevedo-Rodríguez & Strong 2012). We furthermore investigated the chromosome numbers in *Chromolaena*, *Koanophyllon* and *Praxelis* available in the CCDB (Rice & Mayrose 2023) to evaluate the chance of successful hybridization. Geographic distribution was obtained from the literature (Acevedo-Rodríguez & Strong 2012, Plants of the World Online (POWO) and from

online herbaria in GBIF. The I-Naturalist site (www.inaturalist.org) was searched for images of *Chromolaena*, *Praxelis* and *Koanophyllon* from Hispaniola. Images of herbarium specimens were checked for correct determination.

Results

In the reconstructed phylogeny of the *ndh*F region, *Osmiopsis plumieri* emerged as a member of subtribe Praxelinae (PP=0.83) (Figure 2). If *Chromolaena sagittata,* that is sister to the rest of the Praxelinae, is disconsidered, the remaining clade (clade A) has maximum support (PP=1). Clade A includes 12 species of *Chromolaena* DC. and a nested "*Praxelis* clade" (clade B). This "Praxelis clade" B includes 8 species: four *Praxelis* Cass., *Eitenia praxelioides* R.M.King & H.Rob., *Eupatoriopsis hoffmanniana* Hieron., *Praxeliopsis matogrossensis* G.M.Barroso and *Osmiopsis plumieri* (Urb. & Eckman) R.M.King & H.Rob., with a reasonable support of PP=0.82 (Figure 2). However, in the reconstructed phylogenetic tree of the ITS region, which includes 25 species of Subtribe Praxelinae that were well supported (Figure 3), *Osmiopsis* did not group with them. Instead, it emerged as part of a subtribe Critoniinae clade that includes *Koanophyllon*, *Idiothamnus, Chacoa*, *Steyermarkina, Imeria* (as well as genera from two other subtribes namely *Ageratum* (subtribe Ageratinae) and *Fleischmannia* (subtribe Fleischmanniinae)) with high support of PP=0.99 in the ITS tree, clade A (Figure 3).

Our study also produced a reconstructed phylogeny of the Eupatorieae based on a combined analysis of five molecular markers (two matrices): the nuclear matrix of ITS and ETS and the chloroplast matrix of *ndh*F, *ndh*I and *ndh*I-G IGS (Capitulo 1 appendix 2). This reconstructed phylogeny with the best resolution and support shows *O. plumieri* in a clade among the sampled species of *Koanophyllon*, as well as *Idiothamnus lilloi* and *Chromolaena collina* with support of 0.97 (Figure. 4). These results will be presented elsewhere.

The ILD test results confirmed the incongruence between the ITS and the *ndh*F data matrices with a *p*-value of 0.001. The *ndh*F (a chloroplast marker) phylogenetic tree grouped *Osmiopsis* in a clade (0.82 pp) with four species of *Praxelis* in addition to *Eitenia praxelioides*, *Eupatoriopsis hoffmanniana* and *Praxeliopsis mattogrossensis* (Figure 2). Since, in Angiosperms, chloroplasts are maternally inherited (Greiner & al. 2014) it is a logical assumption that the maternal plant is to be looked for in this clade. However, no species of either *Praxelis*, *Eitenia* ou *Eupatoriopsis* have ever been recorded from Hispaniola (Acevedo-Rodrigues & Strong, 1988). This suggests two possibilities: 1) *P. clematidea,* a widely distributed invasive that is established in Australia, China, Southeast Asia, and Florida (Salgado & al. 2022) may well occur in Hispaniola, or

may have occurred in the past; 2) the parent plant could be a *Chromolaena* that is related to the *Praxelis* clade and shares the same *ndh*F region, since the *Praxelis* clade is shown to be nested within *Chromolaena.* Five species of *Chromolaena* are known from Hispaniola: *C. heterosquamea* (endemic to Hispaniola); *C. corymbosa, C. sinuata,* and *C. ivifolia* (widely distributed in South America), and *C. odorata,* an aggressive alien species (Acevedo-Rodriguez & Strong 2012; POWO 2023). We believe *C. heterosquamea* can be discarded as a possible maternal plant as it shows various characters that suggests that it is not a member of the *Chromolaena* (i.e., it does not share the main diagnostic characteristics of the genus (Table 2)). Hypothetical parent plants are compared in Table 3.

Geographic distribution

Osmiopsis plumieri has been recorded from both northern and southern Haiti and in Montfleury near Port au Prince (GBIF, 2023). In northern Haiti, it was recorded from the vicinity of St. Michel de l'Atalaye and around Môle Saint-Nicolas. In southern Haiti, it was recorded from the Massifs des Matheux, des Cahos, de la Selle, and de la Hotte. In the Massif de la Selle and de la Hotte it was recorded from several mountains: Morne à Cabrits, Morne Rochelois, Morne Sentier, and Morne de l'Hôpital. The 1968 collection made by Alain Liogier in the Dominican Republic (Liogier 12804 at P), identified by an unknown person as *Osmiopsis plumieri*, is in fact a specimen of *Koanophyllon selleana* King & Robinson. The I-Naturalist site (www.inaturalist.org.) was searched for evidence of *Praxelis* on Hispaniola and none was found but suggested that *Chromolaena odorata* is now a very common plant on the island.

Chromosome counts

Chromosome counts for the possible maternal plants are variable, since both *Chromolaena* and *Praxelis* are apomictic (King & & Robinson, 1987, Robinson 2009). Both genera have a base number of X=10 (King & Robinson, 1987), with records of N=10, 20, and 30 recorded in the invasive species *Praxelis clematidea* and *Chromolaena odorata* (Table 3). There are no counts available for any of the species of *Chromolaena* that are native to Hispaniola.

Chromosome counts for either of the most likely paternal parents based on morphology (*Koanophyllon phanioides* or *K. selleana*) were not found. *Koanophyllon* has a base number of X=10 (King & Robinson 1987), which is by far the most common count in the genus, recorded in nine species (see Table 3). Other counts recorded in the genus are 15 (one species), 20 (one species)

and 30 (one species). Two species of *Koanophyllon* from Hispaniola have chromosome counts: *K. sciatraphes* (B. L. Rob.) R. M. King & H. Rob. (N=20; Torres & Liogier 1970) and *K. villosum* (Sw.) R. M. King & H. Rob. (N=10; Keil & al. 1988). However, *Koanophyllon* is very species-rich on the Hispaniola with c. 35 species (Acevedo-Rodriguéz & Strong 2012).

Discussion

Hybridization, often thought of as an occasional and inconsequential event, is a fundamental feature of plant evolution and one of the main ways that species evolve (Stace & al. 2015). Robinson (1983) believed that much more hybridization takes place in the Asteraceae than botanists believe, and that hybridization is probably an important contributing factor to the family's success. Inter-generic hybrids, however, are uncommon in nature; in the British Flora, where hybrids have been well studied, only 4 inter-generic hybrids (nothogenera) have been recorded, out of a total of 57 Asteraceae hybrids (Stace & al., 2015). These nothogenera are usually morphologically intermediate between parent plants and sterile, with one of the parents native and one frequently introduced (Supplementary Table 2). Within Tribe Eupatorieae, it has been suggested that species belonging to the subtribes with a chromosome count x=10, that are the more derived, are more likely to cross, and might resultin inter-generic or inter-subtribal hybrids (Robinson & al. 2009). As far as we are aware, this is the first case of an inter-subtribal generic hybrid proved with molecular data. Schilling (2011) suggested a hybrid origin for two monotypic genera within Liatrinae: *Hartwrightia* (*H. floridana* A.Gray ex S.Watson) and *Litrisa* (*L. carnosa* Small). He based his hypothesis of a hybrid origin for these two genera on the same principle and method adopted in this study, i.e., incongruity between nuclear and chloroplast marker phylogenetic trees (both highly supported), and then tested with the ILD test. However, the putative parent genera were both within the Liatrinae. The Liatrinae emerged with two major clades, and Schilling (2011) found that the nuclear markers (ITS and ETS) placed *Hartwrightia* and *Litrisa* in one of them (PP=1; BS=88) along with *Trilisa*, while the chloroplast markers placed these genera in its sister clade (BS=99) along with *Carphephorus* and *Liatris*. Morphlogically, *Litrisa* is intermediate between the parent genera *Trilisa* and *Carphephorus*. *Hartwrightia*, however, is morphologically transgressive to either of the parent genera, showing a loss of several features present in either or both, such as leaf punctuation, pales, floral pigment, anther appendages, bristles on the pappus, and simple hairs on the cypselae, as well as a reduction in series of involucral bracts (from 2-3 to 1) and cypselae ribs (from 8-10 to 5).

Taxonomic Treatment

x Koanoxelis Neves Ribeiro & Proença, **nothogen. nov.**
(= *Osmiopsis* King & H.Rob., Phytologia 32: 250. 1975, *Eupatorium plumieri* Urb. & Elman, **nom. illeg.**

According to Article H.6.1 of the Internationational Code of Nomenclature for algae, fungi and plants (Turland & al., 2018), a name at generic rank for a hybrid taxon is a condensed formula of the two parental genera, so the name *Osmiopsis* is illegal and a replacement name is needed. We have not indicated a type because, according to Article 9, nothogenera do not have types. It is possible that *Chromolaena collina* represents a second species of *Koanoxelis*. It shows the same pattern, i.e., in the ITS phylogeny it emerged in the same polytomy that included *Osmiopsis* and three other species of *Koanophyllon*, nested within the Critoniinae. However, this was a GenBank sequence and no chloroplast sequences are available for *C. collina*. Furthermore, although we know that the voucher specimen of *C. collina* is from Sonora, Mexico (TEX 00115225) and was collected in 1997, it has apparently been misplaced at TEX and we have not been able to examine it. It might be merely a *Koanophyllon* that was misidentified as *C. collina*.

The genus is also to be removed from subtribe Praxelinae due to its hybrid status. We have chosen *Praxelis* to compose the condensed formula (over *Chromolaena*) for two reasons: (i) the *ndh*F phylogenetic inference showed affinity with the *Praxelis* clade; (ii) growing evidence that *Chromolaena* might have to be synonymized under *Praxelis*, the older name, unless conserved.

Koanoxelis plumieri (Urban & Ekman) Neves Ribeiro & V.L.Rivera, **comb. nov.** *Osmiopsis plumeri* (Urban & Ekman) R.M King & H. Robinson (1975:251). *Chromolaena plumieri* (Urban & Ekman) R.M. King & H. Robinson (1970:209). *Eupatorium Plumieri* Urban & Ekman (1931: 52). Type: Hispaniola Civ. Haiti, Montagnes du Trou d'Eau, Morne à Cabrits, at Terre Rouge 580 m. E.L. Ekman sn. (Holotype, S (H 2252) Photo!)

Comments: *Osmiopsis plumieri* shares some vegetative characters with *Chromolaena/Praxelis*, such as the imbricate involucre and the deciduous involucral bracts (Table 4). However, in subtribe Critoniinae there are species with an imbricate involucre, and internal involucral bracts that are deciduous as well. On the other hand, the reproductive characters, namely the shape of the corolla, of the lobes and the anther appendages, are shared with *Koanophyllon* (Table 4), and cannot be found in any of the Praxelinae genera. Among the 35 species of genus *Koanophyllon* known to grow on Hispaniola (Acevedo-Rodriguéz & Strong 2012), *K. phanioide*s is the one that

morphologically most resembles *O. plumieri* in our opinion. Besides the reproductive characteristics that King and Robinson (1987) cited, we can add the ovate to lanceolate leaf blade with a lobed base that becomes entire towards the apex and the long petioles. Among the *Chromolaena* species that are reported for Hispaniola, *C. odorata* and *C. corymbos*a are similar to *O. plumieri* because of the involucral bracts strongly superimposed, but differ in the reproductive characters as mentioned earlier.

Conclusion

Because the more recent Asteraceae collections of the Dominican Republic and Haiti are only available as physical specimens for *in loco* examination, and we have not been able to visit the island, it has not been possible to ascertain if *Osmiopsis plumieri* persists in the Hispaniola flora. However, its occurrence as documented in the 1920's was widespread in Haiti. This suggests that it was then either an established, successful fertile hybrid or species of hybrid origin, or that the parents were common enough for multiple hybridization events to occur. Modern collections of this species would be highly desirable, as well as chromosome counts and ideally experimental artificial hybridization between putative parents plants.

Our evidence (obtained from GBIF, I-Naturalist and the fact that it is not cited in the Catalogue of Seed Plants of the West Indies) that *Praxelis* does not occur on Hispaniola is suboptimal, so botanists collecting in Hispaniola are urged to look for species of this genus.

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Table 1: Protocol for the PCR reactions performed. Quantities of reagents are specified followed by specifications of the PCR cycles.

Reagent	**ITS**	***ndh*F**
H_2O Buffer 10x DMSO BSA ITS-4 & ITS-5 *ndh*F1212 & *ndh*F52 $MgCl_2$ Taq dNTP DNA	8µl 2µl 1,75µl 0 2.5 µl 0 1µl 0,25 µl 2µl 1µl	11.5µl 2.5µl 0 1.25µl 0 2.5 µl 1µl 0,25 µl 2µl 1µl
Total:	**20**µl	**25**µl
Protocol of the PCR Reactions		
Cycles	**ITS**	**ndhF**
1 (1 x)	94 °C / 5:00 m	95 °C /3:00 m
2 (35 x)	94 °C / 00:45 s 50 °C / 0:45 s 72 °C / 1:00 m	95 °C / 0:30 s 54 °C / 0:40 s 72 °C / 1:00 m
3 (1x)	72 °C / 10:00 m 4°C (∞)	72 °C / 5:00 m 4°C (∞)

Table 2. Morphological comparison of the main characters of genus *Chromolaena* and *C. heterosquamea* that suggest that this species is not a member of *Chromolaena.*

Morphological Characters	***Chromolaena***	***Chromolaena heterosquamea***
Involucre	**Imbricate**	**Subimbricate**
Number of involucral bracts series	**4–7**	**2–3**
Corolla shape	**Cylindrical**	**Funnelform**
Corolla color	**Lilac or white**	**White to greenish yellow**
Corolla lobes shape	**Oblong or Oval**	**Triangular**

Table 3. Comparison of possible parental plants. O = *Osmiopsis*; C. = *Chromolaena*; K. = *Koanophyllon*; P. = *Praxelis*. **P?** = paternal; **M?** = maternal. **n** = haploid chromosome count.

Species / chromosome counts	**Habit**	**Leaf shape**	**Leaf margins**	**Involucral bracts (series)**	**Comp. Involucre (mm)**	**Larg. Involucre (mm)**
O. plumieri **n=?**	**Scandent shrubs**	**Ovate to lanceolate**	**Often with lobed bases, upper margins entire**	**4–5**	**3 to 5**	**2–3**
C. corymbosa **(M?) n=20**	**Shrubs**	**Deltoid to cordate**	**Base rouded margins Often crenate**	**6–7**	**7 to 9**	**3.3 to 4**
C. ivifolia **(M?) (n=25)**	**Shrubs**	**Lanceolate**	**Often Base acute margins entire or serrate**	**6–7**	**5.5 to 7.8**	**2.7 to 4**
C. odorata **(M?) n=20,29,30,31 40,51,60**	**Scandent shrubs**	**Ovate to lanceolate**	**Often Base rouded margins serrate**	**5–7**	**8.2 to 9.6**	**2.6 to 3.5**
C. sinuata **(M?) (n=?)**	**Shrubs**	**Ovate**	**Often Base cuneate to truncate Margins sinuately lobed**	**3–5**	**3–4**	**2**
K. selleana **(P?) (n=?)**	**Scandent Shrubs**	**Ovate to elliptical**	**Basi subcordate margins entire**	**3**	**3 to 5**	**2–3**
K. phanioides **(P?) (n=?)**	**Scandent Shrubs**	**Ovate to lanceolate**	**Often with lobed bases, upper margins entire**	**3**	**2 to 4**	**2–3**

Table 4: Differences and similarities in vegetative and reproductive characteristics of genera *Osmiopsis* in comparison to *Chromolaena*/ *Praxelis* and *Koanophyllon*.

Characteristics	***Chromolaena/Praxelis***	***Koanophyllon***	***Osmiopsis***
Involucral bracts (persistence)	Only the internal persisting	All persistent or at least external persistent	None persisting (deciduous)
Involucral bracts (position)	Imbricate	Eximbricate	Eximbricate or Subimbricate
Corolla shape	Cylindrical with a slightly narrower base	Funnelform with a cylindrical base	Funnelform with a cylindrical base
Corolla lobes	Oblong or Ovate (longer than broader)	Triangular (broader than longer)	Triangular (broader than longer)
Anther appendices	Oblong (longer than broader)	Emarginate (broader than longer)	Semicircular (broader than longer)

Figure 1. Isoparatype of *Osmiopsis plumieri* deposited in the herbarium of the University of Texas at Austin (TEX) *Ekman 6490*, voucher material for the DNA sample.

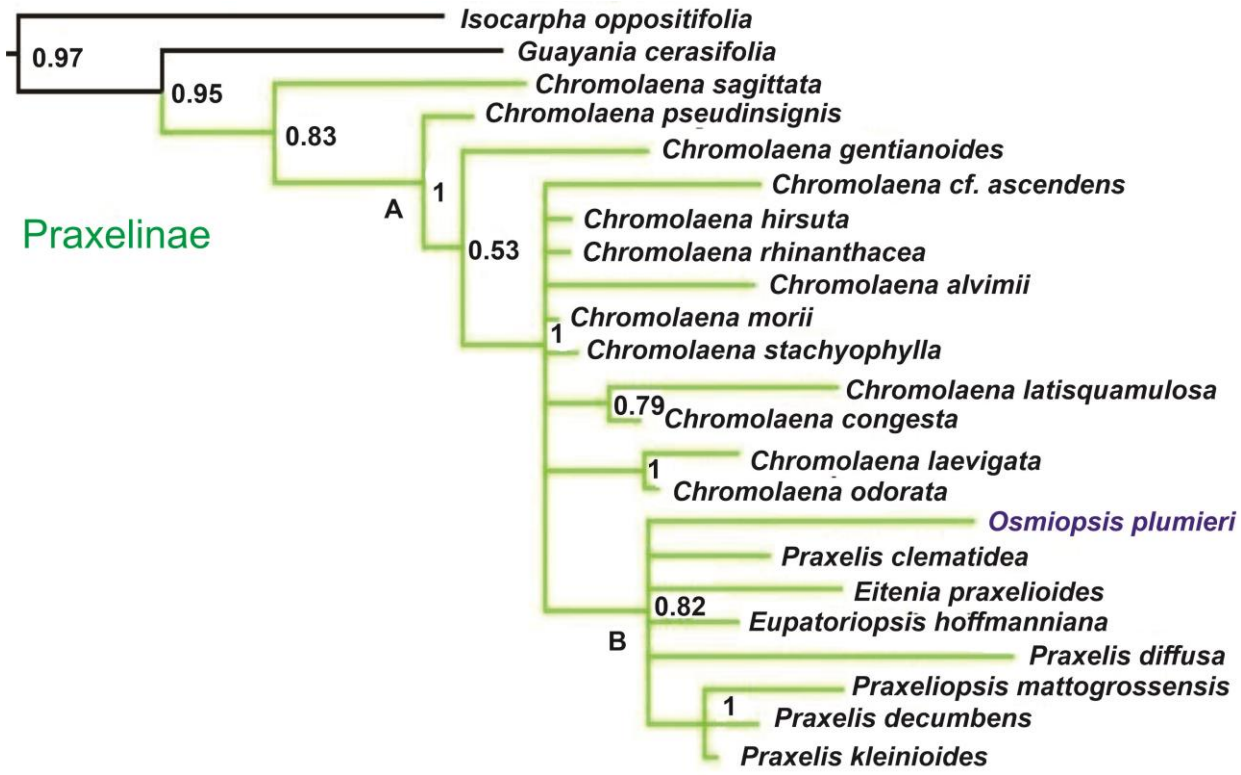


Figure 2. Bayesian 50% majority rule consensus *ndh*F tree. Posterior probabilities are indicated on the branches. *Osmiopsis plumieri* is highlighted in blue, within clade A. Branches from subtribe Praxelinae's clade are colored in green.

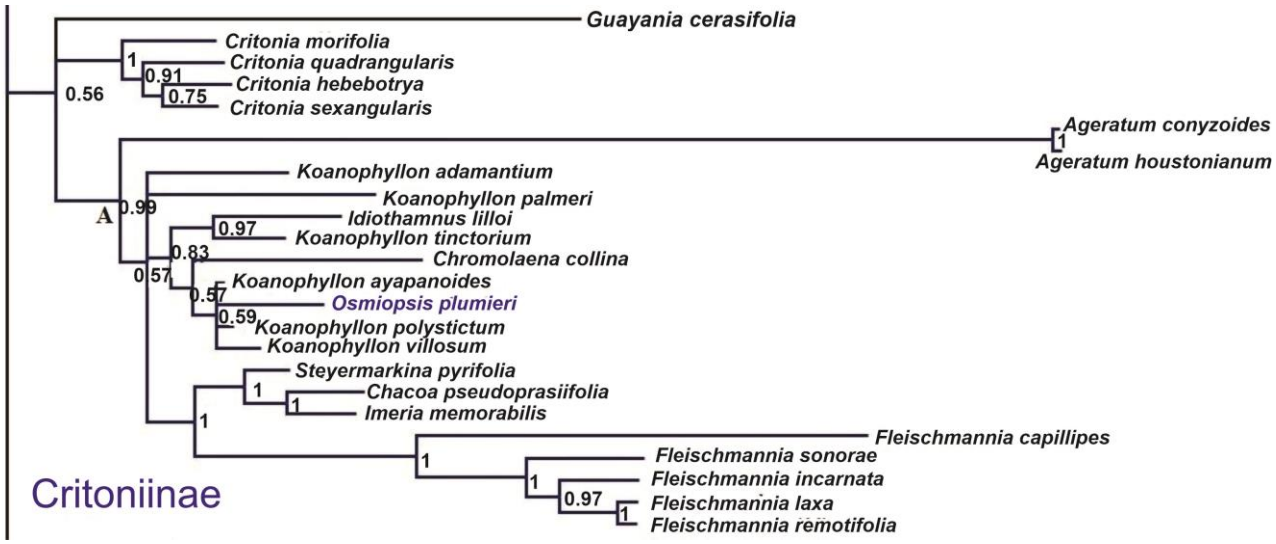


Figure 3. Bayesian 50% majority rule consensus ITS tree. Posterior probabilities are indicated on the branches. *Osmiopsis plumieri* is highlighted in blue, within clade A.

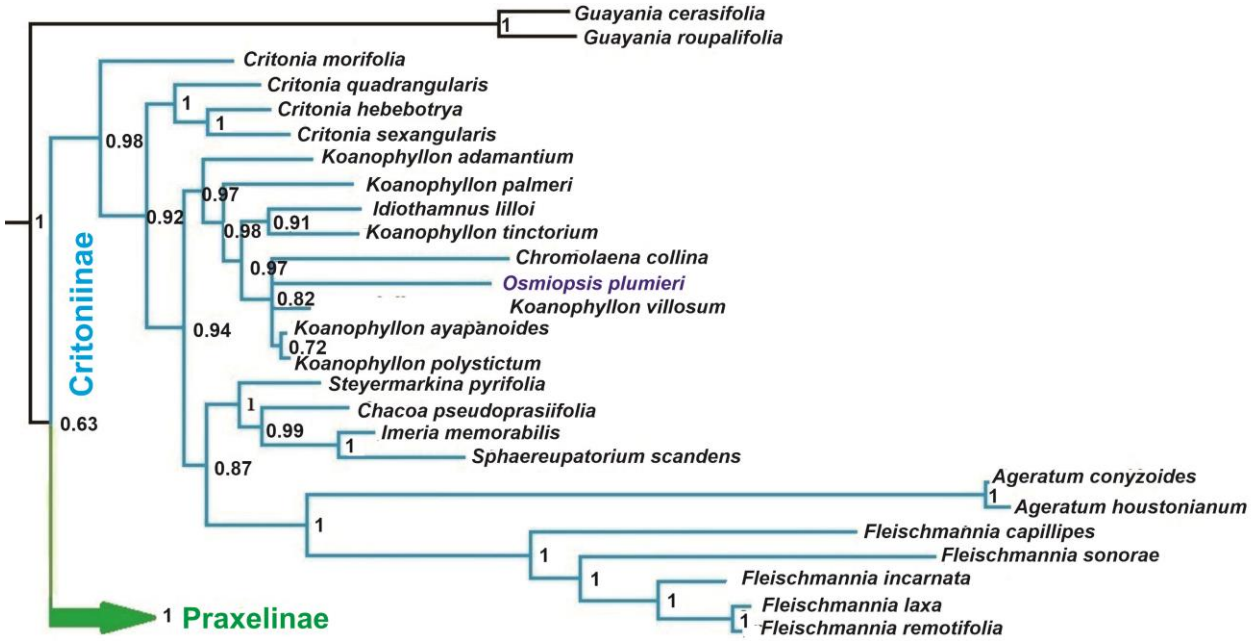


Figure 4. Bayesian 50% majority rule consensus ITS, ETS, *ndh*F, *ndh*I, *ndh*I-*ndh*G tree. Posterior probabilities are indicated on the branches. *Osmiopsis plumieri* is highlighted in blue, within clade A. Branches from subtribe Critoniinae's clade are colored in light blue.

Supplementary Table 1 (appendix)

Supplementary Table 2

Intergeneric Asteraceae hybrids in the British isles (adapted from Stace & al. 2015).

Hybrid species	**Parent genus 1**	**Parent genus 2**	**Morphology**
***Conyzigeron bilboana* J. Rémy**	***Conyza floribunda* Kunth (alien)** **2N=54**	***Erigeron acris* L. (native)** **2N=18**	**Intermediate between parents**
***Conyzigeron hulsenii* (Vatke) Rauschert** **2N=18** **sterile (Roper, I.M. 1911. J.Bot.)**	***Conyza canadensis* (L.) Cronquist (alien)** **2N=18**	***Erigeron acris* L.** **(native)** **2N=18**	**Intermediate between parents**
***Conyzigeron* sp.** **Sterile**	***Conyza sumatrensis* (Retz.) Walker** **(alien)** **2N=54**	***Erigeron acris* L.** **(native)** **2N=18**	**Intermediate between parents**
***Tripleurothemis maleolens* (P. Fourn) Stace 2N=18** **highly sterile**	***Anthemis cotula* (L.) Sch. Bip. 2N=18** **90% SI**	***Tripleurospermum inodorum*** **2N=18** **90% SI**	**Intermediate between parents but less vigorous**

Appendix

1) Supplementary Table Vouchers for species included in the Praxelinae phylogeny.

2) Bayesian 50% majority rule consensus ITS, ETS, *ndh*F, *ndh*I, *ndh*I-*ndh*G tree (202 species)

3) Understanding *Praxelis* (Asteraceae Eupatorieae): an updated taxonomy with lectotypifications and morphological and distributional clarifications

1) Supplementary Table Vouchers for species included in the Praxelinae phylogeny.

X= in submission

Species	Voucher specimen	ITS 1	ITS 2	ETS	*ndh*I	*ndh*I-*ndh*G	*ndh*F	*ndh*F-*ycf*1
Acanthostyles buniifolius (Hook. ex Arn.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8472	KP454294	KP454447	KP454595	KP454160	KP454753	KP454883	KP454055
Acritopappus catolesensis D.J.N. Hind & Bautista	V.L. Rivera 219	KP454295	KP454448	KP454596	KP454161	KP454754	KP454884	KP454056
Acritopappus confertus (Gardner) R.M. King & H. Rob.	V.L. Rivera 121	KP454296	KP454449	KP454597	KP454162	KP454755	KP454885	KP454057
Acritopappus connatifolius (Soares Nunes) R.M. King & H. Rob.	Bautista (2000)	Bautista (2000)	Bautista (2000)	NS	NS	NS	NS	NS
Acritopappus diamantinicus H. Bautista	S. Ortiz & Rodr. Oubiña, Bautista (2000)	Bautista (2000)	Bautista (2000)	NS	NS	NS	NS	NS
Acritopappus heterolepis (Baker) R.M. King & H. Rob.	M.D. de Moraes 730	KP454297	KP454450	KP454598	KP454163	KP454756	KP454886	KP454058
Acritopappus longifolius (Gardner) R.M. King & H. Rob.	V.L. Rivera 163	KP454298	KP454451	KP454599	KP454164	KP454757	KP454887	KP454059
Acritopappus micropappus (Baker) R.M. King & H. Rob.	J.L. Ferreira 161	KP454299	KP454452	KP454600	KP454165	KP454758	NS	NS
Acritopappus pereirae H. Bautista	S. Ortiz & Rodr. Oubiña, R.M. Bautista (2000)	Bautista (2000)	Bautista (2000)	NS	NS	NS	NS	NS
Acritopappus subtomentosus King & H. Rob.	J.B.Bringel 902	KP454300	KP454453	KP454601	KP454166	KP454759	KP454888	KP454060
Acritopappus teixeirae R.M. King & H. Rob.	Bautista (2000)	Bautista (2000)	Bautista (2000)	NS	NS	NS	NS	NS
Adenostemma involucratum R.M. King & H. Rob.	M.D. de Moraes 679	KJ637168	KJ637168	KP454602	NS	NS	KP454889	KP454061
Ageratum conyzoides L.	J.L. Panero 8827	KP454301	KP454454	KP454603	KP454167	KP454760	KP454890	KP454062
Ageratum fastigiatum (Gardner) R.M. King & H. Rob.	V.L. Rivera 91	KP454302	KP454455	KP454604	KP454168	KP454761	KP454891	KP454063
Ageratum houstonianum Miller	E.E. Schilling 04-24	AF177789	AF177829	NS	KP454169	KP454762	EU337042	NS
Agrianthus carvalhoi D.J.N. Hind	V.L. Rivera 136.1	KP454303	KP454456	KP454605	KP454170	KP454763	KP454892	KP454064
Agrianthus empetrifolius Mart. ex DC.	V.L. Rivera 117	KP454304	KP454457	KP454606	NS	NS	NS	NS
Agrianthus giuliettiae D.J.N. Hind	V.L. Rivera 136.2	KP454305	KP454458	KP454607	KP454171	KP454764	KP454893	KP454065
Agrianthus luetzelburgii Mattf.	V.L. Rivera 139	KP454306	KP454459	KP454608	KP454172	KP454765	KP454894	KP454066
Alomia ageratoides Kunth	J.L. Panero & Schilling 8861	KP454307	KP454460	KP454609	KP454173	KP454766	KP454895	NS
Alomiella regnellii (Malme) R.M. King & H. Rob.	N.F.O. Mota 2120	Fernandes (2014)	Fernandes (2014)	NS	NS	NS	NS	NS
Arrojadocharis praxeloides (Mattf.) Mattf.	M.D. de Moraes 726	KP454308	KP454461	KP454610	KP454174	KP454767	KP454896	KP454067
Arrojadocharis santosii R.M. King & H. Rob.	A.M. de Carvalho 6646	KP454309	KP454462	KP454611	NS	NS	KP454897	NS
Austrobrickellia patens (D. Don ex. Hook. & Arn.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8469	KP454310	KP454463	KP454612	KP454175	KP454768	KP454898	KP454068

Austroeupatorium inulifolium (Kunth) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8516	KP454311	KP454464	KP454613	KP454176	KP454769	KP454899	KP454069
Austroeupatorium laetevirens (Hook. & Arn.) R.M. King & H. Rob.	R. Wasum 1023	KP454312	KP454465	KP454614	KP454177	KP454770	KP454900	KP454070
Austroeupatorium picturatum (Malme) R.M. King & H. Rob.	G. Hatschbach 44925	KP454313	KP454466	KP454615	NS	NS	NS	NS
Ayapana amygdalina (Lam.) R.M. King & H. Rob.	M.D. de Moraes 759	KP454314	KP454467	KP454616	KP454178	KP454771	KP454901	KP454071
Ayapana lanceolata R.M. King & H. Rob.	J.J. Strudwick 3907	KP454315	KP454468	KP454617	KP454179	KP454772	NS	NS
Ayapanopsis oblongifolia (Gardner) R.M. King & H. Rob.	R. Harley 25786	KP454316	KP454469	KP454618	NS	NS	NS	NS
Bahianthus viscosus ((Spreng.) R.M. King & H. Rob.	M.D. de Moraes 737	KP454317	KP454470	KP454619	KP454180	KP454773	KP454902	KP454072
Barrosoa betoniciformis (DC.) R.M. King & H. Rob.	M.D. de Moraes 814	KP454318	KP454471	KP454620	KP454181	KP454774	KP454903	KP454073
Barrosoa candolleana (Hook. & Arn.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8533	KP454319	KP454472	KP454621	KP454182	KP454775	KP454904	KP454074
Bartlettina oresbia (B. L. Rob.) R.M. King & H. Rob.	J.L. Panero 5523	KP454320	KP454473	KP454622	KP454183	KP454776	KP454905	NS
Bartlettina sordida (Less.) R.M. King & H. Rob.	J.L. Panero 2762	NS	NS	KP454623	KP454184	KP454777	KP454906	NS
Bejaranoa balansae (Hieron.) R.M. King & H. Rob.	J.L. Panero 8517	KP454321	KP454474	KP454624	KP454185	KP454778	NS	NS
Bejaranoa semistriata (Baker) R.M. King & H. Rob.	M.D. de Moraes 722	KP454322	KP454475	KP454625	KP454186	KP454779	KP454907	KP454075
Bishopiella elegans R.M. King & H. Rob.	M.D. de Moraes 710	KP454323	KP454476	KP454626	KP454187	KP454780	KP454908	KP454076
Brickellia coulteri A. Gray	J.L.Panero 2836	KP454324	KP454477	KP454627	KP454188	KP454781	KP454909	NS
Brickellia diffusa (Vahl) A. Gray	V.L. Rivera 210	KP454325	KP454478	KP454628	KP454189	KP454782	KP454910	KP454077
Brickellia filipes B. L. Rob.	J.L.Panero & Schilling 8843	KM668947	KM668947	KM669046	KP454190	KP454783	KP454911	KP454078
Campovassouria cruciata (Vell.) R.M. King & H. Rob.	M.D. de Moraes 675	KP454326	KP454479	KP454629	KP454191	KP454784	KP454912	KP454079
Campuloclinium campuloclinioides (Baker) R.M. King & H. Rob.	H.S. Irwin 22823	KP454327	KP454480	NS	NS	NS	NS	NS
Campuloclinium chlorolepis (Baker) R.M. King & H. Rob.	N.P. Lopes 146	KP454328	KP454481	KP454630	KP454192	KP454785	KP454913	KP454080
Campuloclinium hirsutum Gardner	M.D. de Moraes 720	KP454329	KP454482	KP454631	KP454193	KP454786	KP454914	KP454081
Campuloclinium macrocephalum (Less.) DC.	R. Wasum 5459	KP454330	KP454483	NS	KP454194	KP454787	KP454915	KP454082
Campuloclinium megacephalum (Mart. ex Baker) R.M. King & H. Rob.	V.L. Rivera 145	KP454331	KP454484	KP454632	KP454195	KP454788	KP454916	NS
Catolesia huperzioides Roque, H.Rob. & A.A. Conceição	A.A. Conceição 1179	KP454332	NS	KP454633	KP454196	KP454789	NS	NS
Catolesia mentions D.J.N. Hind	S.C. Ferreira 360	KP454333	KP454485	KP454634	NS	NS	KP454917	NS
Cavalcantia glomerata (G.M. Barroso & R.M. King) R.M. King & H. Rob.	R.S. Secco 142	NS	NS	KP454635	NS	NS	NS	NS
Chacoa pseudoprasiifolia (Hassl.) R.M. King & H. Rob.	T.M. Pedersen 5070	KP454334	KP454486	KP454636	NS	NS	NS	NS
Chromolaena alvimii R.M. King & H. Rob.	M.D. de Moraes 711	KP454335	KP454487	KP454637	KP454197	KP454790	KP454918	KP454083
Chromolaena arrayana (Gardner) R.M. King & H. Rob.	J.B. Bringel 935	KP454336	KP454488	KP454638	NS	NS	NS	NS
Chromolaena cf. *ascendens* (Sch. Bip ex Baker) R.M. King & H. Rob.	A.L.Christ 622			x	x	x	x	x

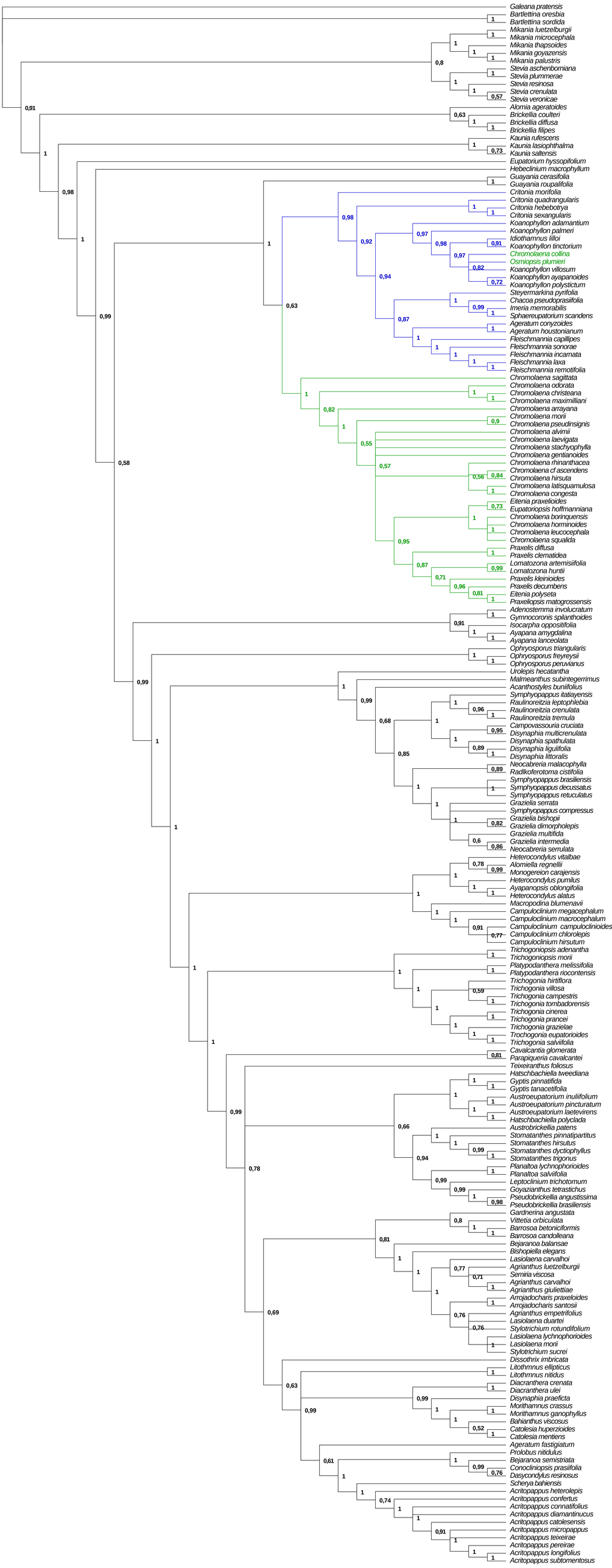
Chromolaena borinquensis (Britton) R.M. King & H. Rob.	Barker et al. 2005	AY576844.1	AY576844.1					
Chromolaena christieana (Baker) R.M. King & H. Rob.	A.L.Christ 526	x	x					
Chromolaena collina (DC.) R.M. King & H. Rob.	Barker et al. 2005	AY576855.1	AY576855.1					
Chrmolaena rhinanthacea (DC.) R.M. King & H. Rob.	A.L.Christ 480			x	x	x	x	x
Chromolaena hirsuta (Hook & Arn.) R.M. King & H. Rob.	A.L.Christ 494			x	x	x	x	x
Chromolaena horminoides DC	S.C.Ferreira 346	KP901193.1	KP901193.1					
Chromolaena latisquamulosa (Hieron) R.M. King & H. Rob.	A.L.Christ 502				x	x	x	x
Chromolaena congesta (Hook. & Arn.) R.M. King & H. Rob.	A.L.Christ 483				x	x	x	x
Chromolaena gentianoides (B. L. Rob.) (DC.) R.M. King & H. Rob.	A.L.Christ 600			x	x	x	x	x
Chromolaena decumbens Gardner. M.D. de Moraes 699	TEX	KP454558	KP454712	KP454260	KP454850	KP454976	KP454133	
Chromolaena laevigata (Lam.) R.M. King & H. Rob.	N.P. Lopes 125	KP454337	KP454489	KP454639	KP454198	KP454791	KP454919	KP454084
Chromolaena leucocephala Gardner	R.N Ribeiro 620	x	x					
Chromolaena maximilianii (Schrad. ex DC.) R.M. King & H. Rob.	R.N Ribeiro 621	x	x					
Chromolaena morii R.M. King & H. Rob.	V.L. Rivera 118	KP454338	KP454490	KP454640	KP454199	KP454792	KP454920	KP454085
Chromolaena odorata (L.) R.M. King & H. Rob.	J.L. Panero 2004-2	KP454339	KP454491	KP454641	KP454200	KP454793	KP454921	KP454086
Chromolaena pseudinsignis R.M. King & H. Rob.	V.L. Rivera 152	NS	NS	KP454642	NS	NS	KP454922	NS
Chromolaena sagittata (A. Gray) R.M. King & H. Rob.	J.L. Panero 6178	AF177786	AF177826	KP454643	KP454201	KP454794	KP454923	KP454087
Chromolaena squalida (DC.) R.M. King & H. Rob	R.N. Ribeiro 603	x	x					
Chromolaena stachyophylla (Spreng.) R.M. King & H. Rob.	M.D. de Moraes 767	KP454340	KP454492	KP454644	KP454202	KP454795	KP454924	KP454088
Conocliniopsis prasiifolia (DC.) R.M. King & H. Rob.	M.D. de Moraes 701	KP454341	KP454493	KP454645	KP454203	KP454796	KP454925	KP454089
Critonia hebebotrya DC.	J.L. Panero & E.E. Schilling 8852	KP454342	KP454494	KP454646	NS	NS	NS	NS
Critonia morifolia (Mill.) R.M. King & H. Rob.	G. Hatschbach 19801	KP454343	KP454495	KP454647	KP454204	KP454797	NS	NS
Critonia quadrangularis (DC.) R.M. King & H. Rob.	J.L. Panero & E.E. Schilling 8825	KP454344	KP454496	KP454648	KP454205	KP454798	KP454926	KP454090
Critonia sexangularis (Klatt) R.M. King & H. Rob.	J.L. Panero & Campos 2770	KJ637169	KJ637169	KP454649	KP454206	KP454799	EU337039	NS
Dasycondylus resinosus (Spreng.) R.M. King & H. Rob.	R. L. Esteves 2283	Ferreira (2010)	Ferreira (2010)	NS	NS	NS	NS	NS
Diacranthera crenata (Schltdl. ex Mart.) R.M. King & H. Rob.	E. de Melo 3010	KP454345	KP454497	KP454650	NS	NS	NS	NS
Diacranthera ulei R.M. King & H. Rob.	A.M. Miranda 5148	KP454346	NS	KP454651	NS	NS	NS	NS
Dissothrix imbricata (Gardner) B.L. Rob.	F.S. Araújo 1467	KP454347	KP454498	KP454652	NS	NS	NS	NS
Disynaphia ligulifolia (Hook. & Arn.) R.M. King & H. Rob.	G. Hatschbach 23944	KP454348	NS	KP454653	NS	NS	NS	NS
Disynaphia littoralis (Cabrera) R.M. King & H. Rob.	R.F. Vieira 313	NS	NS	KP454654	NS	NS	NS	NS
Disynaphia multicrenulata (Sch. Bip. ex Baker) R.M. King & H. Rob.	R. Vanni 4593	KP454349	KP454499	KP454655	KP454207	KP454800	KP454927	NS
Disynaphia praeficta (B.L. Rob.) R.M. King & H. Rob.	E. Guarçoni 1959	KP454350	KP454500	KP454656	KP454208	KP454801	KP454928	KP454091
Disynaphia spathulata (Hook. & Arn.) R.M. King & H. Rob.	V.L. Rivera 96, 148	NS	NS	KP454657	KP454209	KP454802	KP454929	KP454092
Eitenia polyseta R.M. King & H. Rob.	H.S. Irwin 15645	KP454351	KP454501	NS	NS	NS	NS	NS
Eitenia praxelioides R.M. King & H. Rob.	Simom, M.F. et al. 2874	x	x				x	
Eupatoriopsis hoffmanniana Hieron	J.P.L. Braga 800							

Eupatorium hyssopifolium L.	Siripun 02-Eup-157	AF177812	AF177852	HQ416395	HQ416237	HQ416237	EU337035	NS
Fleischmannia capillipes (Benth.) R.M. King & H. Rob.	J.L. Panero & E.E. Schilling 8859	KP454352	KP454502	KP454658	KP454210	KP454803	KP454930	KP454093
Fleischmannia incarnata (Walter) R.M. King & H. Rob.	E.E. Schilling 95-21	AF177788	AF177828	KP454659	KP454211	KP454804	EU337043	NS
Fleischmannia laxa (Gardner) R.M. King & H. Rob.	V.L. Rivera 199	KP454353	KP454503	KP454660	KP454212	KP454805	KP454931	KP454094
Fleischmannia remotifolia (DC.) R.M. King & H. Rob.	M.D. de Moraes 758	KP454354	KP454504	NS	KP454213	KP454806	KP454932	KP454095
Fleischmannia sonorae (A. Gray) R.M. King & H. Rob.	J.L. Panero & E.E. Schilling 8821	KP454355	KP454505	KP454661	KP454214	KP454807	KP454933	KP454096
Galeana pratensis (Kunth) Rydb.	B. Baldwin 980	AF374873	AF374873	KP454662	AF383791	AF383666	AF384726	NS
Gardnerina angustata (Gardner) R.M. King & H. Rob.	P.H.A. Melo 4422	KP454356	KP454506	KP454663	KP454215	KP454808	KP454934	NS
Goyazianthus tetrastichus (B.L. Rob.) R.M. King & H. Rob.	V.L. Rivera 97	KP454357	KP454507	KP454664	KP454216	KP454809	KP454935	KP454097
Grazielia bishopii R.M. King & H. Rob.	V.L. Rivera 153	KP454358	KP454508	KP454665	KP454217	KP454810	KP454936	NS
Grazielia dimorpholepis (Baker) R.M. King & H. Rob.	M.D. de Moraes 718	KP454359	KP454509	KP454666	KP454218	KP454811	KP454937	KP454098
Grazielia intermedia (DC.) R.M. King & H. Rob.	G. Hatschbach 50897	KP454360	KP454510	KP454667	KP454219	KP454812	NS	NS
Grazielia multifida (DC.) R.M. King & H. Rob.	J.M. Cruz 65	KP454361	KP454511	KP454668	KP454220	KP454813	KP454938	NS
Grazielia serrata (Spreng.) R.M. King & H. Rob.	G. Hatschbach 28238	KP454362	KP454512	NS	NS	NS	NS	NS
Guayania cerasifolia (Sch. Bip. ex Baker) R.M. King & H. Rob.	M.L. Kawasaki 124	KP454363	KP454513	KP454669	KP454221	KP454814	KP454939	NS
Guayania roupalifolia (B.L. Rob.) R.M. King & H. Rob.	B. Maguire 60491	NS	NS	KP454670	NS	NS	NS	NS
Gymnocoronis spilanthoides (D. Don ex Hook. & Arn.) DC.	J.L. Panero & B. Crozier 8370	KJ637170	KJ637170	NS	KP454222	KP454815	KP454940	KP454099
Gyptis pinnatifida Cass.	M.D. de Moraes 793	KP454364	KP454514	KP454671	KP454223	KP454816	KP454941	KP454100
Gyptis tanacetifolia (Gilles ex Hook. & Arn.) D.J.N. Hind. & Flann	J.L. Panero & B. Crozier 8378	KP454365	KP454515	KP454672	KP454224	KP454817	KP454942	KP454101
Hatschbachiella polyclada (Dusen ex Malme) R.M. King & H. Rob.	J.M. Silva 506	KP454366	KP454516	KP454673	NS	NS	NS	NS
Hatschbachiella tweedieana (Hook. & Arn.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8381	KP454367	KP454517	KP454674	KP454225	KP454818	KP454943	KP454102
Hebeclinium macrophyllum (L.) DC.	J.M. Poole 1437	KP454368	KP454518	KP454675	NS	NS	KP454944	KP454103
Heterocondylus alatus (Vell.) R.M. King & H. Rob.	M.D. de Moraes 757	KP454369	KP454519	KP454676	KP454226	KP454819	KP454945	KP454104
Heterocondylus pumilus (Gardner) R.M. King & H. Rob.	M.D. de Moraes 715	KP454370	KP454520	KP454677	KP454227	KP454820	KP454946	KP454105
Heterocondylus vitalbae (DC.) R.M. King & H. Rob.	J.G. Jardim 3729	KP454371	KP454521	KP454678	NS	NS	NS	NS
Idiothamnus lilloi (B.L. Rob.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8511	KP454372	KP454522	KP454679	KP454228	KP454821	KP454947	KP454106
Imeria memorabilis (Maguire & Wurdack) R.M. King & H. Rob.	V. Funk 6404	KP454373	KP454523	KP454680	NS	NS	NS	NS
Isocarpha oppositifolia (L.) Cass.	J.L. Panero 2004-1	KJ637171	KJ637171	KP454681	KP454229	KP454822	KP454948	KP454107
Kaunia lasiophthalma (Griseb.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8489	KP454374	KP454524	KP454682	KP454230	KP454823	KP454949	KP454108

Kaunia rufescens (P.W. Lund ex DC.) R.M. King & H. Rob.	M.D. de Moraes 766	KP454375	KP454525	KP454683	KP454231	NS	KP454950	KP454109
Kaunia saltensis (Hieron.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8494	KP454376	KP454526	KP454684	KP454232	KP454824	KP454951	KP454110
Koanoxelis plumieri (Urb. & Ekmnan) R. Neves-Ribeiro & V.L. Rivera	E.L. Ekman 6490	x	x					
Koanophyllon adamantium (Gardner) R.M. King & H. Rob.	V.L. Rivera 161	KP454377	KP454527	KP454685	NS	NS	KP454952	KP454111
Koanophyllon ayapanoides (Griseb.) R.M. King & H. Rob.	Bennet 7582	KJ637172	KJ637172	KP454686	KP454233	KP454825	EU337038	NS
Koanophyllon palmeri (A. Gray) R.M. King & H. Rob.	J.L. Panero & E.E. Schilling 8839	KP454378	KP454528	KP454687	KP454234	NS	KP454953	KP454112
Koanophyllon polystictum (Urb.) R.M. King & H. Rob.	Bennet 7578	KP454379	KP454529	KP454688	KP454235	KP454826	KP454954	KP454113
Koanophyllon tinctorium Arruda	Y. Mexia 4655	KP454380	KP454530	NS	KP454236	KP454827	NS	NS
Koanophyllon villosum (Sw.) R.M. King & H. Rob.	Hite s. n.	KP454381	KP454531	KP454689	KP454237	KP454828	KP454955	KP454114
Lasiolaena carvalhoi D.J.N. Hind	W. Ganev 901	KP454382	KP454532	KP454690	KP454238	KP454829	NS	NS
Lasiolaena duartei R.M. King & H. Rob.	V.L. Rivera 122	KP454383	KP454533	KP454691	KP454239	KP454830	KP454956	KP454115
Lasiolaena lychnophorioides Roque, S.C. Ferreira & H. Rob.	E.C. Oliveira 106	KP454384	KP454534	KP454692	NS	NS	NS	NS
Lasiolaena morii R.M. King & H. Rob.	M.D. de Moraes 736	KP454385	KP454535	KP454693	KP454240	KP454831	KP454957	KP454116
Leptoclinium trichotomum (Gardner) Benth.	V.L. Rivera 87	KP454386	KP454536	KP454694	KP454241	KP454832	KP454958	KP454117
Litothamnus ellipticus R.M. King & H. Rob.	M.D. de Moraes 705	KP454387	KP454537	KP454695	KP454242	KP454833	KP454959	KP454118
Litothamnus nitidus (DC.) W.C Holmes	A.M. Amorim 3526	KP454388	KP454538	NS	NS	NS	NS	NS
Lomatozona artemisiifolia Baker	H.S. Irwin 11786	KP454389	KP454539	NS	NS	NS	NS	NS
Lomatozona huntii R.M. King & H. Rob.	H.S. Irwin 17271	KP454390	NS	NS	KP454243	KP454834	NS	NS
Macropodina blumenavii (Hieron.) R.M. King & H. Rob.	W. Hahn 2043	KP454391	KP454540	KP454696	NS	NS	NS	NS
Malmeanthus subintegerrimus (Malme) R.M. King & H. Rob.	A. Krapovickas 17100	KP454392	KP454541	NS	NS	NS	NS	NS
Mikania goyazensis (B.L. Rob.) R.M. King & H. Rob.	J.B. Bringel 968	NS	NS	KP454697	KP454244	KP454835	KP454960	KP454119
Mikania luetzelburgii Mattf.	M.D. de Moraes 723	KP454393	KP454542	KP454698	KP454245	KP454836	KP454961	KP454120
Mikania microcephala DC.	J.B. Bringel 1004	NS	NS	KP454699	KP454246	KP454837	KP454962	KP454121
Mikania palustris (Gardner) R.M. King & H. Rob.	J.B. Bringel 951	KP454394	KP454543	NS	KP454247	KP454838	KP454963	KP454122
Mikania thapsoides DC.	J.L. Panero & B. Crozier 8525	KP454395	KP454544	KP454700	KP454248	KP454839	KP454964	KP454123
Monogereion carajensis G.M. Barroso & R.M. King	C.R. Sperling 5596	KP454396	KP454545	NS	NS	NS	KP454965	KP454124
Morithamnus crassus R.M. King, H. Rob. & G.M. Barroso	M.D. de Moraes 742	KP454397	KP454546	KP454701	KP454249	KP454840	KP454966	KP454125
Morithamnus ganophyllus (Mattf.) R.M. King & H. Rob.	S.C. Ferreira 375	KP454398	KP454547	KP454702	NS	NS	NS	NS
Neocabreria malacophylla (Klatt) R.M. King & H. Rob.	M. Sobral 5951	KP454399	KP454548	KP454703	KP454250	KP454841	KP454967	NS
Neocabreria serrulata (DC.) R.M. King & H. Rob.	M.D. de Moraes 695	KP454400	KP454549	KP454704	KP454251	KP454842	KP454968	KP454126
Ophryosporus freyreysii (Thunb.) Baker	R. Harley 25330	KP454401	KP454550	KP454705				NS

					KP454252	KP454843	KP454969	
Ophryosporus peruvianus (J.F. Gmel.) R.M. King & H. Rob.	J.L. Panero 875	KP454402	KP454551	KP454706	KP454253	NS	KP454970	KP454127
Ophryosporus triangularis Meyen	J.L. Panero & B. Crozier 8434A	KP454403	KP454552	KP454707	KP454254	KP454844	KP454971	KP454128
Parapiqueria cavalcantei R.M. King & H. Rob.	P.L. Viana 5237	Fernandes (2014)	Fernandes (2014)	NS	NS	NS	NS	NS
Planaltoa lychnophorioides G.M. Barroso	Gates & Eastbrook 205	KP454404	KP454553	KP454708	KP454255	KP454845	NS	NS
Planaltoa salviifolia Taub.	J.B. Bringel 799	KP454405	KP454554	KP454709	KP454256	KP454846	KP454972	KP454129
Platypodanthera melissifolia (DC.) R.M. King & H. Rob. ssp. *melissifolia*	V.L. Rivera 125	KP454406	KP454555	KP454710	KP454257	KP454847	KP454973	KP454130
Platypodanthera melissifolia (DC.) R.M. King & H. Rob. ssp. *riocontensis*	V.L. Rivera 137	KP454407	KP454556	KP454711	KP454258	KP454848	KP454974	KP454131
Praxelis clematidea R.M. King & H. Rob.	V.L. Rivera 146	KP454408	KP454557	NS	KP454259	KP454849	KP454975	KP454132
Praxelis diffusa (Rick.) Pruski	R.N Ribeiro 604	x	x					
Praxelis kleinioides (Kunth) Sch. Bip.	N.P. Lopes 132	NS	NS	NS	KP454261	KP454851	KP454977	KP454134
Praxelis kleinioides (Kunth) Sch. Bip.	R.N. Ribeiro 611	X	X					
Praxeliopsis mattogrossensis G.M. Barroso	J.E.Q. Faria 3493	x	x					
Prolobus nitidulus (Baker) R. M. King & H. Rob.	S.A. Mori 14059	KP454410	NS	KP454713	KP454262	KP454852	NS	NS
Pseudobrickellia angustissima (Spreng. ex Baker) R.M. King & H. Rob.	J.E. Faria 1903	KP454411	KP454559	KP454714	KP454263	KP454853	KP454978	KP454135
Pseudobrickellia brasiliensis (Spreng.) R.M. King & H. Rob.	V.L. Rivera 89	KP454412	KP454560	KP454715	KP454264	KP454854	KP454979	NS
Radlkoferotoma cistifolium (Less.) Kuntze	M.D. de Moraes 813	KP454413	KP454561	KP454716	KP454265	KP454855	KP454980	KP454136
Raulinoreitzia crenulata (Spreng.) R.M. King & H. Rob.	M.D. de Moraes 721	KP454414	KP454562	KP454717	KP454266	KP454856	KP454981	KP454137
Raulinoreitzia leptophlebia (B.L. Rob.) R.M. King & H. Rob.	J. Cordeiro 1420	KP454415	KP454563	KP454718	KP454267	KP454857	KP454982	NS
Raulinoreitzia tremula (Hook. & Arn.) R.M. King & H. Rob.	J.B. Bringel 815	KP454416	KP454564	KP454719	KP454268	KP454858	KP454983	KP454138
Scherya bahiensis R.M. King & H. Rob.	A. Rapini 972	KP454417	KP454565	KP454720	KP454269	KP454859	KP454984	KP454139
Semiria viscosa D.J.N. Hind	S.C. Ferreira 365	KP454418	KP454566	KP454721	NS	NS	NS	NS
Sphaereupatorium scandens (Gardner) R.M. King & H. Rob.	M. Hopkins 77	NS	NS	KP454722	NS	NS	NS	NS
Stevia aschenborniana Sch. Bip.	J.L. Panero & E.E. Schilling 8864	KP454419	KP454567	KP454723	NS	NS	KP454985	NS
Stevia crenulata Baker	J.B. Bringel 848	KP454420	KP454568	KP454724	KP454270	KP454860	KP454986	KP454140
Stevia plummerae A. Gray	Schilling NM7	KP454421	KP454569	KP454725	KP454271	KP454861	KP454987	KP454141
Stevia resinosa Gardner	J.B. Bringel 990	KP454422	KP454570	KP454726	KP454272	KP454862	KP454988	KP454142
Stevia veronicae DC.	J.B. Bringel 779	KP454423	KP454571	KP454727	KP454273	KP454863	KP454989	KP454143
Steyermarkina pyrifolia (DC.) R.M. King & H. Rob.	A.M. de Carvalho 4598	KP454424	KP454572	KP454728	KP454274	KP454864	KP454990	NS
Stomatanthes dyctiophyllus (DC.) H. Rob.	M.D. de Moraes 768	AF177787	AF177827	KP454729	NS	NS	KP454991	KP454144
Stomatanthes hirsutus H. Rob.	V.L. Rivera 147	KP454425	KP454573	KP454730				

					KP454275	KP454865	KP454992	KP454145
Stomatanthes pinnatipartitus (Sch. Bip. ex Baker) R.M. King & H. Rob.	S.C. Ferreira 424	KP454426	KP454574	KP454731	KP454276	KP454866	KP454993	KP454146
Stomatanthes trigonus (Gardner) H. Rob.	V.L. Rivera 95	KP454427	KP454575	KP454732	NS	NS	KP454994	KP454147
Stylotrichium rotundifolium Mattf.	M.D. de Moraes 746	KP454428	KP454576	KP454733	KP454277	KP454867	KP454995	KP454148
Stylotrichium sucrei R.M. King & H. Rob.	S.C. Ferreira 350	NS	NS	KP454734	NS	NS	NS	NS
Symphyopappus brasiliensis (Gardner) R.M. King & H. Rob.	J.B. Bringel 908	KP454429	KP454577	KP454735	KP454278	KP454868	KP454996	KP454149
Symphyopappus compressus (Gardner) B. L. Rob.	V.L. Rivera 133	KP454430	KP454578	KP454736	KP454279	KP454869	NS	NS
Symphyopappus decussatus Turcz.	J.E. Faria 2212	KP454431	KP454579	KP454737	KP454280	KP454870	KP454997	KP454150
Symphyopappus itatiayensis (Hieron.) R.M. King & H. Rob.	C. Proença 4045	KP454432	KP454580	KP454738	KP454281	KP454871	NS	NS
Symphyopappus reticulatus Baker	C.M. Sakuragui 15197	KP454433	KP454581	KP454739	KP454282	KP454872	NS	NS
Teixeiranthus foliosus (Gardner) R.M. King & H. Rob.	Pohl s/n	KP454434	KP454582	KP454740	KP454283	KP454873	KP454998	NS
Trichogonia campestris Gardner	J.B. Bringel 740	KP454435	KP454583	KP454741	KP454284	KP454874	KP454999	KP454151
Trichogonia cinerea (Gardner) R.M. King & H. Rob.	V.L. Rivera 83	KP454436	KP454584	KP454742	KP454285	KP454875	KP455000	KP454152
Trichogonia eupatorioides (Gardner) R.M. King & H. Rob.	M.D. de Moraes 676	KP454437	KP454585	KP454743	NS	NS	KP455001	KP454153
Trichogonia grazielae R.M. King & H. Rob.	V.L. Rivera 149	KP454438	KP454586	KP454744	KP454286	KP454876	KP455002	KP454154
Trichogonia hirtiflora (DC.) Sch. Bip. ex Baker	J.E. Faria 2213	KP454439	KP454587	KP454745	KP454287	KP454877	KP455003	KP454155
Trichogonia prancei G.M. Barroso	V.L. Rivera 90	KP454440	KP454588	KP454746	KP454288	KP454878	KP455004	KP454156
Trichogonia salviifolia Gardner	V.L. Rivera 127	KP454441	KP454589	KP454747	KP454289	NS	KP455005	NS
Trichogonia tombadorensis R.M. King & H. Rob.	V.L. Rivera 217	KP454442	KP454590	KP454748	KP454290	KP454879	KP455006	KP454157
Trichogonia villosa Sch. Bip. ex Baker	J.E. Faria 2234	KP454443	KP454591	KP454749	KP454291	KP454880	KP455007	KP454158
Trichogoniopsis adenantha (DC.) R.M. King & H. Rob.	M.D. de Moraes 764	KP454444	KP454592	KP454750	KP454292	KP454881	KP455008	KP454159
Trichogoniopsis morii R.M. King & H. Rob.	N. Hind 3597	KP454445	KP454593	KP454751	NS	NS	NS	NS
Urolepis hecatantha (DC.) R.M. King & H. Rob.	J.L. Panero & B. Crozier 8493	KP454446	KP454594	KP454752	KP454293	KP454882	KP455009	NS
Vittetia orbiculata (DC.) R.M. King & H. Rob.	J. Mazinek 41	Ferreira (2014)	Ferreira (2014)	NS	NS	NS	NS	NS


Galeana pratensis
Bartlettina oresbia
Bartlettina sordida
Mikania luetzelburgii
Mikania microcephala
Mikania thapsoides
Mikania goyazensis
Mikania palustris
Stevia aschenborniana
Stevia plummerae
Stevia resinosa
Stevia crenulata
Stevia veronicae
Alomia ageratoides
Brickellia coulteri
Brickellia diffusa
Brickellia filipes
Kaunia rufescens
Kaunia lasiophthalma
Kaunia saltensis
Eupatorium hyssopifolium
Hebeclinium macrophyllum
Guayania cerasifolia
Guayania roupalifolia
Critonia morifolia
Critonia quadrangularis
Critonia hebebotrya
Critonia sexangularis
Koanophyllon adamantium
Koanophyllon palmeri
Idiothamnus lilloi
Koanophyllon tinctorium
Chromolaena collina
Osmiopsis plumieri
Koanophyllon villosum
Koanophyllon ayapanoides
Koanophyllon polystictum
Steyermarkina pyrifolia
Chacoa pseudoprasiifolia
Imeria memorabilis
Sphaereupatorium scandens
Ageratum conyzoides
Ageratum houstonianum
Fleischmannia capillipes
Fleischmannia sonorae
Fleischmannia incarnata
Fleischmannia laxa
Fleischmannia remotifolia
Chromolaena sagittata
Chromolaena odorata
Chromolaena christeana
Chromolaena maximilliani
Chromolaena arrayana
Chromolaena morii
Chromolaena pseudinsignis
Chromolaena alvimii
Chromolaena laevigata
Chromolaena stachyophylla
Chromolaena gentianoides
Chromolaena rhinanthacea
Chromolaena cf ascendens
Chromolaena hirsuta
Chromolaena latisquamulosa
Chromolaena congesta
Eitenia praxelioides
Eupatoriopsis hoffmanniana
Chromolaena boninquensis
Chromolaena horminoides
Chromolaena leucocephala
Chromolaena squalida
Praxelis diffusa
Praxelis clematidea
Lomatozona artemisiifolia
Lomatozona huntii
Praxelis kleinioides
Praxelis decumbens
Eitenia polyseta
Praxeliopsis matogrossensis
Adenostemma involucratum
Gymnocoronis spilanthoides
Isocarpha oppositifolia
Ayapana amygdalina
Ayapana lanceolata
Ophryosporus triangularis
Ophryosporus freyreysii
Ophryosporus peruvianus
Urolepis hecatantha
Malmeanthus subintegerrimus
Acanthostyles buniifolius
Symphyopappus itatiayensis
Raulinoreitzia leptophlebia
Raulinoreitzia crenulata
Raulinoreitzia tremula
Campovassouria cruciata
Disynaphia multicrenulata
Disynaphia spathulata
Disynaphia ligulifolia
Disynaphia littoralis
Neocabreria malacophylla
Radlkoferotoma cistifolia
Symphyopappus brasiliensis
Symphyopappus decussatus
Symphyopappus retuculatus
Grazielia serrata
Symphyopappus compressus
Grazielia bishopii
Grazielia dimorpholepis
Grazielia multifida
Grazielia intermedia
Neocabreria serrulata
Heterocondylus vitalbae
Alomiella regnellii
Monogereion carajensis
Heterocondylus pumilus
Ayapanopsis oblongifolia
Heterocondylus alatus
Macropodina blumenavii
Campuloclinium megacephalum
Campuloclinium macrocephalum
Campuloclinium campuloclinioides
Campuloclinium chlorolepis
Campuloclinium hirsutum
Trichogoniopsis adenantha
Trichogoniopsis morii
Platypodanthera melissifolia
Platypodanthera riocontensis
Trichogonia hirtiflora
Trichogonia villosa
Trichogonia campestris
Trichogonia tombadorensis
Trichogonia cinerea
Trichogonia prancei
Trichogonia grazielae
Trochogonia eupatorioides
Trichogonia salviifolia
Cavalcantia glomerata
Parapiqueria cavalcantei
Teixeiranthus foliosus
Hatschbachiella tweediana
Gyptis pinnatifida
Gyptis tanacetifolia
Austroeupatorium inuliifolium
Austroeupatorium pincturatum
Austroeupatorium laetevirens
Hatschbachiella polyclada
Austrobrickellia patens
Stomatanthes pinnatipartitus
Stomatanthes hirsutus
Stomatanthes dyctiophyllus
Stomatanthes trigonus
Planaltoa lychnophorioides
Planaltoa salviifolia
Leptoclinium trichotomum
Goyazianthus tetrastichus
Pseudobrickellia angustissima
Pseudobrickellia brasiliensis
Gardnerina angustata
Vittetia orbiculata
Barrosoa betoniciformis
Barrosoa candolleana
Bejaranoa balansae
Bishopiella elegans
Lasiolaena carvalhoi
Agrianthus luetzelburgii
Semiria viscosa
Agrianthus carvalhoi
Agrianthus giuliettiae
Arrojadocharis praxeloides
Arrojadocharis santosii
Agrianthus empetrifolius
Lasiolaena duartei
Stylotrichium rotundifolium
Lasiolaena lychnophorioides
Lasiolaena morii
Stylotrichium sucrei
Dissothrix imbricata
Litothmnus ellipticus
Litothmnus nitidus
Diacranthera crenata
Diacranthera ulei
Disynaphia praeficta
Morithamnus crassus
Morithamnus gardnerianus
Bahianthus viscosus
Catolesia huperzioides
Catolesia mentiens
Ageratum fastigiatum
Prolobus nitidulus
Bejaranoa semistriata
Conocliniopsis prasiifolia
Dasycondylus resinosus
Scherya bahiensis
Acritopappus heterolepis
Acritopappus confertus
Acritopappus connatifolius
Acritopappus diamantinucus
Acritopappus catolesensis
Acritopappus micropappus
Acritopappus teixeirae
Acritopappus pereirae
Acritopappus longifolius
Acritopappus subtomentosus

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Understanding *Praxelis* (Asteraceae, Eupatorieae): an updated taxonomy with lectotypifications and morphological and distributional clarifications

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ABSTRACT

The South American genus *Praxelis* Cass. (Asteraceae, Eupatorieae) includes 18 species and is the second-largest genus of subtribe Praxelinae. It is distributed from Colombia, Venezuela and the Guianas, to central Argentina, southern Brazil and north-western Uruguay. Over the past 40 years, one species, *P. clematidea*, has invaded several countries around the world. To understand *Praxelis* and its species, this study provides an updated taxonomy with the re-establishment of *P. urticeafolim* var. *nanum* as a synonym of *P. ostenii*, 16 lectotypifications, clarification of morphology and geographical distribution, brief descriptions, and the first key to all the species in the genus.

Keywords: Compositae, *Eupatorium*, lectotypification, nomenclature, *Ooclinium*, Praxelinae, South America, taxonomy.

Introduction

South American *Praxelis* Cass. (Asteraceae, Eupatorieae) includes 18–21 species (Teles *et al.* 2016; Ribeiro *et al.* 2021) and is the second-largest genus of the subtribe Praxelinae (Hind and Robinson 2007; Robinson *et al.* 2009; Mandel *et al.* 2017, 2019; Susanna *et al.* 2020). It thrives in warm or temperate-warm environments of South America, from Colombia, Venezuela and the Guianas, to southern Brazil, north-western Uruguay and central Argentina (Table 1; Dillon and Hensold 1993; Cabrera *et al.* 1996; Freire and Ariza Espinar 2014; Robinson 2014; Christ and Ritter 2019; Salgado *et al.* 2020). There are no records for Chile, Ecuador and Patagonia (Robinson 1999; Abbott 2008; Freire 2008; Rodriguez 2018). The centre of diversity is in Brazil with 15 species, 8 of which are endemic to that country (Abreu 2019; Ribeiro *et al.* 2021).

Praxelis clematidea R.M. King & H.Rob. is a well-known species because of its invasive behaviour around the world (Zhang *et al.* 2021), with established populations in Australia, south-eastern Asia (e.g. China, Singapore and Taiwan) and Florida in the USA (Corlett and Shaw 1995; Waterhouse 2003; Wang *et al.* 2006; Abbott *et al.* 2008; Gardner and Williges 2015). This species, *P. diffusa* (Rich.) Pruski and *P. kleinioides* (Kunth) Sch.Bip. behave as a segetal or ruderal weed in its natural range (e.g. Marzocca 1976; Moreira and Bragança 2010; De Egea *et al.* 2016; Salgado *et al.* 2020; Ribeiro *et al.* 2021).

The genus *Praxelis* was first described by Cassini (1826), who placed it within his 'Eupatoriées' section and identified it by involucral characteristics, including deciduous phyllaries, and highly conical receptacle. *Praxelis villosa* Cass. was designated the type species (now a synonym of *P. diffusa*). However, the taxonomic history of *Praxelis* has an earlier starting point. Some of its current species were described under the large genus *Eupatorium* L. at the end of the 18th century, for example, *E. urticifolium* L.f. in 1781 and *E. pauciflorum* Kunth and *E. kleinioides* Kunth in 1818. The first two species are now synonyms of *P. diffusa* and the latter is the basionym of *P. kleinioides*.

Table 1. Natural distribution of *Praxelis* species per country.

Species	Argentina (Freire 2008; Freire and Ariza Espinar 2014)	Bolivia (Hind 2011, 2014; Robinson 2014)	Brazil (Troncoso Oliveira 2010; Abreu 2019; Ribeiro *et al.* 2021)	Colombia (Avila *et al.* 2019)	French Guiana (Funk *et al.* 2007)	Guyana (Funk *et al.* 2007)	Paraguay (Cabrera *et al.* 1996; Freire 2008)	Peru (Dillon and Hensold 1993)	Suriname (Funk *et al.* 2007)	Uruguay (Salgado *et al.* 2020)	Venezuela (Badillo 2001)
P. asperulacea		Excluded[A]	×			×					×
P. basifolia			×								
P. capillaris			×								
P. chiquitensis		×									
P. clematidea	×	×	×				×	×		×	
P. conoclinanthia		×									
P. decumbens			×								
P. diffusa			×	×	×	×		×	×		×
P. insignis		×	×								
P. kleinioides	×	×	×	×[B]			×	×[B]			×
P. minima			×								
P. missionum	×		×				×				
P. odontodactyla			×								
P. ostenii	×		×				×				
P. porophylloides		×									
P. sanctopaulensis			×								
P. scaturicola			×								
P. splettii			×								
Number of species	4	6	15	2	1	2	4	2	1	1	3

[A]Previous records were misidentifications of *P. chiquitensis* (Robinson 2014).
[B]Doubtful record (see notes under the respective species).

In 1836, de Candolle described the genus *Ooclinium* including *P. villosa* (as a dubious species), and five new species and one combination, namely, *O. grandiflorum* DC., *O. paucidentatum* DC., *O. pedunculare* DC., *O. sideritis* DC. and *O. capillare* DC. (all being currently included in *Praxelis*), and *O. rigidum* (Sw.) DC. (now a synonym of *Chromolaena rigida* (Sw.) R.M.King and H.Rob.). This author also transferred *E. kleinioides* and *E. urticifolium* to *Campuloclinium* DC., a genus of the subtribe Gyptidiinae (King and Robinson 1987; Calvo and Roque 2018). Years later, Schultz (1866) reinstated the genus *Praxelis*, using a wide taxonomic circumscription and including *P. villosa*, all the species of *Ooclinium*, and *E. kleinioides* within it.

In his treatment of the Brazilian species, Baker (1876) considered *Praxelis* a section within the wide concept of *Eupatorium* established by Bentham (1873). This section was characterised by two- or three-seriate involucres, deciduous phyllaries, and prominent receptacles. Baker also proposed several new synonyms, particularly in *E. kleinioides* (currently *Praxelis kleinioides)* and *E. urticifolium* (currently *P. diffusa)*. Section *Praxelis* was maintained throughout the 20th century (e.g. Hoffmann 1894; Robinson 1918, 1923, 1925; Malme 1932; Cabrera and Vittet 1954), until a series of studies (e.g. King and Robinson 1970, 1987) re-established *Praxelis* at genus level, characterising it by its deciduous phyllaries, conical receptacles and pappus with numerous capillary bristles.

King and Robinson's taxonomic concept of the tribe Eupatorieae (King and Robinson 1987) included the dismemberment of the formerly large genus *Eupatorium* into ~100 new genera described partly on the basis of floral characters. This was not fully accepted by southern South American botanists (Cabrera *et al.* 1996; Freire 2008; Novara 2009) until the early 21st century (e.g. Troncoso Oliveira 2010; Grossi *et al.* 2011; Freire and Ariza Espinar 2014; Grossi *et al.* 2020).

Praxelis is morphologically well circumscribed by its deciduous phyllaries, conical and epaleate receptacles, tubular–funnelform corollas, balusterform anther collars, asymmetrical carpopodia, densely papillose on the inner surface corolla lobes, and laterally inserted on the receptacle cypselae (Grossi *et al.* 2020; Salgado *et al.* 2020; Ribeiro *et al.* 2021). Nevertheless, species-level circumscription is often unclear. Many characters overlap, making species delimitation difficult. For example, the following two macroscopic characters widely used in species identifications have been described in very different ways: phyllotaxy and type of capitulescence.

The phyllotaxy in *Praxelis* has been described as opposite, opposite-decussate, alternate, rosulate, semirosulate, and verticillate as well as whorled, pseudowhorled, in pseudoverticils or in a rosette (e.g. Robinson 2006; Freire and Ariza Espinar 2014; Teles *et al.* 2016; Abreu and Esteves 2017; Salgado *et al.* 2020). Some terms are synonymous (i.e. verticillate and whorled) or similar in appearance; for example, pseudowhorled leaves only appear to be whorled; when closely examined, it is possible to see the opposite leaves arising from the axillary shoots. Capitula have been described as solitary, isolated in terminal branches, or scapiform (i.e. Freire and Ariza Espinar 2014). When capitula are grouped, the capitulescences have been described as corymbs, corymbose, corymbiform, dichasial cymes, simple dichasia, umbellate, thyrsoid, paniculate, or in secondary capitulescences (King and Robinson 1987; Hind and Robinson 2007; Freire and Ariza Espinar 2014; Teles *et al.* 2016; Christ and Ritter 2019; Salgado *et al.* 2020; Ribeiro *et al.* 2021).

Recent studies have addressed the taxonomic and morphological diversity of *Praxelis* at regional levels (i.e. Freire and Ariza Espinar 2014; Teles *et al.* 2016; Abreu and Esteves 2017; Christ and Ritter 2019; Abreu 2019; Salgado *et al.* 2020; Ribeiro *et al.* 2021), but until now, a complete treatment of the genus is lacking. Additionally, the aggressive invasive behaviour of *P. clematidea* around the world makes a robust, workable taxonomy of the group highly desirable. To begin to understand *Praxelis*, this study aims to (1) conduct a taxonomic update with nomenclatural readjustments and lectotypifications where required, (2) re-evaluate some morphological characters with taxonomic value, (3) provide distributional clarifications, and (4) provide the first key to all species of the genus.

Materials and methods

We analysed specimens (types and non-types) and photographs from the following herbaria: ALCB, B, BHCB, BM, BONN, BR, CORD, E, F, G, GH, GOET, HAL, HUEG, HUFG, IAN, K, L, LD, LIL, LINN, M, MPU, MO, MVM, MY, NY, OXF, P, R, RB, S, TCD, UB, UC, UFG, US, V, VEN, W and Z (Index Herbariorum, see http://sweetgum.nybg.org/science/ih/). In addition, high-resolution images were obtained from JSTOR (see http://plants.jstor.org/, accessed July 2019), virtual herbaria B (see https://www.bgbm.org/en/herbarium), BM (http://www.nhm.ac.uk/research-curation/scientific-resources/collections/botanical-collections/index.html), BR (http://www.botanicalcollections.be/#/en/search/specimen), E (http://elmer.rbge.org.uk/bgbase/vherb/bgbasevherb.php), F (https://collections-botany.fieldmuseum.org/), G (http://www.ville-ge.ch/musinfo/bd/cjb/chg/?lang=en), GH (https://huh.harvard.edu/pages/gray-herbarium-gh), GOET (https://www.uni-goettingen.de/de/157034.html), HAL (http://www.botanik.uni-halle.de/herbarium/?lang=en), K (http://apps.kew.org/herbcat/navigator.do), L (https://bioportal.naturalis.nl/), MPU (https://collections.umontpellier.fr/collections/botanique/herbier-mpu/base-herbier-mpu), NY (http://sweetgum.nybg.org/science/vh/), P (https://science.mnhn.fr/all/search), S (https://www.nrm.se/en/forskningochsamlingar/botanik/samlingar.565.html), UC (https://webapps.cspace.berkeley.edu/ucjeps/publicsearch/publicsearch/), US (http://collections.nmnh.si.edu/search/botany/), or digital

images were requested from curators of herbaria for further analysis. Specimens or images seen are indicated with '!'. All protologues were cross-checked with label information on type material.

Field trips in Argentina, Brazil and Uruguay were undertaken during 2017, 2018, 2019 and 2020; and vouchers were deposited in BA, LP, MVFA, MVM or UB. Macro- and micromorphological characters were analysed, especially those previously used for delimiting species of *Praxelis* (i.e. leaves, capitulescences, involucres, phyllaries, florets and pubescence). Leaves and capitula were rehydrated, treated with a clearing process and stained with 2% safranin (Zarlavsky 2014). For light microscope examination, the samples were examined with a Nikon Eclipse E200 microscope.

Accepted names are listed alphabetically.

Results

Praxelis currently includes the following 18 species: *P. asperulacea* (Baker) R.M.King & H.Rob, *P. basifolia* (Malme) R.M.King & H.Rob., *P. capillaris* (DC.) Sch.Bip., *P. chiquitensis* (B.L.Rob.) M.R.King & H.Rob., *P. clematidea* R.M.King & H.Rob., *P. conoclinanthia* (Hieron.) R.M.King & H.Rob., *P. decumbens* (Gardner) A.M.Teles & R. Esteves, *P. diffusa* (Rich.) Pruski, *P. insignis* (Malme) R.M.King & H.Rob., *P. kleinioides* (Kunth) Sch.Bip., *P. minima* A.M.Teles & P.L.Viana, *P. missionum* (Malme) R.M.King & H.Rob., *P. odontodactyla* (B.L.Rob.) R.M.King & H.Rob., *P. ostenii* (B.L.Rob.) R.M.King & H.Rob., *P. porophylloides* (B.L.Rob.) Hind, *P. sanctopaulensis* (B.L.Rob.) R.M.King & H.Rob., *P. scaturicola* Neves Ribeiro & V.L.Rivera and *P. splettii* H.Rob.

All species can be recognised by key features of habit, stem branching, length of internodes, shape and arrangement of leaves, general shape of capitulescences, length of peduncles, shape of involucres, leaf and stem pubescence, quantity and size of florets, and colour of the corolla (Fig. 1). Two characters with proven taxonomic relevance within *Praxelis*, namely persistence of the phyllaries (deciduous in the majority of species) and the presence of a xylopodium (i.e. *P. chiquitensis, P. decumbens* and *P. sanctopaulensis*), were excluded from the key because they are difficult to observe in herbarium specimens. To conclude our study, we briefly discuss some features that have had different and conflicting interpretations in previous studies.

Habit, phyllotaxis and leaf traits

Praxelis is composed of mostly perennial herbs, rarely subshrubs.

In previous studies, phyllotaxis, the arrangement of leaves on a stem, has been described in very different ways. We found that *Praxelis* has opposite leaves that can be arranged in the following three different patterns: (1) Leaves conspicuously opposite (alternate in the upper leaves in the case of *P. splettii*), petiolate or pseudopetiolate (Fig. 2*a*) as in *P. asperulacea, P. clematidea, P. conoclinanthia, P. decumbens, P. diffusa, P. insignis, P. kleinipoides, P. minima, P. ostenii, P. sanctopaulensis, P. scaturicola* and *P. spletii;* (2) leaves clustered at the plant base, sometimes in a rosette-like shape (Fig. 2*b*) as in *P. basifolia* and *P. missionum*; and (3) leaves and axillary buds producing pseudowhorls (Fig. 2*c*) as in *P. capillaris* and *P. odontodactyla*. In the latter type, the leaves of the secondary branches, which do not elongate, are usually smaller than those of the main stem. There are many intermediate leaf arrangements among the above-mentioned types, including stems with conspicuously opposite leaves and smaller leaves on lateral branches with short internodes (Fig. 2*d*), for example, *P. chiquitensis* and *P. porophylloides*.

We identified three main types of leaves. (1) Sessile with linear or very narrowly oblong laminas, entire margins and inconspicuous veins, associated with pseudowhorled phyllotaxy (as defined above). This leaf type is present in *P. capillaris* and *P. porophylloides*. (2) Sessile or pseudopetiolate (i.e. with a decurrent leaf base) with narrowly elliptic laminas, entire or somewhat serrate margins and one-veined or with inconspicuous veins, that is associated with a conspicuously opposite phyllotaxy as in *P. asperulacea, P. basifolia, P. chiquitensis, P. insignis, P. odontodactyla, P. sanctopaulensis* and *P. spletti*. (3) Petiolate, pseudopetiolate or sessile with ovate, obovate, rhomboid or elliptic laminas, serrate or crenulate margins, and three-veined; associated with a conspicuously opposite phyllotaxy. This combination is present in *P. clematidea, P. conoclinanthia, P. decumbens, P. diffusa, P. kleinioides, P. minima, P. missionum* and *P. ostenii*. In the last case, when laminas are narrow, the three-veined pattern is noticeable only at the base (for example, in some specimens of *P. kleinioides*).

Capitulescences

The group of capitula arranged on a stem has been called an inflorescence, secondary inflorescence or capitulescence; in this study, we use the last term to avoid confusion with the basic inflorescence in Asteraceae, the capitulum.

Some species of *Praxelis* have solitary capitula as in *P. insignis, P. minima, P. missionum* and *P. porophylloides* (Fig. 3*a*). The rest of the species have two types of capitulescences. (1) Dense corymbiform cymes, with many capitula, usually more than five, clustered at the top of main and lateral branches (Fig. 3*b*) with short peduncles (1.5 cm or less). This is found in *P. clematidea and P. conoclinanthia*. (2) Lax corymbiform cymes, with few (usually four or less) long pedunculate capitula (2 cm or more) distributed at the top of main and lateral branches as in *P. capillaris, P. chiquitensis, P. diffusa, P. odontodactyla, P. ostenii, P. sanctopaulensis* and *P. spletii* (Fig. 3*c*). Some species can present either solitary capitula or lax corymbiform cymes, for example, *P. basifolia, P. decumbens, P. kleinioides* and *P. scaturicola*.

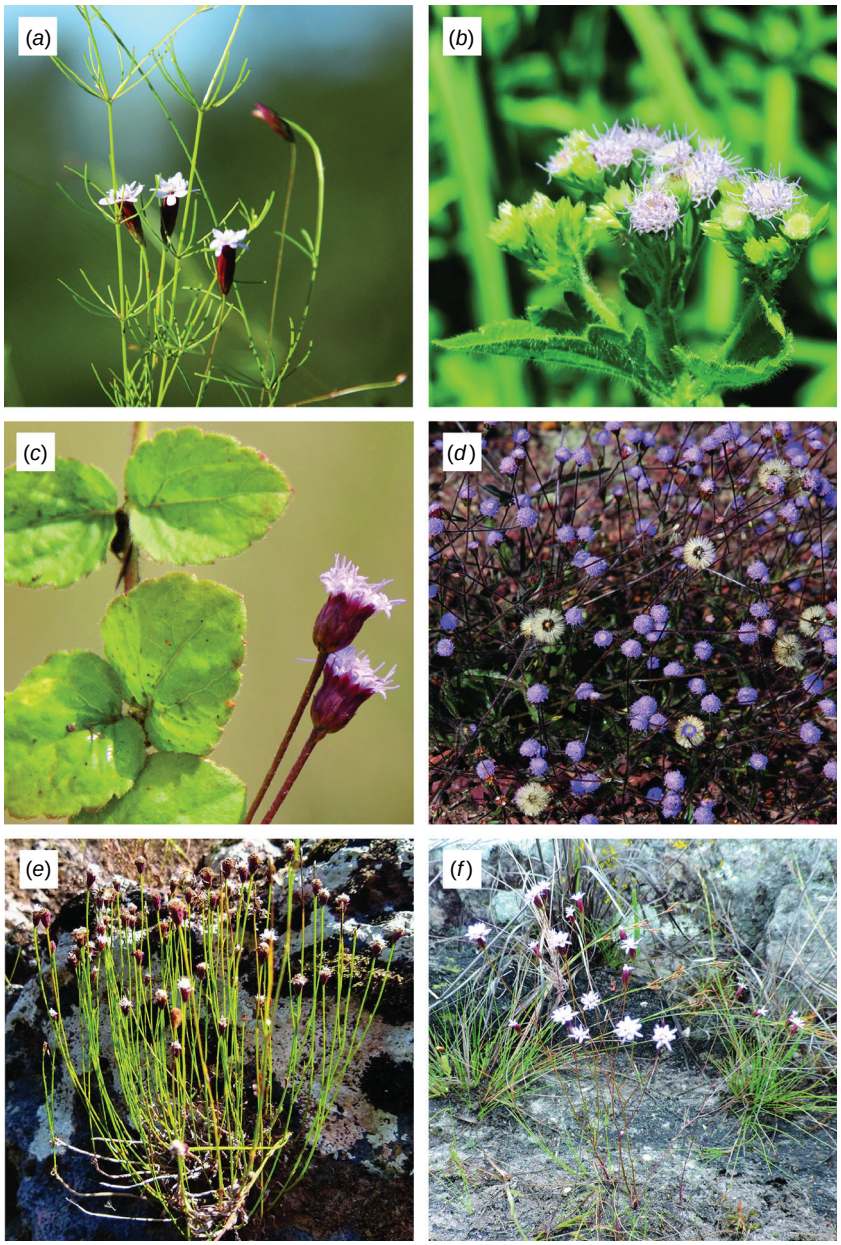

Fig. 1. Diversity of *Praxelis*. (*a*) *P. capillaris*, (*b*) *P. clematidea*, (*c*) *P. decumbens*, (*d*) *P. kleinioides*, (*e*) *P. scaturicola*, (*f*) *P. splettii*. Photo: H. J. C. Moreira (*a*, *c*, *d*), R. N. Ribeiro (e, *f*) and V. G. Salgado (*b*).

Taxonomic treatment

Praxelis Cass., *Dict. Sci. Nat.*, 2nd edn 43: 261 (1826)

Eupatorium sect. *Praxelis* (Cass.) Benth. ex Baker in C.F.P. de Martius (ed.), *Fl. Bras.* 6(2): 341 (1876). *Type: Praxelis villosa* Cass. (=*Praxelis diffusa* (Rich.) Pruski).

Ooclinium DC., Prodr. 5: 133 (1836). *Type: Ooclinium grandiflorum* DC. (=*Praxelis grandiflora* (DC.) Sch.Bip.).

Haberlea Baker in C.F.P. de Martius (ed.), *Fl. Bras.* 6(2): 341 (1876), *nom. inval., nom. nud.*

Annual or perennial herbs, rarely subshrubs, branched or unbranched, slightly woody at the base, rarely with xylopodium. Stems erect, ascendant or decumbent, terete, striate, glabrous or hairy. Leaves opposite or upper leaves rarely alternate, sometimes densely grouped or rosette-like at the plant base, or pseudowhorled, sessile, pseudopetiolate, or petiolate; laminas ovate, obovate, elliptic, rhomboid, oblong or linear, herbaceous or rarely subcoriaceous, glabrous or hairy on both surfaces, 1 or 3-veined or with inconspicuous veins, apex acute, base rounded, cuneate or decurrent, margins entire, serrate, crenate or incised-crenate. Capitulescences of lax or dense corymbiform cymes, few or many-headed, or sometimes solitary terminal capitula. Capitula homogamous, discoid, pedunculate, the peduncles short or long. Involucres campanulate or cylindrical; phyllaries 15–25, usually in 3–4(–8) series, imbricate,

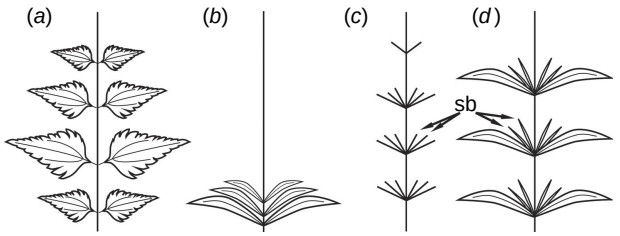

Fig. 2. Phyllotaxy and main leaf arrangements in *Praxelis*. (*a*) Conspicuously opposite leaves. (*b*) Opposite leaves, densely grouped at the plant base or rosette-like. (*c*) Leaves pseudowhorled, with inconspicuous, very short secondary branches showing a pair of leaves in the axil of each leaf. (*d*) Intermediate leaf arrangement, stem with conspicuously opposite leaves and small leaves on lateral branches with short internodes. sb, pair of opposite leaves of inconspicuous secondary branch.

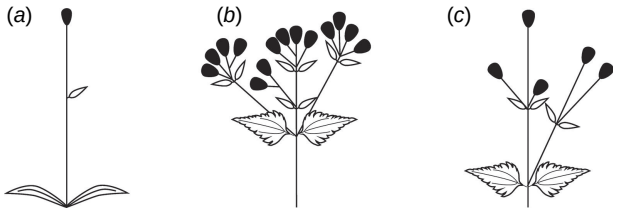

Fig. 3. Capitula arrangement and capitulescences in *Praxelis*. (*a*) Solitary. (*b*) Dense corymbiform cyme. (*c*) Lax corymbiform cyme.

increasing gradually in length, the outer ovate, pubescent mainly at the apex, margins entire, the inner narrowly oblong, glabrescent margins entire, usually deciduous, sometimes persistent. Receptacles conical, epaleate, glabrous. Florets 20–100, bisexual, corolla tubular–funnelform, lilac, purple, violet or white, limb slightly broadened, shortly 5-lobed, lobes densely papillose internally, glandular externally; stamens with ovate apical anther appendage, apices obtuse, base rounded, anther collar balusterform; style with each branch long, filiform or apically clavate, papillose, stylopod not broadened and glabrous. Cypselae obcompressed, 3–5-ribbed, carpopodium distinct, asymmetric, laterally inserted on the receptacle, hairy mainly on the ribs. Pappus 1-seriate, bristles barbellate (10–)15–40, scabrid, not or scarcely broadened distally, persistent, white.

Key to species of *Praxelis*

1. Leaf laminas linear or narrowly oblong or elliptic, 1-veined or sometimes inconspicuously 3-veined.....2
   Leaf laminas ovate, obovate, rhomboid or elliptic, conspicuously 3-veined, rarely penninerved.....10
2. Leaves opposite at base and alternate in the upper portion of the stem.....***P. splettii***
   Leaves all opposite.....3
3. Leaves densely grouped at the plant base or rosette-like.....***P. basifolia***
   Leaves evenly distributed along the main stem and branches, sometimes pseudowhorled.....4
4. Secondary branches with very short internodes; leaves pseudowhorled.....5
   Branches with short or long internodes; leaves not pseudowhorled.....6
5. Leaf laminas less than 0.5 mm wide with margins entire; involucres cylindrical or campanulate.....***P. capillaris***
   Leaf laminas less than 2 mm wide with margins dentate; involucres campanulate.....***P. odontodactyla***
6. Capitula solitary.....7
   Capitula grouped in capitulescences.....8
7. Leaf laminas 0.6–1 mm wide, margins entire.....***P. porophylloides***
   Leaf laminas 3–4 mm wide, margins serrate.....***P. insignis***
8. Subshrubs up to 100 cm tall, stems hairy, phyllaries in 5–6 series.....***P. sanctopaulensis***
   Herbs or subshrubs up to 50 cm tall, stems glabrous or glabrescent, phyllaries in 3–4(−5) series.....9
9. Herbs or subshrubs to 25 cm tall; leaf laminas 0.5–0.9 cm wide, margins entire.....***P. chiquitensis***
   Herbs up to 50 cm tall; leaf laminas 0.1–1 cm wide, margins sparsely serrate… .....***P. asperulacea***
10. Capitula grouped in corymbiform cymes with peduncles less than 1.5 cm long.....11
    Capitula solitary in terminal branches or grouped in corymbiform cymes with peduncles more than 1.5 cm long.....13
11. Herbs or subshrubs up to 100 cm tall; leaf laminas ovate, 3–6 × 1.5–4 cm.....***P. clematidea***
    Herbs or subshrubs up to 0.35 m tall; leaf laminas ovate or rhomboid, 1.5–4 × 0.5–1.5 cm.....12
12. Herbs or subshrubs; capitula of 35–50 florets.....***P. conoclinanthia***
    Herbs; capitula of ~20 florets.....***P. ostenii***
13. Herbs with stems decumbent; leaves subcoriaceous.....***P. decumbens***
    Herbs with stems erect or ascendent; leaves herbaceous.....14
14. Leaves usually densely grouped at the plant base or rosette-like; capitula of ~60–100 (−209) florets.....***P. missionum***
    Leaves evenly spread along the main stems and secondary branches; capitula 20–50 (−70) florets.....15
15. Herbs 5.5–8.5 cm tall, unbranched.....***P. minima***
    Herbs more than 15 cm tall, branched.....16
16. Leaf laminas ovate.....***P. diffusa***
    Leaf laminas obovate or elliptic.....17
17. Stems and leaves glabrous; corolla white.....***P. scaturicola***
    Stems and leaves hairy; corollas lilac or purple.....***P. kleinioides***

Praxelis asperulacea (Baker) R.M.King & H.Rob., *Phytologia* 20: 194 (1970)

Eupatorium asperulaceum Baker in C.F.P. de Martius (ed.), *Fl. Bras.* 6(2): 342 (1876). *Type citation: 'Habitat in prov do Alto Amazonas ad S. Carlos secus ripas fluminis Rio Negro: Spruce n. 3005; etiam in Guiana britannica ad sinum Cucuya: Appun n. 984'* [It inhabits in province of Upper Amazonas in San Carlos by the banks of the river Rio Negro: Spruce n. 305 and also in British Guiana in Cucuya creek: Appun n. 984]. *Type*: Venezuela, Amazonas State, June 1853, *R. Spruce 3005* (lecto, here designated: P 02476789, photo!; isolecto: BR 0000005267989, photo!; GH 00007545, photo!; K 001092383, photo!; K 001092384, photo!; NY 00168902, photo!; TCD 0005999, photo!); British Guiana, Cucuya creek, 1863, *Appun 984* (syn: K 000486863, photo!).

Eupatorium karuaiense Badillo, *Bol. Soc. Venez. Ci. Nat.* 10: 294 (1946); *Praxelis karuaiensis* (Badillo) R.M.King & H.Rob., *Phytologia* 20: 195 (1970). *Type citation:* 'sabanas cerca del bosque del río Karuai entre

Santa Teresita de Kabanayén y la base del Ptare-tepui. 1220 m. noviembre 8 de 1944 (*J. Steyermark 60311*, tipo)' [savannas near the forest of the Karuai river between Santa Teresita de Kabanayén and the base of Ptare –tepui. 1220 m. November 8 of 1944 (*J. Steyermark 60311*, typus)]. *Type:* Venezuela, Bolivar State, 1220 m, 18 Nov. 1944, *J.A. Steyermark 60311* (lecto, here designated: F V0050161F, photo!; isolecto: NY 00169073, photo!; US 00147658, photo!).

Herbs up to 50 cm tall, *stems* erect, glabrescent. *Leaves* opposite, sessile; laminas linear, 2–2.5 × 0.1–1 cm, herbaceous, glabrescent, margins serrate, 1-veined with lateral veins inconspicuous, rarely 3-veined. *Capitula* grouped in a capitulescences, peduncles 0.5–1.5 cm long, hairy. *Involucres* cylindrical or campanulate, phyllaries in 4 or 5 series. *Florets* 15–28, corollas lilac.

Illustration citations

Oliveira Cruz *et al.* (2016, p. 1233).

Distribution and habitat

This species occurs in northern South America, including northern and central Brazil, Guyana and Venezuela (Table 1). It inhabits the Cerrado and Amazonian regions (Badillo 2001; Funk *et al.* 2007; Troncoso Oliveira 2010; Teles *et al.* 2016).

Notes

Baker (1876) cited two gatherings in the protologue, namely, a Spruce collection from Venezuela, near the borders of Brazil and Colombia, and an Appun collection from 'Guiana Britannica' (currently the Cooperative Republic of Guyana). We found seven sheets with the first locality and collector (BR 0000005267989, GH 00007545, K 001092383, K 001092384, NY 00168902, P 02476789, TCD 0005999), and one with the second (K 000486863). We select for lectotypification the collection made by Spruce because it is represented by several specimens kept at many herbaria. We here designate the Spruce specimen deposited in P (02476789) as the lectotype because it matches the protologue, the specimen bears more capitula and leaves than the other original specimens, and Spruce's gathering is widely distributed across several herbaria.

The protologue of *P. karuaiensis* indicates the gathering *J.A. Steyermark 60311* as the type, without an indication of where the type is lodged. We found three sheets with matching collector, number and locality information in F (V0050161F), NY (NY 169073) and US (US 00147658). J. A. Steyermark´s types are held mostly in VEN where he worked (Rodríguez and Hokche 2006) and in several other herbaria (i.e. COL, F, GH, MO, UMO and US) (Stafleu and Cowan 1985). Material matching the protologue was not located in VEN (N. Avendaño, pers. comm., October 2019) or in MY, where Badillo worked (L. Hernández-Chong, pers. comm., August 2019). We here designate the specimen deposited in F (V0050161F) as the lectotype, because it matches the protologue and has more capitula and leaves than do the other original specimens.

Specimens examined

BRAZIL. Amazonas, Manaus-Caracaraí km 10. Near Igarapé Leão, 19 Oct. 1966, *C.K. Allen 2702, G.T. Prance, B.S. Pena & J.F. Ramos* (K 000931917); banks of Rio Taruma and Praia Dourado, 14 Dec. 1974, *A. Gentry 13286 & J. Ramos* (US 01665238). **GUYANA.** Cuyuni-Mazaruni, Utshe River, S side overlooking Guyana and Venezuela, 25 May 1990, *T. McDowell 2854 & D. Gopaul* (U 0158664); Upper Mazaruni River region, Karowtipu Mountain, 12 Apr. 1987, *B. Boom 7587 & D. Gopaul* (US 00600853). **VENEZUELA.** Amazonas, 2 km E of San Carlos de Rio Negro, 13 Nov. 1977, *R. Liesner 3426* (US 00768210); Bolivar, Ocoine River, Pie de la Roca, SE base of Auyan-tepui, 24 Nov. 1982, *G. Davidse 22596 & O. Huber* (MO 3297039).

Praxelis basifolia (Malme) R.M.King & H.Rob., *Phytologia* 20: 194 (1970)

Eupatorium basifolium Malme, *Ark. Bot.* 24a: 30 (1932). *Type citation:* 'Cuyabá, in campis glareoso-argillaceis plus minusve humidis, 19 39/403 (II3198), 196/703 (II:3198a)' [Cuiabá, in gravel-clay grasslands more or less humid]. *Type*: Brazil, Mato Grosso State, Cuiabá, 29 Apr. 1903, *G.O.A. Malme II 3198* (lecto, here designated: S 10–19992, photo!; isolecto: LD 1012419, photo!; S -PL-25581, photo!; S -R-9005, photo!); Brazil, Mato Grosso State, Cuiabá, 6 July 1903, *G.O.A. Malme II* 3198 (syn:S -R-9006, not seen).

Herbs up to 50 cm tall, stems erect, glabrescent. *Leaves* opposite, densely grouped at the plant base or rosette-like, sessile; laminas linear or narrowly oblong, 2.5–3.5 × 0.8–1.2, herbaceous, glabrescent, margins serrate, 1-veined. *Capitula* grouped in a capitulescence, peduncles 10–15 cm long, glabrescent. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* ~60, corollas violet.

Distribution and habitat

This species is endemic to the central west and south-east of Brazil (Table 1). It inhabits the Cerrado region (Teles *et al.* 2016; Abreu 2019).

Notes

From 1901 to 1903, G. O. A. Malme explored South America (Argentina, Brazil and Paraguay) in a series of botanical expeditions as a Regnellian scholar; plants from these expeditions are currently held at The Regnellian Herbarium of S (dos Santos 2016). He described *Eupatorium basifolium* on the basis of material collected in Brazil during those journeys. Four sheets at S match the protologue, three of them with collecting number 3198 (S 10-19992, S -PL-25581 and S -R-9005) and one with collecting number 3198a (S -R-9006). We designate as the lectotype the sheet S 10-19992 because it matches the protologue, shows more data on the label and has more capitula and leaves than do the other two specimens.

Specimens examined

BRAZIL. Minas Gerais, Uberlândia, road to Campo Florido, 8 Oct. 1999, *G.M. Araujo 2786 & A.F. Amaral* (HUFU00049349); Mato Groso, Poconé Municipality Route BR-070, km 584, 4 May 1995, *G. Hatschbach 62222, A. Pott, V. Pott & J.M. Silva* (US 01665236).

Praxelis capillaris (DC.) Sch.Bip., *Jahresber. Pollichia* 22–24: 254 (1866)

Ooclinium capillare DC., *Prodr.* 5: 134 (1836); *Eupatorium capillare* (DC.) Baker in C. F. P. de Martius (ed.), *Fl. Bras*. 6(2): 341 (1876), *nom. illeg.*, *non* Desv. ex Ham. (1825). *Type:* Brazil, Minas Gerais State, Serro, *A.C. Vauthier 311* (lecto, here designated: G-DC G 00464701, photo!; isolecto: P 02476410, photo!).

Haberlea sperguloides Baker in C. F. P. de Martius (ed.), *Fl. Bras*. 6(2): 341 (1876), *nom, inval., pro syn*.

Ooclinium quinquepartitum Baker in C. F. P. de Martius (ed.), *Fl. Bras*. 6(2): 341 (1876), *nom. inval., pro syn.*

Praxelis macrocarpa Abreu & Esteves, *Phytotaxa* 303: 78 (2017). *Type:* Brazil, Federal District, Brasília, Campus da Universidade, 16 Apr. 1963, *J.M. Pires et al. 9123* (lecto, here designated: UB 0125637!; isolecto: IAN 116015 [not seen]; P 02476432, photo!; RB 00427089, photo!; UB 0125638!).

Herbs up to 50 cm tall, stems erect, glabrescent. *Leaves* opposite, pseudowhorled, sessile; laminas linear, 1.5–6.5 × 0.5 cm, herbaceous, glabrescent, margin entire and revolute, 1-veined. *Capitula* solitary, peduncles 2–8.5 cm long, glabrescent. *Involucres* cylindrical, phyllaries in 3 or 4 series. *Florets* 23–26, corollas lilac or white.

Illustration citations

King and Robinson (1987, p. 381, fig. 153); Ribeiro and Teles (2015, p. 899, fig. 1*a*).

Distribution and habitat

This Brazilian endemic species (Table 1) inhabits the central, south and south-east of the country, from Mato Grosso to Paraná states. It grows in the Cerrado region (Teles *et al.* 2016; Abreu 2019).

Notes

De Candolle (1836) described *Ooclinium capillare* on the basis of a collection *A.C. Vauthier 311* from Serra do Frio (current municipality of Serro), in Minas Gerais, Brazil. Original materials are deposited in G (G 00464701) and P (P 02476410) and were previously considered holotype and isotype (Ribeiro *et al.* 2021), but de Candolle did not identify any of them as typus, so they are actually syntypes. We here designate the material G 00464701 as lectotype of the name *Ooclinium capillare*, because it is a well-preserved specimen that shows many of the species diagnostic characters.

Praxelis macrocarpa was described by Abreu and Esteves (2017) on the basis of material *J.M. Pires et al. 9123* that they cited as the holotype. This type collection is in UB in two sheets (UB 0125637 and UB 0125638) that correspond to two different specimens and the publication lacks indication of which one is the holotype, making them syntypes. Therefore, we designated as lectotype specimen UB 0125637.

Specimens examined

BRAZIL. Goiás, 15 km (straight line) N of Corumbá de Goiás, 14 May 1973, *W.R. Anderson 10272* (LIL 565466); Minas Gerais, Serra do Cipo 10–20 km N of Cardeal Mota, 16 May 1990, *M.M. Arbo 4221 & R. Silva, A. Schinini, V.C. Souza* (SI 160030).

Praxelis chiquitensis (B.L.Rob.) M.R.King & H.Rob., *Phytologia* 37: 458 (1977)

Eupatorium chiquitensis B.L.Rob., *Contr. Gray Herb*. 68: 11 (1923). *Type:* Bolivia, Santa Cruz Department, Chiquitos Province, Cerro Pesenema near Santiago de Chiquitos, 800 m, May 1907, *T.C.J. Herzog 25* (lecto, here designated: Z-000003344, photo!; isolecto: GH 00007591, photo!, fragment).

Herbs or subshrubs up to 25 cm tall, stems erect or ascendent, glabrescent. *Leaves* opposite, sessile; laminas linear, 1.5–2 × 0.5–0.9 cm, herbaceous, glabrescent, margins entire, 1-veined. *Capitula* grouped in a capitulescences, peduncles 0.8–2 cm long, glabrous. *Involucres* campanulate, phyllaries in 3–5 series. *Florets* 25, corollas white.

Illustration citations

Mamani *et al.* (2010, p. 61).

Distribution and habitat

This is a narrow endemic species restricted to western Bolivia (Table 1). It inhabits tropical savannas and hills of the Serranía Santiago de Chiquitos and the Serranía San Lorenzo, Ñuflo de Chávez (Mamani *et al.* 2010; *Soto & Escobar 922*, UB).

Notes

In the protologue of *E. chiquitensis*, Robinson indicated that original materials were collected in Bolivia by T. C. J. Herzog, with collecting number 25 and cited herbaria Z (the original specimen) and GH (a single leaf and a photo of the one at Z). We here designate the specimen in Z (Z-000003344) as the lectotype of *Eupatorium chiquitensis*, because the sheet in GH (GH 00007591), where B. L. Robinson's types are preserved, (Stafleu and Cowan 1983) is a fragment that lacks some of the diagnostic characters.

This species is categorised as vulnerable (Mamani *et al.* 2010).

Specimens examined

BOLIVIA. Santa Cruz, Velasco, 22 Mar. 1994, *R. Guillén 1100* (SI 1600414); Santiago, 2 Feb. 1958, *A. Krapovickas 9338* (LIL 460654).

Praxelis clematidea R.M.King & H.Rob., *Phytologia* 20: 194 (1970)

Eupatorium clematideum Griseb., *Abh. Königl. Ges. Wiss. Göttingen* 24: 172 (1879), *nom. illeg., non* (Wall. ex DC.) Sch.Bip. (1866); *Eupatorium urticifolium* var. *clematideum* Hieron. ex Kuntze, *Rev. Gen. Pl.* 3(3): 148 (1898); *Eupatorium urticifolium* var. *clematideum* Chodat, *Bull. Herb. Boissier* sér. 2, 3: 711 (1903), isonym; *Eupatorium catarium* Veldkamp, *Gard. Bull. Singapore* 51: 121 (1999), *nom. nov. Type:* Argentina, Córdoba Province, *s. loc., s. dat., P.G. Lorentz 81* (lecto: GOET 001494, photo!, *fide* S.E.Freire & L.Ariza Espinar in F. O. Zuloaga *et al.*, (eds) *Fl. Argentina* 7(1): 404 (2014); isolecto: GOET 001493, photo!; P 02700149, photo!); Tucumán province, near Tucumán, *s. dat.*, P.G. Lorentz, *G.H.E.W. Hieronymus 1119* (syn: GOET001492, photo!; CORD00006421, photo!; CORD00006422, photo!; CORD00006423, photo!); Paraguay, Asunción, 02 Apr. 1875, *B. Balansa 936* (syn: GOET001495, photo!).

Herbs or subshrubs up to 100 cm tall, stems erect, hairy. *Leaves* opposite, petiolate; laminas ovate, 3–6 cm × 1.5–4 cm, herbaceous, hirsute, margins serrate or incised-crenate, 3-veined. *Capitula* grouped in a capitulescence, peduncles 0.2–2 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 20–55, corollas lilac.

Illustration citations

Burkart (1974, p. 176, fig. 85i–l, as *Eupatorium clematideum*); Cabrera (1978, p. 113, fig. 46F–H, as *E. clematideum*); Cabrera *et al.* (1996, p. 60, fig. 19F–H, as *E. clematideum*); Freire and Molina (2009, p. 311, fig. 13, as *E. clematideum*); Novara (2009, p. 46, fig. 14, as *E. clematideum*); Freire and Ariza Espinar (2014, p. 404); Contro and Nakajima (2017, p. 152); Christ and Ritter (2019, p. 146, fig. 2A–D, 147, fig. 3A–C); Salgado *et al.* (2020, p. 482, fig. 1b).

Distribution and habitat

This species is native to and widely distributed in South America (Table 1). Its original distribution is central and northern Argentina, Bolivia, Brazil, Paraguay, Peru, and extreme north-western Uruguay. It grows in subtropical rainforests, Chaco forests and northern Pampas, as well as on roadsides and in disturbed or cultivated areas (Dillon and Hensold 1993; Cabrera *et al.* 1996; Freire 2008; Troncoso Oliveira 2010; Freire and Ariza Espinar 2014; Robinson 2014; Salgado *et al.* 2020). It is an aggressive invasive species in Australia and Southeast Asia, with established populations in China, Indonesia, Singapore, Taiwan, Thailand and the south-eastern USA (i.e. Florida) (Corlett and Shaw 1995; Waterhouse 2003; Wang *et al.* 2006; Abbott *et al.* 2008; Wu *et al.* 2010; Changtragoon *et al.* 2012; Gardner and Williges 2015; Chen *et al.* 2018; Tjitrosoedirdjo and Wahyuni 2018).

Specimens examined

ARGENTINA. Jujuy, Parque provincial Potrero de Yala, Provincial Route 4 on the way to Lagoon Yala, 28 Feb. 2019, *D.G. Gutiérrez 1508* (BA 95370); Misiones, 8 km E of Concepción de la Sierra, 24 Feb. 2020, *D.G. Gutiérrez 1661* (BA 95347). **BOLIVIA.** Santa Cruz, Ñuflo de Chávez, 34 km E of Concepción, on the road to San Ignacio, 23 July 2003, *M. Dematteis 1044, M. Ferrucci & A. Schinini* (SI 460020); Regional Park Lomas de Arena, 16 km S of Santa Cruz, 18 Mar. 1994, *J. Hunziker 12997 & A.F. Wulff* (SI 160035). **BRAZIL.** Minas Gerais, Santa Rita do Sapucaí Municipality, Timburé, 26 Feb. 2001, *O.S. Ribas 3298 & A.M.S. Ponchon* (US 01665403); Mato Grosso do Sul, Campo Grande, UEMT, 24 Jan. 1979, *A.L. Cabrera 29990 & E.M. Zardini* (SI 16064). **PARAGUAY.** Central, Tavarory, 0.78 km from administration on the direction to Arroyo Abai, 9 Dec. 1991, *E. Zardini 29384 & P. Aquino* (SI 084629); San Pedro, Colonia Primavera, 23 Mar. 1956, *A. Woolston 114a* (SI 160049). **PERU.** Piura, 57 km E of Olmos on road to Pucara, E of Abra de Porculla, 10 June 1978, *A. Gentry 22675, M. Dillon, J. Aronson & C. Diaz* (US 01665428); San Martín, Mariscal Casares, outskirts of Toache, 14 Mar. 1979, *A. Gentry 25756 & J. Aronson* (US 01665429). **URUGUAY.** Artigas, Arroyo Itacumbú, roadside of Route 3 km 613, 13 Jan. 2020, *A. González s.n.* (MVM 23485); Salto, Route 3, 6 km W of Monteclaro and 12 km NW of Palomas, 27 Feb. 2020, *D.G. Gutiérrez 1707* (BA 95338).

Praxelis conoclinanthia (Hieron.) R.M.King & H.Rob., *Phytologia* 20: 194 (1970)

Eupatorium conoclinanthium Hieron., *Bot. Jahrb. Syst.* 40: 388 (1908). *Type citation:* 'in parte australi reipublicae loco accuratius non indicate (K. FIEBRIG n. 3514 et 3515); prope Pinos baud procul ab urbe Tarija, alt. s. m. 2200 m, locis lapidosis humidis apricis (K. FIEBRIG n. 3152 et 3152[a]; 21. M. Martii 1904)' [in the southern part of the state, accurate location not indicated (K:FIEBRIG n 3514 and 3515); near Pinos, not far from the city of Tarija, 2200 m above sea level, humid and sunny stony places (K.FIEBRIG n. 3152 and 3152[a], 21 Mar. 1904)]. *Type:* Bolivia, Tarija Department, 2200 m, 21 Mar. 1904, *K.A.G. Fiebrig 3152* (lecto, here designated: K 000373102, photo!; isolecto: B (destroyed, Field Museum photo negatives collection 16230, photo!); E 00433270, photo!; GH 00007608, photo!; GH 00257068, photo!; GOET 001498, photo!; M 0029577, photo!; P 02476661, photo!; S R-2110, photo!; US 00409849, photo!); Bolivia, Tarija Department, 2200 m, 21 Mar. 1904, *K.A.G. Fiebrig 3152a* (syn: K 000486860, photo!); Bolivia, *s. dat.*, *K.A.G. Fiebrig 3153* (syn: not found); Bolivia, *s. dat.*, *K.A.G. Fiebrig 3154* (syn: not found).

Herbs or subshrubs up to 35 cm tall, stems erect, hairy. *Leaves* opposite, petiolate; laminas subrhomboid or narrowly ovate, 3 × 1.5 cm, herbaceous, hairy, mainly on the nerves, margins serrate, 3-veined. *Capitula* grouped in a capitulescence, peduncles 0.6–2 cm long, hairy. *Involucres* campanulate, phyllaries in 3–5 series. *Florets* 46–48, corollas deep purple.

Distribution and habitat

This species is endemic to western, southern and central-eastern Bolivia (Table 1) in La Paz, Santa Cruz and Tarija Departments (Robinson 2014). It inhabits xeric valleys.

Notes

Hieronymus cites four gatherings made by K. A. G. Fiebrig in the protologue of *E. conoclinanthium*. *Fiebrig 3152* and *3152a* were collected in Pinos (Tarija Department, Bolivia), and *Fiebrig 3153* and *3154* in unknown localities

in southern Bolivia. We here designate as lectotype *Fiebrig 3152* (K 000373102; Fig. 4*a*) because it matches the protologue and is widely distributed in several herbaria.

Specimens examined

BOLIVIA. Santa Cruz, Florida Province, 110 km from Santa Cruz to Cochabamba, 23 Mar. 1981, *G. Beck 6768* (US 01665332); Vallegrande, road from Vallegrande to Piramiri 2 km west from the peak, 4 Mar. 2005, *J.R.I. Wood 21735, H. Huaylla & A. Haigh* (US 01665319).

Praxelis decumbens (Gardner) A.M.Teles & R.Esteves in Teles *et al.*, *Phytotaxa* 278: 49 (2016)

Chromolaena decumbens Gardner, *London J. Bot.* 5: 466 (1846); *Eupatorium decumbens* (Gardner) Baker in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 344 (1876). *Type:* Brazil, Minas Gerais State, dry hills near Morro Velho, Sep. 1840, *G. Gardner 4754/3* (holo: BM 000541018, photo!).

Campyloclinium decumbens Baker in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 344 (1876), *nom. inval., pro syn.*

Herbs up to 30 cm tall, stems decumbent, hairy. *Leaves* opposite, sessile or very shortly petiolate; laminas ovate or oblong, 0.1–0.4 × 0.1–1.6 cm, subcoriaceous, glabrescent, margins serrate-crenate, 3-veined. *Capitula* solitary or grouped in a capitulescence, peduncles 5–20 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 40–60, corollas violet.

Illustration citations

Baker (1876, table 90, fig. 2, as *Eupatorium decumbens*); Fig. 1*c*.

Distribution and habitat

This species is endemic to Minas Gerais and São Paulo States in south-eastern Brazil (Table 1). It inhabits the Cerrado region (Teles *et al.* 2016; Chaves *et al.* 2019).

Notes

Gardner assigned the same collecting number to several gatherings, representing three different species of Asteraceae (*Vernonia burchelliana* Gardner and *V. martiana* Gardner

Fig. 4. (*a*) Lectotype of *Eupatorium conoclinanthium* in K. (*b*) Lectotype of *Eupatorium odontodactylum* in GH.

(Gardner 1846), both synonyms of *Piptolepis oleaster* (Mart. ex DC.) Sch.Bip.), so caution should be exercised when interpreting these Gardner specimens and their status as types. A single specimen corresponding to the protologue is held at BM and is here treated as the holotype.

Specimens examined

BRAZIL. Minas Gerais, lower cut-over slopes of Serra de Caraça, ~10 km W of Barao de Cocalis, 22 Jan. 1971, *H.S. Irwin 28850, R.M. Harley & E. Onishi* (LIL 565465); Lima Duarte, Parque Estadual do Ibitipoca, Lago dos Espelhos, 16 May 2006, *M.M. Saavedra 253, R.A.X. Borges, R.C. Forzza, A.R. Pereira, P.C. Ribeiro & M. Alvear* (NY 0113974).

Praxelis diffusa (Rich.) Pruski, *Brittonia* 50: 475 (1998)

Cacalia diffusa Rich., *Actes Soc. Hist. Nat. Paris* 1: 112 (as page '105') (1792). *Type:* French Guyana, Cayenne arrondissement, Cayenne, 1792, *J.B. Leblond 344* (lecto: G 00222773, photo!, *fide* J.F. Pruski, *Brittonia* 50:475 (1998)).

Eupatorium pauciflorum Kunth in A. Humboldt, A. Bonpland and C. S. Kunth (eds), *Nov. Gen. Sp.* (folio ed.) 4: 94 (1820); *Praxelis pauciflora* (Kunth) R.M.King & H.Rob., *Phytologia* 20: 195 (1970). *Type citation:* '*Crescit in Nova Granata?'* [New Granada]. *Type: s. loc.* [probably Colombia], *s. dat.*, *A. Humboldt & A. Bonpland s.n.* (holo: P 00320079, photo!).

Praxelis villosa Cass., *Dict. Sci. Nat*. 2nd ed, 43: 261 (1826); *Ooclinium villosum* (Cass.) DC., *Prodr.* 5: 134 (1836). *Type:* Guyane [French Guiana], July 1824, *P.A. Poiteau s.n.* (holo: K 00768722, photo!).

Ooclinium sideritis DC., *Prodr.* 5: 134 (1836); *Praxelis sideritis* (DC.) Sch.Bip., *Jahresber. Pollichia* 22–24: 254 (1866). *Type:* Brazil, Bahia State, 1830, *P.Salzmann s.n.* [Compos. 50] (lecto, here designated: G-DC barcode G 00464682, photo!; ~~i~~solecto: HAL 0111855, photo!; K 000069515, photo!; MPU 023492, photo!; P 02476874, photo!).

Ooclinium depressum Gardner, *London J. Bot.* 6: 437 (1847). *Type citation:* 'In open sandy places common, near the Villa de Arrayas, Province of Goyaz. April, 1840.' *Type*: Brazil, Tocantins State, Goyaz, near the Villa de Arrayas, Apr. 1840, *G.Gardner 3814* (lecto, here designated: W 0065631, photo!; isolecto: HAL 0111637, photo!; K 000484711, photo!; K 000484712, photo!; K 000484713, photo!; NY 00230817, photo!; NY 02491472, photo!; P 00708637, photo!; P 02406498, photo!; US 00146285, photo!).

[*Eupatorium urticifolium auct. non* Baker, *nom. illeg.*, in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 334 (1876)].

Herbs up to 50 cm tall, stems erect, hairy. *Leaves* opposite, petiolate; laminas ovate, 2.5–5 × 0.8–2 cm, herbaceous, hairy, margins serrate, 3-veined. *Capitula* grouped in a capitulescence, peduncles 1.2–8 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 30–45, corollas lilac.

Illustration citations

Delessert *et al.* (1820, table 14, as *Ooclinium sideritis*); Wawra (1866, tafel 77, as *Ooclinium villosum*); Baker (1876, table 91, as *Eupatorium urticifolium*); Jung and Kao (2013, p. 65); Ribeiro and Teles (2015, p. 899).

Distribution and habitat

This species is widely distributed in South America (Table 1), throughout Brazil (Cerrado region), Colombia, French Guyana, Guyana, Peru, Surinam and Venezuela (Dillon and Hensold 1993; Cabrera *et al.* 1996; Funk *et al.* 2007; Abreu 2019; Avila *et al.* 2019). It has also been reported as naturalised in Taiwan (Jung and Kao 2013).

Notes

De Candolle (1836) described *Ooclinium sideritis* on the basis of a collection *Salzmann* without number from near Bahia, Brazil. Original materials are deposited in G (G 00464682) where de Candolle worked and many other herbaria (i.e. HAL 0111855, K 000069515, MPU 023492, P 02476874). All specimens are complete and match protologue information. We here designate G 00464682 as lectotype of the name *Ooclinium sideritis*.

Regarding the type of *Ooclinium depressum*, Gardner collected throughout Brazil for 5 years, from 1836 to 1841. Most of his gatherings have a large number of duplicates that were sold to many herbaria and private collectors (Hind 2012). We found nine sheets of *Gardner 3814* which match the protologue for this species (i.e. HAL 0111637, K 000484711, K 000484712, K 000484713, NY 230817, NY 2491472, P 00708637, US 00146285 and W 0065631). We herein designate W 0065631 as lectotype of the name *O. depressum* Gardner because it is a well-preserved specimen that shows many of the species diagnostic characters.

Specimens examined

BRAZIL. Brazil, Maranhão, Lorêto Municipality, Ilha de Balsas region, between the Rio As Balsas and Parnaíba, ~2 km S of main house of Fazenda Moros, ~35 km S of Loreto, 27 Apr. 1962, *G. Eiten 4423 & L.T. Eiten* (US 01665552); Santa Catarina, Araranguá, 9 July 1996, *R. dosSantos 254 & C.M. Martinello* (CRI 001154). **COLOMBIA.** Antoloquia, Río Negro, 27 July 1930, *W.A. Archer 466* (US 01665534); Caldas, La Dorada Municipality, valley of La Miel River, 'Miel 1' Proyect, 5 Oct. 1989, *J. Estrada 544 & J.M. Cardiel* (MO 6607095). **FRENCH GUIANA.** Cayenne, vicinity of Cayenne, 30 May 1921, *W.E. Brodway 334* (US 00600862); Organabo, 17 Mar. 1986, *C. Feuillet 3559* (US 00600861). **PERU.** Cuzco, Santa Ana, 3 July 1915, *O.F. Cook 1606 & G.B. Gilbert* (US 01665549); Sahuayaco, 18 May 1963, *C. Vargas 14480* (US 01665548). **SURINAME.** Para, Zanderij airfield, 30 Dec. 1955, *A.M.E. Jonker 320 & F.P. Jonker* (USF). **VENEZUELA.** Bolivar, 5 km west of Upata, 31 July 1944, *J.A. Steyemark 57526* (US 00777914); Cojedes, San Carlos, 26 Mar. 1946, *A. Burkart 16251* (SI 160065).

Praxelis insignis (Malme) R.M.King & H.Rob., *Phytologia* 20: 195 (1970)

Eupatorium insigne Malme, *Ark. Bot.* 24a: 28. (1932). *Type citation:* 'Serra da Chapada, Cascata Grande, pr. Buriti in fissuris rupium apricarum, $19^{3}/_{6}03$ (II:3477)' [Serra da Chapada, Cascata Grande, near Buriti in sunny clefts]. *Type:* Brazil, Matos Grosso State, Cuiabá, Chapada dos Guimarães, 8 June 1903, *G.O.A. Malme II 3477*

(lecto, here designated: S -R-8997, photo!; isolecto: BHCB 000053, photo!; GH 00007719, photo!; LD 1035764, photo!; R 000026271, photo!; RB 00282960, photo!; S -R-8997, photo!; S 10-20091, photo!).

Herbs up to 40 cm tall, stems erect or ascendent, hairy. *Leaves* opposite, sessile; laminas linear or narrowly oblong, 2.5–3.5 × 0.3–0.4 cm, herbaceous, glabrescent, margins serrate, 1-veined. *Capitula* solitary, peduncles 1.5–20 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 70–120, corollas lilac.

Illustration citations

Malme (1932, p. 29, as *Eupatorium insigne*).

Distribution and habitat

This species occurs in central-eastern Bolivia (Santa Cruz Department), and the central-west, south-east and south of Brazil (Goiás, Mato Grosso, Mato Grosso do Sul, Minas Gerais and Paraná States; Table 1). It inhabits the Cerrado region (Malme 1932; Troncoso Oliveira 2010; Abreu 2019).

Notes

Malme (1932) described *Eupatorium insigne* in 'Die Compositen der zweiten Regnellschen Reise. II. Matto Grosso'. The locality mentioned in the protologue is 'Serra da Chapada, Cascata Grande pr. Buriti' (Malme 1932, p. 29). In the introduction, G. O. A. Malme explained that he spent most of his time in 'Cuyabáaun der Serra da Chapada (Santa Anna da Chapada)' (Malme 1932, p. 1). This locality corresponds to the current municipality of Chapada dos Guimarães near Buriti in the Brazilian State of Mato Grosso. Type material of *Eupatorium insigne* was collected by Malme on his 'second expedition Regnelliana' (dos Santos 2016) to Brazil. Specimens from this expedition are deposited in S, particularly in the Regnellian collection. Several sheets matching the protologue are held at S, of which we designate S -R-8997 as the lectotype for *E. insigne* (Fig. 5*b*, *d*), because it is well preserved and shows many of the species diagnostic characters.

Specimens examined

BOLIVIA. Santa Cruz, Ñuflo de Chavez 10 km S of Concepción, 14 Apr. 1987, *T. Killen 2463* (US 01665450). **BRAZIL.** Goiás, Alto Paraiso Municipality, Capada dos Veadeiros, 20 Feb. 1975, *G. Hatschbach 36333, W. Anderson, R. Barneby & B. Gates* (NY 00861228); Serra do Caiapó 33 km S of Caiaponia on road to Jataí, 19 Oct. 1964, *H.S. Irwin 7078* (NY 00805327).

Praxelis kleinioides (Kunth) Sch.Bip. *Jahresber. Pollichia* 22–24: 254 (1866)

Eupatorium kleinioides Kunth in A. Humboldt, A. Bonpland & C. S. Kunth (eds), *Nov. gen. sp.* (folio ed.) 4: 94 (1820); *Campuloclinium kleinioides* (Kunth) DC., Prodr. 5: 137 (1836). *Type citation: 'Crescit in aridis montium Cocollar et Tumiriquiri, alt. 600 hex.* (*Nova Andalusia*)'. [New Andalusia, the Cocollar and Turimiquire mountains, 1100 m]. Type: Venezuela, Sucre State, Montes municipality, Cocollar, Turimiquire, *s. dat., A. Bonpland & A. Humboldt 271* (probable holo: P 00320078, photo!).

Ooclinium grandiflorum DC., *Prodr.* 5: 134 (1836). *Praxelis grandiflora* (DC.) Sch. Bip. *Jahresber. Pollichia* 22–24: 254 (1866); *Praxelis grandiflora* (DC.) R.M.King & H.Rob., *Phytologia* 20: 194 (1970), isonym. *Type:* Brazil, São Paulo State, *s. loc.*, *s. dat., F. Sellow 434* (lecto, here designated: P 02476807, photo!; ~~iso~~isolecto: G-DC barcode G 00464699, photo).

Ooclinium paucidentatum DC., *Prodr.* 5: 134 (1836). *Praxelis paucidentata* (DC.) Sch.Bip., *Jahresber. Pollichia* 22–24: 254 (1866). *Type citation:* 'in Peruviâ legit olim cl. Haenke … (v. s. in h. Acad. reg. Monac.)'. *Type:* [Probably] Peru, *s. dat.*, *leg. ign. s.n.* (probable syn: G-DC barcode G 00464700, photo!).

Ooclinium pedunculare DC., *Prodr.* 5: 134 (1836); *Praxelis pedunculare* (DC.) Sch.Bip., *Jahresber. Pollichia* 22–24: 254 (1866). *Type:* Brazil, Minas Gerais State, Sabará municipality, 1833, *A.C. Vauthier 311* (lecto: GH 00010766, photo!, *fide* S.E.Freire & L.Ariza Espinar in F. O. Zuloaga *et al.* (eds) *Fl. Argentina* 7(1): 405 (2014); isolecto: G-DC barcode G 00464681, photo!; GH 00010765, photo!; P 02476791, photo!; P 02399558, photo!).

Eupatorium kleinioides var. *subglabratum* Hieron., *Bot. Jahrb. Syst.* 22: 782 (1897); *Eupatorium sanctopaulense* var. *subglabratum* (Hieron.) Malme, *Kongl. Svenska Vetensk. Handl.* 12: 46 (1933); *Eupatorium subglabratum (Hieron.) Cabrera & Vittet, Revista Mus. La Plata, Secc. Bot.* 8: 243 (1954). *Type*: Brazil, São Paulo State, Ypanema [currently Sorocaba], 1819, *F. Sellow* [B] 825 [c] 1040, (lecto: K 000802924, photo!, *fide* S.E.Freire & L.Ariza Espinar in F. O. Zuloaga *et al.* (eds) *Fl. Argentina* 7(1): 405 (2014); isolecto: P 00708623, photo!; P 02476799, photo!); Argentina, Misiones, near Salto Moconá, Apr. 1887, *G. Niederlein* 1384 (syn: not found).

Eupatorium kleinioides var. *latifolium* Chodat, *Bull. Herb. Boissier* ser. 2, 2: 307 (1902). *Type citation:* '… in campo pr. fl. Corrientes. Déc., 5844.' *Type:* Paraguay, San Pedro Department, Sierra de Maracayú, near Corrientes river, Dec. 1898–1899, *E. Hassler 5844* (lecto, here designated: G 00392274, photo!; isolecto: BM 000096257, photo!; GH 00257093, photo!; K 000768721, photo!; P 02399580, photo!; P 02476870, photo!; S R-2168, photo!; UC 944921, photo!).

Eupatorium kleinioides var. *microcephalum* Chodat, *Bull. Herb. Boissier* ser. 2, 3: 711 (1903) *Type:* Paraguay, Amambay Department, Apa river, Nov 1901–1902, *E. Hassler 7786* (lecto: G 00392200, photo!, *fide* A.L.Cabrera *et al. Fl. Paraguay* 25: 90 (1996); isolecto: MO 714624, photo!; S R-2139, photo!).

Eupatorium kleinioides var. *lasiolepis* B.L.Rob., *Proc. Amer. Acad. Arts* 51: 534 (1916). *Type:* Brazil, Goyaz State, on the road called Caminho do Bocãpãrý, 1828, *W.J. Burchell 6885* (holo: GH 00257092, photo!; iso: K 000955360, photo!; K 000955361 [not seen]; NY 00805345, photo!; P 00148858, photo!).

Eupatorium variegatum Malme, *Kongl. Svenska Vetensk. Acad. Handl., n.s.* 12(2): 46 (1933). *Type citation:* Capão Grande $^{3}/_{3}$ 04 (n.3972), Jaguariahyba $^{15}/_{1}$ 15 (n.16356, 16387). *Type:* Brazil, Paraná State, Jaguariaíva, 15 Jan. 1915, *P.K.H. Dusén 16386* (lecto, here designated: MO 1960318, photo!; isolecto: S 15-63948, not seen; S 15-65717, photo!).

[*Eupatorium capillare auct. non* (DC.) Baker, *nom. illeg*: J.G.Baker in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 342 (1876), *p.p.*].

Herbs up to 60 cm tall, stems erect, hirsute. *Leaves* opposite, sessile or very shortly petiolate; laminas obovate or elliptic, 2–3 × 0.3–2 cm, herbaceous, hairy, margins sparsely serrate, 3-veined, more conspicuously so at the base. *Capitula* solitary or grouped in a capitulescence,

Fig. 5. (*a*) Holotype of *Praxelis villosa* (right) and isolectotype of *Ooclinium sideritis* (left) in K. (*b*) Lectotype of *Eupatorium insigne* at S. (*c*) Label data for *P. villosa* holotype. (*d*) Label data for *E. insigne* lectotype.

peduncles 3–8 cm long, glabrous. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 50–60(−70), corollas lilac, purple or white.

Illustration citations

Baker (1876, table 90, fig. 1, as *Eupatorium kleinioides*); Cabrera *et al.* (1996, p. 91, fig. 31, as *E. kleinioides*); Freire and Ariza Espinar (2014, p. 405, fig. 1*d*).

Distribution and habitat

This species is widely distributed in South America (Table 1), in north-eastern Argentina, Bolivia, Brazil, Paraguay and Venezuela. Records of its occurrence in Peru and Colombia are doubtful (see Notes below). It inhabits the Caatinga, Cerrado and Chaco regions (Cabrera *et al.* 1996; Freire and Ariza Espinar 2014; Robinson 2014; Abreu 2019).

Notes

The locality mentioned in the protologue of *Eupatorium kleinioides* is 'montium Cocollar et Tumiriquiri, Nova Andalusia' (Kunth 1818, p. 94). New Andalusia was a South American Province first claimed by the Spanish Empire (from 1537 up to 1864), and later by Gran Colombia, and, finally, Venezuela. This province included the current Venezuelan States of Anzoátegui, Monagas and Sucre. Tumiriqui refers to the current Turimiquire Peak in Montes municipality, Sucre State. According to Stafleu and Cowan (1976), the original collections of A. Bonpland and A. Humboldt from the Americas are held at B and P. We found one sheet of original material of *Eupatorium kleinioides* in P (P 00320078) from the A. Humboldt and A. Bonpland 'Ameriqué equatorial' herbarium, labelled 'Cocollar' and 'no. 271'; this number is not mentioned in the protologue. This specimen is here treated as a probable holotype, in the absence of any other original material.

In the protologue of *Ooclinium grandiflorum*, de Candolle stated 'in Brasiliæ pro. Sancti-Pauli… (v. s. in h. Mus. Reg. Par. á Mus. imp. Bras. sub n. 434 miss)' (de Candolle 1836, p. 134), indicating that original material from São Paulo, Brazil, with number 434 seen in P. A specimen in P (P 02476807) and one in G (G 00464699) match the protologue information. The label on the specimen in P reads '(Herbier Impérial du BRÉSIL N°434) HERB. MUS. PARIS. C. GAUDICHAUD 1833'; according to Luis (1958), specimens with this indication correspond to a collection organised by Gaudichaud by using duplicates from F. Sellow and should be attributed to the latter. We here designate the specimen in P (P 02476807) as lectotype of *O. grandiflorum* because it is a complete specimen that bears more information on the label than does the one in G.

Baker (1876) regarded *Ooclinium grandiflorum* as a synonym of *Eupatorium kleinioides*. This was not adopted by recent authors, who have treated them as different species (e.g. King and Robinson 1987; Cabrera *et al.* 1996; Abreu 2019). The characters typically used to differentiate these two species are variable and unsupportive of a clear distinction between the two species; Ribeiro *et al.* (2021) provided a detailed discussion of this issue. Until further morphological, molecular and cytogenetic studies are conducted, we agree with Ribeiro *et al.* (2021) and follow Baker (1876) in considering *O. grandiflorum* a synonym of *P. kleinioides*.

In the protologue of *Ooclinium paucidentatum*, de Candolle stated 'in Peruviâ legit olim cl. Haenke … (v. s. in h. Acad. reg. Monac.)' (de Candolle 1836, p. 134), indicating that original material for this name was collected by T. Haenke and seen in M ('v. s. in h. Acad. Reg. Monac.'). Collections made by Haenke are held at PR and PRC (Stafleu and Cowan 1979), but the material is not in the PRC database or in PR (O. Šída, pers. comm., August 2019). Hind (2011) and Freire and Ariza Espinar (2014) noted that original material (incorrectly the 'holotype') was held at M, but this material cannot currently be located (A. Fleischmann, pers. comm., June 2019). A single specimen in G-DC (G 00464700), matching the protologue and identified as *O. paucidentatum*, is labelled 'Perou h. mun' (i.e. Peru, herb, Munich (Botanische Staatssammlung München)), but lacks any other identifying information. This specimen matches the protologue, and may represent original material of this name.

The presence of *Praxelis kleinioides* in Colombia and Peru, and the supposed Peruvian type locality of *Ooclinium paucidentatum*, is doubtful. Dillon and Hensold (1993) noted that even though King and Robinson (1987) recorded this species as occurring in Peru, they were unable to find any Peruvian records, and the material here treated as a probable syntype of *O. paucidentatum* lacks definite locality information. Haenke was part of the Malaspina´s Pacific Ocean Expedition from 1790 to 1793, and subsequently settled in Cochabamba (Bolivia), until he died in 1816. He collected extensively in the Americas, mainly in Brazil, Bolivia and Peru (Harmond *et al.* 1997). At the time, the Viceroyalty of Peru included most of modern-day Peru and parts of other South American countries. The political delimitation of these countries has undergone several changes throughout history, and it is impossible to determine exactly where Haenke collected material of this taxon, in terms of current political and geographical boundaries.

Baker (1876) recorded this species for Colombia (as *Eupatorium kleinioides*) on the basis of material collected by Humboldt and Bonpland and 'Funk' (*sic*) 223. Robinson (1918) suspected that these specimens came from Venezuela. We found one sheet in K (K000931968), *N. Funcke 223*, of this species, labelled as having been collected in Venezuela, and this is probably the specimen referred to by Baker and Robinson under the mis-spelled colletctor's name 'Funk'. Recently, Avila *et al.* (2019) also recorded this species for Colombia on the basis of material collected by Humboldt and held at P. Herbarium P lacks records for the species in Colombia; the material collected by Humboldt and Bonpland in their collection being the probable holotype from Venezuela. So, the presence of the species in Colombia should be regarded as doubtful until new records are found.

Six specimens matching the the protologue of *Eupatorium kleinioides* var. *latifolium* Chodat have been located in several herbaria. We designate the specimen G 36010/1 as the lectotype of this name because it is a well-preserved specimen that shows many diagnostic characteristics for this species.

Cabrera *et al.* (1996) cited 'In regione cursus superioris fluminis Apa' … XI.1901–02, *Hassler*, *E. 7786* HOLOTYPUS de *E. kleinioides* var. *microcephalum* Chodat' (p. 90) under specimens examined for *E. kleinioides*. This is here treated as inadvertent lectotypification by Cabrera *et al.* in accordance with ICN Art. 7.11 (Turland *et al.* 2018). Because the citation of Cabrera *et al.* (1996) meets the relevant requirements of ICN Art. 7.11, their use of the term 'HOLOTYPUS' is correctable under ICN Art. 9.10.

Malme lists three gatherings in the protologue for *E. variegatum*, including two from Jaguariahyba (*Dusén 16386* and *Dusén 16387*), currently Jaguariaíva, and one from Capão Grande (no. 3972), both collected by P. K. H. Dusén. Both G. O. A. Malme and P. K. H. Dusén collections are held at S (Stafleu and Cowan 1976). We found three sheets at S and one sheet in MO, collected by Dusén and which match the protologue. Specimens at S are currently unavailable for examination because of the renovation of the herbarium building (A. Anderberg, pers. comm., July 2019), and, accordingly, we select herein as lectotype the material deposited in MO (MO – 1960318).

Specimens examined

ARGENTINA. Misiones, San Ignacio, Gobernador Roca, 11 Oct. 1948, *G.J. Scwarz 6355* (LIL 268381); Cainguás, Puerto Mineral, 24 Aug. 1950, *G.J. Scwarz 10690* (LIL 347371). **BOLIVIA.** Beni, Ballivián Province, San Borja 19 km to La Paz, 22 July 1981, *G. Beck 6964* (US 0165506); Santa Cruz, Buena Vista, Mar. 1915, *J. Steinbach 1125* (LIL 16478). **BRAZIL.** Minas Gerais, Fazenda do Diamante, base of Sierra do Angico, 16 Apr. 1931, *Y. Mexia* 5633 (LIL 228247); Paraná, Timbú, 23 Apr. 1953, *G. Hatschbach 3150* (LIL 473893). **PARAGUAY.** Amambay, San Luis, Mar. 1908/1909, *F. Fiebrig 5160* (L 3682826); Concepción, Villa Sana, 22 Jan. 1908/1909, *K. Fiebrig 4674* (L 3682827). **VENEZUELA.** *s. loc.,* Mar. 1842, *N. Funcke 223* (K 000931968).

Praxelis minima A.M.Teles & P.L.Viana in Teles *et al.*, *Phytotaxa* 278: 49 (2016)

Type: Brazil, Minas Gerais State, Aiurouca, Parque Estadual do Papagaio, subida para o Pico do Papagaio, saindo do Retiro das Pedraos [climb to Pico do Papagaio, leaving from Retiro das Pedras], 22°02´S, 44°39´W, 1900 m, 12 Mar. 2008, *P.L. Viana et al. 3923* (holo: BHCB 034930, photo!; iso: UFG 65042!; US 01919619, photo!).

Herbs up to 5.5–8.5 cm tall, stems erect, hairy. *Leaves* opposite, petiolate; laminas ovate or oblong, 0.4–1 × 0.1–0.5 cm herbaceous, hairy, margins serrate, revolute, penninerved. *Capitula* solitary, peduncles 0.5–3.8 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* ~22, corollas lilac.

Illustration citations

Teles *et al.* (2016, p. 50, fig. 1, p. 51, fig. 2).

Distribution and habitat

This Brazilian species is endemic to Minas Gerais State. It is known only from the Parque Estadual da Serra do Papagaio, where it is found on granite rock outcrops (Teles *et al.* 2016).

Notes

The protologue cites an isotype deposited in K; however, this specimen could not be located (Sue Frisby, pers. comm., June 2019).

Specimens examined

BRAZIL. Minas Gerais, Aiuruoca, Parque Estadual do Papagio, climb to Pico do Papagaio leaving Retiro dos Pedros, 12 Mar. 2008, *P.L. Viana 3923, N.F.O. Mota, L.A. Ecternacht, L.V.C. Silva & G.M. Maciel* (US 01919619).

Praxelis missionum (Malme) R.M.King & H.Rob., *Phytologia* 20: 195 (1970)

Eupatorium missionum Malme, *Ark. Bot.* 24a: 35 (1932). *Type:* Argentina, Misiones Province, Posadas, 12 Nov. 1907, *E.L. Ekman 1119* (lecto: S -R-8992, photo!, *fide* S.E.Freire & L.Ariza Espinar in F. O. Zuloaga *et al.* (eds) *Fl. Argentina* 7(1): 405 (2014); isolecto: S 10-20101, photo!); Brazil, Rio Grande do Sul State. Alegrete to Misiones, May–Nov. 1826, F. Sellow 3652 (syn: K 000486862, photo!, B, not seen; P 02476809, photo!).

Eupatorium kleinioides var. *hecatantha* Baker in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 343 (1876). *Type:* Brazil, Rio Grande do Sul State. Alegrete to Misiones, May–Nov. 1826, *F.Sellow 3652* (lecto: K 000486862, photo!, *fide* A.L.Christ & M.R.Ritter, *Phytotaxa* 148 (2018); isolecto: B, not seen; P 02476809, photo!).

Herbs up to 15–30 cm tall, stems erect, hairy. *Leaves* opposite, densely grouped at the plant base or rosette-like, sessile; laminas oblong or elliptic, 3–5 × 0.5–1.5 cm, herbaceous, hairy, margins sparsely serrate, 3-veined. *Capitula* solitary, peduncles 5–20 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 60–100(–209), corollas lilac.

Illustration citations

Cabrera *et al.* (1996, p. 125, fig. 45, as *Eupatorium missionum*); Freire and Ariza Espinar (2014, p. 406); Christ and Ritter (2019, p. 146, fig. 2E–H, p. 147, fig. 3D, E).

Distribution and habitat

This species inhabits north-eastern Argentina, southern Brazil and south-eastern Paraguay (Table 1). It is found in the Cerrado and Pampas regions (Cabrera *et al.* 1996; Freire 2008; Troncoso Oliveira 2010).

Notes

The species epithet is correctly spelled '*missionum*', rather than '*missiona*', as commonly cited. The specific epithet is a genitive plural noun and it should retain its gender and termination, despite *Praxelis* being a feminine noun (Turland *et al.* 2018, Art. 23.5; Christ and Ritter 2019). Malme chose the specific epithet to refer to the type locality in the Argentine territory of 'Misiones' (currently Misiones Province). Jesuit missions or reductions were a type of settlement for indigenous people, in this case for the Guaraní people in north-eastern Argentina and Brazil (i.e. western Rio Grande do Sul State), and south-eastern Paraguay, from the beginning of the 17th century to the 18th century.

Specimens examined

ARGENTINA. Misiones, Cainguás, UNLP Private Reserve in Capito 5, 17 Mar. 2000, *F. Biganzoli 927, P. Peralta, G. Irrazabal, G. Massaccesi & B. Zucchuno* (SI 081252); San Ignacio, Menocchio, 12 Sep. 1945, *G. Schwarz 1259* (LIL 139526). **BRAZIL.** Rio Grande do Sul, Santo Angelo Municipality, São João Velho, 15 Nov. 1976, *T.M. Pedersen 11495* (L 3683587); Santa Cararina, Chepecó Municipality 9 km W of Campo Erê, 20 Feb. 1957, *L.B. Smith 11530 & R. Klein* (US 01665581). **PARAGUAY.** Caaguazú, Yhú, Feb 1932, *P. Jorgensen 7804* (US 01665588); in region of Alto Paraná River, Oct. 1909, *K. Fiebrig 5916* (L 3683586).

Praxelis odontodactyla (B.L.Rob.) R.M.King & H.Rob., *Phytologia* 20: 195 (1970)

Eupatorium capillare var. riedelii Sch.Bip. ex Baker, *Fl. Bras.* 6: 341 (1876); *Eupatorium odontodactylum* B.L.Rob., Contr. Gray Herb. 75: 10 (1925), *nom. nov., non Eupatorium riedelii* Baker (1876). *Type citation: 'In prov. S. Paulo ad Ypanema: Martius; locis non indicatis: Lund, Riedel.' Type*: Brazil, São Paulo State, Jan. 1826, *L. Riedel 1405* (lecto: GH 00007849, *fide* H.Robinson, Contr. *Gray Herb.* 75: 10 (1925), photo!).

Praxelis riedelii Baker in C. F. P. de Martius (ed.), *Fl. Bras.* 6(2): 342 (1876), *nom. inval., pro syn.*

Herbs up to 50 cm tall, stems erect, glabrescent. *Leaves* opposite, pseudowhorled, sessile; laminas linear or narrowly oblong, 3–5 cm × 0.2 cm, herbaceous, hairy, margins serrate, 3-veined. *Capitula* solitary, peduncles 1.5–8 cm long, glabrescent. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* ~25, corollas lilac.

Distribution

This species is endemic to central and eastern Brazil (Table 1). It inhabits the Atlantic Forest region of São Paulo (Troncoso Oliveira 2010) and the Cerrado region in the Federal District and the State of Goiás (Abreu 2019).

Notes

Baker cited three gatherings in the protologue of *E. capillare* var. *riedelii*. Robinson (1925) stated that 'Riedel's no. 1405 collected 'in saxosis humidis prope Ypanema,' Jan. 1826 (Gr.) may be taken as the type' (p. 10). This is here treated as inadvertent lectotypification by Robinson in accordance with ICN Art. 7.11 (Turland *et al.* 2018). Several specimens (i.e. C 10023137, GH 00007851, K 000931970, NY 00168916, US 00147524) representing original material collected by L. Riedel are labelled 'Brasilia', but lack collecting numbers. These specimens are regarded as syntypes rather than isolectotypes on that basis.

Specimens examined

BRAZIL. Goiás, Morro Feio, 10 May 1988, *R.R. Brooks 272 & R.D. Reeves* (MO 4296707); Cromini–Mairipotaba, transect from Site 2B to 2A, 27 Apr. 1988, *R.D. Reeves 197 & A.J.M. Baker* (MO 4296705).

Praxelis ostenii (B.L.Rob.) R.M.King & H.Rob., *Phytologia* 20: 195 (1970)

Eupatorium ostenii B.L.Rob., *Ostenia* 356 (1933). *Type:* Paraguay, Cordillera Department, San Bernardino, along the lake Ypacarí, 16 Aug. 1916, *C. Osten & T. Rojas 8779* (lecto: CORD 00005349, photo!, *fide* S.E.Freire & L.Ariza Espinar in F. O. Zuloaga *et al.* (eds) *Fl. Argentina* 7(1): 406 (2014).

Eupatorium urticifolium var. *nanum* Hieron., *Bot. Jahrb.* Syst. 22: 783 (1897), as '*nana*'. *Type:* Paraguay, Misiones Department, Villa Florida, Sep. 1892, *O. Kuntze s.n.* (holo: NY 04083638, photo!).

Herbs up to 35 cm tall, stems erect, hairy. *Leaves* opposite, petiolate; laminas ovate or obovate, 1.5–4 × 0.5–1.5 cm herbaceous, glabrescent above and hairy below, margins serrate, 3-veined. *Capitula* solitary or grouped in a capitulescence, peduncles 0.3–2 cm long, hairy. *Involucres* campanulate, phyllaries in 3 or 4 series. *Florets* 20–30, corollas lilac.

Illustration citations

Cabrera *et al.* (1996, p. 138, fig. 50, as *Eupatorium ostenii*); Freire and Ariza Espinar (2014, p. 406).

Distribution and habitat

This species occurs in north-eastern Argentina (Corrientes Province), north-eastern, central-western and southern Brazil, and eastern and south-eastern Paraguay (Table 1). It inhabits the Cerrado and humid Chaco regions (Cabrera *et al.* 1996; Ribeiro *et al.* 2021).

Notes

In the protologue of *E. urticifolium* var. *nanum*, Hieronymus indicates as type material a collection made by O. Kuntze in September 1892 from an unspecified locality in southern Paraguay. This material was reported to be at B (Hind 2011), but it was not found there and was probably lost in the fire of the Berlin Botanical Museum during World War II (Robert Vogt, pers. comm., June 2019). Most of Kuntze's type collections were purchased by the New York Botanical Garden in 1809 (Zanoni 1980). In NY, there is a specimen labelled *E. urticifolium* var. *nanum*. dated September 1892 from Villa Florida, a Paraguayan town in the south of the country. This specimen is the holotype (NY 04083638).

Eupatorium urticifolium var. *nanum* has been regarded as a synonym of *Praxelis clematidea* by several authors (e.g. Cabrera and Vittet 1954; Hind 2011; Freire and Ariza Espinar 2014). However, B. L. Robinson indicated in the protologue of *E. ostenii*:

> *E. ostenii* is with scarcely a doubt the same plant as, or at least conspecific with, the one collected by Dr Otto Kuntze and described by Hieronymus (1897) in *Engl.*

Bot. Jahrb. XXII, 783 under the wholly erroneous name *E. urticifolium* var. *nana* … *E. ostenii* has characters other than those of nanism to separate it from *E. clematideum*. It is a smoother plant with lanceolate rather than ovate leaves, looser inflorescences 3 striate rather than 4- or 5-striate phyllaries and perceptibly shorter achenes [Robinson 1933, p. 386].

The characters mentioned by Robinson can be clearly distinguished in the holotype (Fig. 6) of *E. urticifolium var. nanum*, especially those related to the shape of leaves and capitulescences. Therefore, we follow Robinson (1933) and consider this variety a synonym of *P. ostenii*.

Specimens examined

ARGENTINA. Corrientes, Ituzaingó, Estancia San Pedro, 10–13 Nov. 1976, *M.M. Arbo 1119* (SI 020147). **BRAZIL.** Goiás, Biquinha, 2 km S of Cristalina, 11 Apr. 1981, *G. Hatschbach 43783* (USF); Mato Grosso do Sul, around Aldeia Indigena São João, 9 Oct. 2003, *G. Hatschbach 76098, M. Harschbach & E. Barbosa* (US 01665569). **PARAGUAY.** Concepción, Itapucumí, Mar. 1917, *T. Rojas 2952* (LP 081006, SI 043294); Cordillera, San Bernardino, June 1915, *T. Rojas 1204* (LIL 63277).

Fig. 6. Holotype of *Eupatorium urticifolium* var. *nanum* in NY.

Praxelis porophylloides (B.L.Rob.) Hind, *Kew Bull.* 69: 9549 (2014)

Eupatorium porophylloides B.L.Rob., *Contr. Gray Herb.* 68: 29 (1923); *Chromolaena porophylloides* (B.L.Rob.) R.M.King & H.Rob., *Phytologia* 49: 4 (1981). *Type:* Bolivia, Santa Cruz Department, Chiquitos Province., Cerro de Santiago, 800 m, May 1907, *T.C.J. Herzog 24* (lecto; here designated: Z 000003365, photo!; isolecto: GH 00007924, photo!, fragment).

Herbs up to 30 cm tall, stems erect or ascendant, glabrous. *Leaves* opposite, sessile; laminas linear, 1–3.5 cm × 0.5–1 mm, herbaceous, glabrous, margins entire, 1-veined. *Capitula* solitary, peduncles 4–7.5 cm long, glabrous. *Involucres* campanulate, phyllaries in 5 series. *Florets* 25–30, corollas violet.

Illustration citations

Hind (2014, p. 2, fig. 1).

Distribution and habitat

This species is endemic to the east of Bolivia (Table 1). It inhabits tropical savannas and hills of the Serranía de Santiago de Chiquitos and the nearby Cerro de Chochís (Hind 2014).

In the protologue of *E. porophylloides*, Robinson indicated that original materials were collected in Bolivia by T. C. J. Herzog with collecting number 24 and cited herbaria Z (the original specimen) and GH (a single leaf and a photo of the one at Z). We here designate the specimen in Z (Z-000003365) as the lectotype of *Eupatorium porophylloides*, since the sheet in GH (GH 00007924), where B. L. Robinson's types are preserved (Stafleu and Cowan 1983), is a fragment that lacks some of the diagnostic characters.

Specimens examined

BOLIVIA. Santa Cruz, Cerro de Santiago (Chiquitos), May 1907, *T. Herzog 24* (Z000003365).

Praxelis sanctopaulensis (B.L.Rob.) R.M.King & H.Rob., *Phytologia* 65: 488 (1989)

Eupatorium sanctopaulense B.L.Rob., *Contr. Gray Herb.* 68: 32 (1923); *Chromolaena sanctopaulensis* (B.L.Rob.) R.M.King & H.Rob., *Phytologia* 20: 206 (1970). *Type citation:* 'BRAZIL: prov. São Paulo, *A. de Saint-Hilaire*, Cat. C^{2}, No. 1401 (Par., phot. Gr.).' *Type:* Brazil, São Paulo State, au bord du Tararé (Rio Itararé) [on the banks of the Tararé (Itararé River)], 1820, *A. de Saint-Hilaire Catal. C^{2}' No. 1401* (lecto, here designated: P 00742637, photo!; isolecto: GH 00007963, photo!; P 00742639, photo!; P 00742640, photo!; P 02411371, photo!).

Subshrubs up to 100 cm tall, stems erect, hairy. *Leaves* opposite, sessile; laminas linear, ~1.5–3 × 0.1 cm, herbaceous, glabrescent above and hairy below, margins serrate with small teeth, 1-veined. *Capitula* grouped in a capitulescence, peduncles 3–8 cm long, hairy. *Involucres* campanulate, phyllaries in 5 or 6 series. *Florets* 19–39, corollas lilac.

Distribution and habitat

This species is endemic to central and southern Brazil (Table 1) in the Cerrado region (Abreu 2019; Ribeiro *et al.* 2021).

Notes

In the protologue of *E. sanctopaulensis*, Robinson indicated original materials collected by *A. de Saint-Hilaire* number 1401, with additional information in his field notebook number 2 'Cat. C^{2}' (i.e. field notebook 2). We found five specimens that match the protologue, including four at P (P 02411371, P 00742637, P 00742639 and P 00742640) and a fragment at GH (GH 00007963) with a photo of P 00742637.

Both the protologue and label information from the specimens cite the locality as São Paulo, Brazil. The field notebook number 2 of *A. de Saint-Hilaire* contains further information: 1820, on the banks of the Tararé (Itararé River; Pignal *et al.* 2013).

We designate P 00742637 as the lectotype of the name *E. sanctopaulense* because it is a well-preserved specimen that shows many of the species diagnostic characters.

Specimens examined

BRAZIL. Paraná, Yaguariahyva [Jaguariaíva], 18 Apr. 1911, *P. Dusén 28470* (LIL 28470); Santa Catarina, Urubici Municipality, Aguas Brancas, 8 Mar. 2005, *G. Hatschbach 78929, E. Barbosa & E.F. Costa* (US 01665567).

Praxelis scaturicola Neves Ribeiro & V.L.Rivera, *Systematic Botany* 46 (4): 1131 (2021)

Type: Brazil, Goiás: Paraúna, ~2 km do Bar Restaurante Ponte de Pedra, [~2 km of Bar Restaurant Ponte de Pedra], Mata Ciliar, 17°179723S, 50°836857W, 25 May 2020, *R.N. Ribeiro & R.N. Ribeiro 610* (holo: UB!).

Herbs up to 50 cm tall, stems erect or decumbent, glabrous. *Leaves* opposite, petiolate; laminas linear or elliptic, 0.3–3 × 0.1–2 cm, herbaceous, glabrous, margins entire or sparsely dentate, 3-veined. *Capitula* usually solitary, or grouped in a capitulescence, peduncles 0.5–5 cm long, glabrous. *Involucres* campanulate, phyllaries in 3 series. *Florets* 30–42, corollas white.

Illustration citations

Ribeiro *et al.* (2021, fig. 1e).

Distribution and habitat

This species is endemic to Goiás State in Brazil (Table 1) and is known only from riverbanks on the Ponte de Pedra River, in the municipality of Paraúna.

Specimens examined

BRAZIL. Goias, Parauna Municipality, ~2 km from Bar Restaurante Ponte de Pedra, May 2020, *Rogerio N. Ribeiro 610 & Rodrigo N. Ribeiro* (UB).

Praxelis splettii H.Rob., *Phytologia* 88: 148 (2006)

Type: Brazil, Goiás State, estrada para Campos Belos (GO 118), 15.5 km ao norte de Alto Paraiso [road to Campos Belos (GO 118), 15.5 km north of Alto Paraiso] 13°46′S, 47°30′W, ~1100 m, 29 May 1994, *S. Splett 271* (lecto, here designated: US 00811155, photo!).

Herbs up to 15 cm tall, stems erect, glabrous. *Leaves* mostly alternate, opposite near base, sessile; laminas linear, 0.5–1.2 × 0.07–0.1 cm, herbaceous, glabrous above and glandular-hairy below, margins entire, 1-veined. *Capitula* solitary, peduncles 2–5 cm long, glabrous. *Involucres* cylindrical, phyllaries in 5 series. *Florets* ~15, corollas purple.

Illustration citations

Robinson (2006, p. 149, fig. 6, fig. 1d).

Distribution and habitat

This species is endemic to the State of Goiás in central-western Brazil (Table 1), recorded only in the Chapada dos Veadeiros. It is endemic to the Cerrado region (Troncoso Oliveira 2010; Abreu 2019).

Notes

The protologue records the holotype as being lodged in UB, but after a thorough search, we were unable to find it. Robinson cites two isotypes, one deposited in BONN, which could not be located (T. Joßberger, pers. comm., June 2019) and the other in US (US 00811155). The specimen at US is herein designated as the lectotype.

Specimens examined

BRAZIL. Goiás, 15.5 km N of Alto Paraiso, 29 May 1994, *S. Splett 271* (US 0081155).

Notes on *Ooclinium*

The type of *Ooclinium* and most of the species that have been described or attributed to this genus are now included in *Praxelis*. However, *Ooclinium rigidum* (Sw.) DC. and *O. clavatum* Benth. are currently placed in *Chromolaena* DC., as *C. rigida* (Sw.) R.M.King & H.Rob. and *C. ivifolia* (L.) R.M.King & H.Rob. respectively. Our studies support this generic placement.

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Data availability. The data that support this study will be shared upon reasonable request to the corresponding author.

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