Systematics of *Tanaecium* Sw. emend L.G. Lohmann (Bignonieae, Bignoniaceae)

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Tese apresentada ao Instituto de Biociências da Universidade de São Paulo, para a obtenção de Título de Doutor em Ciências Biológicas, na Área de Botânica.

Orientadora: Profa. Dra. Lúcia Garcez Lohmann

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Comissão Julgadora:

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Aos meus pais, *Alcides Frazão* e
Celma Assumpção, meus eternos
incentivadores, dedico.

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Índice

RESUMO

Tanaecium Sw. emend L.G. Lohmann é um gênero monofilético de lianas neotropicais pertencente à tribo Bignonieae (Bignoniaceae). O gênero é caracterizado por uma mistura de gemas axilares com profilos em formato tanto subulados quanto em rosetas (*bromeliad-like*), sendo uma sinapomorfia morfológica putativa. Na sinopse mais recente de *Tanaecium*, 17 espécies foram reconhecidas; trabalhos subsequentes incluíram quatro novas espécies ao gênero, elevando para 21 espécies em *Tanaecium*. Apesar de alguns estudos filogenéticos terem amostrado representantes de *Tanaecium* no passado, estes estudos não focaram em reconstruir a filogenia de *Tanaecium* e, com isso, as relações taxonômicas e filogenéticas entre suas espécies persistem incertas. Os componentes taxonômicos desta tese resultaram em: (i) descrição de uma nova espécie (*Tanaecium decorticans* Frazão & L.G. Lohmann), (ii) combinação de uma espécie em *Fridericia* (i.e., *Fridericia mutabilis* (Bureau & K. Schum.) Frazão & L.G. Lohmann, (iii) elucidação da tipificação do gênero, e (iv) sinopse revisada que trata todas as 21 espécies reconhecidas para *Tanaecium*. O componente filogenético desta tese combinou bancos de dados de Sanger e sequenciamento em larga escala (HTS) para reconstruir a filogenia mais abrangente do gênero até o presente. Essa filogenia foi baseada em sequências de 28 plastomas (16 *Tanaecium* e 12 grupos-externo) e 176 sequências geradas com Sanger para três marcadores moleculares (i.e., *ndh*F, *rpl32-trn*L e *pep*C), representando 92 indivíduos e 17 espécies de *Tanaecium.* Os 16 plastomas de *Tanaecium* montados neste estudo revelaram cinco diferentes padrões de organização de regiões de cópia única maior (LSC), cópias invertidas e repetidas (IR) e cópia única menor (SSC). Adicionalmente, quarto principais mudanças nos limites das IRs foram encontradas, com contrações das IRs associadas à expansões das SSC e LSC. As topologias reconstruídas usando os três bancos de dados montados neste estudo (i.e., Sanger, plastomas e Sanger e plastomas combinados) reconstruíram quatro grandes clados no *core Tanaecium*. A topologia reconstruída a partir das análises de dados combinados de plastoma e Sanger recuperou a filogenia melhor resolvida e suportada de *Tanaecium* até o momento. Esta tese destaca a importância de estudos aprofundados de linhagens individuais, incluindo estudos detalhados em taxonomia, distribuição e relações evolutivas, para o entendimento da compisição de biotas de regiões megadiversas tais como o Neotrópico.

Palavras-chaves: Amazônia, lianas, Neotrópicos, filogenômica, taxonomia.

ABSTRACT

Tanaecium Sw. emend L.G. Lohmann is a monophyletic genus of Neotropical lianas within the tribe Bignonieae (Bignoniaceae). The genus is characterized by mixed subulate and bromeliad-like prophylls of the axillary buds, putative morphological synapomorphy. In the most recent synopsis of *Tanaecium*, 17 species were recognized; subsequent works included four new species into the genus leading to 21 species in *Tanaecium*. Even though some phylogenetic studies sampled representatives of *Tanaecium* in the past, these studies were not focused on reconstructing the phylogeny of *Tanaecium* as whole and phylogenetic relationships among its species remain unclear. In this thesis I undertook taxonomic and phylogenetic studies to better understand the systematics and evolution of *Tanaecium*. The taxonomic component of this thesis resulted in: (i) the description of one new species (*Tanaecium decorticans* Frazão & L.G. Lohmann), (ii) the combination of one species in *Fridericia* (i.e., *Fridericia mutabilis* (Bureau & K. Schum.) Frazão & L.G. Lohmann, (iii) the elucidation of the genus typification, and (iv) a revised synopsis that treated all 21 species for *Tanaecium* recognized. The phylogenetic component of this thesis combined Sanger and High-Throughput Sequencing (HTS) datasets to reconstruct the most comprehensive phylogeny of the genus to date. This phylogeny was based on sequences of 28 plastomes (16 *Tanaecium* and 12 outgroups), and 176 sequences generated with Sanger for three molecular markers (i.e., *ndh*F, *rpl32-trn*L, and *pep*C) representing 92 individuals and 17 species of *Tanaecium*. The 16 plastomes of *Tanaecium* assembled in this study revealed five different patterns of organization of the Large Single Copy (LSC), Inverted Repeat (IR), and Small Single Copy (SSC) regions. Additionally, four main IR boundary shifts were found, with contractions of the IRs associated to expansions of the SSC and LSC. The topologies reconstructed using the three datasets assembled in this study (i.e., Sanger, plastome, and combined plastome and Sanger) reconstructed four major clades within the core *Tanaecium*. The topology reconstructed through the analysis of the combined plastome and Sanger dataset provides the most resolved and supported phylogeny of *Tanaecium* to date. This thesis highlights the importance of in-depth studies of individual lineages, including detailed studies of the taxonomy, distribution, and evolutionary relationships, for the understanding of the assembly of the biotas of megadiverse regions such as the Neotropics.

Keywords: Amazonia, lianas, Neotropics, phylogenomic, taxonomy.

A região Neotropical está entre as mais ricas em biodiversidade no planeta (Antonelli & Sanmartín 2011). Essa região inclui as Américas Central e do Sul, estendendo-se desde o centro do México até o sul do Brasil (Morrone 2014). O Neotrópico abriga uma alta diversidade de ecossistemas, incluindo desde áreas áridas, como a Caatinga, até as mais úmidas do planeta, como a Floresta Amazônica (Fiaschi *et al.* 2015). A alta diversidade dessa região vem despertando grande interesse nos cientistas ao longo do tempo, inspirando levantamentos de hipóteses para explicá-la tais como a influência de fatores edáficos (*e.g.*, Burnett *et al.* 1998; Fine *et al.* 2005; Laurance *et al.* 2010), de interações planta-polinizadores (*e.g.*, Smith *et al.* 2008; Tripp & Manos 2008; Alcantara & Lohmann 2010) e/ou de planta-dispersores (ver Pennington & Dick 2004), ou ainda da história biogeográfica da região (Hoorn *et al.* 2010; Antonelli & Sanmartín 2011).

Uma das abordagens para o estudo da biodiversidade Neotropical é o uso de grupos-modelo para testar hipóteses específicas e, consequentemente, tentar responder questões mais gerais sobre a região. Nesse contexto, a tribo Bignonieae, composta de arbustos e lianas exclusivamente Neotropicais, e que pertencente à família do ipê-amarelo (Bignoniaceae), tem sido utilizada em diversos estudos de evolução da biota Neotropical (*e.g.* Lohmann 2006; Alcantara & Lohmann 2010; Lohmann *et al.* 2013; Medeiros & Lohmann 2015a; Fonseca & Lohmann 2018; Thode *et al.* 2019). Bignonieae contém 21 gêneros e cerca de 400 espécies (Lohmann & Taylor 2014), ocorrendo desde florestas úmidas na América Central até vegetações sazonalmente secas na América do Sul (Lohmann 2006).

Tanaecium Sw. emend L.G.Lohmann é um dos gêneros pertencentes à tribo Bignonieae. Apresenta distribuição Neotropical, ocorrendo desde o México e Antilhas até a Argentina, contendo 22 espécies atualmente reconhecidas (Lohmann & Taylor 2014; Pace *et al.* 2016; Frazão & Lohmann 2018; Kaehler *et al.* 2019) (Fig. 1). A maior diversidade deste gênero é encontrada na região Amazônica, onde ocorrem 11 espécies (Lohmann & Taylor 2014) (Fig. 2).

Algumas espécies de *Tanaecium* apresentam distribuição restrita, como é o caso de *Tanaecium affine* (A.H. Gentry) L.G. Lohmann, *Tanaecium apiculatum* A.H. Gentry, *Tanaecium caudiculatum* (Standl.) L.G. Lohmann, *Tanaecium crucigerum* Seem., *Tanaecium decorticans* Frazão & Lohmann, *Tanaecium exitiosum* Dugand, *Tanaecium neobrasiliense* L.G. Lohmann, *Tanaecium paradoxum* (Sandwith) Kaehler & Lohmann e *Tanaecium parviflorum* (Mart. ex. DC.) Kaehler & Lohmann (Lohmann & Taylor 2014; Pace at al. 2016; Frazão & Lohmann 2018; Lohmann, dados não publicados) (Fig. 2). Por outro lado, há também espécies com distribuição disjunta, como é o caso de *Tanaecium cyrtanthum* (Mart. ex DC.) Bureau & K.Schum. e

Tanaecium duckei A. Samp (Fig. 2). As 11 espécies restantes estão distribuídas amplamente pela região Neotropical (Lohmann & Taylor 2014) (Fig. 2).

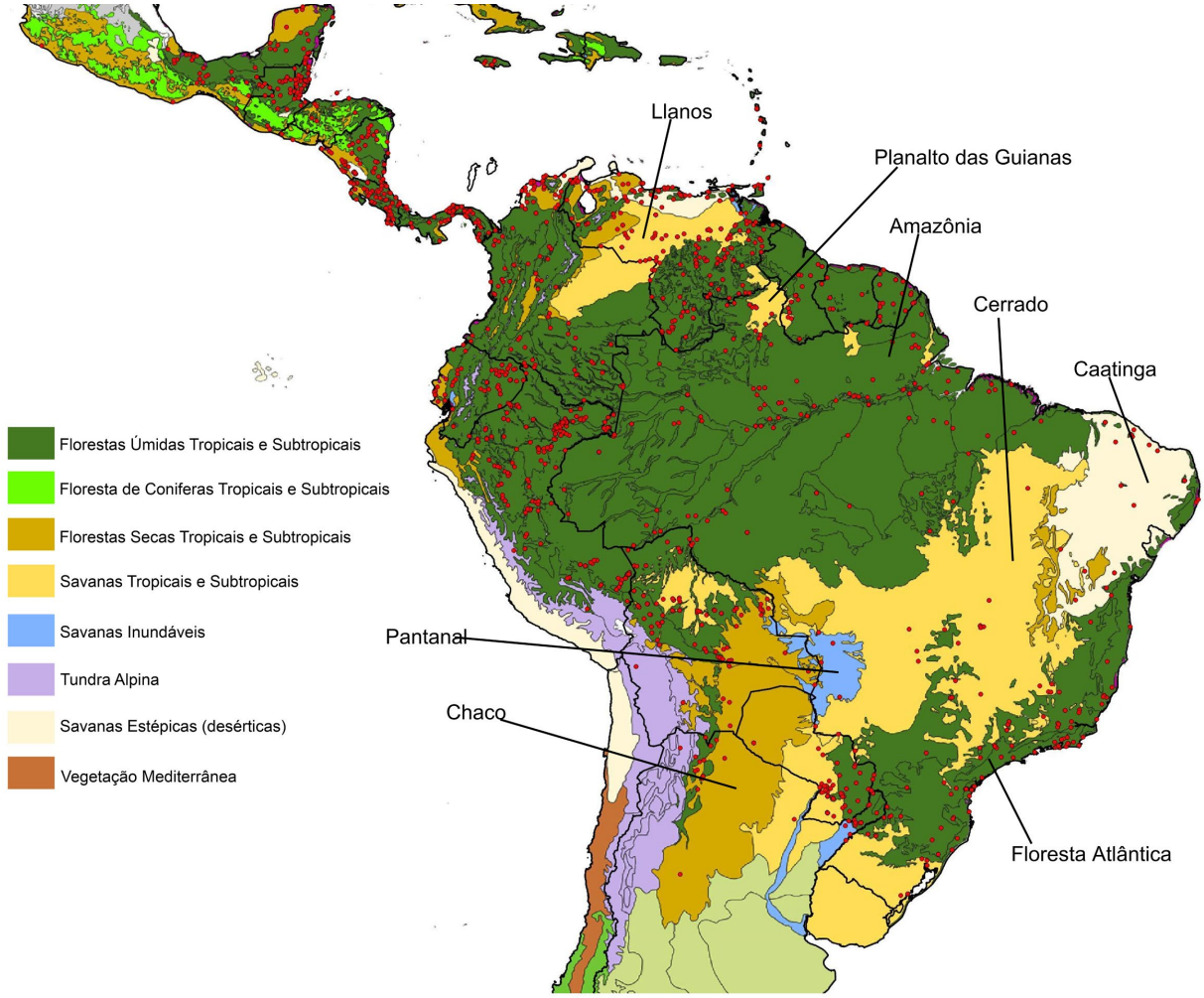

Figura 1: Mapa de distribuição conhecida para as espécies de *Tanaecium* nas diferentes ecorregiões Neotropicais. Pontos vermelhos representam as distribuições conhecidas para todas as espécies de *Tanaecium*. Alguns biomas onde existem grande representatividade do gênero são assinalados. Mapa modificado a partir do disponível no Wikimedia Commons (http://commons.wikimedia.org/wiki/File%3ANeotropic_biomes.svg).

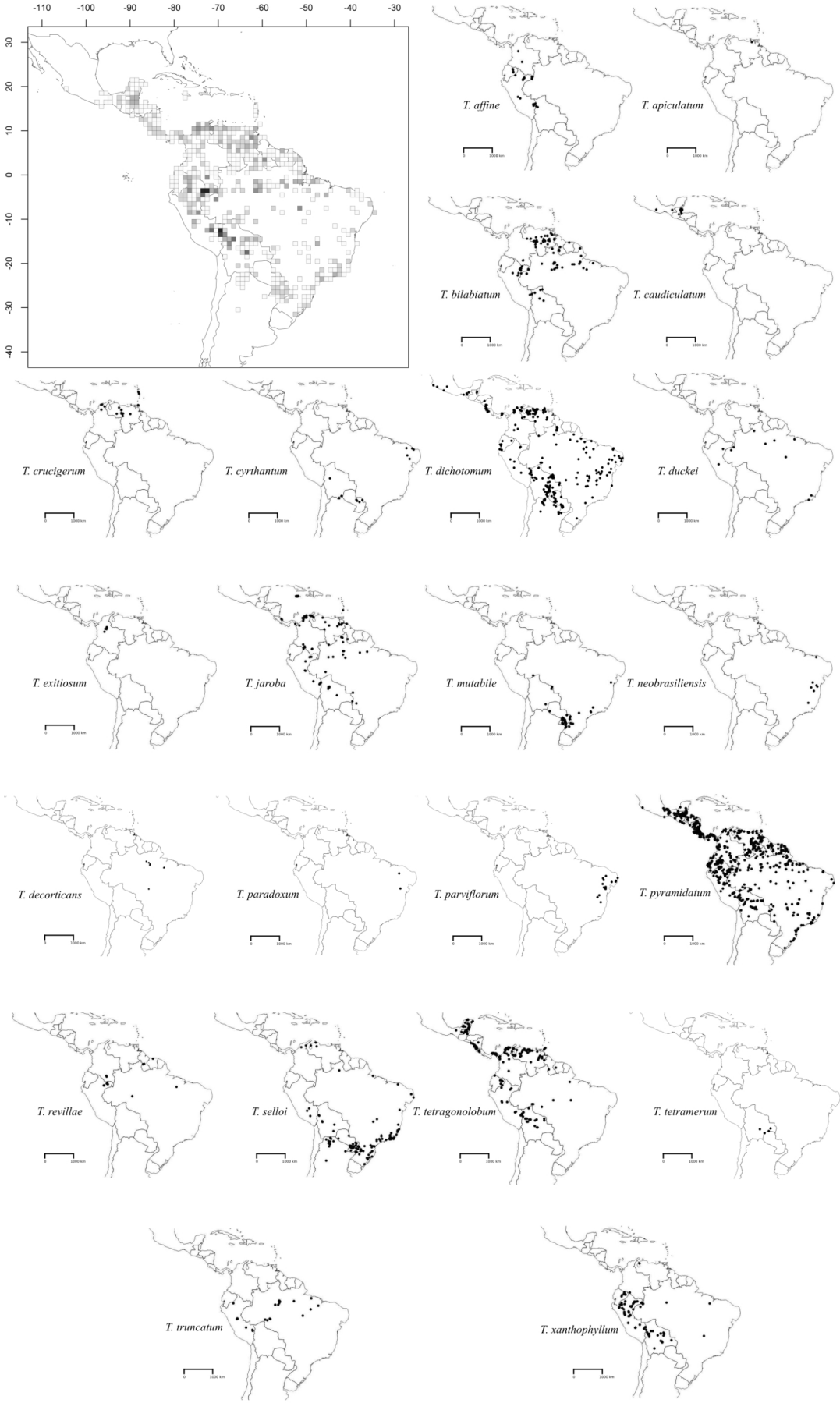

Figura 2: Distribuição geográfica das espécies de *Tanaecium*. O mapa maior à esquerda superior mostra a concentração de espécies de *Tanaecium* por área na região Neotropical. Tons mais escuros indicam maior riqueza de espécies.

Taxonomia e morfologia de *Tanaecium*

A circunscrição original de *Tanaecium* era mais restrita do que a atual, com apenas seis espécies reconhecidas (ver Gentry 1973; Gentry 1976). Destas seis espécies, cinco permanecem incluídos no gênero de acordo com a atual circunscrição (Lohmann & Taylor 2014), enquanto *Tanaecium nocturnum* (Barb. Rodr.) Bureau & K. Schum. foi transferida para o gênero *Bignonia* L. (Lohmann & Taylor 2014). Além das cinco espécies tradicionalmente classificadas como *Tanaecium*, 12 espécies dos antigos gêneros *Arrabidaea*, *Ceratophytum*, *Pseudocatalpa*, *Paragonia*, *Periarrabidaea* e *Spathicalyx* foram também incluídas em *Tanaecium* (Lohmann & Taylor 2014). Recentemente, Kaehler e colaboradores (2019) verificaram a reconstrução de três espécies do gênero *Fridericia* em meio à diversidade de *Tanaecium*. Com isso, as espécies incluídas no gênero foram: *Tanaecium dichotomum* (Jacq.) Kaehler & L.G.Lohmann, *T. paradoxum* (Sandwith) Kaehler & L.G.Lohmann e *T. parviflorum* (Mart. ex DC) Kaehler & L.G.Lohmann. Outra recente combinação em *Tanaecium* foi a espécie do gênero monotípico *Sphingiphila tetramera* A.H.Gentry [=*Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann] (Pace *et al.* 2016). Por fim, uma nova espécie para o gênero foi descrita recentemente, *i.e. Tanaecium decorticans* Frazão & Lohmann (Frazão & Lohmann 2018), somando o total de 22 espécies pertencentes ao gênero.

A inclusão dessas espécies no gênero e a atual circunscrição de *Tanaecium* é sustentada por caracteres moleculares e por uma provável sinapomorfia morfológica que é a presença de profilos das gemas axilares subulados (Fig. 3B) ou em forma de roseta (do inglês, bromeliad-like) (Fig. 3E) (Lohmann & Taylor 2014). Além disso, as espécies de *Tanaecium* também são caracterizadas pelo caule com quatro cunhas de floema em secção transversal (Fig. 3A), folíolos com nervuras retas-percurrentes e glândulas esparsamente distribuídas pelo cálice fortemente bilabiado (Fig. 3F), corola vilosa, pólen colpado e sementes opacas (Lohmann & Taylor 2014).

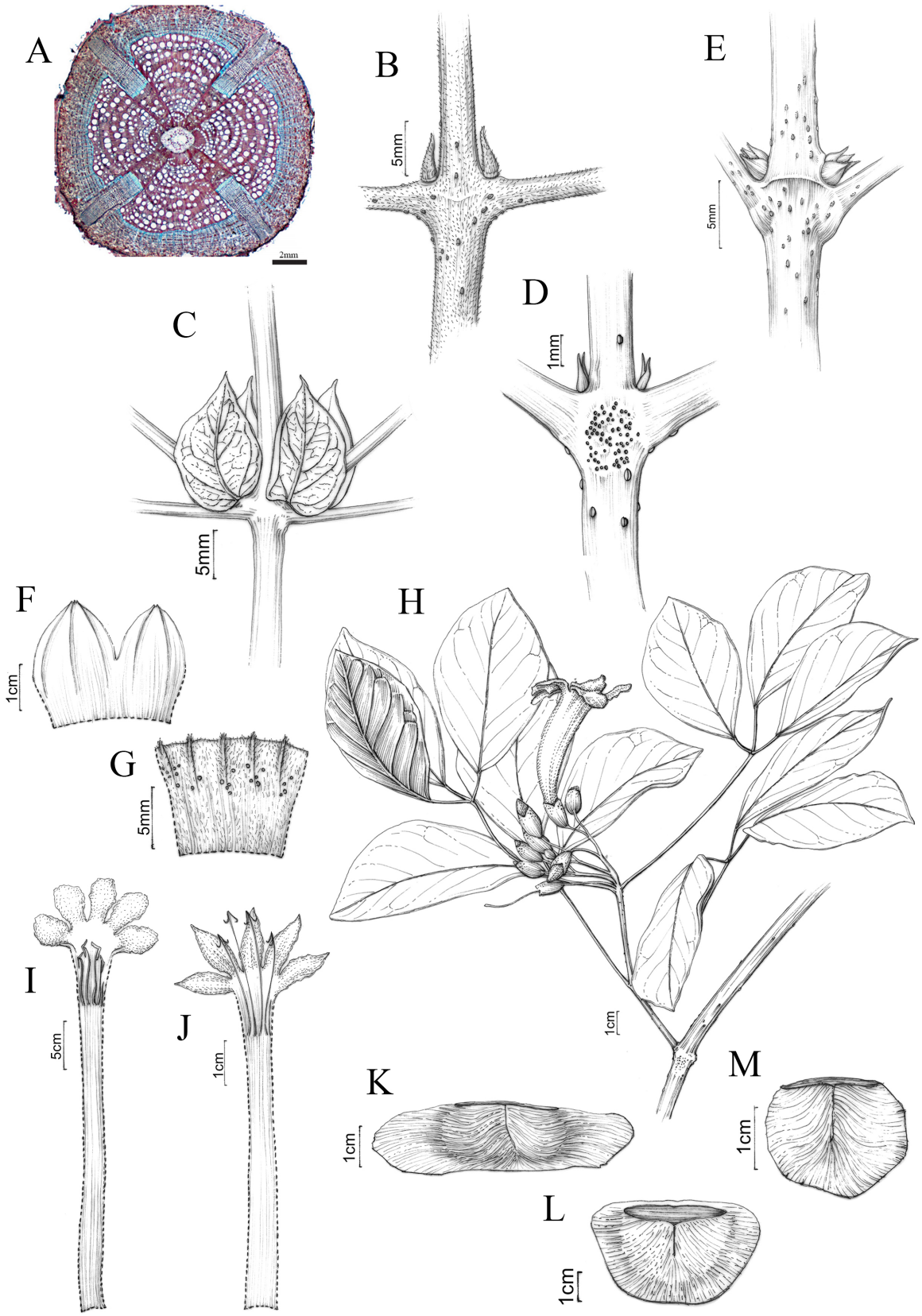

Figura 3: Alguns caracteres diagnósticos de *Tanaecium*. A. Caule com quatro cunhas de floema em secção transversal, *T. pyramidatum*. B. Profilos das gemas axilares subulado, *T. duckei*. C. Profilos das gemas axilares foliáceo, *T. selloi*. D. Região interpeciolar com tricomas pateliformes, *T. tetragonolobum*. E. Profilos das gemas axilares m roseta (*bromeliad-like*), *T. bilabiatum*. F. Cálice bilabiado, *T. bilabiatum*. G. Cálice truncado, *T. jaroba*. H. Inflorescência corimbiforme, *T. tetragonolobum*. I. Corola com androceu inserto, *T. jaroba.* J. Corola com androceu exserto, *T. duckei*. K. Semente com alas presentes, *T. cyrtanthum*. L. Semente com alas vestigiais, *T. bilabiatum*. M. Semente com alas ausentes, *T. jaroba*. Imagem A por M. Pace. Ilustrações por Klei.

Apesar de esses caracteres serem os mais frequentes, há variação de seus estados entre as espécies de *Tanaecium*. Os profilos das gemas axilares podem ser também foliáceos (Fig. 3C), como observado em *T. selloi* (Frazão 2019). Outro caractere que varia em *Tanecium* é a presença de região interpeciolar com tricomas pateliformes (Fig. 3D), como observado, por exemplo, nas espécies *T. tetragonolobum* e *T. truncatum* (Frazão 2019). O cálice, além de bilabiado, pode ser também truncado (Fig. 3G), ocorrendo,por exemplo, na espécie *T. jaroba*, ou ainda espatáceo, como observado em *T. duckei* (Frazão 2019). As variações desses caracteres é essencial para a dignose das espécies do gênero.

Além desses caracteres, também há outros que apresentam variações que fazem das espécies de *Tanaecium* diagnosticáveis. Por exemplo, as inflorescências de *Tanaecium* podem ser do tipo tirso, o qual pode ter diferentes conformações dos tamanhos dos internós, podendo ser corimbiformes (Fig. 3H), como é o caso de *T. tetragonolobum*. Outra variação pouco frequente é a posição do androceu em relação a fauce da corola, a qual geralmente é inserto (Fig. 3I), podendo ser exserto (Fig. 3J) em *T. duckei* (Frazão 2019). As sementes também apresentam variação quanto à presença de alas, podendo estar presentes (Fig. 3K; *e.g. T. cyrtanthum*), vestigiais (Fig. 3L; *e.g. T. bilabiatum*) ou ausentes (Fig. 3M; *e.g. T. jaroba*) (Frazão 2019).

Apesar de o gênero ter sido tratado em uma sinopse recente incluindo toda a tribo Bignonieae (Lohmann & Taylor 2014), nenhum tratamento taxonômico compreensivo de *Tanaecium* foi realizado até o momento. O gênero foi descrito por Swartz (1788) e originalmente caracterizado pela presença de flores com corola tubulares e com cálice truncado, no mesmo trabalho em que descreveu a espécie tipo do gênero, *T. jaroba*, a qual tem flores alvas e longo-infundibuliformes. Estudos filogenéticos recentes indicaram, no entanto, que a coloração e morfologia floral são altamente variáveis em Bignonieae, enquanto caracteres vegetativos como os profilos da gema axilar parecem ser constantes em clados genéricos, representando sinapomorfias para essas linhagens (Lohmann 2006; Alcantara & Lohmann 2010; Alcantara & Lohmann 2011). Assim, na classificação mais atual para o gênero (Lohmann & Taylor 2014), as espécies incluídas em *Tanaecium* apresentam profilos da gema axilar com morfologia relativamente constante, mas alta variação morfológica no que diz respeito à morfologia floral. Por exemplo, o tamanho do tubo da corola varia de 1,6 cm em *T. affine* (A.H. Gentry) L.G. Lohmann (Gentry 1992) até 30 cm em *T. jaroba* Sw. (Gentry 2009). Além disso, a corola pode ser branca, amarela, rosa ou magenta e, ainda, apresentar variação no número de estames, como é o caso de *T. caudiculatum* (Standl.) L. G. Lohmann, uma espécie que tem apenas dois estames em vez de quatro, como as demais Bignoniaceae (Lohmann & Taylor 2014).

Em relação ao posicionamento dentro da tribo, *Tanaecium* está inserido no clado "*Fridericia* & allies" (Lohmann 2006), o qual inclui ca. de 140 espécies e 1/3 da diversidade

encontrada na tribo Bignonieae (Lohmann & Taylor 2014) (Fig. 4). O clado é sustentado como monofilético por um grande número de caracteres moleculares (Lohmann 2006). Estão incluídos neste clado os gêneros *Cuspidaria*, *Lundia*, *Fridericia*, *Tanaecium*, *Tynanthus* e *Xylophragma*. Além de *Tanaecium*, o qual tem tratamento taxonômico apresentado nesta tese, revisões taxonômicas e filogenias já foram realizadas ou estão em andamento para *Tynanthus* (Medeiros & Lohmann 2015a; Medeiros & Lohmann 2015b), *Lundia* (Kaehler *et al.* 2012; Kaehler & Lohmann 2015), *Cuspidaria* (Francisco & Lohmann in prep.), e *Xylophragma* + *Fridericia* (Kaehler *et al.* 2019).

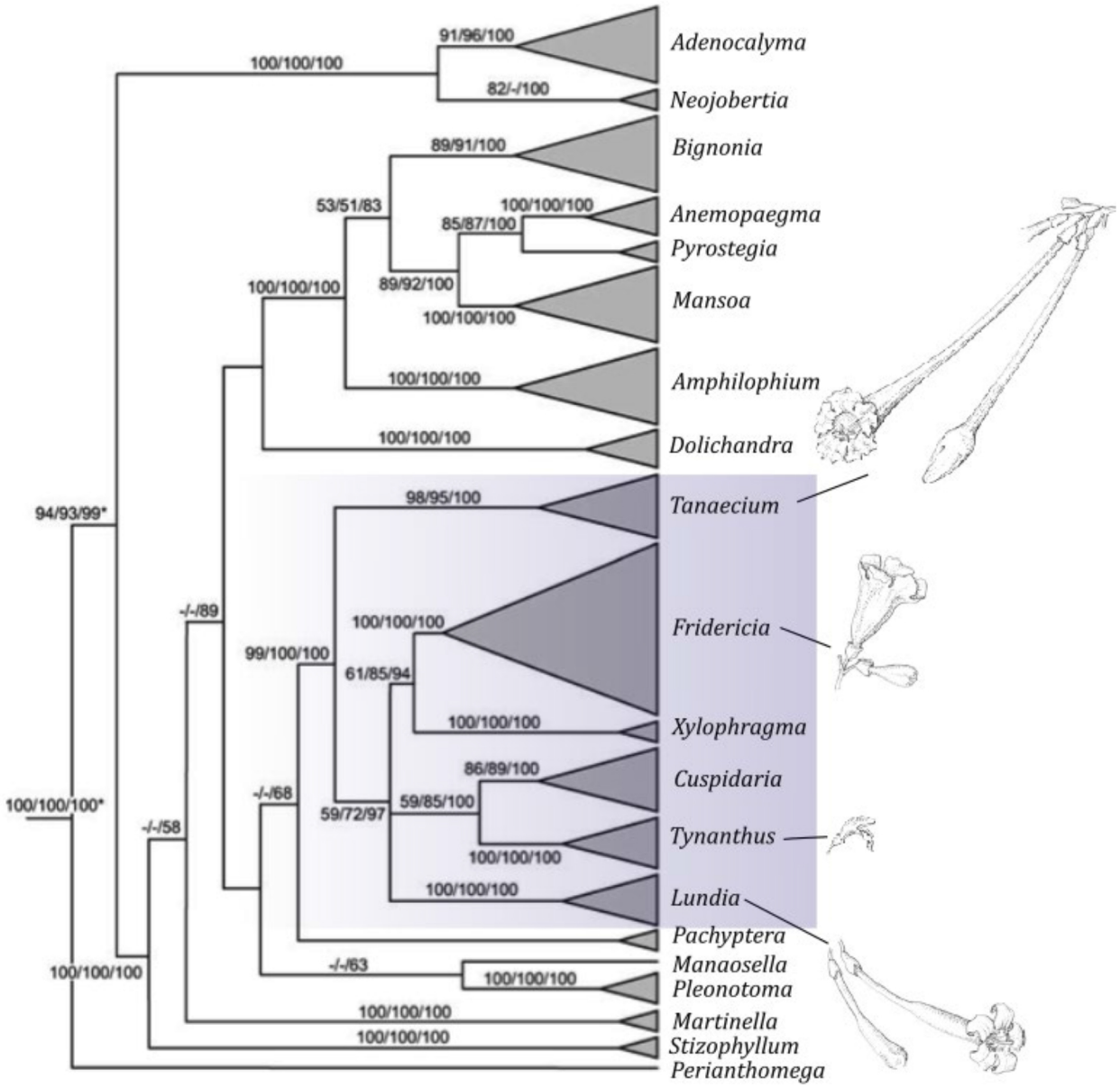

Figura 4: Representação da filogenia da tribo Bignonieae (Bignoniaceae) (Lohmann 2006). Os valores mostrados nos nós representam, respectivamente, valores de suporte de bootstrap da análise de parcimônia, bootstrap da análise de máxima verossimilhança e probabilidade posterior bayesiana. Em destaque o clado "*Fridericia* & allies", ao qual *Tanaecium* pertence.

Filogenia de *Tanaecium*

Tanaecium emergiu como grupo monofilético em todas as filogenias em que foi amostrado (Fig. 5). A primeira filogenia que amostrou o gênero (Lohmann 2006) encontrou três clados, no qual (i) *T. crucigerum* foi reconstruído como grupo-irmão de *T. revillae* mais *T. selloi*, (ii) *T. bilabiatum* irmão de *T. caudiculatum* e (iii) *T. pyramidatum* irmão de *T. truncatum* mais *T. affine* grupo-irmão de *T. tetragonolobum* (Fig 5A). O relacionamento entre esses clados foi (i) irmão de (ii) mais (iii) (Fig. 5A). Nos estudos subsequentes (Pace *et al.* 2016; Frazão & Lohmann 2018; Kaehler *et al.* 2019), as divergências mais profundas de *Tanaecium* não tiveram boa resolução (Fig. 5B-D). Entretanto, o clado formado por *T. truncatum*, *T. affine* e *T. tetragonolobum* foram consistentes em todos os estudos (Lohmann 2006; Pace *et al.* 2016; Frazão & Lohmann 2018; Kaehler *et al.* 2019). Similarmente, o clado (i), *i.e.* formado por *T. crucigerum*, *T. revillae* e *T. selloi*, emergiu na maioria dos estudos (Lohmann 2006; Pace *et al.* 2016; Frazão & Lohmann 2018). O clado (ii), *i.e. T. bilabiatum* mais *T. caudiculatum*, também foi recuperado na filogenia de Frazão & Lohmann (2018).

O estudo mais recente, incluindo a maior amostragem para *Tanaecium* até o momento (Kaehler *et al.* 2019), encontrou que *T. xanthophyllum* foi a primeira linhagem de *Tanaecium* a divergir, sendo grupo-irmão de todas as outras espécies (Fig. 5D). Em seguinda, a segunda linhagem que emergiu foi *T. parviflorum*, o qual seria grupo-irmão de uma tricotomia composta de: (1) *T. pyramidatum* + *T. caudiculatum*; (2) *T. truncatum* irmão de *T. affine* + *T. tetragonolobum*; e *T. crucigerum* + *T. cyrtanthum* grupo-irmão de *T. selloi* irmão de *T. paradoxum* irmão de *T. revillae* + *T. selloi* (Fig. 5D). Esse estudo trouxe novidades quanto ao relacionamento filogenético do gênero, como a reconstrução de *T. pyramidatum* como grupo-irmão de *T. caudiculatum*, enquanto, na hipótese anterior, a última espécie formou um clado com *T. bilabiatum* (Lohmann 2006; Frazão & Lohmann 2018). Além disso, *T. cyrtanthum* emergiu como irmão de *T. crucigerum*, ambas espécies pertencentes à antiga e mais restrita circunscrição do gênero (ver Gentry 1973; Gentry 1976).

Apesar de os inúmeros estudos filogenéticos que amostraram *Tanaecium* terem sido realizados nos últimos 13 anos, os relacionamentos entre seus clados permanece não esclarecida. Além disso, algumas espécies, como *T. tetramerum*, não apresenta nenhuma hipótese para seu posicionamento no gênero (Pace *et al.* 2016; Frazão & Lohmann 2018), enquanto outras nunca foram amostradas, como *T. duckei* e *T. jaroba*.

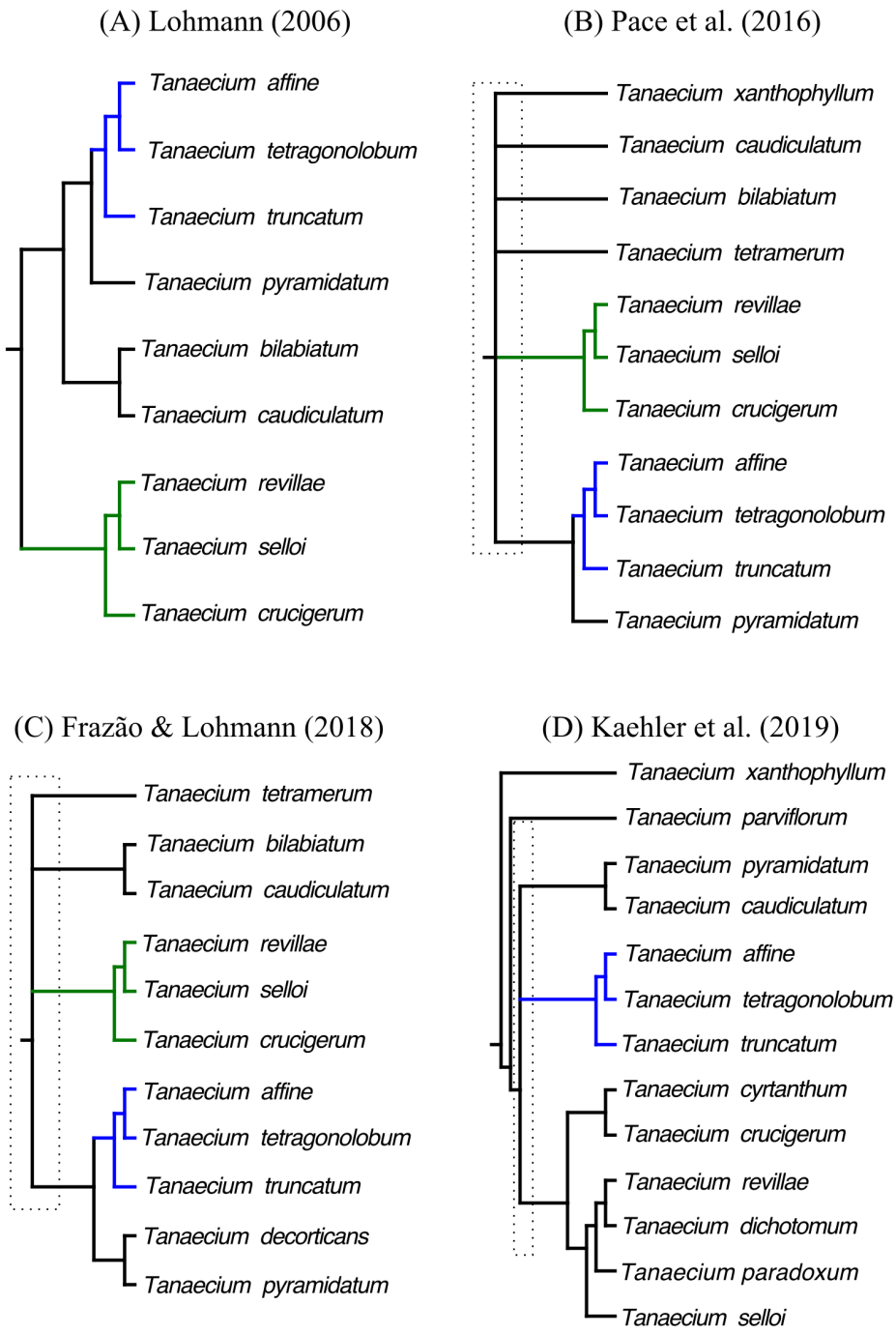

Figura 5: Sumário com as filogenias de *Tanaecium.* A. Topologia de Lohmann (2006). B. Topologia de Pace *et al.* (2016). C. Topologia de Frazão & Lohmann (2018). D. Topologia de Kaehler *et al.* (2019). Politomias estão destacadas com a linha pontilhada. Clados recuperados em mais de uma filogenia estão destacados em azul ou verde.

Aspectos evolutivos de *Tanaecium*

Apesar do reduzido número de espécies, *Tanaecium* apresenta uma alta diversidade morfológica, principalmente no que diz respeito aos caracteres reprodutivos. Além disso, é um grupo distribuído por toda a região Neotropical. Esses fatores fazem do gênero um modelo atraente para estudos evolutivos.

A alta diversidade floral existente em *Tanaecium* sugere que a evolução morfológica das flores do gênero pode estar associada a interações com polinizadores (Alcantara *et al.* 2010).

Baseado nas variações das morfologias das flores de Bignonieae, Gentry (1974) caracterizou sete tipos de morfologia das flores da tribo: (1) "*Amphilophium*-type", (2) "*Anemopaegma*-type", (3) "*Cydista*-type", (4) "*Martinella*-type", (5) "*Pithecoctenium*-type", (6) "*Tynanthus*-type" e (7) "*Tanaecium*-type".

Flores "*Amphilophium*-type" são tubulares, coriáceas e profundamente bilabiadas, apresentando antese fechada, permitindo que apenas polinizadores com tamanhos corporais maiores consigam abrir e, portanto, acessar a flor internamente, como abelhas da subfamília Xylocopinae (Gentry 1974). As do tipo "*Anemopaegma*-type" são flores membranáceas, com fauce aberta quando em antese e com anteras inclusas, podendo apresentar cores desde brancas até magenta e fauce podendo apresentar coloração contrastante com a da flor. São polinizadas por abelhas de tamanho corporal grande ou médio (Gentry 1974). As flores do tipo "*Cydista*-type" têm tubo longo, dorso-ventralmente comprimidas, infundibuliformes e com fauce ampla porém estreita, apresentado muitas vezes guias de néctar e o disco nectarífero está ausente. São polinizadas por abelhas de grande e médio porte, como aquelas da tribo Euglossini (Gentry 1974). Flores "*Martinella*-type" são vermelhas a alaranjadas ou vináceas, cartáceas, glabras externamente, com fauce aberta em antese, base do tubo floral estreito e ligeiramente mais longa do que o cálice, o androceu é exserto ou sub-exserto e polinização por beija-flores (Gentry 1974). Já as flores do tipo "*Pithecoctenium*-type" são brancas ou amareladas, coriáceas, curvadas, androceu inserto, frequentemente com o cálice coberto por tricomas pateliformes e são polinizadas por abelhas de tamanho médio (Gentry 1974). Flores "*Tynanthus*-type" são caracterizadas por corolas brancas ou magenta, pequenas, bilabiadas, androceu sub-exserto e são polinizadas por pequenas abelhas e borboletas (Gentry 1974). Por fim, as flores do tipo "*Tanaecium*-type" são brancas, com o tubo floral estreito e longo, antese noturna, com androceu sub-exserto e são polinizadas por mariposas (Gentry 1974).

Baseado nessa classificação de tipos de flores e suas putativas associações com polinizadores, as espécies de *Tanaecium* estão distribuídas pelas categorias (2) "*Anemopaegma*-type", (7) "*Tanaecium*-type" e uma mistura entre mais de um tipo de flor proposta por Gentry, o "mixed-type" (Gentry 1974, Alcantara & Lohmann 2010) (Fig. 6).

Alcantara & Lohmann (2010) apresentaram um estudo no qual investigaram a evolução das flores de Bignonieae com base nos tipos florais propostos por Gentry (1974). Nesse estudo elas hipotetizaram que a flor ancestral de *Tanaecium* possivelmente era do tipo "*Anemopaegma*-type", assim como para o ancestral da tribo. Na reconstrução de caracteres ancestrais realizada por elas, o "*Tanaecium*-type" e o "mixed-type" evoluíram independentemente ao longo da história evolutiva do gênero (Alcantara & Lohmann 2010).

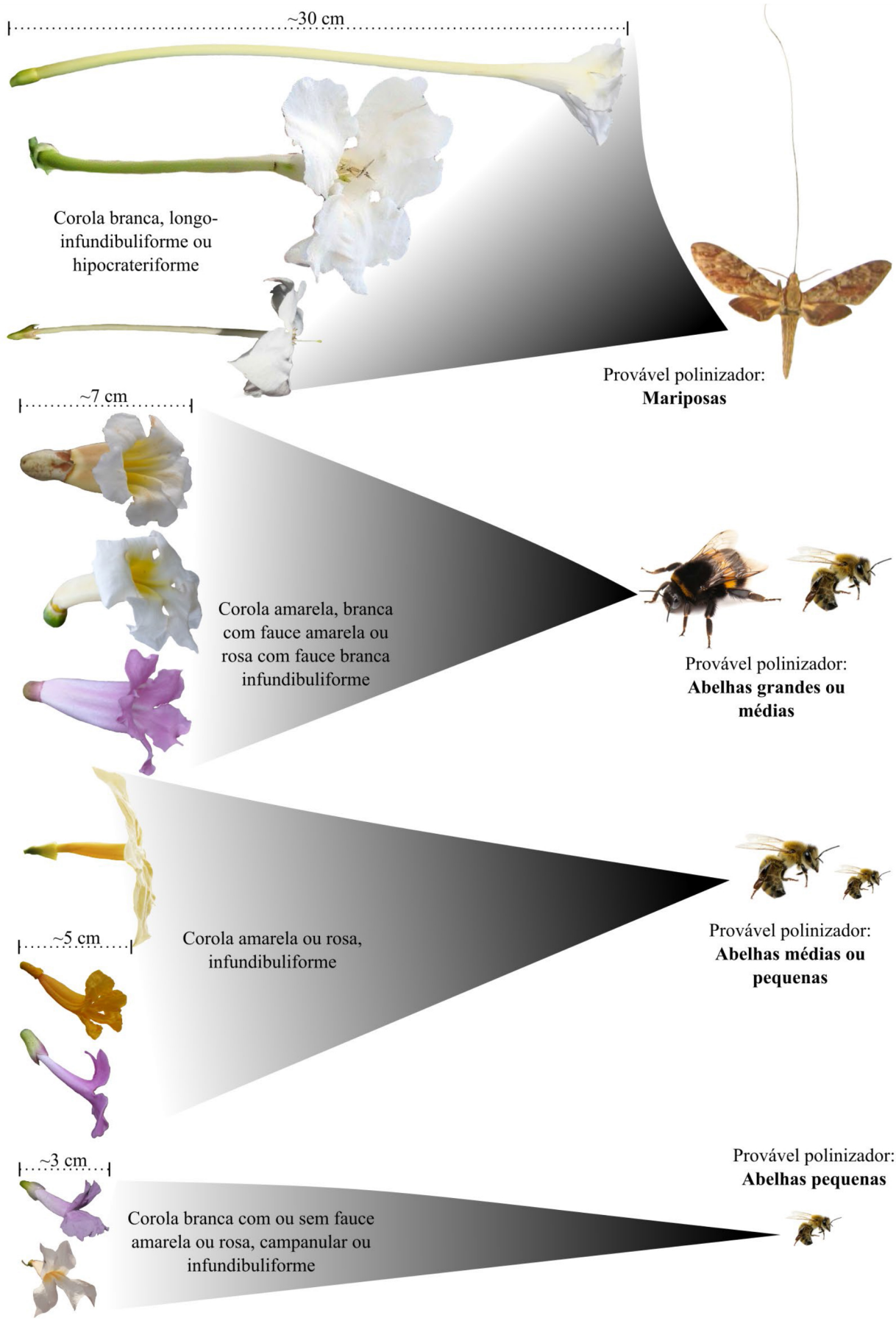

Figura 6: Representação gráfica dos tipos de flores existentes em *Tanaecium* e os prováveis polinizadores de acordo com os tipos morfológicos florais propostos por Gentry (1974).

O ancestral de *Tanaecium* possivelmente estava na Amazônia, sendo que a maioria das especiações no gênero devem ter ocorrido também na Amazônia (Lohmann *et al.* 2013) (Fig. 7). Apesar disso, a reconstrução da área para o ancestral de *T. crucigerum* foi ambígua (Lohmann *et al.* 2013) (Fig. 7). A reconstrução ancestral para o clado *T. revillae* + *T. selloi* também foi ambíguo, com o ancestral podendo estar amplamente distribuído, ou na Amazônia + leste da América do Sul, ou ainda na Amazônia + diagonal sazonalmente seca da América do Sul (Lohmann *et al.* 2013) (Fig. 7). Já o ancestral de *T. bilabiatum* + *T. caudiculatum* possivelmente estava distribuído na Amazônia + oeste da América do Sul até a América Central (Lohmann *et al.* 2013) (Fig. 7).

Interessantemente, quando comparamos as hipóteses de evolução floral para *Tanaecium* (Alcantara & Lohmann 2010) com os encontrados para a história biogeográfica do grupo (Lohmann et al 2013), algumas coincidências são observadas. As mudanças geográficas reconstruídas para os ancestrais das linhagens de *Tanaecium* ocorreram majoritariamente no Mioceno, entre aproximadamente 20 e 23 Ma, exceto a mais recente especiação entre *T. tetragonolobum* + *T. affine*, a qual foi estimada para o Plioceno (Lohmann *et al.* 2013) (Fig. 7). Quando comparadas com as reconstruções dos tipos florais de Gentry, a maioria das mudanças de tipos florais teriam ocorrido no mesmo período, *i.e.* no início do Mioceno (Fig. 7). Apesar de nenhuma análise ter sido realizada comparando essas informações, essa coincidência pode ser uma possível explicação para o surgimento de tanta variação na flor dos *Tanaecium*, podendo estar associada não somente à interação das espécies com seus polinizadores, mas também em resposta a mudanças geográficas históricas no grupo. Ambas explicações para o surgimento da variação morfológica, ou seja, tanto a hipótese da mudança morfológica associando interação com polinizador quanto a hipótese de ser resposta a história biogeográfica do grupo, já foram investigadas para outros grupos distribuídos na região Neotropical (*e.g.* Pennington & Dick 2004; Smith *et al.* 2008; Tripp & Manos 2008; Hoorn *et al.* 2010; Antonelli & Sanmartín 2011; Rull 2011). Nesse sentido, em estudos futuros, *Tanaecium* pode ser um excelente modelo para testar as hipóteses que melhor explicaria o surgimento de variação morfológica.

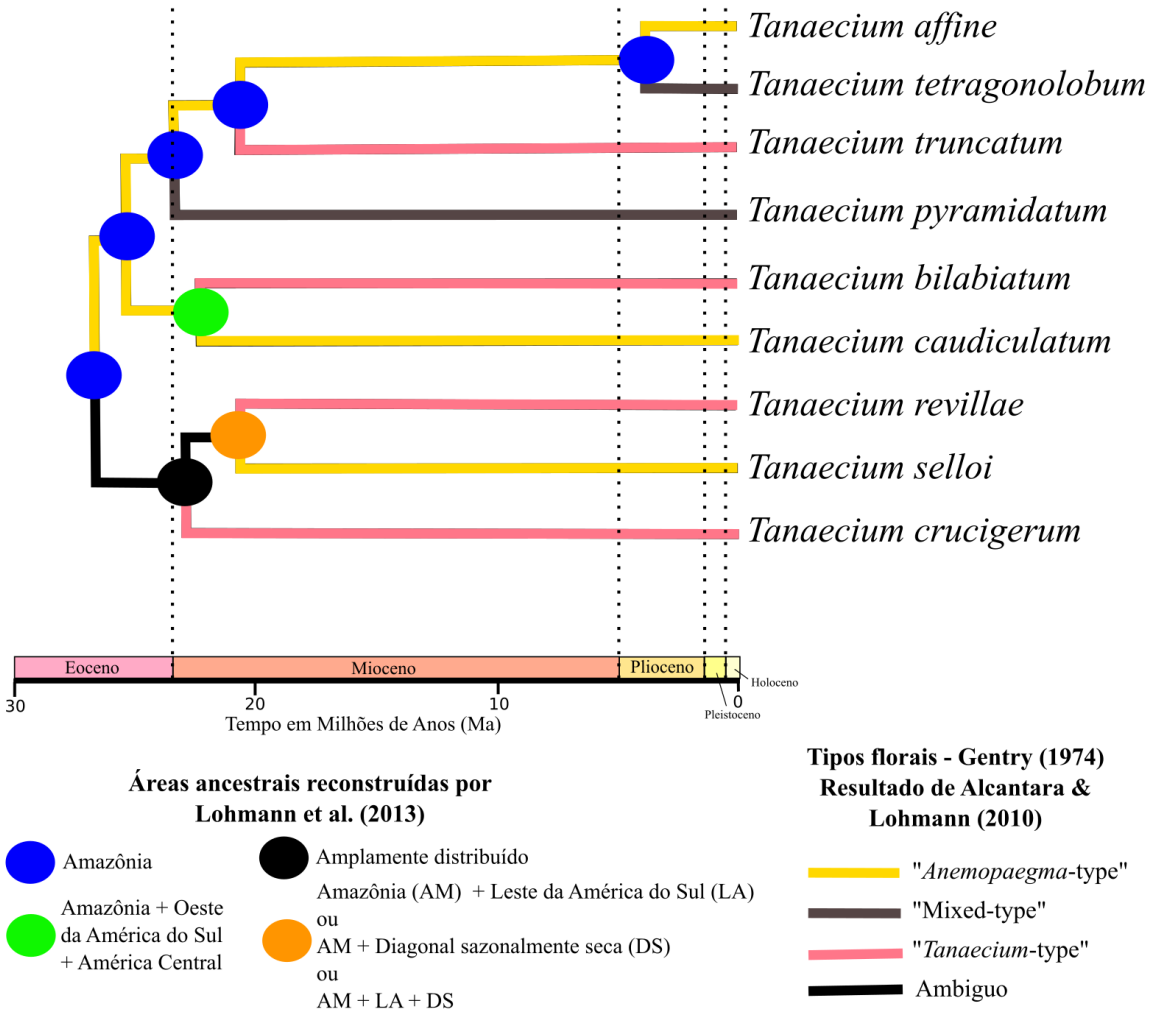

Figura 7: Sumário com os resultados encontrados no estudo biogeográfico (Lohmann *et al.* 2013) e no de evolução dos tipos florais (Alcantara & Lohmann 2010) para a tribo Bignonieae (Bignoniaceae). Somente resultados para *Tanaecium* foram compilados. Codificação das cores foram adaptadas.

Objetivos e organização da tese

O objetivo desta tese é apresentar (i) um estudo taxonômico detalhado para *Tanaecium*, além de (ii) um estudo filogenético para o gênero. Para isso, utilizamos uma extensa amostragem de materiais de herbário e coletados em trabalhos de campo tanto para os estudos taxonômicos quanto para o filogenético. Para o estudo filogenético, utilizamos uma combinação de sequências geradas pelo método Sanger com aquelas geradas por sequenciamento de nova geração (NGS), o qual nos permitiu também a realização de um detalhado estudo dos genomas de cloroplasto (=plastomas) das espécies de *Tanaecium.*

Esses resultados estão organizados da seguinte forma:

Capítulo 1 – Estudos taxonômicos de *Tanaecium*. Este capítulo é um compêndio de quatro estudos taxonômicos os quais propuseram: (1) a descrição de uma nova espécie; (2) a nova combinação de *T. mutabile* para o gênero *Frideria*; (3) a elucidação da tipificação do gênero; e (4) uma sinopse atualizada para as espécies de *Tanaecium*.

Capítulo 2 – Filogenia de *Tanaecium.* Esta capítulo é composto por um manuscrito no qual utilizamos dados de sequenciamento Sanger e de NGS para reconstruir a filogenia para *Tanaecium.* Também descrevemos os plastomas das espécies amostradas para o gênero e apresentamos um estudo comparativo com as outras espécies da família Bignoniaceae que têm plastomas sequenciados. Apresentamos quatro formas de mudança das fronteiras entre as quatro cópias dos plastomas de *Tanaecium* por ocorrência de redução das regiões Invertidas e Repetidas. Esse resultado demonstra que a estrutura dos plastomas em Bignoniaceae são mais lábeis do que se imaginava. Esses resultados também demonstram que *Tanaecium* apresenta não só uma grande variação tanto de suas características morfológicas externas quanto genômicas.

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Chapter 1.1. A New Species of *Tanaecium* (Bignonieae, Bignoniaceae) from the Brazilian Amazon and its Phylogenetic Placement

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Running title: New species of *Tanaecium* from the Amazon

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Abstract – *Tanaecium* Sw. emend L.G. Lohmann (Bignonieae, Bignoniaceae) is a genus of Neotropical lianas, that is centered in Amazonia. The genus exhibits interesting patterns of morphological variation, especially in terms of flower morphology. Despite that, the group remains poorly known, lacks a phylogeny and a taxonomic revision. While working on the systematics of *Tanaecium*, we encountered a morphological variant of *Tanaecium pyramidatum* (Rich.) L.G. Lohmann from the Brazilian Amazon that represents an independent evolutionary lineage and differs significantly from this species in various morphological traits. This taxon is here described as *Tanaecium decorticans* Frazão & L.G. Lohmann. While *T. decorticans* is sister and most morphologically similar to *T. pyramidatum*, it differs in the peeling epidermis (vs. not-peeling in *T. pyramidatum*), presence of an arrow-shaped petiolule (vs. absence of an arrow-shaped petiolule in *T. pyramidatum*), and interpetiolar region covered with fields of glandular trichomes (vs. aglandular interpetiolar region in *T. pyramidatum*), among other characters. This finding highlights the importance of in-depth taxonomic studies of individual lineages for an improved understanding of biodiversity.

Keywords – Amazonia, lianas, Neotropical biodiversity, taxonomy.

INTRODUCTION

Tanaecium Sw. emend L.G. Lohmann (Bignonieae, Bignoniaceae) is a genus of Neotropical lianas that includes 18 species distributed from Mexico and the Antilles to Argentina (Lohmann and Taylor 2014; Pace et al. 2016). The genus is centered in the Amazon, where 11 species are found (Lohmann and Taylor 2014; Frazão et al. in prep.). The genus exhibits particularly diverse flower morphology and pollination systems that range from bee to hawkmoth pollination (Alcantara and Lohmann 2010). Seeds can be winged or wingless and corky (Lohmann and Taylor 2014), likely wind and water dispersed, respectively.

Until the publication of a synopsis of the whole tribe Bignonieae (Lohmann and Taylor 2014), the genus was circumscribed more narrowly and included six species (Gentry 1973; Gentry 1976). Among these, five remain in *Tanaecium*, i.e., *T. apiculatum* A.H. Gentry, *T. crucigerum* Seem., *T. cyrthanthum* (Mart. ex DC.) Bureau & K. Schum., *T. duckei* A.Samp., and *T. exsitiosum* Dugand, while one species, i.e., *T. nocturnum* (Barb. Rodr.) Bureau & K. Schum., was transferred to *Bignonia* L. [= *B. nocturna* (Barb. Rodr.) L.G. Lohmann]. In addition to the five species with white and long-tubular corollas traditionally classified as *Tanaecium*, twelve species from six different genera (i.e., *Arrabidaea* DC., *Ceratophytum* Pittier, *Pseudocatalpa* A.H.Gentry, *Paragonia* Bureau, *Periarrabidaea* A. Samp. and *Spathicalyx* J.C.Gomes) were transferred to *Tanaecium* (Lohmann and Taylor 2014). Furthermore, the monotypic genus *Sphingiphila* A.H. Gentry was shown to fall within *Tanaecium* and an additional species, *Tanaecium tetramerum* (A.H. Gentry) Zuntini & L.G. Lohmann, was included within the genus (Pace et al. 2016).

The monophyly of *Tanaecium* is supported by molecular characters (Lohmann 2006). The prophylls of the axillary buds that are subulate or bromeliad-like represent a putative morphological synapomorphy of the genus (Lohmann and Taylor 2014). Species of *Tanaecium* are also characterized by the wood with four phloem wedges in cross-section, well-developed interpetiolar ridges, leaflets with straight-percurrent venation and sparsely distributed glands, thick bilabiate calyx, villose corolla, colpate pollen, and opaque corky seeds (Lohmann and Taylor 2014).

While working on the systematics of *Tanaecium* (Frazão et al., in prep.), we encountered a morphological variant of *T. pyramidatum* (Rich.) L.G. Lohmann from the Brazilian Amazon that represents an independent evolutionary lineage and differs significantly from this species in various morphological traits. This taxon is here described as *Tanaecium decorticans* Frazão & L.G. Lohmann.

MATERIALS AND METHODS

Molecular Data and Phylogenetic Analyses – We compiled a dataset with published sequences of *ndh*F and *Pep*C for 10 out of the 18 species of *Tanaecium* currently recognized (Lohmann and Taylor 2014; Pace et al. 2016). In addition, we obtained new sequences of four accessions of the putative new species and six new accessions of *T. pyramidatum*, the most morphologically similar taxon. This led to a final dataset with 36 accessions, representing 10 currently recognized taxa plus the putative new species and outgroup (Table 1).

Total DNA was extracted from silica-dried leaf tissue using a Spin Plant Mini Kit (Invisorb) following the manufacturer's protocol. PCR conditions of the *ndh*F and *pep*C followed Zuntini et al. (2013). For *pep*C, we first used a nested PCR approach that started with an amplification using primers 4F and 5R as described by Ayres et al. (2009). Second, we used 1 ul of the product of the first PCR as basis for a second PCR that used primers IV119F and V25R described by Zuntini et al. (2013). Whenever the second PCR failed, we conducted a third PCR that also used 1 ul of the product of the first PCR using primers IV197F and V25R described by Zuntini et al. (2013). Samples were purified and sequenced at Macrogen Inc. (Korea). Sequences were assembled and edited using Geneious 7.0 (Kearse et al. 2012) and aligned using MAFFT 7 (Katoh and Toh 2008) with the default parameters. The concatenated molecular matrix was constructed using Seaview 4.0 (Gouy et al. 2010). All sequences, vouchers and GenBank accessions are summarized in Table 1.

The best-fit models of nucleotide substitution for the individual data partitions were determined with jModelTest 2.0 (Guindon et al. 2010; Darriba et al. 2012) using the Akaike Information Criterion (AIC). The GTR+G+I and GTR+G were identified as the most appropriate models of evolution for the *ndh*F and *pep*C datasets, respectively. Bayesian inference (BI) was performed with MrBayes 3.2.2 (Ronquist and Huelsenbeck 2003) and the online server CIPRES (Miller et al. 2010) using three datasets: (i) *ndh*F, (ii) *pep*C, and (iii) combined dataset (*ndh*F + *pep*C). Two independent MCMC runs were conducted, each composed of four linked chains that ran for 10,000,000 generations with sampling every 1000 generations. Likelihood values were monitored graphically to detect stationarity with Tracer 1.7 (Rambaut et al., 2018. Posterior probabilities (PP) were used to assess clade support.

Taxonomic Treatment – We follow the evolutionary species concept of de Queiroz (2007) and considered isolated evolutionary lineages that are diagnosed by morphological characters as separate species. We analyzed botanical specimens deposited at the INPA and SPF herbaria (acronyms following Thiers 2018). Morphological descriptions follow the terminology adopted by Lohmann and Taylor (2014) for tribe Bignonieae. Maps with geographical distribution were

prepared using QGis (2018). The conservation status was assessed using the IUCN criteria (IUCN 2018 IUCN Standards and Petitions Subcommittee 2017, and the GeoCAT software (Bachman and Moat 2011).

RESULTS

The *ndh*F dataset includes 31 terminals and 2,111 pb, while the *pep*C dataset includes 29 terminals and 776 pb. The combined dataset includes 32 terminals and 2,887pb. The combined matrix is available for download at Figshare (https://1.6084/m9.figshare.5813604).

Topologies that resulted from the analyses of the *ndh*F, *pep*C and combined dataset led to very similar results (Fig. 1), although the topology that resulted from the analysis of the combined dataset is more strongly supported. As such, only the topology that resulted from the combined analysis is described here. Minor differences between topologies are noted below.

Tanaecium decorticans emerged as monophyletic (PP=1.0) and strongly supported as sister to *T. pyramidatum* (PP=1.0; Fig. 1a). Both of these taxa represent independent evolutionary lineages that are strongly supported as reciprocally monophyletic (PP=1.0). This clade is, in turn, sister to a clade composed of *T. truncatum* (A.Samp.) L.G.Lohmann sister to *T. affine* (A.H.Gentry) L.G.Lohmann plus *T. tetragonolobum* (Jacq.) L.G.Lohmann (PP=0.72). Two other clades are recovered within *Tanaecium*: (i) a clade composed of *T. bilabiatum* (Sprague) L.G.Lohmann and *T. caudiculatum* (Standl.) L.G.Lohmann (PP=0.61; Fig. 1a), and (ii) a clade composed of *T. crucigerum* sister to *T. revillae* (A.H.Gentry) L.G.Lohmann plus *T. selloi* (Spreng.) L.G.Lohmann (PP=0.95; Fig. 1a). *Tanaecium tetramerum* has an unclear placement in all topologies (Fig. 1a).

The topology reconstructed based on the *ndh*F and *pep*C markers individually was very similar to the topology that resulted from the analysis of the combined dataset except from the following relationships: (i) the clade composed of *T. truncatum* sister to *T. affine* plus *T. tetragonolobum* was not recovered in the topology that resulted from the analysis of the *pep*C dataset (Fig. 1b); (ii) the clade composed of *T. crucigerum* sister to *T. revillae* plus *T. selloi* was not recovered in the topology that resulted from the analysis of the *ndh*F dataset (Fig. 1c); and, (iii) the sister-group relationship between *T. bilabiatum* and *T. crucigerum* was only recovered in the topology that resulted from the analysis of the *ndhF* dataset (PP=0.81; Fig. 1c).

DISCUSSION

In this study, we used morphological and molecular data to identify a new species of *Tanaecium* (Bignonieae, Bignoniaceae). The new species is well characterized by morphological

features and constitutes a separate species, following the evolutionary species concept of de Queiroz (2007). The sister-group relationship between *T. decorticans* and *T. pyramidatum* corroborates previous expectations based on morphology. While *T. decorticans* is restricted to forests from Eastern Amazon, its sister-species, *Tanaecium pyramidatum*, is broadly distributed throughout the Neotropics (Lohmann and Taylor 2014).

Tanaecium decorticans is characterized by a series of morphological features, including interpetiolar region with fields of glandular trichomes (Fig. 2b), stem with peeling epidermis (Figs. 2c, 3d), petiolules with arrow-shaped apex toward the leaflets base (Figs. 2d, e, 3d), leaflets drying grayish in adaxial surface and brownish on the abaxial surface, flowers with acute lobes (Fig. 2f), and flattened fruits with peltate and patelliform glandular trichomes concentrated along the margin (Fig. 2l, m). The peeling epidermis is one of the most distinctive features. Even though this character is also found in *Pleonotoma* Miers and *Pachyptera* DC. ex Meisn. (Lohmann and Taylor 2014; Francisco and Lohmann 2018), *T. decorticans* is easily distinguished from other members of these genera. Namely, *Tanaecium decorticans* is easily distinguished from *Pleonotoma* by the cylindrical stems and 2-foliolated leaves, instead of the tetragonal stems and biternately compound leaves in *Pleonotoma* (Lohmann and Taylor 2014), and from *Pachyptera* by the subulate and curved prophylls of the axillary buds not arranged in series instead of the ensiform prophylls of axillary buds arranged in series of 3(-5) in *Pachyptera* (Francisco and Lohmann 2018). The homoplastic nature of the peeling epidermis within Bignonieae should be further investigated through future morpho-anatomical studies.

Our findings support the need of in depth taxonomic studies throughout the Brazilian Amazon. Detailed species-level studies of Amazonian lineages can provide key insights into the origin and evolution of this important Biome. Ongoing phylogenetic studies based on genomic data, morphological, and systematic studies of *Tanaecium* should provide additional insights into the evolution and biogeographic history of this interesting Neotropical genus (Frazão et al. in prep.).

TAXONOMIC TREATMENT

Tanaecium decorticans Frazão & L.G. Lohmann, **sp. nov.** – HOLOTYPE: Brasil, Pará, Belterra, Entrada da estrada de Aramanaí para Pindobal, próximo a Fazenda São Sebastião, 41 m a. s. l., 2°38′24.7″S, 54°59′06.6″W, 20 Sep 2015, *A. Frazão* et al *210* (holotype: SPF!; isotype: RB!, MO!). Fig. 2.

Etymology: The species epithet refers to the stem with peeling epidermis.

Description: Liana. Branchlets terete, with peeling epidermis, sparse lenticels, glabrous; interpetiolar region with fields of patelliform glandular trichomes, and discontinuous

interpetiolar ridge; prophylls of the axillary buds subulate and curved, 1.2-3.53 mm. *Leaves* 2-foliolate, with the terminal leaflet modified into a trifid tendril; petioles 0.5–1.9 cm long, with simple eglandular trichomes, pubescent in the canalicule or glabrous, and glandular patteliform trichomes at the apex; petiolules 0.3-1.8 cm long, with an arrow-shaped apex towards the leaflet base; leaflets ovate, elliptic or obovate, 6-14.5 × 2.3-6.6 cm, coriaceous, with margin entire and revolute, apex acute, base rounded, cuneate or cordate, primary venation pinnate, secondary venation brochidodromous, tertiary venation randomly reticulated, adaxial surface drying grayish and abaxial surface brownish, both glabrous with glandular peltate and patelliform trichomes throughout the lamina. *Inflorescence* thyrsoid, axillary or terminal; peduncle 0.6-8.5 cm; rachis 0.3-9 cm, with simple eglandular trichomes, puberulent, and peltate glandular trichomes; floral bracts caducous or persistent, elliptic, 9-11.6 × 2.1-3.2 mm, membranous, puberulent, with patteliform glandular trichomes, 0.4-0.5 mm diam.; bracts caducous or persistent, linear, 1.5–2 mm, with simple eglandular trichomes, villose, and peltate glandular trichomes; bracteole persistent, ovate, 0.5-1 mm; pedicel 4-8 mm long. *Calyx* vinaceous at base and whitish at apex or green and vinaceous at base, coriaceous, campanulate or cupular, 0.5-0.9 × 0.6-1.2 cm, truncate or 5-mucronate, 0.3 mm long, with simple eglandular trichomes, puberulent, sparse peltate and patteliform glandular trichomes grouped in line or grouped at the apex. *Corolla* tube pink with white base, 3.2-5.1 cm long, 0.8-1.5 cm wide at tube apex, and 4.3-5.5 mm wide at calyx base, velutinous, with simple eglandular trichomes, and peltate glandular trichomes externally, villose, with simple eglandular trichomes internally; lobes pink, aestivation imbricate, 1.3-2.6 × 1-1.9 cm, apex acute, with eglandular simple trichomes externally, velutinous, and glandular peltate trichomes internally; mouth white, 3-4.2 cm diameter, with peltate glandular trichomes. *Androecium* didynamous, included, inserted at 3.5-8 mm, shorter filaments 1-1.6 cm long, longer filaments 1.6-2 cm long, with stiptate glandular trichomes; staminode 3.5-6 mm long, with stipitate glandular trichomes; anthers with theca straight, 2-3.5 × 0.4-0.8 mm, with connective thick, round, with peltate glandular trichomes throughout. *Nectar disk* 1-1.5 mm height. *Gynoecium* with ovary linear-elliptic, 2.5-4.5 × 0.9-1.5 mm, with peltate and patelliform glandular trichomes densely distributed, with two series of ovules in each placenta; style 1.6-2.3 cm long, with sparsely distributed peltate glandular trichomes; stigma rhomboid, 2.1-3.4 × 1.1-1.7 mm. *Fruit* green, linear, flattened, tuberculate, straight, 42 × 1.3 cm, apex atenuate, with peltate and patelliform glandular trichomes concentrated at the margin, calyx persistent. *Seeds* not seen. Figs. 2 and 3.

Diagnosis: Tanaecium decorticans is similar to *Tanaecium pyramidatum*, but can be distinguished by the stem with peeling epidermis (Figs. 2c, 3d) (vs. not peeling epidermis in *T. pyramidatum*), interpetiolar region with fields of glandular trichomes (Fig. 2b) (vs. interpetiolar

region without glandular trichomes in *T. pyramidatum*), petiolules with arrow-shaped apex toward the leaflet base (Figs. 2d-e) (vs. without arrow-shaped apex toward the leaflet base in *T. pyramidatum*), leaflets with adaxial surface drying grayish and abaxial surface brownish (vs. a variety shades of brown and gray on the both surfaces in *T. pyramidatum*), prophylls of the axillary buds ≤ 3.5 mm (Figs. 2b, 3d) (vs. prophylls of the axillary buds generally > 3 mm of *T. pyramidatum*), flowers with acute lobes (Fig. 2f) (vs. rounded lobes in *T. pyramidatum*), and flattened fruits, with peltate and patelliform glandular trichomes concentrated at margin (Fig. 2l) (vs. inflated fruits, without glandular trichomes in *T. pyramidatum*).

Phenology: Flowering and fruiting specimens were collected in September.

Habitat and distribution: *Tanaecium decorticans* is known from the Brazilian Amazon, where it is restricted to the state of Pará (Fig. 4).

Additional specimens examined: BRAZIL. Pará. Óbidos, Serra da Escama, trilha para os canhões, 24 m a. s. l., 1°54′54.20″S, 55°30′31.64″W, 24 Sep 2015, *Frazão* et al. *220* (SPF). Oriximiná, Mineração Rio do Norte, Porto Trombetas, 1994, *Evandro* and *Knowles 1249* (INPA); *Evandro* and *Knowles 516*, 1991 (INPA); *Evandro* and *Knowles 764*, 1990 (INPA). Santarém, Alter do Chão, Rio Tapajós, Lago Verde, 7 m a. s. l., 2°30′35.7″S, 54°56′2.4″W, 18 Sep 2015, *Frazão* et al. *196* (SPF); 15 m a. s. l., 2°29′7.2″S, 54°56′51.5″W, 18 Sep 2015, *Frazão* et al. *197* (SPF).

Conservation status: Tanaecium decorticans is known from only a few localities (Fig. 4). Its conservation status is near threatened [NT], according to IUCN criteria (IUCN 2018; IUCN Standards and Petitions Subcommittee 2017.

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Table 1. Taxon, voucher, locality and GenBank accessions for DNA sequences. Slash indicates missing data.

Taxa	Voucher	Locality	Accession numbers	
			ndhF	***PepC***
Bignonia capreolata L.	Lohmann 356 (MO)	Johnson County, Illinois, USA	DQ222566	—
Bignonia nocturna (Barb.Rodr.) L.G. Lohmann	Lohmann 451 (MO, NY, SPF, UFAC)	Rio Juruá, Acre, Brazil	DQ222641	DQ222814
Cuspidaria convoluta (Vell.) A.H. Gentry	Lohmann 713 (MO, SPF)	Cultivated Instituto Plantarum, São Paulo, Brazil	DQ222573	DQ222712
Fridericia speciosa Mart.	Lombardi 2521 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222584	DQ222731
Lundia densiflora DC.	Lohmann 82 (INPA, MO)	Ducke Forest Reserve, Amazonas, Brazil	DQ222592	DQ222744
Manaosella cordifolia (DC.) A.H. Gentry	Lombardi 2546 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222596	DQ222751
Martinella iquitoensis A. Sampaio	Lohmann 616 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222605	DQ222761
Pachyptera aromatica Barb.Rodr.	Lohmann 28 (INPA, MO, SPF)	Ducke Forest Reserve, Amazonas, Brazil	DQ222589	DQ222740
Pleonotoma jasminifolia (Kunth) Miers	Lohmann 122 (INPA)	Ducke Forest Reserve, Amazonas, Brazil	DQ222625	DQ222794
Stizophyllum perforatum (Cham.) Miers	Lombardi 2431 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222639	DQ222810
Tanaecium affine (A.H. Gentry) L.G. Lohmann	Lohmann 633 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222539	DQ222666
Tanaecium bilabiatum (Sprague) L.G. Lohmann	Lohmann 92 (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222540	DQ222668
Tanaecium caudiculatum (Standl.) L.G. Lohmann	Whitefoord 9231 (BRH, MO)	Grano de Oro Camp, Cayo District, Belize	DQ222630	—
Tanaecium crucigerum Seem.	Lohmann 355 (MO)	Cult. Missouri Botanical Garden, Missouri, USA	DQ222640	DQ222812
Tanaecium decorticans 1	Frazão 188 (SPF)	Brasil, Pará, Belterra	—	—
Tanaecium decorticans 2	Frazão 197 (SPF)	Brasil, Pará, Santarém	—	—
Tanaecium decorticans 3	Frazão 210 (SPF)	Brasil, Pará, Belterra	—	—
Tanaecium decorticans 4	Frazão 220 (SPF)	Brasil, Pará, Óbidos	—	—

Tanaecium pyramidatum (Rich.) L.G. Lohmann 1	Fonseca 315 (SPF)	Amazonas, Novo Airão	—	—
Tanaecium pyramidatum (Rich.) L.G. Lohmann 2	Fonseca 321 (SPF)	Amazonas, Novo Airão, Parque Nacional de Anavilhanas	—	—
Tanaecium pyramidatum (Rich.) L.G. Lohmann 3	Francisco 44 (SPF)	Brasil, Roraima, Caracaraí	—	—
Tanaecium pyramidatum (Rich.) L.G. Lohmann 4	Forzza 6785 (RB)	Brasil, Roraima, Caracaraí	—	—
Tanaecium pyramidatum (Rich.) L.G. Lohmann 5	Lohmann 264 (SPF)	Brasil, Minas Gerais, Uberlândia	—	—
Tanaecium pyramidatum (Rich.) L.G. Lohmann 6	Lohmann 274 (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222618	DQ222782
Tanaecium pyramidatum (Rich.) L.G. Lohmann 7	Silva 1 (HUFU)	Brasil, Minas Gerais, Delfinópolis	—	—
Tanaecium revillae (A.H. Gentry) L.G. Lohmann	Lohmann 265a (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222558	DQ222695
Tanaecium selloi (Spreng.) L.G. Lohmann	Lohmann 702 (MO, SPF)	Guarabira, Paraíba, Brazil	DQ222560	DQ222697
Tanaecium tetragonolobum (Jacq.) L.G. Lohmann	Lohmann 619 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222568	—
Tanaecium tetramerum (A.H. Gentry) Zuntini & L.G. Lohmann	Pace 32 (SPF)	Bolívia, Santa Cruz, Valle Grande	KU757039	KU757041
Tanaecium truncatum (A. Samp.) L.G. Lohmann	Lohmann 33 (INPA, K, MG, MO, NY, SPF)	Ducke Forest Reserve, Amazonas, Brazil	DQ222620	DQ222784
Tynanthus elegans Miers	Lohmann 663 (CVRD, MO)	Vale do Rio Doce Forest Reserve, Espirito Santo, Brazil	DQ222643	DQ222816
Xylophragma myrianthum (Cham.) Sprague	Lohmann 649 (CVRD, MO)	Vale do Rio Doce Forest Reserve, Espirito Santo, Brazil	DQ222648	DQ222823

Figure Captions

Fig. 1. Bayesian topologies resulting from the analysis of 20 accessions of *Tanaecium* Sw. emend L.G. Lohmann plus 12 outgroups. **a** Topology that resulted from the analysis of the combined dataset (i.e., *ndh*F plus *pep*C); **b** Topology that resulted from the analysis of the *pep*C marker; **c** Topology that resulted from the analysis of the *ndh*F marker. Green shading highlights the monophyly of *Tanaecium decorticans* Frazão & L.G. Lohmann, and pink shading highlights the monophyly of *Tanaecium pyramidatum* (Rich.) L.G. Lohmann. Numbers next to nodes are posterior probabilities; circles on nodes indicate PP=1.0.

Fig. 2 *Tanaecium decorticans*. **a** Flowering branch; **b** Detail of node; **c** Detail of peeling epidermis; **d** Detail of arrow-shaped apex of petiolule at adaxial face; **e** Detail of arrow-shaped apex of petiolule at abaxial face; **f** Flower in pre-anthesis; **g** Detail of calyx; **h** Detail of calyx apex and glandular trichomes; **i** Detail of corolla showing stamen insertion; **j** Nectar disk, ovary, style, and stigma; **k** Detail of ovary trichomes; **l** Fruit; **m** Detail of fruit trichomes at the margin. Illustrated from Frazão *et al.* 210 (SPF)

Fig. 3. Key morphological features of *Tanaecium decorticans* Frazão & L.G. Lohmann. **a** Flowering branch; **b** Side view of flowers; **c** Flower buds showing the acute apices. White arrow indicates the patteliform glandular trichomes found in the calyx; **d** Branch with peeling epidermis. White arrow indicates the arrow-shaped petiolule apex while black arrow indicates the subulate prophylls of the axillary buds. Photos: A. Frazão.

Fig. 4. Known occurrences of *Tanaecium decorticans* Frazão & L.G. Lohmann. Yellow star indicates the type locality.

Fig.1.

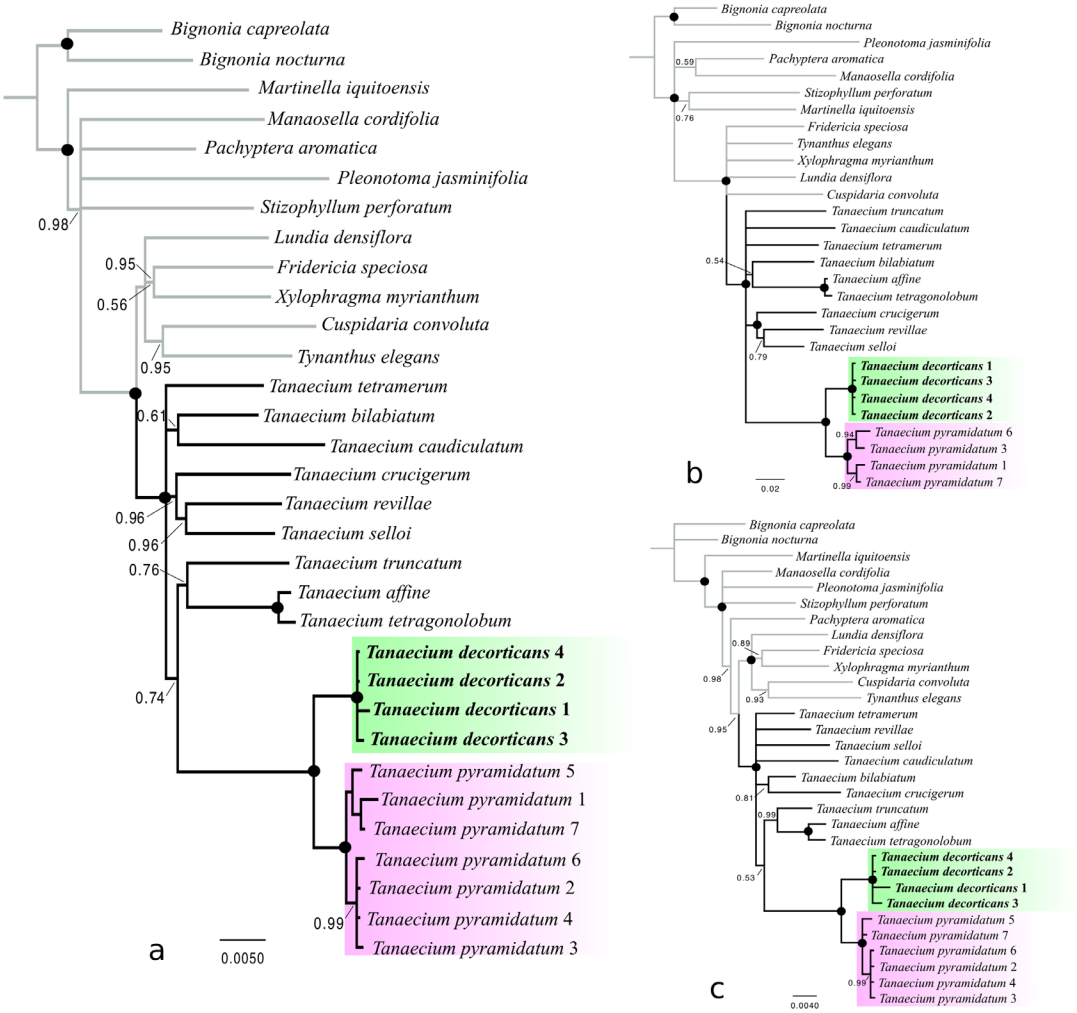
Bignonia capreolata
Bignonia nocturna
Martinella iquitoensis
Manaosella cordifolia
Pachyptera aromatica
Pleonotoma jasminifolia
Stizophyllum perforatum
Lundia densiflora
Fridericia speciosa
Xylophragma myrianthum
Cuspidaria convoluta
Tynanthus elegans
Tanaecium tetramerum
Tanaecium bilabiatum
Tanaecium caudiculatum
Tanaecium crucigerum
Tanaecium revillae
Tanaecium selloi
Tanaecium truncatum
Tanaecium affine
Tanaecium tetragonolobum
Tanaecium decorticans 4
Tanaecium decorticans 2
Tanaecium decorticans 1
Tanaecium decorticans 3
Tanaecium pyramidatum 5
Tanaecium pyramidatum 1
Tanaecium pyramidatum 7
Tanaecium pyramidatum 6
Tanaecium pyramidatum 2
Tanaecium pyramidatum 4
Tanaecium pyramidatum 3
0.98
0.95
0.56
0.95
0.61
0.96
0.96
0.76
0.74
0.99
a
0.0050
0.59
0.76
0.54
0.79
0.94
0.99
b
0.02
0.89
0.98
0.93
0.95
0.81
0.99
0.53
0.99
c
0.0040

Fig.2.

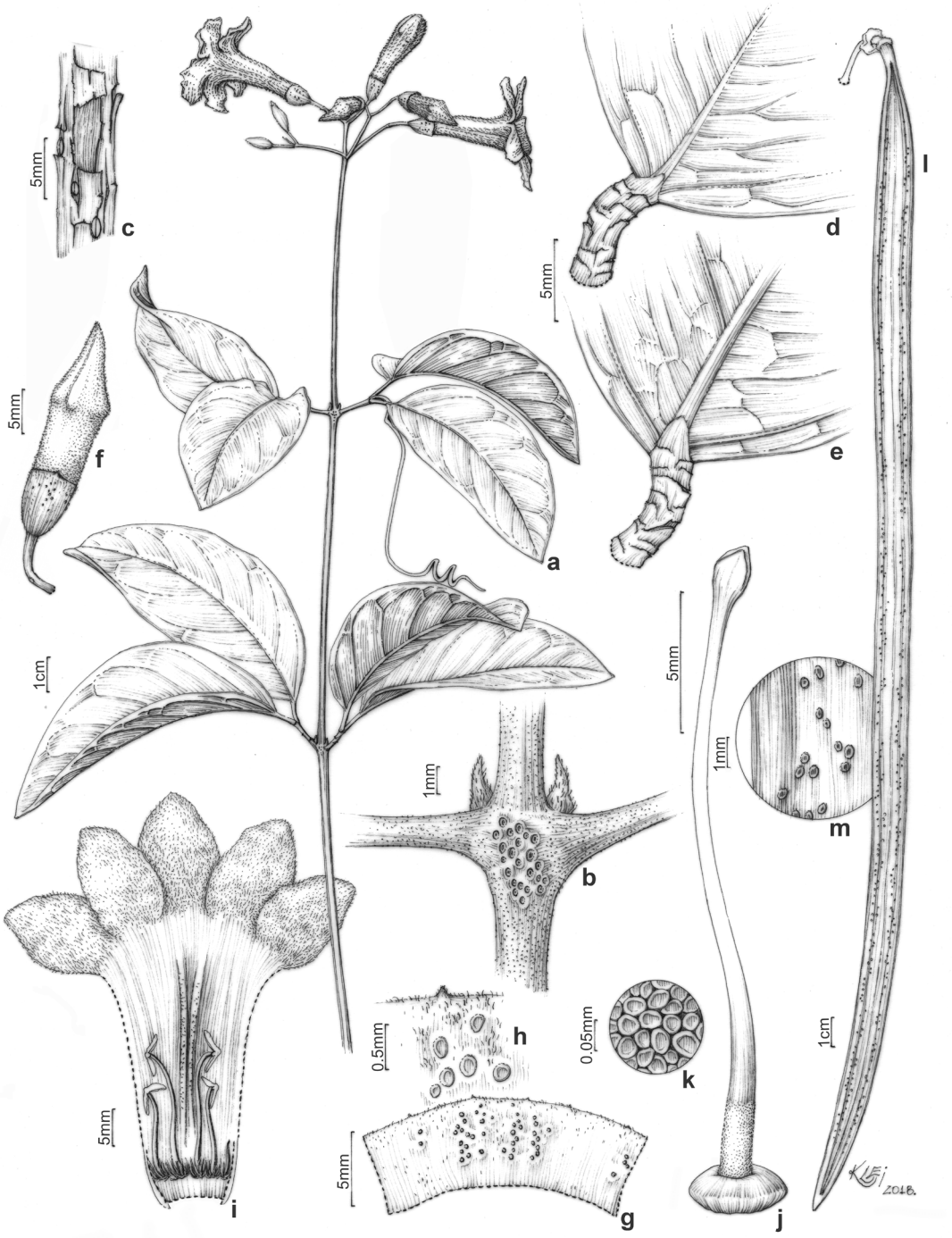
5mm
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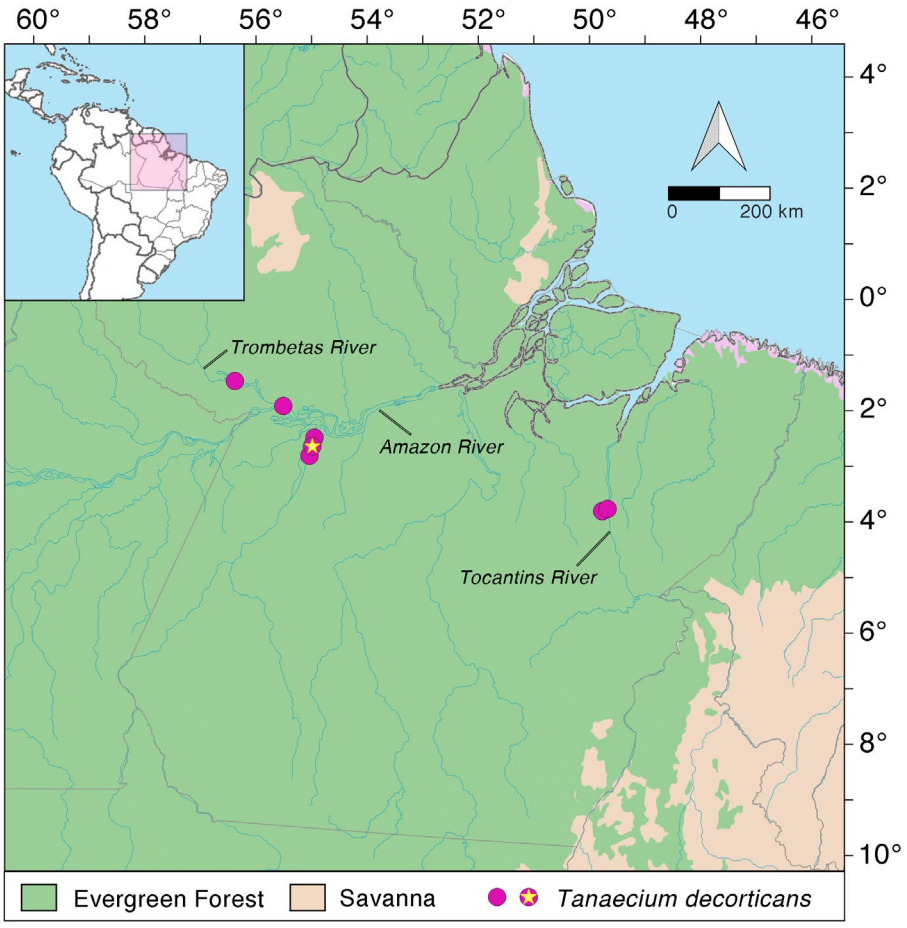
Fig.3.


a
b
c
d

Fig.4.


60°
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46°
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4°
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8°
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0
200 km
Trombetas River
Amazon River
Tocantins River
Evergreen Forest
Savanna
Tanaecium decorticans

Chapter 1.2. Taxonomic placement of *Tanaecium mutabile* (Bignonieae, Bignoniaceae) based on new morphological and phylogenetic data

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Abstract

During ongoing taxonomic studies with *Tanaecium* we identified some morphological disparities between *Tanaecium mutabile* (Bureau & K.Schum.) L.G.Lohmann and the remaining species of the genus. *Tanaecium mutabile* (previously *Arrabidaea mutabilis*) has a complicated taxonomic history, for which a detailed revision is greatly needed. Here, we reconstruct a molecular phylogeny of *Tanaecium* based on the *ndh*F and *pep*C genes, including a broad sampling of taxa within the "*Fridericia* and allies," where *Tanaecium*, *Fridericia*, *Lundia*, *Tynanthus*, *Cuspidaria*, and *Xylophrgama* are included. In the phylogenetic framework reconstructed here, *Tanaecium mutabile* is nested within *Fridericia.* These findings are further supported by new morphological data, indicating that *T. mutabile* is best placed within *Fridericia*. The appropriate taxonomic changes are proposed, including a new lectotypes for *Arrabidaea muehlbergiana*. Morphological comparisons between *T. mutabile* and other species commonly misidentified with this taxon are also presented.

Keywords: *Arrabidaea*, *Fridericia*, Lianas, Phylogeny, *Tanaecium*, Typification.

Introduction

During ongoing taxonomic studies in *Tanaecium* Sw. emend L.G. Lohmann (Frazão and Lohmann, in prep.) we identified some morphological disparities between *Tanaecium mutabile* (Bureau & K.Schum.) L.G.Lohmann and the remaining species of the genus. *Tanaecium mutabile* has a complicated taxonomic history. The basionym for this name is *Arrabidaea mutabilis* Bureau & K.Schum published in the *Flora Brasilienses* (1896). Two centuries later, *A. mutabilis* was treated as *Fridericia mutabilis* (Bureau & K.Schum.) L.G.Lohmann (Arbo & Lohmann 2008; Lohmann 2010), although these new combinations are *illegitimate* given that did not include a full and direct reference to the basionym (article 41 of the Shenzhen Code, Turland et al. 2017). Finally, *A. mutabilis* was transferred into *Tanaecium* and the new combination *Tanaecium mutabil*e was proposed (Lohmann & Taylor 2014).

The original description for this species (Bureau & Schumann 1896) provides adequate characters for its identification such as the leaflets with round to acute bases, generally glabrous, except from lepidote trichomes sparsely distributed throughout the lamina, calyx campanulate and membranaceous, corolla sub-obliqua campanulate, and capsule with the central valve ridges prominent. Bureau & Schumann (1896) called attention to the fact that some of the morphological features of *A. mutabilis* [= *Tanaecium mutabile*] overlap with features from other species included in the then accepted *Arrabidaea*. More specifically, Bureau & Schumann (1896) indicated that the leaflet morphology of *A. corymbifera* [= *Lundia corymbifera* (Vahl) Sandwith] and *A. conjugatae* [= *Fridericia conjugata* (Vell.) L.G.Lohmann] could led to the misidentifications of these taxa. Despite the morphological divergences between *T. mutabile* and other *Tanaecium* species, this species shares bromeliad-like prophylls of the axillary buds and bilabiate calyces with *Tanaecium*. Both of these traits are putative synapomorphies to *Tanaecium* (Lohmann & Taylor 2014), providing support for the inclusion of this species within *Tanaecium*.

Considering the patterns of morphological overlap, taxonomic, and nomenclatural confusion, we here reconstruct a phylogeny of *Tanaecium* and conduct morphological studies in this genus in order to determine the best possible placement for *T. mutabile*.

Materials and Methods

Molecular sampling

To investigate the phylogenetic placement of *Tanaecium mutabile*, we compiled a molecular dataset composed of published sequences deposited in GenBank (Benson et al. 2005) plus sequences of three individuals of *Tanaecium mutabile* that were newly generated for this study. Our final dataset included 51 sequences, i.e., 26 sequences for *ndh*F and 25 sequences for

*pep*C, representing 10 species of *Tanaecium* (Lohmann and Taylor 2014; Frazão and Lohmann 2018; Pace et al. 2016) and 12 outgroups (Table 1).

DNA extraction and alignment

Genomic DNA was extracted from silica-dried leaf tissue from herbarium specimens (Table 1) using a Spin Plant Mini Kit (Invisorb) following the manufacturer's protocol. PCR conditions for the amplification of *ndh*F and *pep*C followed Frazão and Lohmann (2018). PCR products were purified and sequenced by Macrogen Inc. in Korea. Sequences were assembled and edited in Geneious 7.0 (Kearse et al. 2012), and aligned with MAFFT 7 (Katoh and Toh 2008) using default parameters. The concatenated molecular matrix was constructed using Geneious 7.0 (Kearse et al. 2012). All sequences, vouchers, and GenBank accession numbers are available in Table 1.

Phylogenetic analyses

The best-fit model of DNA substitution for the individual data partitions were selected usin the Akaike Information Criterion (AIC) in jModelTest 2.0 (Guindon et al. 2010; Darriba et al. 2012). The GTR + G was identified as the most appropriate model of DNA substitution for both the *ndh*F and *pep*C. We used a combined *ndh*F and *pep*C dataset to perform a Bayesian inference (BI) using MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) on the online server CIPRES (Miller et al. 2010). Two independent MCMC runs were conducted, each composed of four linked chains that ran for 10,000,000 generations, sampling every 1000 generations. Likelihood values were monitored graphically to detect stationarity with Tracer 1.7 (Rambaut et al. 2018). Posterior probabilities (PP) were used to assess clade support.

Taxonomic treatment

We studied the original publication of the name *Tanaecium mutabile* (Lohmann and Taylor 2014), which included the details of the lectotype selected by Lohmann and Taylor (2014). We then searched for all images of vouchers associated with the lectotype at Jstor Global Plants (2019), and analyzed the isolectotypes deposited at F and MO herbaria [a photocopy in the last] (acronyms following Thiers 2018). Synonyms were studied based on a compilation of names associated with *Tanaecium mutabile* available online (Lohmann and Ulloa 2006 onwards).

We analyzed samples deposited at MO and SPF in order to compare *Tanaecium mutabile* with the morphologically similar *Fridericia conjugata* (Vell.) L.G.Lohmann, *Lundia*

corymbifera (Vahl) Sandwith (see Bureau & Schummann 1896), and *Tanaecium selloi* (Frazão & Lohmann, in prep.) (Table 2). Morphological terminology followed that adopted by Lohmann and Taylor (2014) for Bignonieae. Distribution maps for *F., conjugata*, *L. corymbifera*, and *T. selloi* were prepared using on a geo-referrenced database compiled by Lohmann (unpubl. data). This same database was complemented with additional specimens from MO and SPF to prepare a distribution map of *T. mutabile*. All maps were built using QGis (2019). Nomenclatural proposals follow the *International Code of Nomenclature for algae, fungi, and plants* (Turland et al. 2018).

Results and Discussion

Molecular phylogeny

The *ndh*F dataset included 26 terminals and 2,111 bp, while the *pep*C dataset included 25 terminals and 773 bp. The final combined dataset included 26 terminals and 2,883 bp. *Tanaecium* emerged as polyphyletic in the molecular phylogeny reconstructed here (Fig. 1). *Tanaecium mutabile* was reconstructed as sister to *Fridericia speciosa* Mart., the type species of *Fridericia*, with maximum posterior probability (PP 1; Fig. 1). The clade that contains *F. speciosa* plus *Tanaecium mutabile* is sister to *Lundia densiflora* DC. (PP 1; Fig 1), which is in turn reconstructed within a polytomy that also contains *Cuspidaria convoluta* (Vell.) A.H.Gentry, sister to *Tynanthus elegans* Miers (PP 0.94; Fig. 1), and *Xylophragma myrianthum* (Cham.) Sprague (PP 0.96; Fig. 1). This whole clade is sister to *Tanaecium s.s.*, which includes three main clades with unclear relationships (PP 1.0; Fig. 1). The first clade includes *Tanaecium bilabiatum* (Sprague) L.G.Lohmann sister to *Tanaecium caudiculatum* (Standl.) L.G.Lohmann with low support (PP 0.65; Fig. 1). The second clade includes *Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann sister to *Tanaecium crucigerum* Seem. (PP 0.62; Fig. 1), which is in turn sister to a clade composed by *Tanaecium revillae* (A.H.Gentry) L.G.Lohmann and *Tanaecium selloi* (Spreng.) L.G.Lohmann (PP 0.95; Fig. 1). The sister group relationship between *T. tetramerum* and *T. crucigerum* is novel as earlier studies recovered *T. tetramerum* within a polytomy (Pace et al. 2016; Frazão & Lohmann 2018). The third clade includes *Tanaecium decorticans* Frazão & L.G.Lohmann sister to *Tanaecium pyramidatum* (Rich.) L.G.Lohmann (PP 1.0; Fig. 1), which is sister to a clade composed of *Tanaecium truncatum* (A.Samp.) L.G.Lohmann (PP 0.92), *Tanaecium tetragonolobum* (Jacq.) L.G.Lohmann, and *Tanaecium affine* (A.H.Gentry) L.G.Lohmann (PP 1.0; Fig. 1).

Morphological studies

In the protologue of *Arrabidaea mutabilis* (= *Tanaecium mutabile*), Bureau & Schummann (1896) commented that this species was morphologically similar to *Arrabidaea conjugata* (= *Fridericia conjugata*) and *Arrabidaea corymbifera* (= *Lundia corymbifera*). Despite that, these species differ from *T. mutabile* by the raised primary venetion on adaxial side in *F. conjugata* (vs. flat in *T. mutabile*), and lax inflorescence in *F. conjugata* (vs. condensed inflorescence in *T. mutabile*), and cordate leaflet bases of *Lundia corymbifera* (vs. rounded, truncate or acute leaflet bases in *T. mutabile*) (Bureau & Schumann 1896). *Tanaecium mutabilis* is often also confused with *Tanaecium selloi*, but these can be distinguished by the absence of interpetiolar patelliform trichomes (vs. presence of interpetiolar patelliform trichomes in *F. mutabilis*), triangular or foliaceous prophylls (vs. bromeliad-like prophylls in *F. mutabilis*), second venation with narrow acute angle (vs. moderate acute to *F. mutabilis*).

Tanaecium mutabile is often confused with the sympatric *F. conjugata*, *L. corymbifera* and *T. selloi*. Even though herbarium specimens of these taxa are often misidentified, all three species are easily distinguishable in the field due to the different corolla color (Fig. 2). Furthermore, *T. mutabile* shows a series of unique diagnostic characters, namely the: (i) bromeliad-like prophylls of the axillary buds, (ii) ovate or obovate leaflets with rounded, truncate or asymmetrical bases and acuminate to retuse apices, (iii) basal secondary venation recurved, (iv) flowers with curved corollas and only the longest stamens subexserted, (v) fruits with flat margins and conspicuous middle ridges, and (vi) greenish seeds.

Despite these diagnostic features, *T. mutabile* was placed in *Tanaecium* due to the presence of bromeliad-like prophylls of the axillary buds and bilabiate calyces, putative morphological synapomorphies for the genus (Lohmann & Taylor 2014). However, the bromeliad-like prophylls are homoplastic in the tribe Bignonieae, having evolved independently in *Bignonia* L. (Zuntini et al. in prep.), *Fridericia* Mart. emend L.G. Lohmann (Kaehler et al. in prep.), and *Xylophragma* Sprague (Lohmann & Taylor 2014). Similarly, the bilabiate calyces are also labile in the tribe, also occuring in species of *Adenocalymma* Mart. ex Meisn. emend L.G. Lohmann, *Amphilophium* Kunth emend L.G. Lohmann, *Bignonia*, *Dolichandra* Cham. emend L.G. Lohmann, *Fridericia*, and *Stizophyllum* Miers (Lohmann & Taylor 2014; Fonseca et al. 2017). Despite that, the curved corolla of *T. mutabilis*, is not found in any other *Tanaecium* (Frazão & Lohmann, in prep), while being common in *Fridericia*, as observed in *F. conjugata*, for example (Fig. 2). A comparison between *F. mutabilis* and the most morphologically similar species is presented in Table 2. Key-characters to distinguish these taxa are shown in Figure 2.

Taxonomic treatment

Our phylogenetic results recovered three main clades in *Tanaecium*, corroborating earlier findings (Lohmann 2006; Pace et al. 2016; Frazão & Lohmann 2018), as well as recovered *T. mutabile* within *Fridericia*. Even though *T. mutabile* shares a series of features with members of *Tanaecium* (e.g., bromeliad-like prophylls and bilabiate calyx), other morphological features shared with *Fridericia* support its placement within the genus, namely the interpetiolar patelliform trichomes, simple tendrils, thyrsoid inflorescences, pink flowers, lepidote ovaries with a single series of ovules on each placenta, and aglandular lepidote fruits (Lohmann & Taylor 2014). Our phylogenetic findings combined with the new morphological observations support the placement of *T. mutabile* within *Fridericia*. Below, we present the necessary nomenclatural changes, along with information on the distribution and taxonomic notes.

Fridericia mutabilis (Bureau & K.Schum.) Frazão & L.G. Lohmann, comb. nov. Basionym: *Arrabidaea mutabilis* Bureau & K.Schum., Fl. Bras. 8(2): 38. 1896. ≡*Tanaecium mutabile* (Bureau & K. Schum.) L.G.Lohmann. Ann. Missouri Bot. Gard. 99: 465. LECTOTYPE: Brazil. São Paulo, Campinas ["Brésil méridional" on sheet], 16 Sep 1868, *J. Correia de Méllo 44* (lectotype designated by Lohmann & Taylor 2014 P barcode 00468542!,; isolectotypes, P barcode 00468543!, P barcode 00468544!, P barcode 00468545!, P barcode 00468546!, S S09-21566 [image!], S as photocopy MO–2909990!, F 999017!; F 784134!).

= *Arrabidaea muehlbergiana* Hassl. Bull. Herb. Boissier 6 (4, App. 1): 25. 1898. TYPE: Paraguay. Paraguary: In silva prope Cerro Sº Tomas, Sep. 1885–1895, *E. Hassler 964.* LECTOTYPE: designated here, G barcode G00094021 [image!]; isolectotype, G barcode G00008853 [image!], G barcode G00008854 [image!], G barcode G00085508 [image!]), LP 11267 [image!], NY barcode NY00313100!, US barcode US01108028!.

Distributional and habitat: *Fridericia mutabilis* is distributed in South America occurring in seasonal vegetation and occasionally in wet forests in Argentina (Corrientes, Missiones), Brazil (Espírito Santo, Minas Gerais, Paraná, Santa Catarina, São Paulo), Bolivia (Chuquisaca), and Paraguay (Alto Paraná, Caazapá, Canindeyú, Central, Concepción, Cordillera, Guairá, Itapúa, Paraguarí). The distribution of *T. mutabilis* forms an arc in the Southern portions of South America, which is consistent with the "southern connection" thought to have connected the Atlantic Forest and the Amazon in the past (e.g., Batalha-Filho et al 2013; Ledo & Colli 2017; Peres et al 2017; Thomé et al 2016; Fine & Lohmann 2018).

Phenology: *Fridericia mutabilis* was collected with flowers in September and October and with fruits between May and September.

Nomenclatural notes. When Hassler (1898) described *Arrabidaea muehlbergiana*, he did select a holotype. We here selected the collection *E. Hassler 964* desposited at G (barcode G00094021) as the lectotype because it is a high-quality material allowing the accurate identification of this species, and this material is likely to be part of the Hassler's original material (Index of Botanists 2019).

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Figure captions

Figure 1. Phylogeny of the *Fridericia* and allies clade including intensive sampling of *Tanaecium* based on a combined *ndh*F and *pep*C dataset. The green box highlights the *Tanaecium* s.s. clade while the grey box highlights the outgroups. The phylogenetic placement of *Tanaecium mutabile* is highlighted in red. Numbers near nodes are posterior probabilities.

Figure 2. Comparison between *Fridericia mutabilis* (Bureau & K.Schum.) Frazão & L.G.Lohmann and morphologically similar taxa. A-F. *Fridericia mutabilis*: A. habit; B. distribution map; C-D. leaflet; E. detail of fruit; F. seed. G-K. *Fridericia conjugata* (Vell.) L.G.Lohmann: G. habit; H. distribution map; I. leaflet; J. detail of fruit; K. seed. L-O. *Lundia corymbifera* (Vahl) L.G.Lohmann: L. habit; M. distribution map; N. leaflet; O. detail of fruit. P-T. *Tanaecium selloi* (Spreng.) L.G.Lohmann: P. habit; Q. distribution map; R. leaflet; S. detail of fruit; T. seed. Photo A by D. Grasel, B by L.G. Lohmann, C by G. Gerlach, and D by A. Frazão.

Table 1. Taxon, voucher, locality, and GenBank accessions for DNA sequences.

Taxa	Voucher	Locality	Access number	
			ndhF	*PepC*
Bignonia capreolata L.	Lohmann 356 (MO)	Johnson County, Illinois, USA	DQ222566	DQ222706
Bignonia nocturna (Barb.Rodr.) L.G.Lohmann	Lohmann 451 (MO, NY, SPF, UFAC)	Rio Juruá, Acre, Brazil	DQ222641	DQ222814
Cuspidaria convoluta (Vell.) A.H.Gentry	Lohmann 713 (MO, SPF)	Cult. Instituto Plantarum, São Paulo, Brazil	DQ222573	DQ222712
Fridericia speciosa Mart.	Lombardi 2521 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222584	DQ222731
Lundia densiflora DC.	Lohmann 82 (INPA, MO)	Ducke Forest Reserve, Amazonas, Brazil	DQ222592	DQ222744
Manaosella cordifolia (DC.) A.H.Gentry	Lombardi 2546 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222596	DQ222751
Martinella iquitoensis A.Sampaio	Lohmann 616 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222605	DQ222761
Pachyptera aromatica Barb.Rodr.	Lohmann 28 (INPA, MO, SPF)	Ducke Forest Reserve, Amazonas, Brazil	DQ222589	DQ222740
Pleonotoma jasminifolia (Kunth) Miers	Lohmann 122 (INPA)	Ducke Forest Reserve, Amazonas, Brazil	DQ222625	DQ222794
Stizophyllum perforatum (Cham.) Miers	Lombardi 2431 (BHCB, MO)	State Park of Rio Doce, Minas Gerais, Brazil	DQ222639	DQ222810
Tanaecium affine (A.H.Gentry) L.G.Lohmann	Lohmann 633 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222539	DQ222666
Tanaecium bilabiatum (Sprague) L.G.Lohmann	Lohmann 92 (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222540	DQ222668
Tanaecium caudiculatum (Standl.) L.G.Lohmann	Whitefoord 9231 (BRH, MO)	Grano de Oro Camp, Cayo District, Belize	DQ222630	DQ222800
Tanaecium crucigerum Seem.	Lohmann 355 (MO)	Cult. Missouri Botanical Garden, Missouri, USA	DQ222640	DQ222812

Tanaecium decorticans Frazão & Lohmann	Frazão 188 (SPF)	Brasil, Pará, Belterra	MH790868	MH765565
Tanaecium pyramidatum (Rich.) L.G.Lohmann	Lohmann 274 (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222618	DQ222782
Tanaecium revillae (A.H.Gentry) L.G.Lohmann	Lohmann 265a (MO, NY, SPF, UNIP)	Rio Solimões, Amazonas, Brazil	DQ222558	DQ222695
Tanaecium selloi (Spreng.) L.G.Lohmann	Lohmann 702 (MO, SPF)	Guarabira, Paraíba, Brazil	DQ222560	DQ222697
Tanaecium tetragonolobum (Jacq.) L.G.Lohmann	Lohmann 619 (MO, MOL)	Manu National Park, Madre de Dios, Peru	DQ222568	DQ222707
Tanaecium tetramerum (A.H.Gentry) Zuntini & L.G.Lohmann	Antezana-Valera 1327 (BOLV, MO)	Bolívia, Cochabamba, Campero	KU757040	KU757043
Tanaecium truncatum (A.Samp.) L.G.Lohmann	Lohmann 33 (INPA, K, MG, MO, NY, SPF)	Ducke Forest Reserve, Amazonas, Brazil	DQ222620	DQ222784
Tynanthus elegans Miers	Lohmann 663 (CVRD, MO)	Vale do Rio Doce Forest Reserve, Espirito Santo, Brazil	DQ222643	DQ222816
Xylophragma myrianthum (Cham.) Sprague	Lohmann 649 (CVRD, MO)	Vale do Rio Doce Forest Reserve, Espirito Santo, Brazil	DQ222648	DQ222823
Tanaecium mutabile (Bureau & K.Schum.) L.G.Lohmann 1	Carneiro (SPF)	Brasil, Paraná, Londrina, Fazenda Figueira-Paiquerê	–	–
Tanaecium mutabile (Bureau & K.Schum.) L.G.Lohmann 2	de Souza s.n. (UPCB)	Brasil, Paraná, Maringá, Horto Florestal	–	–
Tanaecium mutabile (Bureau & K.Schum.) L.G.Lohmann 3	Zardini 15207 (SPF)	Paraguai, Guaira, Cordillera de Ybytyruzú	–	–

Table 2. Morphological comparison of shared and unshared character states between *Fridericia mutabilis* (Bureau & K.Schum.) Frazão & L.G.Lohmann and its closer species. Bold highlighted exclusive character states for each species. Vouchers: *Fridericia mutabilis* - Zardini 8342, SPF, MO, G, PY; Zardini 15207, SPF, MO, G, PY; Zardini 12382, SPF, MO, G, FCQ. *Fridericia conjugata* - Guillén 1430, MO; Pirani 3315, NY, SPF; Zuntini 209, SPF. *Lundia corymbifera* - Lorenzi 5015, SPF, HPL; Forzza 2042, SPF, CESJ; Gentry 10759, MO; Scudeller 407, VIC (image! VIC16058). *Tanaecium selloi* Frazão 235, SPF; Udulutsch 356, SPF, HRCB.

Characters	**Species**			
	Fridericia mutabilis	*Fridericia conjugata*	*Lundia corymbifera*	*Tanaecium selloi*
Tendril apex	simple	simple	simple	simple
Patelliform glandular interpetiolar field	present	present	present	**absent**
Prophylls	**bromeliad-like**	subulate	minute and triangular	minute and triangular or foliaceous
Leaflet morphology	ovate to **obovate**	ovate	ovate	ovate
Leaflet base	rounded, **truncate** or **asymmetrical**	round or cordate	round or cordate	round or cordate
Leaflet apex	acuminate to **retuse**	acuminate	acuminate or cuspidate	acute or cuspidate
Secondary venation - type	basal and suprabasal actinodrom	basal and suprabasal actinodrom	basal and suprabasal actinodrom	basal and suprabasal actinodrom
Secondary basal venetion - angle of divergence	moderate acute (45-65º)	80-100º	moderate acute (45-65º)	**narrow acute (<45º)**
Secondary supra basal venetion - angle of divergence	narrow acute (< 45º)	moderate acute (45-65º)	moderate acute (45-65º)	narrow acute (< 45º)
Secondary basal venation - course	**recurved**	curved	curved	**straight**
Secondary supra basal venation - course	recurved or straight	recurved	recurved or straight	straight
Primary venetion on adaxial side	flat	**rised**	flat	flat
Calyx apex	bilabiate	truncate	truncate or **spataceous**	bilabiate
Calyptra	absent	absent	**present**	absent
Adaxial surface	glabro	glabro	**puberulent**	**glabrescent to pubescent only on veins**
Abaxial surface	glabro	glabro	puberulent only on veins	puberulent to pubescent
Domatia	absent	absent	**membrane-like**	**tuft domatia**
Curved corolla	**present**	**present**	absent	absent
Longest stamens subexerted	**present**	absent	absent	absent
Fruit central ridge conspicuous	present	present	present	**absent**
Fruit margin	**flat**	raised	raised	raised
Seeds color	**greenish**	light brown yellowish	**brownish**	light brown yellowish

Figure 1.

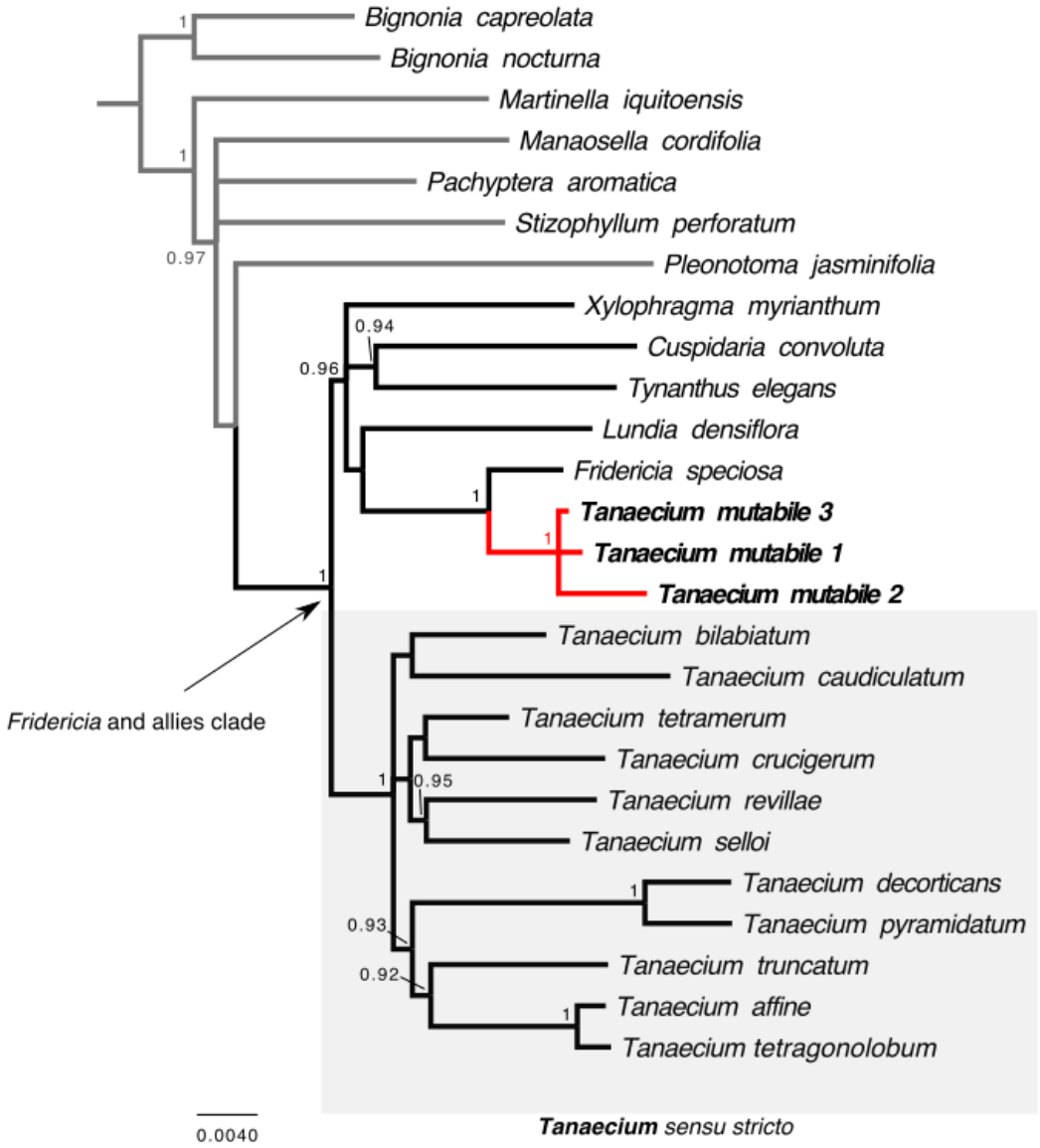
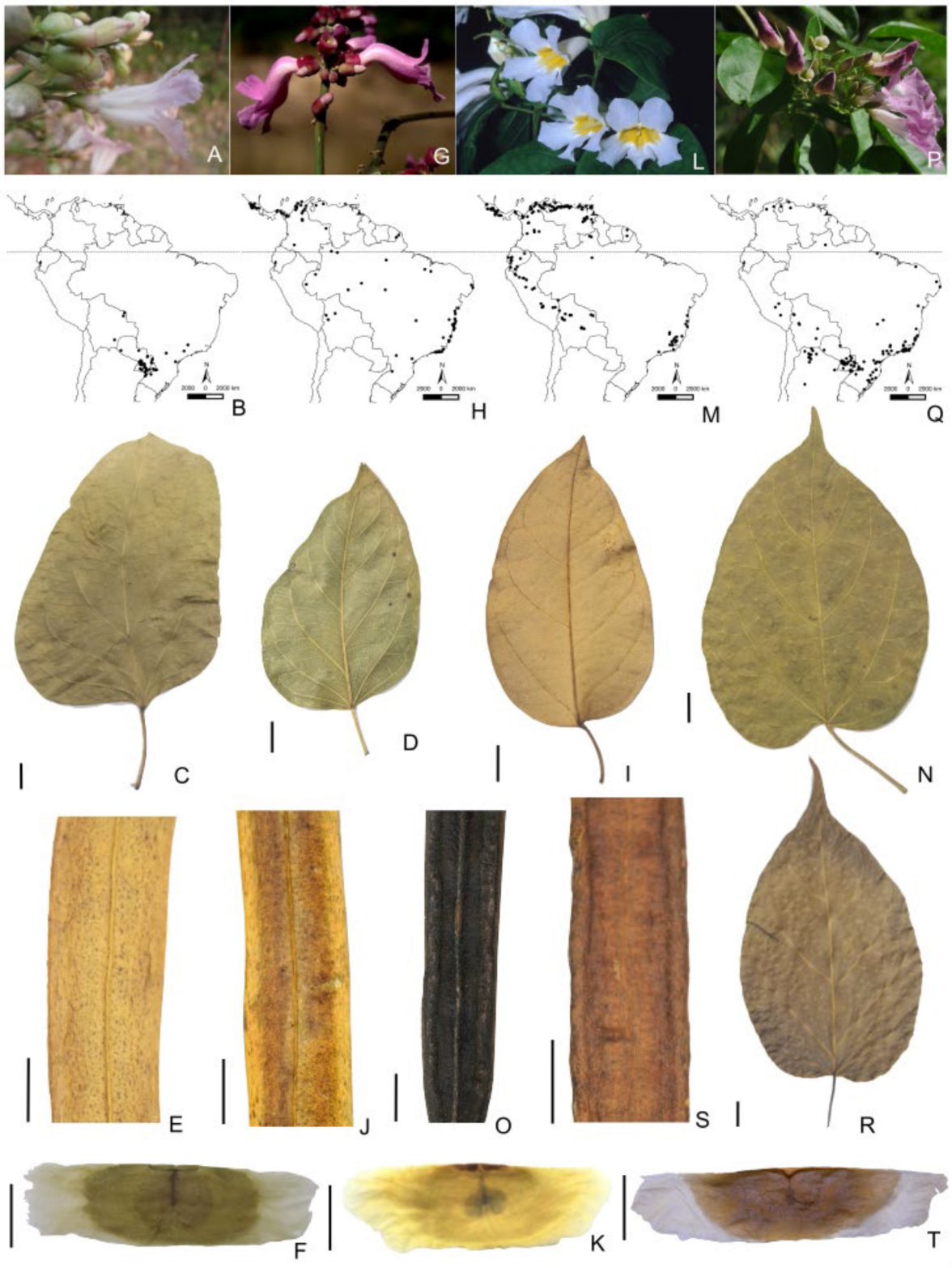

Bignonia capreolata
Bignonia nocturna
Martinella iquitoensis
Manaosella cordifolia
Pachyptera aromatica
Stizophyllum perforatum
Pleonotoma jasminifolia
Xylophragma myrianthum
Cuspidaria convoluta
Tynanthus elegans
Lundia densiflora
Fridericia speciosa
Tanaecium mutabile 3
Tanaecium mutabile 1
Tanaecium mutabile 2
Tanaecium bilabiatum
Tanaecium caudiculatum
Tanaecium tetramerum
Tanaecium crucigerum
Tanaecium revillae
Tanaecium selloi
Tanaecium decorticans
Tanaecium pyramidatum
Tanaecium truncatum
Tanaecium affine
Tanaecium tetragonolobum
1
1
0.97
0.94
0.96
1
1
1
1
0.95
1
0.93
0.92
1
Fridericia and allies clade
0.0040
Tanaecium sensu stricto

Figure 2.



Chapter 1.3. Deciphering the typification of the Neotropical genus *Tanaecium* (Bignonieae, Bigoniaceae)

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ABSTRACT

Ongoing studies on the systematics of *Tanaecium* indicated that this name has a doubtful type. Materials from Jamaica and Brazil were cited in the protologue of the genus, but none of the cited specimens were located in the herbaria where these materials were supposedly deposited. Those materials are presumed destroyed, and we here designate an epitype to *Tanaecium*. We further present a historical overview on the problems associated with the typification of the genus.

Keywords: Neotropical flora, taxonomy, typification, epitype.

INTRODUCTION

Tanaecium Sw. emend L.G. Lohmann is a Neotropical genus that comprise 19 species (Lohmann & Taylor 2014; Pace & al 2016; Frazão & Lohmann 2018). The genus name (from greek Τανανηχης – tanaekes: long) refers to the long corollas (Swartz 1800), as the genus was originally described to accommodate species with white, long, narrow, and infundibuliform corollas. However, subsequent phylogenetic data indicated that the genus was not monophyletic as originally circumscribed (Lohmann 2006), leading to a more broadly circumscribed *Tanaecium* that also includes species with different flower morphologies (Lohmann & Taylor 2014). The genus basionym is *Tanaecium jaroba* Sw. (Lohmann & Taylor 2014, p. 463), which has an abstruse history.

Swartz (1788) listed four samples in the protologue of *Tanaecium jaroba* (as "Iaroba"), two samples from Brazil (collections *Marcgrave 25* and *Piso 173*) and two from Jamaica (collections *Brown 266* and *Sloan 207*). While the Jamaican samples were clearly described as a liana with ternate leaves and terminal tendrils, the first samples from Brazil (*Marcgrav 25*) included a note that said "Cucurbifera," while the second sample (*Piso 173*) included the annotation "Crescentia?".

De Candolle (1845) cited Swartz's *Flora Indiae Occidentalis* (1800) instead of the original publication (Swartz 1788) in his treatment. Furthermore, De Candolle (1845) renamed *Tanaecium jaroba* as *Tanaecium albiflorum* DC. and excluded the collection *Marcgrave 25*, which he thought belonged to the Passifloraceae instead.

Swartz (1788) also described *Tanaecium parasiticum*, which was later synonymized as *Schlegelia parasitica* (Sw.) Miers ex Griseb. (Grisebach 1864). However, before this synonymization, Seemann (1857) treated *Tanaecium parasiticum*, as well as described *Tanaecium lilacinum* Seem, even though *Tanaecium lilacinum* was thought to be best placed in *Schlegelia* by Miquel in sched. (Seemann 1856). Nevertheless, fruit morphological studies of Miers (1861) questioned Brown's collection cited in the protologue, which was also thought to represent *Schlegelia* instead of *Tanaecium*.

In a wide study of Bignoniaceae morphology, Miers (1861) indicated that there was a problem with *Tanaecium*'s type. More specifically, he noted that the collection *Brown 266* represented mixed material, and that the morphological description of Seemann (1857) clearly applied to *Schlegelia* instead. Miers (1861) further noted that he could not locate the Jamaican collections listed in the protologue (*Brown 266* and *Sloan 207*). Despite that, Miers (1861) followed the descriptions of these materials conducted earlier by Swartz (1800) and De Candolle (1845). Miers (1861) added fruit and seed descriptions of *Tanaecium albiflorum* (= *Tanaecium jaroba*) based on one unnumbered collection of Robins deposited at BM. Seemann (1856, 1857) cited the same Robins material in his treatment.

In De Candolle's work (1845), he cited a plate from *Flora Indiae Occidentalis* (Swartz 1800) as a reference for *Tanaecium jaroba*, which was followed in all subsequent treatments. Despite that, Howard [1989: 335] was the first to explicitly indicate that this plate represented a type for *Tanaecium*. In modern terminology, Howard [1989: 335] selected the plate of the *Flora Indiae Occidentalis* (Swartz 1800) as the lectotype of *Tanaecium jaroba* and the genus as a whole. Despite that, the plate does not contain the diagnostic characters of the genus, nor enough information to allow the accurate identification of *Tanaecium jaroba*. Given all the uncertainty associated with the type of *Tanaecium*, we here select an epitype to complement the type series currently available for the genus. We also provide notes to further elucidate the nomenclatural and taxonomic history of the genus.

MATERIALS AND METHODS

This work is based on the study of specialized literature and specimens deposited at BM, GOET, K, NY, P, and S (acronyms following Thiers 2019). The type was selected based on the similarity with the description presented in the protologue, which was consulted using the Biodiversity Heritage Library (BHL 2019). We used the Jstor Platform (2019) and the online databases from the herbaria BM (Natural History Museum 2014), K (Royal Botanic Gardens 2019), NY (The New York Botanical Garden 2019), and P (Muséum national d'Histoire naturelle 2019) to study images of all specimens. Nomenclatural rules follow the Shenzhen Code (Turland & al 2018). The name, herbaria, and authors were confirmed using the online Taxonomic Literature II (TL-2 2019) and the Index of Botanists (2019).

TYPIFICATION

Tanaecium jaroba Sw., Prodr. 92: 1788. ≡ *Tanaecium albiflorum* DC. Prodr. 9: 245. 1845. **Lectotype (designated by Howard 1989: 335)**: Jamaica. Sw. Fl. Ind. Occ. 2: *t. 20*, *f. 1*. 1800. **Epitype (designated here):** Jamaica. Saint Elizabeth. Black River, 17 Jul 1915, *Herris 12092* (epitype, NY barcode 01350477!, isoepitype, P barcode 05090714 [photo]!).

= *Tanaecium praelongum* Miers, Ann. Mag. Nat. Hist., ser. 3, 8: 117. 1861. **Type**: Guiana Britannica. Sin loc., s.d., *Schomburgk 829* (holotype, K – [barcode] 000449542 image!).

= *Tanaecium exsertum* Griseb. Fl. Brit. W. I.: 450. 1864 [1862]. **Type**: Jamaica. Sin loc., s.d., *March. 1070* (holotype, GOET– [barcode] 000372 image!; K– 449537 image!).

Swartz (1788) cited materials collected by Browne, Marcgrave, Piso, and Sloane in the protologue of the genus. However, the numbers cited are publication pages from voyage notes

through Brazil by Marcgrave (1648) and through Jamaica and the Lesser Antilles by Sloane (1725). The Piso material cited is a citation from his publication (Pisonis 1658) and carries the same information as Marcgrave (1648). As indicated by De Candolle (1845), the Marcgrave collection does not correspond to *Tanaecium jaroba*. While Swartz (1788) cited "Brown.266," De Candolle (1845) and Seemann (1856) cited "Brown. 266 n.6" and Miers (1861) cited "Brown. 267." None of the cited materials were located, and the accuracy of this information remains doubtful. The sole *Tanaecium jaroba* material from Jamaica containing an annotation by Swartz is a collection from the Herbarium of the Linnean Society of London (LINN-HS1060-2 [photo]!). However, this specimen actually corresponds to *Schlegelia parasiticum* instead of *Tanaecium jaroba*.

Miers (1861) cited an unnumbered collection by Robins deposited at BM to describe the mysterious *Tanaecium jaroba* fruit. We analyzed a photo from BM that showed two fruits from Jamaica identified as *Tanaecium albiflorum* (= *Tanaecium jaroba*). Like Miers (1861), we were also unable to locate the physical specimens though. Nevertheless, the image allowed us to verify that only one of these fruits represents *Tanaecium jaroba*. Miers (1861) seems to have already noted this problem, as his description did not include the other fruit, which actually belongs to *Amphilophium paniculatum* (L.) Kunth. Because we were unable to locate the actual specimen associated with this photograph, which is presumed lost, we here selected the material *Herris 12092* as epitype. This material includes all diagnostic characters of *Tanaecium jaroba*, allowing immediate identification of this species. In contrast, the illustration presented in the *Flora Indiae Occidentalis* (Swartz 1800, t. 20, f. 1) seems to represent *Tanaecium crucigerum* Seem. Even though the selected epitype does not include a fruit, there are credible descriptions of the fruit and seeds of *T. jaroba* in publications where this species or synonyms are treated (Gentry 1973; Howard 1989; Miers 1861).

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We thank the curators from NY for permission to examine the selected epitype specimen, and to the BM vascular plant curator Mrs. Prakash for providing us with photos from the fruit collections. We also thank the Missouri Botanical Garden for hosting A.F.N. during a five-month internship. We are also grateful to the following funding agencies: Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES,1525151), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, 142224/2015-4, 310871/2017-4), Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP, 2011/50859-2, 2012/50260-6, 2015/10914-5, 2018/11110-5), International Association for Plant Taxonomy (IAPT 2016), Systematic Research Fund (SRF 2016), Society of Systematic Biologists (SSB 2017), and American Society of Plant Taxonomists (ASPT 2019).

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Chapter 1.4. An updated synopsis of *Tanaecium* (Bignonieae, Bignoniaceae)

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Abstract

Tanaecium Sw. emend L.G. Lohmann (Bignonieae, Bignoniaceae) is a morphological variable genus of Neotropical lianas, especially in what concerns floral features. The genus is distributed from Mexico and the Antilles to Argentina, and centered in Amazonia. Here, we present an updated overview for *Tanaecium* that recognizes 21 species within the genus. Species delimitation was based on a detailed analysis of protologues and herbarium specimens, including type collections of all taxa. We present a detailed description for the genus and a key for the identification of all species. For each of the 21 species recognized, we present information on the nomenclature, phenology, habitat, distribution, and taxonomic notes. Furthermore, *Spathicalyx kuhlmannii* J.C. Gomes is transferred into *Tanaecium kuhlmannii* (J.C. Gomes) Frazão & L.G. Lohmann. A lectotype is proposed for *Tanaecium crucigerum* Seem.

Keywords: *Tanaecium*, lianas, Lamiales, lectotype, Neotropical flora, nomenclature, taxonomy.

Introduction

Tanaecium Sw. emend L.G.Lohmann is a monophyletic genus, well supported by molecular characters, as well as the presence of subulate or bromeliad-like prophylls of the axillary buds putative morphological synapomorphy (Lohmann & Taylor 2014). Species of the genus are lianas or shrubs distributed from Mexico and the Antilles to Argentina (Lohmann & Taylor 2014; Pace et al. 2016; Frazão & Lohmann 2018; Kaehler et al. 2019). The genus is centered in Amazonia, where 11 species occur (Lohmann & Taylor 2014; Frazão & Lohmann 2018; Kaehler et al. 2019). While some species show disjunct distributions (e.g., *Tanaecium duckei* A.Samp.), others are broadly distributed (e.g., *Tanaecium pyramidatum* (Rich.) L.G.Lohmann), or endemic to small geographic areas (e.g., *Tanaecium affine* (A.H.Gentry) L.G.Lohmann, *T. apiculatum* A.H.Gentry) (Lohmann & Taylor 2014; Frazão & Lohmann in prep.).

The genus was described by Swartz (1788) and originally characterized by the presence of tubular flowers and truncate calyx. The original circumscription of *Tanaecium* included six species (see Gentry 1973; Gentry 1976), five of which remain in *Tanaecium* (i.e. *T. apiculatum*, *T. crucigerum* Seem., *T. cyrtanthum* (Mart. ex DC.) Bureau & K.Schum., *T. exitiosum* Dugand, and *T. jaroba* Sw.), while *T. nocturnum* (Barb. Rodr.) Bureau & K. Schum. was transferred to *Bignonia* L. (Lohmann & Taylor 2014). In addition to the five species originally classified as *Tanaecium*, twelve species from six previously recognized genera (i.e., *Arrabidaea* DC., *Ceratophytum* Pittier, *Pseudocatalpa* A.H.Gentry, *Paragonia* Bureau, *Periarrabidaea* A.Samp, and *Spathicalyx* J.C.Gomes) were transferred to *Tanaecium* in a revised classification system for the whole tribe Bignonieae (Lohmann & Taylor 2014). As a result, 17 species of *Tanaecium* were recognized in the most recent synopsis of the genus (Lohmann & Taylor 2014).

Subsequent molecular phylogenetic studies combined with novel morphological observations indicated that *Sphingiphila tetramera* A.H.Gentry was best placed in *Tanaecium*, leading to the new combination *Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann (Pace et al 2016). A new species of *Tanaecium* was then described (i.e., *T. decorticans* Frazão & L.G.Lohmann) (Frazão & Lohmann 2018), while *Tanaecium mutabile* (Bureau & K. Schum.) L.G. Lohmann was transferred to *Fridericia mutabile* (Bureau & K.Schum.) Frazão & L.G. Lohmann (Frazão et al., in prep.). Kaehler et al. (2019) subsequently transferred three species of *Fridericia* Mart. emend L.G. Lohmann into *Tanaecium*, i.e., *Tanaecium dichotomum* (Jacq.) Kaehler & L.G.Lohmann, *T. paradoxum* (Sandwith) Kaehler & L.G.Lohmann, and *T. parviflorum* (Mart. ex DC) Kaehler & L.G.Lohmann. However, *T. paradoxa* appeared within *Fridericia* in a recent phylogenetic study (Frazão and Lohmann, in prep.) indicating that this taxon is best treated as *Fridericia paradoxa* (Sandwith) L.G.Lohmann, as proposed in Lohmann

& Taylor (2014). After these recent taxonomic changes, the number of species accommodated in the genus changed from 17 to 21.

Given all the recent taxonomic changes in *Tanaecium*, a new evaluation of the overall circumscription of the genus is needed. Here, we present an overview for the genus and its species. For each of the 21 species recognized, we present information on the nomenclature, synonymy, phenology, habitat, distribution, and taxonomic notes. A lectotype is proposed for *Tanaecium crucigerum* Seem., and the new combination *Tanaecium kuhlmannii* (J.C.Gomes) Frazão & L.G.Lohmann is proposed to accommodate novel morphological observations and recent phylogenetic findings (Frazão & Lohmann, in prep.).

Material and Methods

Materials from the following herbaria were studied using standard taxonomic methods (Acronyms following Thiers 2019): INPA, IAN, MG, UFACPZ, EAC, CEN, IBGE, UB, HERBAM, ESA, RBR, RB, R, SPF, SP, UEC, HRCB, CESJ, BHCB, MBM, PY, FCQ, QCNE, QCA, NY, US, MO, A, and F. Furthermore, images of specimens from AAU, B, BR, COL, G, K, L, M, and P were accessed online through Jstor Global Plants (2019) or the online database of individual herbaria. All protologues were consulted in the Peter Raven Library (Missouri Botanical Garden) or using the online database of BHL (2019). Morphological terminology used here follows Hickey (1974) for leaf venation, Radford (1986) for leaf morphology, Weberling (1989) for inflorescence morphology, Gomes-Silva (2009) for leaflet mite-domatia, Nogueira et al. (2013) for trichomes, and Lohmann & Taylor (2014) for prophyll morphology and other morphological traits. Phenology is based on data gathered from herbarium specimens. Distributions are based in herbaria specimens and information provided in Lohmann & Taylor (2014).

Taxonomic Treatment

Tanaecium **Sw., Prodr. Veg. Ind. Occ. 6: 91. 1788, emend L.G. Lohmann, Ann. Missouri Bot. Gard. 2014: 463.**

Type: *Tanaecium jaroba* Sw.

Paragonia Bureau, Bull. Soc. Bot. France 19: 17. 1872. Type: *Bignonia lenta* Mart. ex DC. [= *Tanaecium pyramidatum* (Rich.) L.G.Lohmann].

Sanhilaria Baill., Hist. Pl. 10: 27. 1888. *Hilariophyton* Pichon, Bull. Soc. Bot. France 92: 228. 1946. Type: *Sanhilaria brasiliensis* Baill. [= *Tanaecium brasiliensis* (Baill.) L.G.Lohmann].

Ceratophytum Pittier, J. Wash. Acad. Sci. 18: 62. 1928. Type: *Ceratophytum capricorne* Pittier [= *Tanaecium tetragonolobum* (Jacq.) L.G.Lohmann].

Periarrabidaea A. Samp., Ann. Acad. Brasil. Sci. 6: 175. 1934. Type: *Periarrabidaea truncata* A. Samp. [= *Tanaecium truncatum* (A. Samp) L.G.Lohmann].

Spathicalyx J.C.Gomes, Notul. Syst. (Paris) 15: 220. 1956. Type: *Spathicalyx kuhlmannii* J. C. Gomes [= *Tanaecium duckei* (A.Samp.) L.G.Lohmann].

Pseudocatalpa A.H.Gentry, Brittonia 25(3): 241. 1973. Type: *Pseudocatalpa caudiculata* (Standl.) A. H. Gentry [= *Tanaecium caudiculatum* (Standl.) L.G.Lohmann].

Lianas or shrubs, without dimorphic juvenile growth; stems with four wedges in cross section (without in *T. tetramerum*), solid (hollow in *T. apiculatum*); branchlets terete or tetragonal, without ridges, with or without striation, without peeling epidermis (present in *T. decorticans*), sparse or dense lenticels, with or without simple eglandular trichomes (dendritic eglandular trichomes in *T. xanthophyllum*); interpetiolar region with or without fields of patelliform glandular trichomes, and discontinuous interpetiolar ridges (sometimes continuous); prophylls of the axillary buds bromeliad-like or subulate (minute and triangular or foliaceous), without patelliform glandular trichomes (present in *T. selloi*). *Leaves* 2–3–foliolate (sometimes simple in *T. tetramerum*) with the terminal leaflet modified into a simple or trifid tendril; leaflets without cartilaginous margin (present in *T. apiculatum*), secondary venation brochidodromous (craspedodromous in *T. parviflorum*). *Inflorescence* terminal (sometimes axillary); calyx bilabiate or truncate (sometimes spathaceous); corolla infundibuliform or wide-infundibuliform (campanulate or hypocrateriform), zygomorphic (actinomorphic in *T. tetramerum*), pentamerous (tetramerous in *T. tetramerum*), aestivation imbricate; androecium didynamous, pollen in monads, 3-colpate, psilate and microperforate (inaperturate and coarse-reticulate in *T. apiculatum*); nectar disk well-developed; gynoecium with ovary without stipe at the base, with one two or many series of ovules in each placenta, stigma papilose. *Capsule* linear (elliptic), with or without lenticels, calyx caducous (persistent); seeds winged or wingless, with body smooth and glabrous, winged hyaline or opaque, linear, wingless seeds corky or woody and rounded.

Key to species of *Tanaecium*

1 Branchlets thorn-tipped; terminal leaflets never replaced by a tendril; corollas hipocrateriform, 4-lobed …..... **19. *T. tetramerum***

– Branchlets not thorn-tipped; terminal leaflets generally replaced by a tendril; corollas campanulate, infundibuliform or wide infundibuliform, 5-lobed **2**

2 Leaflets with caudate apices; corollas campanulate; androecium with two fertile stamens ……..…....…….. **4. *T. caudiculatum***

– Leaflets without caudate apices; corollas infundibuliform or wide infundibuliform; androecium with four fertile stamens …..……..…….…….…… **3**

3 Leaflets with dentate margins; calyces aristate (rarely mucronate); fruit apices caudate ……..…….. **14. *T. parviflorum***

– Leaflets without dentate margins; calyces not aristate; fruit apices not caudate ……... **4**

4 Leaflets with apiculate apices, with cartilagenous margins; calyces with stellate simple trichomes; pollen grains inaperturated ……..... **2. *T. apiculatum***

– Leaflets without apiculate apices, without cartilagenous margins; calyces without stellate simple trichomes; pollen grains colpate …..... **5**

5 Leaflets with emarginated membrane-like domatia; inflorescence nodes with patelliform trichome fields; corollas < 2.6 cm long. …….....……. **1. *T. affine***

– Leaflets without emarginated membrane-like domatia; inflorescence nodes without patelliform trichome fields; corollas > 2,6 cm long. ……..……..... **6**

6 Stems with peeling epidermis; petiolules with arrow-shaped apices; fruits with patelliform and peltate trichomes along the margins ……..…….. **7. *T. decorticans***

– Stems without peeling epidermis; petiolules without arrow-shaped apices; fruits without patelliform and peltate trichomes along the margins …….……....**7**

7 Leaflets 8–15 times larger than the petioles; calyces costate; corollas with cuspidate lobes …….…..... **13. *T. neobrasiliense***

– Leaflets < 8 times larger than the petioles; calyces costate; corollas without cuspidate lobes ……..……..……..……..... **8**

8 Leaflets with yellow dendritic simple trichomes; bracteoles ≥ 4:5 the flower pedicels; corollas with peltate trichomes in the ventral portion internally …….……. **21. *T. xanthophyllum***

– Leaflets without yellow dendritic simple trichomes; bracteoles < 4:5 the flower pedicels; corollas without peltate trichomes in the ventral portion internally ……..…… **9**

9 Leaflets with foveolate domatia abaxially; calyces with constriction on basal or medial portions; corollas pale-yellow …….…….…… **20. *T. truncatum***

– Leaflets without foveolate domatia abaxially; calyces without constriction on basal or medial portions; corollas white, pink or magenta …….……..……. **10**

10 White flowers …….……..……..….. **11**

– Pink or magenta flowers …….……..……... **18**

11 Leaflets with membrane-like and tuft domatia; petioles pulvinate (rarely absent); calyces 1:3 to 2:3 the corolla tubes; ovaries with one ovule series on each placenta …….……. **18. *T. bilabiatum***

– Leaflets without domatia; petioles not-pulvinate; calyces ≤ 1:3 the corolla tubes; ovaries with two or many ovule series on each placenta …….…… **12**

12 Stems with conspicuous patelliform trichomes between petioles; inflorescences in corymbiform thyrses; corollas infundibuliform; fruits 4-lobed at base …. **18. *T. tetragonolobum***

– Stems with inconspicuous patelliform trichomes between petioles; inflorescences not in corymbiform thyrses; corollas wide-infundibuliform; fruits not 4-lobed at base …… **13**

13 Leaflets with basal and suprabasal venation actinodromous; tendrils trifid; calyces spathaceous; anthers curved backwards …….…….….. **14**

– Leaflets without basal and suprabasal venation actinodromous; tendrils simple; calyces not spathaceous; anthers not curved backwards ……..... **15**

14 Abaxial side of leaflets with patelliform trichomes ≥ 0,45 mm diam., with protrusion at the patelliform insertion; anthers > 7 mm long. ...…….…….... **12. *T. kuhlmannii***

– Abaxial side of leaflets with patelliform trichomes < 0,45 mm diam., without protrusion at the patelliform insertion; anthers < 7 mm long. ……..……...…….. **9. *T. duckei***

15 Adaxial side of leaflets bullate; calyces campanulate and bilabiate; anthers exserted ……..…….……. **10. *T. exitiosum***

– Adaxial side of leaflets bullate; calyces cupular or campanulate and truncate; anthers sub-exserted ……...…….…… **16**

16 Caducuous when flowering; abaxial surface of leaflets with patelliform trichomes concentrated at base; calyces campanulate or cupular; fruits linear; seeds linear, with seed body lateral …….……..……. **6. *T. cyrtanthum***

– Not caducuous when flowering; abaxial surface of leaflets without patelliform trichomes concentrated at base; calyces cupular; fruits elliptic; seeds circular, without seed body lateral **17**

17 Abaxial side of leaflets whitish-tomentose; inflorescences in racemes with long internodes …….……..……..... **5. *T. crucigerum***

– Abaxial side of leaflets glabrous; inflorescences in racemes with short internodes ……..……...…….....…….. **11. *T. jaroba***

18 Prophylls of the axillary buds foliaceous or minute and triangular; fruits with raised margins, without central ridges ……...……....……..….. **17. *T. selloi***

– Prophylls of the axillary buds subulate or bromeliad-like; fruits with or without raised margins, with central ridges …….....……..…….. **19**

19 Fruits linear-oblong; seeds with vestigial wings; distributed along riparian areas in the Amazon ……..... **16. *T. revillae***

– Fruits linear; seeds with well-developed wings; distributed in all habitat types throughout the Neotropics …….……..... **20**

20 Petioles with patelliform trichomes at apices; tendrils bifid or trifid; fruits inflated and lenticellated ……...…. **15. *T. pyramidatum***

– Petioles without patelliform trichomes at apices; tendrils simple; fruits flattened and not lenticellated .....……...……..…. **8. *T. dichotomum***

1. *Tanaecium affine* (A.H.Gentry) L.G.Lohmann. Ann. Missouri Bot. Gard. 99: 464. 2014.

Arrabidaea affinis A.H.Gentry, Novon 2(2): 159. 1992. Type: Ecuador. Sucumbios: Lake Agrio, banks of lake, 250 m, 0º6'45.28" N, 76º54'42.81" W, 1 Apr. 1980, *J. Brandbyge & E. Asanza 30393* (holotype, MO [MO-083145]!; isotypes, AAU image!, AAU photo at MO!, NY [NY00000106]!).

Habitat and Distribution: *Tanaecium affine* is known from humid forests. It has been collected in primary and secondary forests with lateritic soil (in Peru: Loreto, Mayanas), growing mainly on forest edges. It is native from Bolivia (La Paz), Colombia (Antioquia, Boyaca), Ecuador (Napo, Pastaza, Sucumbíos), and Peru (Amazonas, Junín, Loreto, Pasco, Puno).

Phenology: Flowering: February to April, September and November; fruiting: February to December.

Notes: This species is morphologically similar to *Fridericia florida* but differs by the bilabiate calyces, stems with conspicuous patelliform trichomes in the interpetiolar region, and preference for rich soils (Gentry 1992). In addition, *T. affine* can also be recognized by the numerous peltate trichomes distributed throughout the leaflets, emarginated membrane-like domatia, and fields of patelliform trichomes that cover the inflorescence nodes. *Tanaecium affine* shares vegetative traits with *Tanaecium tetragonolobum*, a sympatric species (Tab. 1). However, *T. tetragonolobum* can be differentiated by the glabrous leaflets (vs. leaflets covered with peltate trichomes in *T. affine*), petioles longer than petiolules (vs. petioles shorter than petiolules in *T. affine*), and subulate prophylls of the axillary buds (vs. bromeliad-like prophylls of the axillary buds in *T. affine*).

2. *Tanaecium apiculatum* A.H.Gentry, Ann. Missouri Bot. Gard. 63(1): 58, fig. 4. 1976.

Type: Venezuela. Monagas: Caicara, 15 May 1952, *F. D. Smith 226* (holotype, US!; isotype, US!, US photo at MO [MO-067514]!, [MO-067514]!)

Habitat and Distribution: *Tanaecium apiculatum* is known only from the type location, Caicara, Venezuela.

Phenology: Flowering: May; fruiting (immature): May.

Notes: This species shares wide-infundibuliform corollas with *T. crucigerum*, *T. cyrtanthum*, *T. duckei*, *T. exitiosum*, *T. kuhlmanii*, and *T. jaroba*, but can be differentiated from these taxa by the

leaflets with apiculate apices and cartilaginous margins, and tubular calyces with stellate simple trichomes (Tab. 1).

3. *Tanaecium bilabiatum* (Sprague) L.G.Lohmann, Nuevo Cat. Fl. Vasc.Venezuela 274. 2008.

Fig. 1A, L

Memora bilabiata Sprague, Bull. Herb. Boissier (ser. 2) 6: 375. 1906. Type: Brazil. Amazonas: Manaus, s.d., *R. Spruce 1783* (holotype, K [K000492969] image!).

Adenocalymma bilabiatum (Sprague) Sandwith, Recueil Trav. Bot. Néerl. 34: 213. 1937.

Habitat and Distribution: *Tanaecium bilabiatum* grows in wet, flooded, riparian vegetation, or Amazonian lowlands. It occurs in Bolivia (Beni, Pando), Brazil (Acre, Amapá, Amazonas, Pará, Roraima), Colombia (Amazonas, Arauca, Guainía), French Guyana, Guyana, Peru (Madre de Dios, Loreto), Suriname (Sipaliwini, Nickerie), and Venezuela (Amazonas, Apure, Bolívar, Delta Amacuro, Guárico, Monagas, Sucre).

Phenology: Flowering: February to November; fruiting: December to October.

Notes: *Tanaecium bilabiatum* is easily differentiated from other *Tanaecium* species by the pulvinated petioles (typical of *Adenocalymma* but usually lacking in and other Bignonieae; Lohmann & Taylor, 2014), large bilabiate calyces, covering 1:3 to 2:3 of the corolla tube, white corollas with yellow mouths, oblong and flattened fruits, and seeds with vestigial wings (rarely well-developed) (Tab. 1).

4. *Tanaecium caudiculatum* (Standl.) L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 464.

Petastoma caudiculatum Standl. Publ. Field Mus., Bot. 11(4): 141. 1932.

Pseudocatalpa caudiculata (Standl.) A.H.Gentry, Brittonia 25(3): 241. 1973. Type: Belize. Nine Mile, Stann Creek Railway, 30 m, 22 Mar. 1932, *W. A. Schipp S–297* (holotype, F!).

Habitat and Distribution: *Tanaecium caudiculatum* is restricted to Central America. It is known from wet forests that grow in the mountains and sea level in Belize (Belize, Cayo, Stann Creek, Toledo), Guatemala (Alta Vera Cruz), and Mexico (Chiapas, Oaxaca).

Phenology: Flowering: March to May, July to September; fruiting: April, June, and August.

Notes: *Tanaecium caudiculatum* differs from other species in the genus by the caudate leaflets, simple tendrils that bear hooks (otherwise only found in the trifid tendrilled *Dolichandra*; Lohmann & Taylor, 2014; Fonseca et al., 2017), foliaceous inflorescence bracts, stipitate glandular trichomes in the internal ventral surface of the corolla tubes, androecium with only two fertile stamens, and fruits with sinuous margins (Tab. 1).

5. *Tanaecium crucigerum* Seem., Bonplandia (Hannover) 4: 127. 1856.

Type: Lesser Antilles. Dominica, sin. loc., s. d., *J. Imray 94* (lectotype, designated here, K [K000449535] image!).

Habitat and Distribution: *Tanaecium crucigerum* occurs in wet forests in Colombia (Atlántico, Bolívar, César, Magdalena), Lesser Antilles (Dominica, Martinique), Trinidad and Tobago, and Venezuela (Anzoátegui, Apure, Cojedes, Delta Amacuro, Guárico, Portuguesa).

Phenology: Flowering: March to July, and October; fruiting: February, April to July, and October to November.

Notes: Like Lohmann & Taylor (2014), we were also unable to locate the lectotype of *T. crucigerum* selected by Howard (1989: 334), the collection *J. Imray 95* supposedly deposited at K. This collection is presumed lost and we select another Imray collection from Dominica studied by Seemmann (1856) and deposited at K as lectotype. We selected the material *J. Imray 94* as lectotype due to high quality of this material, including the diagnostic racemose inflorescence.

This species is morphologically most similar to *T. jaroba*, from which it can be differtiated by the tomentose leaflets on the abaxial surface (vs. glabrous leaflets on the abaxial surface in *T. jaroba*), and inflorescences with long internodes (vs. inflorescences with short internodes in *T. jaroba*) (Tab. 1).

6. *Tanaecium cyrtanthum* (Mart. ex DC.) Bureau & K.Schum, Fl. Bras. 8(2): 186. 1896.

Fig. 1M, Q.

Tecoma cyrtantha Mart. ex DC., in A. DC., Prodr. 9: 218. 1845. Type: Brazil. Bahia: Pão d'Espinho, caatinga, Oct., *C.F.P. von Martius 1860* (holotype, M [M0088980] image!; isotype, G–DC image!).

Habitat and Distribution: *Tanaecium cyrtanthum* is distributed in dry forests, caatinga, cerrado and chaco in Bolívia (Santa Cruz, Tarija), Brazil (Bahia, Ceará, Goiás, Mato Grosso do Sul, Pernambuco, Rio Grande do Norte), and Paraguay (Alto Paraguay, Amambay, Concepción, San Pedro).

Phenology: Flowering: September to January and April; fruiting: April to August and October.

Notes: This species is generally caducous when flowering, and produces new leaves when fruiting. The tendril is simple and the leaflets have patelliform trichomes concentrated at the base abaxiallly. The calyces are campanulate or cupular, while the fruits are linear and inflated, bearing linear seeds, with a lateral seed body (Tab. 1).

7. *Tanaecium decorticans* Frazão & L.G.Lohmann, Pl. Syst. Evol. 304:1248. fig. 2. 2018.

Type: Brazil. Pará: Belterra, Entrada da estrada de Aramanaí para Pindobal, próximo a Fazenda São Sebastião, 41 m a. s. l., 2°38′24.7″S, 54°59′06.6″W, 20 Sep 2015, *A. Frazão* 210 (holotype: SPF!; isotype: RB!, MO!).

Habitat and Distribution: *Tanaecium decorticans* is known from the Brazilian Amazon (Pará, Maranhão).

Phenology: Flowering: February and September; fruiting: September and December.

Notes: This species is morphologically most similar to *T. pyramidatum*, but can differentiated by the stem with peeling epidermis, petiolules with arrow-shaped apices, and fruits flattened with glandular trichomes and patelliform and peltate trichomes along the margins (Frazão & Lohmann 2018) (Tab. 1).

8. *Tanaecium dichotomum* (Jacq.) Kaehler & L.G.Lohmann. TAXON in press. 2019.

Fig. 1B

Bignonia dichotoma Jacq. Enum. Syst. Pl. 25. 1760 [also in Select. stirp. amer. hist. 183, 1763].

Fridericia dichotoma (Jacq.) L.G. Lohmann, Ann. Missouri Bot. Gard. 99: 436. 2014. Type: Colombia. Magdalena: Cartagena, not located.

Habitat and Distribution: *Tanaecium dichotomum* is commonly found in dry to humid forests in Argentina (Chaco, Corrientes, Formosa, Jujuy, Misiones, Salta), Belize (Cayo), Bolivia (Beni, Chuquisaca, La Paz, Pando, Santa Cruz, Tarija), Brazil (Acre, Alagoas, Amapá, Amazonas, Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo, Tocantins), Colombia (Amazonas, Atlántico, Bolívar, César, Chocó, Huila, La Guajira, Magdalena, Meta, Sucre, Tolima), Costa Rica (Guanacaste, Puntarenas), Ecuador (Guayas, Napo), French Guiana, Guyana (Essequibo, Rupununi), Mexico (Chiapas, Colima, Guerrero, Jalisco, Mexico, Oaxaca, Veracruz), Nicaragua (Boaco, Chontales, Granada, Matagalpa, Nueva Segovia, Río San Juan), Panama (Canal Area, Panama, Los Santos), Paraguay (Alto Paraguay, Amambay, Boquerón, Central, Chaco, Concepción, Cordillera, Ñeembucú, Nueva Asuncion, Paraguarí, Presidente Hayes, San Ramon), Peru (Cusco, Loreto, Madre de Dios, Piura, San Martín, Tumbes, Ucayali), and Venezuela (Amazonas, Anzoátegui, Apure, Aragua, Barinas, Bolívar, Carabobo, Cojedes, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Nueva Esparta, Portuguesa, Sucre, Táchira, Trujillo, Yaracuy, Zulia).

Phenology: Flowering: January to December; fruiting: January to December.

Notes: This species is widespread through the Neotropics, where it is found in many vegetation types. The species encompasses an enormous degree of morphological variation, representing a species complex. Detailed morphological and molecular studies are necessary to sort out the patterns of variation and identify putatively cryptic species.

Tanaecium dichotomum shares many morphological traits with *T. selloi* and *T. revillae* (e.g., tuft domatia in the abaxial side of leaflets, bilabiate calyces), and *T. pyramidatum* (e.g., thyrsoid inflorescences, pink corollas with white mouths). However, *T. dichotomum* differs from these species by the bilabiate and cuspidate calyces, stems with patelliform glandular trichomes between the petioles, and flattened fruits without raised margins or a conspicuous central ridge (Tab. 1).

9. *Tanaecium duckei* A.Samp., Ann. Acad. Brasil. Sci. 7: 125. 1935.

Fig. 1C

Spathicalyx duckei (A.Samp.) A.H.Gentry, Phytologia 35(3): 194. 1977. Type: Brazil. Pará: Óbidos, 21 July 1918, *A. Ducke s.n.* (holotype, MG!; isotypes, MO [MO-077163]!, R!, RB [RB00536923]!, US [US00125782]!).

Habitat and Distribution: *Tanaecium duckei* grows in Amazonian forests with sandy soils and canga vegetation. It occurs in Brazil (Acre, Amazonas, Pará, Mato Grosso), Colombia (Amazonas), and Peru (Loreto, Pasco).

Phenology: Flowering: July and September to October; fruiting: September.

Notes: This species differs from other species of *Tanaecium* by the spathaceous calyces, reflexed anthers, and vegetative structures covered by stipitate glandular trichomes. It is morphologically most similar to *T. kuhlmannii* from which it differs by the absence of patelliform glandular trichomes along the tertiary veins (vs. present in *T. kuhlmannii*), green fruits with sparse stipitate glandular trichomes (vs. yellow fruits covered by stipitate glandular trichomes in *T. kuhlmannii*), small anthers with 4.17–4.34 mm (vs. large anthers with 7.0–10.0 mm in *T. kuhlmannii*), and stamens inserted at the same height (vs. stamens inserted at two different heights in *T. kuhlmannii*) (Tab. 1).

10. *Tanaecium exitiosum* Dugand, Caldasia 1(5): 31, fig. 1. 1942.

Type: Colombia. Santander: Barrancabermeja, 50 m, 5 Apr. 1942, *R. Mora s.n.* (holotype, COL [COL000004390] image!; isotype, COL [COL000004389] image!).

Habitat and Distribution: *Tanaecium exitiosum* is endemic to wet forest vegetation from Colombia (Caldas, Santander).

Phenology: Flowering: March to April and December; fruiting: unknown.

Notes: This species shares wide infundibuliform white flowers with *T. apiculatum*, *T. crucigerum*, *T. cyrtanthum*, *T. duckei*, *T. kuhlmanii*, and *T. jaroba*, from which it differs by the leaflets bullate adaxially, calyces campanulate and bilabiate, and anthers exserted (Tab. 1).

11. *Tanaecium jaroba* Sw., Prodr. 92: 1788.

Fig 1D, N, R

Tanaecium albiflorum DC. Prodr. 9: 245. 1845.

Tanaecium praelongum Miers, Ann. Mag. Nat. Hist., ser. 3, 8: 117. 1861. Lectotype (designated by Howard 1989: 335): Jamaica. Sw. Fl. Ind. Occ. 2: *t. 20*, *f. 1*. 1800.

Habitat and Distribution: *Tanaecium jaroba* is associated to flooded and swampy forests (Gentry 1997) in Bolivia (Beni, La Paz), Brazil (Acre, Amazonas, Mato Grosso, Mato Grosso do Sul, Pará, Rondônia, Roraima), Colombia (Amazonas, Antioquia, Atlántico, Bolívar, Caquetá, La Guajira, Magdalena, Sucre), Costa Rica (Limón), Ecuador (Napo, Orellana), French Guiana (Cayenne), Guyana, Lesser Antilles (Jamaica, St. Vincent), Panamá (Panamá), Peru (Loreto, Madre de Dios, Ucayali), Trinidad and Tobago, and Venezuela (Amazonas, Apure, Bolívar, Carabobo, Delta Amacuro, Guárico, Zulia).

Phenology: Flowering: April to August and November to December; fruiting: March to August and December.

Notes: This species has the longest wide infundibuliform white flowers in the whole tribe Bignonieae (Gentry 1997, Howard 1989). This species is also characterized by the large ellipsoid fruits (ca. 30 diam.), which bear wingless woody seeds. It is most morphologically similar to *T. crucigerum*, from which it can be distinguished by the glabrous or glabrescent leaflets abaxially (vs. tomentose leaflets abaxially in *T. crucigerum*), and inflorescences with short internodes (vs. inflorescences with long internodes in *T. crucigerum*) (Tab. 1).

12. *Tanaecium kuhlmannii* (J.C.Gomes) Frazão & L.G.Lohmann, comb. nov. Basionym: *Spathicalyx kuhlmannii* J.C. Gomes, Arq. Srv. Fl., Rio de Janeiro 10: 200. 1956. Type: Brazil. Rio de Janeiro: Sumaré, 5 Dec. 1932, *J.G. Kuhlmann s.n.* (holotype, RB!; isotype, SPF!, K image!, MO!).

Habitat and Distribution: *Tanaecium kuhlmannii* is known from only a few localities within humid formations of the Atlantic Forest of Brazil (Minas Gerais, Rio de Janeiro).

Phenology: Flowering: December; fruiting: January.

Notes: Gomes (1956) originally described this species as *Spathicalyx kuhlmannii* J.C.Gomes, but Gentry (1977) synonymized it with *Spathicalyx duckei* (A.Samp.) A.H.Gentry. More recently, Lohmann & Taylor (2014) synonymized *Spathicalyx* with *Tanaecium* and recognized a single species, *Tanaecium duckei* (A. Samp.) L.G.Lohmann, following Gentry (1977). A detailed study of these taxa showed that apart from the allopatric distribution (*T. duckei* is restricted to the Amazon, while *T. kuhlmannii* is restricted to the Atlantic Forest of Brazil), *T. kuhlmannii* can be distinguished by the patelliform glandular trichomes along the tertiary veins of leaflets (vs. absent in *T. duckei*), and the ferrugineous stipitate glandular trichomes that cover the fruit surface (vs. ferrugineous stipitate glandular trichomes lacking in *T. duckei*). Furthermore, *T. kuhlmanii* has leaflets with patelliform trichomes ≥ 0,45 mm in diameter abaxially (vs. leaflets with patelliform trichomes < 0,45 mm in diameter abaxially in *T. duckei*), that also show a protrusion at the patelliform insertion (vs. without protrusion at the patelliform insertion in *T. duckei*), and anthers > 7 mm long. (vs. anthers < 7 mm long in *T. duckei*). Based on these morphological features and distribution data, we here recognize both taxa as separate and propose the new combination *Tanaecium kuhlmannii* (J.C.Gomes) Frazão & L.G.Lohmann (Tab. 1).

13. *Tanaecium neobrasiliense* L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 465. 2014.

Sanhilaria brasiliensis Baill., Hist. Pl. 10: 27. 1888.

Paragonia brasiliensis (Baill.) A. H. Gentry, Ann. Missouri Bot. Gard. 63(1): 70. 1976. Type: Brazil. Minas Gerais: Itabira, 1816–1821, *A.St. Hilaire 745* (holotype, P [P00458597] image!; isotypes, P [P00468598] image!, F [F0092570] image!).

Habitat and Distribution: *Tanaecium neobrasiliense* is found in caatinga and cerrado in eastern Brazil (Bahia, Ceará, Distrito Federal, Minas Gerais).

Phenology: Flowering: November to January; fruiting: January to April and June.

Notes: This species is generally confused with *T. pyramidatum* due to its pink corollas. However, it can be differentiated from *T. pyramidatum* by the leaflets 8–15 times longer than the petiole, costate calyces, and corollas with cuspidate lobes. The prophylls of the axillary buds are subulate or bromeliad-like, positioned in an acute angle in relation to the stems (vs. straight angle in *T. pyramidatum*) (Tab. 1).

14. *Tanaecium parviflorum* (Mart. ex DC.) Kaehler & L.G.Lohmann, TAXON in press. 2019.

Fig. 1E

Pithecoctenium parviflorum Mart. ex DC. in A.DC. Prodr 9: 197. 1845.

Arrabidaea parviflora (Mart. ex DC.) Bureau & K.Schum. in Fl. Bras. 8(2): 53. 1896. *Fridericia parviflora* (Mart. ex DC.) L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 441. 2014. **Type**: Brazil. Bahia, Vale do Rio das Contas, October 1818, *C.F.P. von Martius s.n.* (lectotype, selected by Lohmann & Taylor 2014, M [M0086353] image!).

Habitat and Distribution: *Tanaecium parviflorum* occurs in Caatinga vegetation from eastern Brazil (Bahia, Ceará, Minas Gerais, Paraíba, Pernambuco), and is also found disjunctly in Mato Grosso do Sul, in an area with drained soil.

Phenology: Flowering: December to February and April; fruiting: February to March and November to December.

Notes: *Tanaecium parviflorum* can be distinguished from all other species of the genus by the dentate leaflet margins, calyces aristate (rarely mucronate), and fruit apices caudate. Like *T. cyrtanthum* and *T. tetramerum*, this species is also caducous when flowering. However, *T. parviflorum* differs from these two species by the strongly compressed corollas (Tab. 1).

15. *Tanaecium pyramidatum* (Rich.) L.G.Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008.

Fig. 1F

Bignonia pyramidata Rich., Actes Soc. Hist. Nat. Paris 1: 110. 1792.

Tabebuia pyramidata (Rich.) DC., in A. DC., Prodr. 9: 214. 1845.

Paragonia pyramidata (Rich.) Bureau, Konigl. Danske Vidansk. Selsk. Skr., Naturivdensk. Math. Afd., ser. 6, 6: 422. 1892. Type: French Guiana. Cayenne, s. d., *J. B. Leblond 292* (holotype, P–LA [P00358235] image!; isotype, P–LA [P00358236] image!).

Habitat and Distribution: *Tanaecium pyramidatum* is widespread throughout the Neotropics, where it is found in dry and wet vegetation in Belize (Cayo, Toledo, Stann Creek, Belize, Orange Walk, Corozal), Bolivia (Beni, Cochabamba, La Paz, Pando, Santa Cruz), Brazil (Acre, Amapá, Amazonas, Bahia, Ceará, Distrito Federal, Goiás, Maranhão, Mato Grosso, Mato Grosso do Sul, Minas Gerais, Pará, Paraíba, Paraná, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Sul, Rondônia, Roraima, Santa Catarina, São Paulo, Tocantins), Colombia (Amazonas, Antioquia, Atlántico, Boyacá, Caquetá, Chocó, Córdoba, Cundinamarca, Guaviare, Magdalena, Meta, Nariño, Putumayo, Santander, Valle del Cauca, Vaupés), Costa Rica (Alajuela, Guanacaste,

Heredia, Limón, Puntarenas, San José), Ecuador (El Oro, Esmeraldas, Guayas, Loja, Los Ríos, Manabí, Napo, Pastaza, Pichincha, Sucumbíos, Zamora-Chinchipe), El Salvador (Ahuachapán, La Libertad, Usulután), Guatemala (Alta Verapaz, Izabal, Petén), French Guiana (Cayenne, Saint-Laurent-du-Maroni), Guyana (East Berbice, Rupununi, West Demerara), Honduras (Colón, El Paraíso, Gracias a Dios, Islas de la Bahía, Olancho, Yoro), Mexico (Campeche, Chiapas, Colima, Oaxaca, Quintana Roo, Tabasco, Veracruz), Nicaragua (Atlántico Norte, Atlántico Sur, Chontales, Jinotega, Matagalpa, Río San Juan, Rivas), Panama (Bocas del Toro, Canal Area, Chiriquí, Coclé, Colón, Darién, Herrera, Los Santos, Panamá, San Blas, Veraguas), Peru (Amazonas, Cusco, Huánuco, Junín, Loreto, Madre de Dios, Pasco, Puno, San Martín, Ucayali), Suriname (Nickerie, Saramacca, Sipaliwini), Trinidad and Tobago, and. Venezuela (Amazonas, Anzoátegui, Apure, Barinas, Bolívar, Delta Amacuro, Distrito Federal, Falcón, Lara, Miranda, Monagas, Portuguesa, Sucre, Yaracuy, Zulia),

Phenology: Flowering: January to December; fruiting: January to December.

Notes: This species can be distinguished from other *Tanaecium* species by the petioles with patelliform trichomes at the apices, subulate prophylls of the axillary buds, fruits lenticellated, linear, and inflated. Despite that, *T. pyramidatum* is extremely variable morphologically. For example, populations from the Brazilian dry forests and cerrados have pubescent leaflets abaxially, a feature not found in any other population of this species. On the other hand, populations from Mexico are strongly covered by lenticels. Both of these features are found exclusively in these populations. Additional studies of *T. pyramidatum*, including phylogeographic studies based on a broad sampling of individuals collected throughout the range of this species are necessary to identify putative cryptic species (Tab. 1).

16. *Tanaecium revillae* (A.H.Gentry) L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 466.

Fig. 1G, S

Arrabidaea revillae A.H.Gentry, Ann. Missouri Bot. Gard. 65(2): 726, fig. 1. 1978 [1979]. Type: Peru. Loreto: Maynas, distr. Pebas, Río Yahuasyacu, afluente del Río Ampiyacu, 18 Jul. 1976, J. Revilla 718 (holotype, MO [MO-086234]!; isotypes, COL [COL000004271] image!, F–1797223!, NY [00313111]!, AMAZ not seen, USM not seen)

Habitat and Distribution: *Tanaecium revillae* occurs in riparian vegetation and permanently flooded forest of the Amazon region. It occurs in Brazil (Amazonas, Pará, Roraima), Colombia (Caquetá), Guyana (Upper Takutu-Upper Essequibo), Peru (Loreto), and Suriname (Sipaliwini).

Phenology: Flowering: January, April, June to September and November; fruiting: July to August.

Notes: This species is well characterized morphologically and can be separated from other species of *Tanaecium* by the elliptic to ovate leaflets with cuspidate apices, tuft domatia in the abaxial surface of leaflets, fruits linear-oblong covered with peltate and patelliform glandular trichomes, and flat seeds with vestigial wings (Tab. 1).

17. *Tanaecium selloi* (Spreng.) L.G.Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008.

Fig. 1O, T

Bignonia selloi Spreng., Syst. Veg. 2: 831. 1825. Type: Brazil. Sin. loc., 1840, *F. Sellow s. n.* (holotype, B destroyed; lectotype, selected by Arbo 2017 in K [K000402778] image!; isolectotypes, BR [BR0000008764805] image!, G [G00133280] image!, K [K000402780] image!, L [L0412987] image!).

Arrabidaea selloi (Spreng.) Sandwith, Kew Bull. 8(4): 461. 1953 [1954].

Bignonia coriacea Sellow ex Steud. Nomencl. Bot., ed. 2, 1: 204. 1840.

Habitat and Distribution: This species is found in semi-deciduous dry or wet vegetation in Argentina (Chaco, Corrientes, Jujuy, Misiones, Salta), Bolivia (Chuquisaca, La Paz, Santa Cruz, Tarija), Brazil (Bahia, Ceará, Distrito Federal, Espírito Santo, Goiás, Mato Grosso do Sul, Minas Gerais, Paraíba, Paraná, Pernambuco, Rio de Janeiro, Rio Grande do Sul, Roraima, Santa Catarina, São Paulo), Colombia (Cesar), Paraguay (Alto Paraná, Caaguazú, Caazapá, Canindeyú, Central, Cordillera, Guairá, Paraguarí), Peru (Cusco, Junín, Tumbes), and Venezuela (Falcón, Zulia).

Phenology: Flowering: September to May and July; fruiting: January to December.

Notes: *Tanaecium selloi* differs from other *Tanaecium* species by the foliaceous or minute and triangular prophylls of the axillary buds, and fruits without a central ridge but with margins raised. Populations from semi-deciduous and dry areas of Argentina, Southern Brazil, Bolivia, and Paraguay show leaflets that are pubescent abaxially; these features are restricted to those populations (Tab. 1).

18. *Tanaecium tetragonolobum* (Jacq.) L.G.Lohmann, Nuevo Cat. Fl. Vasc. Venezuela 274. 2008.

Fig. 1K, P

Bignonia tetragonoloba Jacq., Fragm. Bot. 36. 1809 [1810]. Type: N. J. Jacquin, Fragm. Bot. 36, tab. 40, fig. 2 1809 [1810]–illustration! (lectotype, selected by Lohmann & Taylor 2014).

Ceratophytum tetragonolobum (Jacq.) Sprague & Sandwith, Bull. Misc. Inform. Kew 1934: 222. 1934.

Habitat and Distribution: *Tanaecium tetragonolobum* is found in dry to evergreen lowland forest vegetation (Gentry 1997) in Belize (Cayo, Orange Walk, Toledo), Bolivia (Beni, Chuquisaca, Cochabamba, La Paz, Pando, Santa Cruz), Brazil (Acre, Mato Grosso, Pará, Rondônia), Colombia (Atlántico, Bolívar, Chocó, La Guajira, Magdalena, Meta, Santander, Sucre), Costa Rica (Alajuela, Guanacaste, Guanaste, Puntarenas, San José), Ecuador (Napo, Pastaza), Guatemala (Petén), Guyana, Lesser Antilles (Grenada), Mexico (Campeche, Chiapas, Quintana Roo, Tabasco, Yucatán), Nicaragua (Atlántico Sur, Carazo, Chinandega, Chontales, Granada, León, Managua, Masaya, Río San Juan, Rivas), Panama (Canal Area, Darién, Herrera, Panama, Panamá, San Blas), Peru (Loreto, Madre de Dios, San Martín, Ucayali), Trinidad and Tobago, and Venezuela (Anzoátegui, Aragua, Barinas, Bolívar, Carabobo, Distrito Federal, Falcón, Guárico, Lara, Mérida, Miranda, Monagas, Portuguesa, Táchira, Yaracuy, Zulia).

Phenology: Flowering: February to November; fruiting: January to December.

Notes: *Tanaecium tetragonolobum* can be confused with two sympatric species, *T. jaroba* and *T. dichotomum*. However, *T. tetragonolobum* can be separated by *T. jaroba* by the membrane-like domatias (vs. lacking in *T. jaroba*), and a lack of glandular peltate trichomes abaxially (vs. present in *T. jaroba*). On the other hand, *T. tetragonolobum* can be confused with *T. dichotomum* as both species share stems with interpetiolular patelliform trichomes and a subulate or bromeliad-like prophylls. However, *T. tetragonolobum* always bears trifid tendrils while *T. dichomotum* has simple tendrils (Tab. 1).

19. *Tanaecium tetramerum* (A.H.Gentry) Zuntini & L.G.Lohmann, TAXON 65(5): 1059. 2016.

Fig. 1I

Sphingiphila tetramera A.H.Gentry, Syst. Bot. 15: 277–279, fig. 1. 1990. Type: Paraguay. Alto Paraguay: Chovoreca, moist sandy soil along pond in open Cerrado vegetation, 19°20′ S 59°05′ W, 12 Aug 1983, *W. Hahn 1600* (holotype, MO [MO–077156]!; isotypes, G [G00094221] image!, MBM–117809 not seen, MO [MO–077155]!, NY [00328929]!, PY–3783!, US [00432848]!).

Habitat and Distribution: *Tanaecium tetramerum* is known from Central South America, where it occurs in Bolivia (Cochabamba, Santa Cruz), and Paraguay (Alto Paraguay, Chaco). This species occurs in xerophytic vegetation along the Chaco, in transition areas between the Chaco and Bolivian Chiquitano, Interandian, and Andean valleys. *Tanaecium tetramerum* generally grows on sandy soils or rocky outcrops.

Phenology: Flowering: January to February, August and November; fruiting: January to February, April and July.

Notes: *Tanaecium tetramerum* is characterized by a series of unique morphological features that allows it to be easily separated from other species of *Tanaecium* such the thorn-tipped branchlets, terminal leaflets never replaced by tendrils, corollas actinomorphic, hipocrateriform, and 4-lobed (Gentry 1990; Pace et al. 2016) (Tab. 1).

20. *Tanaecium truncatum* (A.Samp.) L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 467. 2014.

Fig. 1J

Periarrabidaea truncata A.Samp., Bol. Mus. Nac. Rio de Janeiro 12: 86. 1936. Type: Brazil, Amazonas, Manaus, capoeira além da Villa Municipal, lugar alto, 27 July 1931, *A. Ducke s.n.* (holotype, RB–24093!; isotype, R–28731!).

Habitat and Distribution: This species occurs in humid forest vegetation in Bolivia (Pando), Brazil (Amazonas, Mato Grosso, Rondônia), and Peru (Cusco, Loreto, Madre de Dios, Ucayali).

Phenology: Flowering: November to March, and May to October; fruiting: February, July to August, and October to December.

Notes: This species differs from other *Tanaecium* species by the foveolate domatia, calyces basally constructed, and pale-yellow corollas (Tab. 1).

21. *Tanaecium xanthophyllum* (DC.) L.G.Lohmann, Ann. Missouri Bot. Gard. 99: 467. 2014.

Fig. 1K

Tabebuia xanthophylla DC., in A.DC., Prodr. 9: 214. 1845. Type: Brazil, Amazonas, Alto Amazonas, Rio Negro, Maribi, towards River Japurá, Dec. 1819, *C.F.P. von Martius 2967* (holotype, G [G00133960] image!; isotypes, M [M0088929] image!, M [M0088930] image!, M [M0088931] image!, M [M0088932] image!, M [M0088933] image!, M [M0088934] image!, M [M0088935] image!).

Arrabidaea xanthophylla (DC.) Bureau & K.Schum., Fl. Bras. 8(2): 70. 1896.

Xylophragma xanthophylla (DC.) J.F.Macbr., Publ. Field Mus. Nat. Hist., Bot. Ser., 13 (pt. 5c, no. 1): 65. 1961.

Pithecoctenium xanthophyllum (DC.) Miers, Proc. Roy. Hort. Soc. London 3: 199. 1963.

Spathicalyx xanthophylla (DC.) A.H.Gentry, Phytologia 35(3): 195. 1977.

Habitat and Distribution: This species occurs in wet forest vegetation in Bolivia (Beni, Chuquisaca, La Paz, Santa Cruz), Brazil (Acre, Amazonas, Maranhão, Mato Grosso, Pará,

Rondônia), Colombia (Amazonas, Putumayo), Ecuador (Napo, Pastaza), and Peru (Amazonas, Cusco, Junín, Loreto, Madre de Dios, San Martín, Ucayali).

Phenology: Flowering: October to July; fruiting: February to July and December.

Notes: *Tanaecium xanthophyllum* differs from other species of *Tanaecium* by the leaflets with yellow dendritic simple trichomes, bracteoles with a proportion ≥ 4:5 to the flower pedicel, corollas with peltate trichomes in the ventral portion internally. The species epithet refers to the yellow stems, leaves, inflorescences, and fruits (Tab. 1).

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Figure caption

Fig. 1. Morphological diversity of *Tanaecium*. A-K. Flowers. A. *T. bilabiatum.* B. *T. dichotomum.* C. *T. duckei*. D. *T. jaroba*. E. *T. parviflorum*. F. *T. pyramidatum*. G. *T. revillae*. H. *T. tetragonolobum*. I. *T. tetramerum*. J. *T. truncatum*. K. *T. xanthophyllum*. L-P. Fruits. L. *T. bilabiatum*. M. *T. cyrtanthum*. N. *T. jaroba*. O. *T. selloi*. P. *T. tetragonolobum*. Q-T. Seeds. Q. *T. cyrtanthum*. R. *T. jaroba*. S. *T. revillae*. T. *T. selloi*. Photos by A. Frazão, except: A by B. Gomes; B by R. Lopes; E, M by C. Siniscalchi; G by E. Kataoka; H by Stevens; I by Parada-Gutierrez; and J by L.H.M. Fonseca.

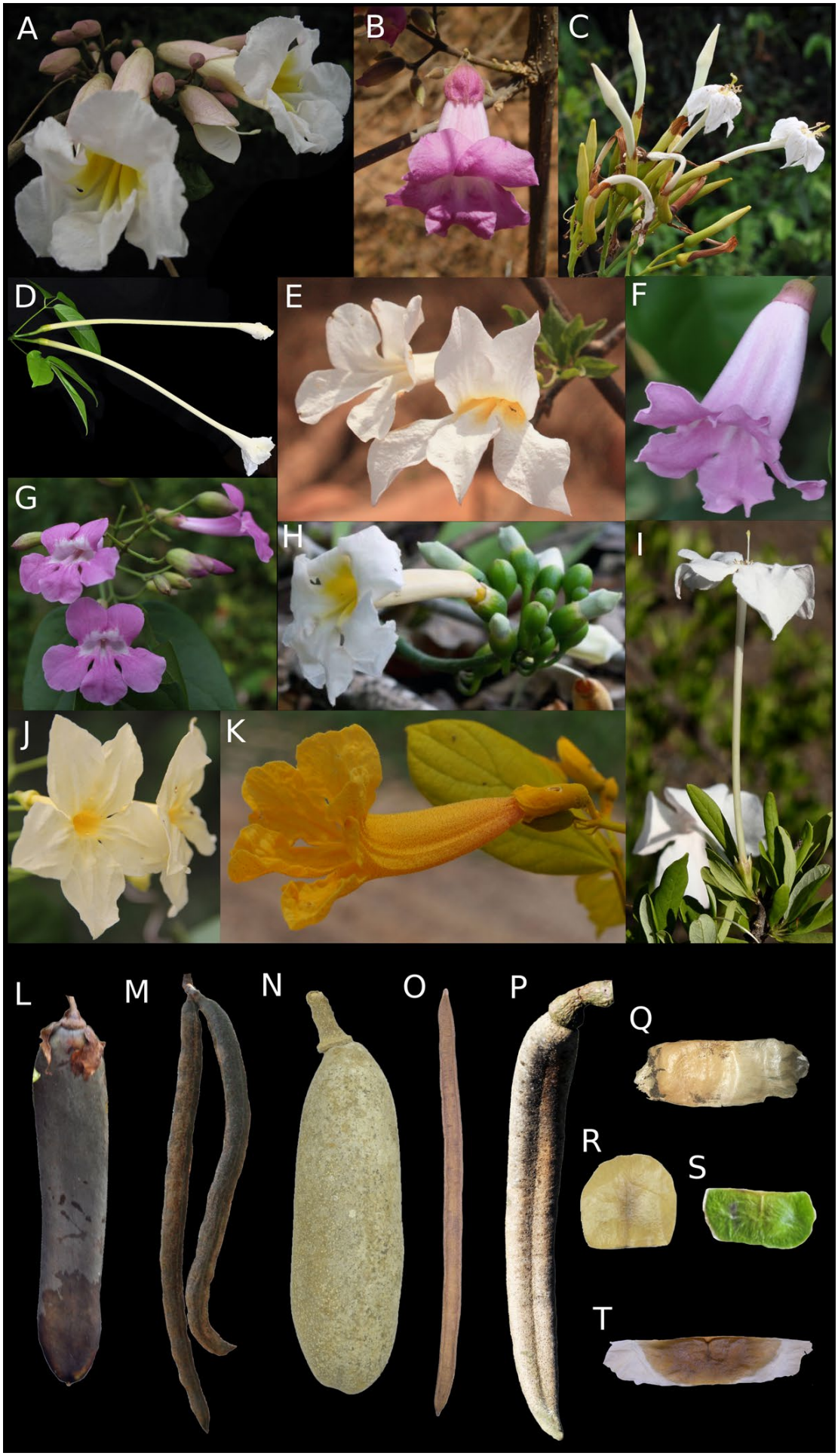
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Table 1. Vegetative and reproductive characters useful in recognizing *Tanaecium* species.

	Tanaecium species	Branchlet section	Interpetiolar glandular field	Prophylls of the axillary buds	Tendril type	Inflorescence type	Calyx shape	Calyx aperture	Corolla color	Corolla mouth color	Corolla shape	Ovules series	Fruit shape	Seeds wings
1.	*Tanaecium affine*	terete or tetragonal	present	subulate or bromeliad-like	simple	compound thyrse	campanulate	bilabiate	white	white	infundibular	one	linear	well-developed
2.	*Tanaecium apiculatum*	terete	absent	-	-	raceme	tubular	truncate	white	white	wide infundibular	many	-	-
3.	*Tanaecium bilabiatum*	terete	absent	subulate or bromeliad-like	simple	thyrse	campanulate or tubular	bilabiate	white	yellow	infundibular	one	linear	vestigial
4.	*Tanaecium caudiculatum*	tetragonal	absent	subulate or bromeliad-like	simple	thyrse	campanulate	truncate	pale yellow	white	campanulate	one	linear	well-developed
5.	*Tanaecium crucigerum*	terete	present	minute and triangular or bromeliad-like	simple	raceme	cupular	truncate	white	white	wide infundibular	many	elliptic	absent
6.	*Tanaecium cyrtanthum*	terete	present	minute and triangular or bromeliad-like	simple	raceme	cupular	truncate	white	white	wide infundibular	many	linear	well-developed
7.	*Tanaecium decorticans*	terete	present	subulate	trifid	thyrse	campanulate or cupular	truncate	pink	white	infundibular	one	linear	well-developed
8.	*Tanaecium dichotomum*	terete	present or absent	subulate or bromeliad-like	simple	thyrse	campanulate	bilabiate	pink	white	campanulate or infundibular	one	linear	well-developed
9.	*Tanaecium duckei*	terete	absent	subulate	trifid	thyrse	tubular	oblique	white	white	wide infundibular	many	linear	well-developed
10.	*Tanaecium exitiosum*	terete	absent	subulate	simple	raceme	campanulate	bilabiate	white	white	wide infundibular	-	-	-
11.	*Tanaecium jaroba*	terete	present	minute and triangular or bromeliad-like	simple	raceme	campanulate	truncate	white	white	wide infundibular	many	elliptic	absent

Table 1. Continued.

12. Tanaecium kuhlmanii	terete	absent	subulate	trifid	thyrse	tubular	oblique	white	white	wide infundibular	many	linear	well-developed
13. Tanaecium neobrasiliense	terete	absent	subulate or bromeliad-like	trifid	compound thyrse	campanulate	truncate	magenta	-	infundibular	two	linear	well-developed
14. Tanaecium parviflorum	terete or tetragonal	absent	subulate or bromeliad-like	simple	raceme	campanulate	truncate	white	yellow	infundibular	two	linear	well-developed
15. Tanaecium pyramidatum	terete	absent	subulate or bromeliad-like	trifid	compound thyrse	campanulate	bilabiate or truncate	pink or magenta	white	infundibular	one	linear	well-developed
16. Tanaecium revillae	terete	absent	subulate or bromeliad-like	simple	thyrse	campanulate	bilabiate	pink	white	infundibular	one	linear-oblong	vestigial
17. Tanaecium selloi	terete	absent	minute and triangular or foliaceous	simple	thyrse	campanulate	bilabiate	pink	white	infundibular	one	linear	well-developed
18. Tanaecium tetragonolobum	terete or tetragonal	present	subulate	simple	fascicle	cupular	truncate	white	yellow	infundibular	many	linear	well-developed
19. Tanaecium tetramerum	terete	absent	subulate or bromeliad-like	absent	fascicule	tubular	truncate	white	white	hipocraterifor m	two	elliptic	well-developed
20. Tanaecium truncatum	terete	present	subulate or bromeliad-like	trifid	thyrse	campanulate	oblique or truncate	pale yellow	yellow	infundibular	two	linear	well-developed
21. Tanaecium xanthophyllum	terete	present	minute and triangular or bromeliad-like	trifid	compound thyrse	campanulate	bilabiate	yellow	yellow	infundibular	two	linear	well-developed

CHAPTER 2 – PHYLOGENY OF *TANAECIUM* AND IMPLICATIONS FOR PLASTOME STRUCTURE IN THE PLANT FAMILY BIGNONIACEAE

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Abstract

The growth of High-Throughput Sequencing (HTS) technologies combined with the high amount of Sanger sequences currently available in public data repositories are allowing comprehensive taxon and character sampling in molecular phylogenetics. Here, we reconstruct the phylogeny of *Tanaecium* (Bignonieae, Bignoniaceae), a genus of Neotropical lianas using a plastome dataset that sampled 2/3 of all species recognized in the genus, plus a comprehensive dataset generated through Sanger sequencing. Our final dataset included 28 plastomes (16 *Tanaecium* and 12 outgroups), and 176 sequences generated with Sanger technology as follows: 61 sequences of the chloroplast gene *ndh*F, 51 sequences of the chloroplast spacer *rpl32-trn*L, and 64 sequenced of the nuclear *pep*C, representing 92 individuals and 17 species of *Tanaecium*, plus 14 outgroups. Topologies reconstructed using the Sanger, plastome, and the plastome and Sanger combined datasets reconstructed the same four clades. The topology reconstructed with the plastome and Sanger combined dataset was the most strongly supported and resolved, representing the best estimate of the phylogeny of the genus. The assembled plastomes showed five different patterns of organization of the Large Single Copy (LSC), Inverted Repeat (IR), and Small Single Copy (SSC) regions. Additionally, four patterns of Inverted Repeat (IR) region boundaries shifts were also found, as follows: (i) IRs with average size of 30,648 bp and a SSC with average size of 12,748 bp (found in most species of *Tanaecium*); (ii) IRs with average size of 24,182 bp and SSC 26,057 bp long (found in *T. bilabiatum*); (iii) IRs with average size of 11,409 bp and SSC 49,868 bp long (found in *T. tetragonolobum*); and (iv) IRs with average size of 28,791 bp and LSC 89,092 bp long (found in *T. tetramerum*). We present the most comprehensive and robust phylogenetic framework of *Tanaecium* to date, along with novelties in Bignoniaceae plastome structure.

Keywords: genome skimming, Lamiales, Neotropical lianas, phylogenomic, plastome.

1. Introduction

The chloroplast is a circular organelle found in plant cells with prokaryotic origin that is responsible for photosynthesis and critical for the biosynthesis of starch, fatty acids, pigments, and amino acids (Qian et al., 2013; Wise, 2006). Chloroplast genomes, also known as plastomes, range from 120 to 180 kb in size, and have a conserved quadripartite structure that consists of a Large Single-Copy (LSC), two Inverted Repeat (IR), and a Small Single-Copy (SCC) region (Green, 2011; Palmer, 1985). Despite that, different patterns, rearrangements, structure organization, size, gene content, and order have been documented in the last few years (e.g., Firetti et al., 2017; Fonseca and Lohmann, 2017; Guisinger et al., 2011; Wicke et al., 2011; Yao et al., 2019). Also, events of IR boundary shifts including IR contraction, expansion, or loss seem to have occurred independently in different lineages, resulting in considerable plastome size variation (e.g., Park et al., 2018; Yao et al., 2019).

In the Bignoniaceae, plastomes range from 153,776 bp in *Callichlamys latifolia* (Rich.) K. Schum. (Nazareno et al., 2015; as *Tanaecium tetragonolobum* (Jacq.) L.G. Lohmann, see Fonseca and Lohmann, 2019) to 168,987 bp in *Anemopaegma acutifolium* DC., the latter figuring among the largest plastomes within Lamiales (Firetti et al., 2017). Bignoniaceae plastomes also show structural rearrangements such as the loss of the *ycf4* gene reported for *Adenocalymma* (Fonseca and Lohmann, 2017; Fonseca and Lohmann, 2019), and variation in gene number, ranging from 132 to 142 genes in different plastomes (Firetti et al., 2017; Fonseca and Lohmann, 2017; Moreira et al., 2016; Nazareno et al., 2015; Thode et al., 2019).

During the past decades, chloroplast data has been extensively used to reconstruct plant phylogenies at different taxonomic levels (e.g., Chase et al., 1993; Lohmann, 2006; Moore et al., 2007; Olmstead et al., 2009; Soltis et al., 2011; Thode et al., 2019; Uribe-Convers et al., 2017). The broad use of chloroplast data in molecular phylogenetics is due to its haploid nature, predominant uniparental inheritance, relatively stable gene structure, and high copy number per cell, which facilitates sequencing. While chloroplast sequencing initially targeted a few genes through Sanger sequencing approaches, the recent development of High-Throughput Sequencing (HTS) technologies allowed for whole plastome sequencing (Straub et al., 2012, 2011).

High-throughput sequencing has already been used in Bignoniaceae phylogenetics (Firetti et al., 2017; Fonseca and Lohmann, 2018, 2017; Thode et al., 2019). Despite that, most Bignoniaceae molecular phylogenies to date were based on selected genes obtained through Sanger sequencing (Callmander et al., 2016; Fonseca & Lohmann, 2015; Kaehler et al., 2012; Lohmann, 2006; Medeiros and Lohmann, 2015; Olmstead et al., 2009; Zjhra et al., 2003), leading to a high amount of published chloroplast DNA sequence data.

Tanaecium Sw. emend. L.G. Lohmann (Bignonieae, Bignoniaceae) is a genus of Neotropical lianas that includes 21 species distributed from Mexico and the Antilles to Argentina, and centered in the Amazon (Frazão and Lohmann, 2018; Frazão and Lohmann, in prep.; Kaehler et al., 2019; Lohmann and Taylor, 2014; Pace et al., 2016). The genus exhibits diverse flower morphologies and pollination systems (Alcantara and Lohmann, 2010), seeds that can be winged or wingless and corky, and bromeliad-like prophylls of the axillary buds, a putative vegetative synapomorphy (Lohmann and Taylor, 2014). The genus was first sampled in a molecular phylogenetic study based on the chloroplast gene *ndh*F and the nuclear *pep*C (Lohmann, 2006). Subsequent molecular phylogenetic studies with this group used the same molecular markers (Frazão and Lohmann, 2018; Frazão and Lohmann, in prep.; Kaehler et al., 2019; Pace et al., 2016). Even though representatives of this genus have been sampled in multiple studies, sampling remains limited. Moreover, *Tanaecium* plastome structure has been little explored.

Here, we reconstruct a comprehensive phylogeny of *Tanaecium* based on a combination of Sanger and plastome data, encompassing the broadest taxon sampling to date. Seventeen of the 21 species recognized are sampled at least once, while broadly distributed or morphologically variable taxa are sampled multiple times. We further characterize the structure of *Tanaecium* plastomes and document novel patterns of plastome variation.

2. Material and Methods

2.1. Taxon sampling

We sampled 17 out of 21 species of *Tanaecium* recognized to date (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann and Taylor, 2014; Pace et al., 2016), only *T. apiculatum* A.H. Gentry, *T. exitiosum* Dugand, and *T. neobrasiliense* L.G. Lohmann were not sampled. We further sampled 14 other Bignoniaceae taxa as outgroups, namely: *Adenocalymma albiflora* (Salzm. ex DC.) L.H. Fonseca & B. Gomes, *Adenocalymma candolleanum* (Mart. ex DC.) L.H. Fonseca & L.G. Lohmann, *Adenocalymma peregrinum* (Miers) L.G. Lohmann, *Anemopaegma arvense* (Vell.) Stellfeld ex J.F. Souza, *Callichlamys latifolia* (Rich.) K. Schum., *Cuspidaria convoluta* (Vell.) A.H. Gentry, *Dolichandra cynanchoides* Cham., *Fridericia ornithophila* (A.H. Gentry) L.G. Lohmann, *Fridericia paradoxa* (Sandwith) L.G. Lohmann, *Fridericia platyphylla* (Cham.) L.G. Lohmann, *Fridericia trichoclada* (DC.) Kaehler & L.G. Lohmann, *Podranea ricasoliana* (Tanfani) Sprague, *Pyrostegia venusta* (Ker Gawl.) Miers, and *Tecomaria capensis* (Thunb.) Spach. All sequences, plastomes, vouchers, and respective GenBank accession numbers are summarized in Table A.1.

Our final plastome dataset included 28 plastomes, 13 of which are outgroups and 16 are *Tanaecium*, representing 15 species given that the morphologically variable *Tanaecium dichotomum* was sampled twice. Outgroups are the same as those from the Sanger dataset, except from *F. paradoxa* for which we were unable to obtain plastome sequences. While all *Tanaecium* plastomes were newly sequenced in this study using genome-skimming, sequences of most of the outgroup taxa were obtained from GenBank, except from *F. ornithophila*, whose plastome was sequenced in this study for the first time.

Our final Sanger dataset included 176 sequences, of which 50 were obtained from GenBank, and 126 were newly obtained in this study. The final dataset included 61 sequences of the chloroplast gene *ndh*F, 51 sequences of the chloroplast spacer *rpl*32-*trn*L, and 64 sequences of the nuclear *pep*C. For broadly distributed and morphologically variable species, samples were selected to represent the breath of the variation. For *T. dichotomum*, the most variable species, we sampled 12 samples covering four morphotypes, i.e., α, β, γ, and δ.

2.2. Sanger sequencing and data treatment

The total DNA was extracted from silica-dried leaf tissue or herbaria samples using a Spin Plant Mini Kit (Invisorb)® following the manufacturer's protocol. PCR conditions for the amplification of *ndh*F and the spacer *rpl32-trn*L followed Zuntini et al. (2013), and *pep*C followed Frazão and Lohmann (2018). Samples were purified and sequenced by Macrogen Inc. (Korea). Sequences were assembled and edited in Geneious 9.0.5 (Kearse et al., 2012). Voucher specimens and GenBank accession numbers are listed in Table A.1.

2.3. NGS sequencing and data treatment

2.3.1. DNA extraction and genomic sequencing

Given the high concentration of DNA necessary for Bignonieae plastome sequencing (Fonseca and Lohmann, 2017; Nazareno et al., 2015; Thode et al., 2019), leaf tissue was initially pulverized with Tissuelyzer® (Qiagen, Duesseldorf, Germany) for 5 min at 50 hz and subsequently extracted following the mini-scale CTAB protocol (Doyle and Doyle, 1987). The protocol was adapted with the inclusion of 2-Mercaptoethanol and polyvinylpyrrolidone (PVP).

DNA was quantified using the Qubit® Fluorometer (Thermo Fisher Scientific, Waltham, MA, USA), and 5 μg of total DNA was fragmented using a Covaris S-series sonicator, generating DNA fragments of approximately 300 bp. Libraries for Illumina platform sequencing were prepared following Nazareno et al. (2015). Sequencing was conducted in an Illumina's HiSeq 2500 Genome Analyzer (Illumina, San Diego, California, USA) as paired-read, with 22 samples per lane, at USP-Esalq (Piracicaba, Brazil). The sequencing of 17 plastomes (i.e., 16

Tanaecium and *Fridericia ornithophila*) was conduced together with other Bignonieae used in other studies (Fonseca and Lohmann, 2018, 2017; Francisco and Lohmann, in prep.; Kataoka and Lohmann, in prep.). Voucher specimens and GenBank accession numbers are listed in Table A.1.

2.3.2. Plastome assembly and annotation

Plastomes were assembled using the Fast-Plast pipeline (McKain and Wilson, unpubl.; https://github.com/mrmckain/Fast-Plast). This pipeline initially uses Trimmomatic 0.35 (Bolger et al., 2014) to remove the adaptors and low quality sequences. The trimmed reads were then mapped against a database that included the published plastomes of *Adenocalymma peregrinum* (MG008314.1; Fonseca and Lohmann, 2017), *Olea europaea* L. (NC_013707.2; Messina, unpublished), *Sesamum indicum* L. (NC_016433.2; Yi and Kim, 2012), *Salvia miltiorhiza* Bunge (NC_020431.1; Qian et al., 2013), and *Callichlamys latifolia* (Rich.) K. Schum. (KR534325; Nazareno et al., 2015) using Bowtie 2.1.0 (Langmead and Salzberg, 2012). Mapped reads were assembled into contigs using SPAdes 3.1.0 (Bankevich et al., 2012). Resulting contigs were assembled with afin (https:// bitbucket.org/afi nit/afin), using the parameters -l 50, -f 0.1, -d 100, -x 100, and -i 2. For species for which it was harder to obtain comprehensive contigs, we tested values between 10 and 20 for minimum overlap of contig (-p) parameters. The final assembly from Fast-Plast or afin was checked, and edited in Geneious 9.0.2 (Kearse et al., 2012). The plastome assembly was verified through a coverage analysis conducted in Jellyfish 2.1.3 (Marçais and Kingsford, 2011) using a 25-bp sliding window of coverage across the plastome of each species. Only sites with depth higher than two were kept.

Plastome annotation was initially conducted in Geneious 9.0.2 (Kearse et al., 2012) using the annotated *Adenocalymma peregrinum* plastome (Fonseca and Lohmann, 2017). The annotated loci were verified in DOGMA (Wyman et al., 2004) and BLAST (Altschul et al., 1997, 1990). For each species, the annotations were checked manually to determine the correct start and stop codons of the Open Reading Frames (ORFs) in Geneious 9.0.2 (Kearse et al., 2012). Spacers between genes were annotated to facilitate subsequent extraction of specific regions.

Because chloroplast DNA can have differences in the SSC orientation due to heteroplasmy (Palmer, 1983; Walker et al., 2015), all plastomes were manually standardized to the same orientation in Geneious 9.0.2 (Kearse et al., 2012). The boundaries between the Large Single Copy (LSC), Inverted Repeat (IR), and Small Single Copy (SSC) regions were verified using the online IRscope (Amiryousefi et al., 2018). The boundary annotations identified by the algorithm were confirmed using the find tool in Geneious 9.0.2 (Kearse et al., 2012). The graphical

representation of *Tanaecium* annotated plastomes was created using OGDRAW (Lohse et al., 2013).

To determine synteny and identify possible rearrangements, we compared the *Tanaecium* plastomes with other Bignonieae plastomes including *Adenocalymma* (MG008314.1; Fonseca and Lohmann, 2017), *Anemopaegma* (MG831872; Firetti et al., 2017), and *Callichlamys* (KR534325.1; Nazareno et al., 2015). These analyses were made using Mauve 2.4.0 (Darling et al., 2004), assuming the settings mauveAligner as alignment algorithm, MUSCLE 3.6 (Edgar, 2004) as the internal aligner, with full alignment, and minimum locally collinear block (LCB) score automatically calculated. Genomes were not assumed to be collinear.

*2.3.3. Assembly of pep*C *from genome-skimming data*

For the samples that we could not access the *pep*C locus using Sanger sequencing and had the genomic sequences in hand, we assembled the *pep*C marker from the genome-skimming data. For that, we selected the published *pep*C sequence of *Tanaecium tetramerum* (A.H. Gentry) Zuntini & L.G. Lohmann (KU757042.1; Pace et al., 2016) as reference. We then used Bowtie 2.1.0 (Langmead and Salzberg, 2012) to map all sequenced reads trimmed using Trimmomatic 0.35 (Bolger et al., 2014). We then used Geneious 9.0.2 (Kearse et al., 2012) to perform the final manual edition and annotation of the assembled sequences. The ambiguities were coded with "N." All *pep*C sequences accessed with this approach are presented in Table A.1.

2.4. Phylogeny reconstruction

Plastome and Sanger sequences were aligned with MAFFT (Katoh and Toh, 2008) assuming the automatic option for the alignment strategy or Q-INS-I for the RNA sequences. The poorly aligned regions were removed using Gblocks (Castresana, 2000; Talavera and Castresana, 2007) assuming the least stringent settings. Alignments were concatenated using SequenceMatrix (Vaidya et al., 2011). Three datasets were assembled: (i) plastome loci; (ii) Sanger sequencing loci; and, (iii) plastome and Sanger loci combined. For dataset (iii), we first extracted the *ndh*F and *rpl*32-*trn*L sequences from the plastomes and aligned those with the Sanger sequences. We estimated the numbers of parsimony informative and variable sites at each locus for all datasets using MEGA 7 (Kumar et al., 2016).

Phylogenies were reconstructed using Maximum Likelihood (ML) in RAxML 8.2.10 (Stamatakis, 2014) using the CIPRES gateway (Miller et al., 2010). The GTRCAT model was implemented for all partitions. The best ML tree was inferred by rapid bootstrap (-f a) using 1,000 non-parametric bootstrap pseudo-replicates. Topologies generated using each of the three datasets were visualized and edited in FigTree 1.4.2 (Rambaut, 2014).

3. Results

3.1. Plastome assembly

We sequenced 16 *Tanaecium* plastomes, of which half were complete and half were partial. The complete plastomes are summarized in Table 2, and correspond to the following taxa: *T. cyrtanthum* (Mart. ex DC.) Bureau & K. Schum., *T. decorticans* Frazão & L.G. Lohmann, two individuals of *T. dichotomum* (Jacq.) Kaehler & L.G. Lohmann, *T. duckei* A. Samp., *T. pyramidatum* (Rich.) L.G. Lohmann, *T. tetragonolobum* (Jacq.) L.G. Lohmann, and *T. xanthophyllum* (DC.) L.G. Lohmann. The partial plastomes correspond to the following taxa: *T. bilabiatum* (Sprague) L.G. Lohmann, *T. crucigerum* Seem., *T. jaroba* Sw., *T. parviflorum* (Mart. ex DC.) Kaehler & L.G. Lohmann, *T. revillae* (A.H. Gentry) L.G. Lohmann, *T. selloi* (Spreng.) L.G. Lohmann, *T. tetramerum* (A.H. Gentry) Zuntini & L.G. Lohmann, and *T. truncatum* (A. Samp.) L.G. Lohmann.

The paired end raw reads sequenced varied between 3,858,109 and 14,350,498 bp, for *T. parviflorum* and *T. tetragonolobum*, respectively (Table 2). After mapping the reads against the references, the mapped reads varied from 101,125 to 660,086 bp for *T. duckei* and *T. revillae*, respectively (Table 2). Average read depth (x) varied between 85 x for *T. tetragonolobum* and 679 x for *T. dichotomum 2β* (Table 2).

3.2. Plastome characteristics

All plastomes have the typical quadripartite structure of Angiosperms, with a pair of IR regions that range from 11,409 bp (*T. tetragonolobum*) to 30,976 bp (*T. pyramidatum*), intercalated by one LSC region that ranges from 83,490 bp (*T. crucigerum*) to 86,213 bp (*T. xanthophyllum*), and one SSC region that ranges from 12,498 bp (*T. parviflorum*) to 49,868 bp (*T. tetragonolobum*) (Table 2, Fig. 1-2). The *Tanaecium* plastomes have an average length of 159,048 bp, with *Tanaecium xanthophyllum* representing the largest plastome, with a total length of 160,935 bp (Table 2). For the newly assembled plastome of *F. ornithophila*, used as outgroup, we obtained a nearly complete plastome that is 158,940 bp long, with IRs 30,311 bp, SSC with 12,748 bp, and LSC 85,570 bp.

The large size of the *T. xanthophyllum* plastome is due to an expansion in the LSC (Table 2). On the other hand, reductions of the IRs were observed for *T. bilabiatum*, *T. tetramerum*, and *T. tetragonolobum* (Table 2, Fig. 1-2). The large plastome of *T. xanthophyllum* is due an expansion of the LSC (Table 2). While IR expansions were reported for other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann, 2017; Nazareno et al., 2015), the exact opposite was observed in *T. bilabiatum*, *T. tetramerum*, and *T. tetragonolobum* (Table 2, Fig. 1-2). *Tanaecium tetragonolobum* showed the shortest IR regions, which are 11,409 bp in length, ranging between

the *ndh*B locus until *rpl*2 (Fig. 1-2). Graphical representations of the *Tanaecium* plastomes showing the IR size variation are presented in Figure 1. The average GC content is 38% for all *Tanaecium* species studied here (Table 2), similar to other Bignoniaceae plastomes sequenced (Firetti et al., 2017; Fonseca and Lohmann, 2018, 2017; Moreira et al., 2016; Nazareno et al., 2015). While Mauve retrieved four synteny blocks, no rearrangements were found in *Tanaecium* plastomes (Fig. S1).

The 16 *Tanaecium* plastomes studied here encode 134 to 135 genes, including 80 to 81 unique coding (CDS) (9 duplicated), 37 tRNA, and four rRNA loci (Table 2). The genes *ycf15* and *ycf68* are found in all *Tanaecium* species, but absent in other Bignoniaceae genera (Firetti et al., 2017; Fonseca and Lohmann, 2017; Thode and Lohmann, 2019). The gene *ycf15* is also found in the plastomes of *C. latifolia* and *Crescentia cujete* L. The number of CDS varies between 86 and 90 due the pseudogenization of the loci *ψndhB, ψrpl2, ψrps15*, *ψycf1*, and *ψycf68* (Table 3). The amount of CDS duplicated in the IRs varies accordingly to the degree of IR retraction and SSC expansion. For most *Tanaecium*, the IRs are composed by ten CDS (i.e., *ndhB*, *rpl2*, *rpl23*, *rps12*, *rps15*, *rps7*, *ycf1*, *ycf2, ycf15*, and *ycf68*), seven tRNA, and four rRNA (Table 3). However, this composition varies for *T. bilabiatum*, which has eight CDS (i.e., *ndhB*, *rpl2*, *rpl23*, *rps12*, *rps7*, *ycf1*, *ycf2*, and *ycf15*), *T. tetramerum,* which has seven CDS (i.e., *ndhB*, *rps12*, *rps15*, *rps7*, *ycf1*, *ycf2*, and *ycf15*), and *T. tetragonolobum,* which has five CDS (i.e., *ndhB*, *rpl2*, *rpl23*, *ycf2*, and *ycf15*) (Table 3, Fig 1-2). All species studied here have 37 tRNA and four rRNA in the IRs (Table 3). The plastomes contain 18 loci with introns, among which 15 loci have one intron, and three loci have two introns (Table 3). The locus *rps12* is trans-spliced with the 5-end located in the LSC region, while the duplicated 3-end located in the IRs (Fig. 1). The same pattern has been observed in other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann, 2018, 2017; Moreira et al., 2016; Nazareno et al., 2015).

Five different LSC/IRb/SSC/IRa boundary patterns and respective loci were detected in *Tanaecium* as follows: (i) In six plastomes (i.e., *T. crucigerum*, *T. cyratanthum*, *T. decorticans*, *T. jaroba*, *T. pyramidatum*, and *T. truncatum*) the LSC/IRb boundary is composed by the *rps19* locus with a spacer of 4-24 bp from the LSC/IRb boundary, a SSC between the *rps15* loci, and an IRa/LSC with the *trnH-GUG* region spaced by 14-18 bp from the boundary (Fig. 2); (ii) In six plastomes (i.e., *T. dichotomum 1α*, *T. dichotomum 2β*, *T. duckei*, *T. revillae*, *T. selloi*, and *T. xanthophyllum*) the LSC/IRb boundary includes 274-275 bp of the *rps19* locus inserted within the LSC, and the remaining 4-5 bp of the *rps19* locus inserted within the IRb. In this arrangement the SSC falls between the *rps15* duplicated loci, while the IRb/LSC includes the *trnH-GUG* locus spaced by 5-6 bp from the boundary (Fig. 2); (iii) In *T. bilabiatum*, the *rps19* includes a spacer with 4 bp located within the IRb, while the SSC is located between the two

copies of the *ycf1*, with the functional copy completely located within the SSC, within the IRb/SSC boundary, and spaced from this boundary by 497 bp. Furthermore, the boundary SSC/IRa falls within the *ψycf1* making it a pseudogene, while the IRb/LSC includes the *trnH-GUG* locus spaced by 14 bp from the boundary (Fig. 2); (iv) In *T. tetragonolobum*, the LSC/IRs boundaries fall within the locus *rpl2*, which is partially located within the LSC and partially within the Ira. The SSC is located between the duplicated *ndhB*. Additionally, the loci *rpl*2 and *ndh*B are pseudogenes, with *ψrpl2* located within the IRa/LSC boundary, with 1187 bp within the IRa and 302 bp within the LSC, while the functional *rpl2* is located within the boundary LSC/IRb, with 1187 bp within the IRb and 303 bp within the LSC. Finally, the *ψndhB* locus is within the IRa/SSC boundary, with 1873 bp within the IRa and 311 bp within the SSC. The functional *ndhB* includes 311 bp within the SSC and 1873 within the IRa (Fig. 2); and, (v) In *T. tetramerum*, the LSC/IRs boundary includes the *rpl23* within the LSC with 76 bp spaced from the LSC/IRb boundary and 44 bp from the LSC/IRa, and the SSC between the two copies of the duplicated *rps15* (Fig. 2).

In all arrangements that showed a SSC located between the duplicated *rps15*, this gene is a pseudogene (*ψrps15*), with the boundary LSC/IRa ranging between 1-58 bp in the SSC and 222-231 bp in the IRa. Furthermore, the functional *rps15* is located within the LSC/IRb, ranging from no SSC expansion and 279 bp long in the IRb (as seen in *T. dichotomum 1α* and *T. revillae*), to having a SSC expansion with 8-56 bp and 222-279 bp long in the IRb for other *Tanaecium* (Fig. 2). The opposite pattern is observed in *T. xanthophyllum*, where the *ψrps15* is located in the IRb/SSC boundary (Fig. 2). The IRb/SSC/IRa boundaries of most *Tanaecium* species studied here are similar to those found in the plastomes of *Anemopaegma* (Firetti et al., 2017), and *Adenocalymma* (Fonseca and Lohmann, 2017). Despite those similarities, the plastomes of *T. bilabiatum, T. tetramerum,* and *T. tetragonolobum* show a unique plastome boundary arrangement (Fig. 2). Nevertheless, the boundary SSC/IRa of *T. bilabiatum* is similar to that found in other Lamiales, where the boundary is within the *ψycf1* making it a pseudogene (Fonseca and Lohmann, 2017; Moreira et al., 2016; Nazareno et al., 2015) (Fig. 2). The gene *ycf68* found in all *Tanaecium* species was not found in any other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann, 2017; Moreira et al., 2016; Nazareno et al., 2015; Thode et al., 2019). In *Tanaecium*, this gene is located within the intron region of the *trnI-GAU*, generally in the IRs, except from *T. tetragonolobum*, where this gene is located within the SSC. For some species, the *ψycf68* is a pseudogene (*T. bilabiatum*, *T. decorticans*, *T. dichotomum 1α* and *2β*, *T. pyramidatum*, *T. revillae*, *T. tetragonolobum*, and *T. tetramerum*).

We found four main IR boundary shifts that led to different length sizes in the LSC, IRs, and SSC. The average length of the IRs for the assembled *Tanaecium* plastomes is 30,648 bp,

while the average length of the SSC is 12,748 bp (Fig. 2). However, a contraction in the IRs resulted in a larger SSC in *T. bilabiatum* and *T. tetragonolobum*. In *T. bilabiatum*, the IRs are 24,182 bp and the SSC is 26,057 bp, which is more than twice the average length size found in other *Tanaecium* plastomes (Tab. 2, Fig. 2). On the other hand, *T. tetragonolobum* shows a more extreme variation, with the IRs being 11,409 bp in length and the SSC 49,868 bp in length (Tab. 2, Fig. 2). In *T. tetramerum*, the contraction of the IRs (28,792 bp) resulted in an expansion of the LSC, which gained the genes *rpl2* and *rpl23* (Fig. 1-2). IR boundary shifts and expansions were also documented in *Anemopaegma* (Firetti et al., 2017), and *Amphilophium* (Thode and Lohmann, 2019).

3.3. Plastome dataset

The final plastome dataset including 28 plastomes (16 *Tanaecium* and 12 outgroups) is 101,649 bp long, representing 12.95% of the proportion of the variable sites of the final alignment (Table 1). The 15 plastome loci with more variable sites in *Tanaecium* are *ycf1*, *ycf2*, *accD*, *rpoA*, *rpoC2*, *ndhF*, *clpP*, *rpoB*, *rpoC1*, *rps18*, *ycf4*, *matK*, *ndhD*, *atpA*, and *ndhH* (Table 1). Between these loci, three showed structural variation when compared to outgroups. The *accD* was proportionally the most variable site (Table 1), showing many poorly aligned regions before the Gblocks analysis (Fig. 3A). The *rpoA* was proportionally the second most variable site (Table 1), showing an expansion between positions 786 and 1,218 before the Gblocks analysis (Fig. 3B). This expansion was also found in *T. duckei* (415 bp), *T. tetragonolobum* (345 bp), *T. truncatum* (264 bp), *T. pyramidatum* (109 bp), and *T. selloi* (127 bp) (Fig. 3B). Finally, the *rps18* was proportionally the fourth most variable site (Table 1). Differently from the *rpoA*, the *rps18* shows an expansion in all *Tanaecium* plastomes assembled here (Fig. 3C). This expansion was also found in *Cuspidaria*, *Fridericia*, *Podranea*, and *Tecomaria* (Fig. 3C), indicating that this represents a frequent expansion event in Bignoniaceae plastomes. The *rps18* gene ranged in size from 429 to 1,440 bp (Fig. 3C), with the longest genes found in *T. duckei* (1,440 bp) and *T. truncatum* (1,344 bp) (Fig. 3C).

3.4. Phylogenetic analyses of the plastome dataset

In the phylogeny that resulted from the analysis of the plastome dataset, *Tanaecium* appears as monophyletic with maximum bootstrap support (BS 100) (Fig. 4A). Most nodes within this topology also show maximum bootstrap support (BS 100). Overall, *Tanaecium xanthophyllum* is sister to a large clade containing the remaining species of *Tanaecium* (Fig. 4A). Four main lineages are recovered within this large *Tanaecium* clade. Clade I includes *T. tetramerum* sister to *T. parviflorum* (Fig. 4A). Clade II includes two subclades, the first (i.e., IIa)

composed of *T. decorticans* and *T. pyramidatum* sister to a second subclade (i.e., IIb) composed of *T. duckei*, *T. truncatum*, and *T. tetragonolobum*; all relationships within this clade are supported by maximum bootstrap values (BS 100), except from the sister relationship between *T. duckei* and *T. truncatum* (BS 98). Clade III includes *T. bilabiatum* which is sister to subclade IIIa composed of *T. jaroba* sister to *T. crucigerum*, which is in turn sister to *T. cyrtanthum*; all relationships within this clade are supported by maximum bootstrap values (BS 100). Clade IV includes *T. selloi* which is sister to subclade IVa composed of *T. dichotomum 2β* sister to *T. revillae*, which is in turn sister to *T. dichotomum 1α*; all relationships in this clade are also supported by maximum bootstrap support (BS 100). Clade I is poorly supported (BS 43) as sister to a clade composed of clade II, and clade III + IV (BS 100) (Fig. 4A).

3.3. Sanger dataset

The *ndh*F dataset includes 61 individuals and 2065 bp, while the spacer *rpl*32-*trn*L includes 54 individuals and 975 bp. The *pep*C includes 64 individuals and 618 bp. The final Sanger dataset includes 65 individuals of *Tanaecium* plus five outgroups and a total size of 3,658 bp. A summary of the final dataset is shown in Table A.1.

The locus with the most variable sites is *ndh*F with 399 variable sites, followed by *pep*C and *rpl*32-*trn*L with 319 and 284 variable sites, respectively. The combined Sanger dataset includes 23% of the total alignment with variable sites. Details about the size, number of parsimony informative sites, variable sites, and the proportion of variable sites in the individual datasets are summarized in Table 1.

3.4. Phylogenetic analyses of the Sanger dataset

The topology that resulted from the ML analysis of the Sanger dataset recovered a paraphyletic *Tanaecium*, with *F. paradoxa* nested within the genus (Fig. 4). More specifically, *F. paradoxa* was recovered as sister to a clade composed of *T. dichotomum 2β* and *T. revillae* (BS 100) (Fig. 4A). The topology recovered using the Sanger dataset is similar to that inferred using the plastome dataset (Fig. 4A-B), with *T. xanthophyllum* also appearing as sister to all remaining *Tanaecium.* Clades IIa, IIb, IIIa, and IVa also emerged in this topology (Fig. 4A-B). Despite the similarities between both topologies, clade IIa formed by *T. pyamidatum* (BS 99) sister of *T. decorticans* plus *T. affine* (BS 80) is the second lineage to diverge in the topology that resulted from the analysis of the Sanger dataset (Fig. 4B). Subsequently, a large clade with short branches and low resolution emerges (Fig. 4B). Seven main lineages are identified within this clade, as follows (i) a monophyletic *T. caudiculatum* (BS 100); (ii) clade I (BS 88), composed of *T. parviflorum* and *T. tetramerum*; (iii) clade IIb (BS 93), composed of *T. tetragonolobum* sister to

T. duckei plus *T. truncatum* (BS 98); (iv) a monophyletic *T. bilabiatum* (BS 100) sister to (v) clade IIIa (BS 100), composed of a monophyletic *T. cyrtanthum* (BS 100), sister of *T. crucigerum* and a monoohyletic *T. jaroba* (BS 100) plus (vi) a monophyletic *T. selloi* (BS 100) sister to (vii) *F. paradoxa* plus clade Iva (BS 98) containing multiple individuals of *T. dichotomum* (BS 98), sister of *T. revillae* plus *T. dichotomum 5β* (BS 90) (Fig. 4B). *Tanaecium dichotomum* emerged as polyphyletic in all topologies, with the *T. dichotomum* morphotype *β* emerging as sister to *T. revillae* in both topologies (Fig. 4A-B).

3.5. Phylogenetic analyses of the plastome and Sanger combined dataset

The Sanger combined dataset including 92 terminals (representing 78 *Tanaecium* individuals and 17 species, plus 14 outgroups) is 103,058 bp long, representing 13.4% of the proportion of the variable sites of the final alignment (Table 1).

The topology obtained from the ML analysis of the plastome and Sanger combined datasets also recovered a monophyletic *Tanaecium* (Fig. 5). Relationships recovered in this topology are identical to those recovered from the analysis of the plastome dataset, although this topology is more resolved and well supported (Fig. 5). This topology shows some discrepancies with the topology that resulted from the analysis of the Sanger dataset (Fig 4A). Most notably, *F. paradoxa* appears as sister to *F. ornithophila* although this relationship is poorly supported (BS < 70) (Fig. 5).

Concordant with all other topologies recovered in this study (Fig. 4), *T. xanthophyllum* is sister to a large clade that contains all remaining *Tanaecium* (Fig. 5); this relationship is weakly supported though (BS < 70). Like the topology that resulted from the analysis of the plastome dataset (Fig. 4B), clades I, IIb, III, IIIa, and IVa emerge with identical composition and relationships among taxa. Clade I is sister to clade A plus clade B (Fig. 5). The composition and relationships within each clade is as follows: clade I, includes *T. parviflorum* sister to *T. tetramerum* (BS 100), representing the second lineage to diverge after *T. xantophyllum*; clade A (BS < 70), includes *T caudiculatum* sister to a monophyletic *T. pyramidatum* (BS 99), sister to *T. decorticans* plus *T. affine* (BS 85), sister to subclade IIb, which includes a monophyletic *T. tetragonolobum* (BS 99) sister to *T. duckei* plus *T. truncatum* (BS 99) (Fig. 5). Clade B includes clade III, with a monophyletic *T. bilabiatum* (BS 99) sister to clade IIIa, which in turn includes a monophyletic *T. cyrtanthum* (BS 100), sister to *T. crucigerum* plus *T. jaroba* (BS 100), plus a monophyletic *T. selloi* (BS 100) sister to a clade composed of *Tanaecium dichotomum 9γ*, which is in turn sister to clade IVa which includes multiple terminals of *T. dichotomum* (BS < 70), sister to *T. dichotomum 2β* + *5β* plus a monophyletic *T. revillae* (BS 94) (Fig. 5).

4. Discussion

In this study we sequenced and assembled 16 plastomes representing 15 species of the 21 species of *Tanaecium* currently recognized (Frazão and Lohmann, 2018; Frazão and Lohmann, in prep.; Kaehler et al., 2019; Lohmann and Taylor, 2014; Pace et al., 2016). These plastomes were compared with other published Bignoniaceae plastomes, providing novel insights into Bignoniaceae plastome structure such as the identification of four main IR boundary shift patterns in *Tanaecium*. In addition, a dataset composed of 61 *ndh*F, 51 *rpl32-trn*L and 64 *pep*C Sanger sequences, representing 65 individuals of *Tanaecium* and 5 outgroups was assembled. Phylogenetic inferences of the three dataset (i.e., Sanger dataset, plastome dataset, and plastome and Sanger dataset) recovered consistent topologies, although some differences emerged, especially between the topology recovered using the Sanger dataset and the two topologies recovered using plastome data. The topology recovered based on the analysis of the plastome and Sanger dataset is the best resovled and most well supported, representing the most estimate of phylogenetic relationships within *Tanaecium* to date.

4.1. Tanaecium plastomes

Land plant plastomes range from 120 to 200 kb (Green, 2011; Palmer, 1985). *Tanaecium* plastomes have an average length of 159,048 bp, ranging between 157,807 bp in *T. crucigerum* and 160,935 bp in *T. xanthophyllum* due to a LSC expansion (Tab. 2). The quadripartite plastome structure found in most angiosperms (e.g., Green, 2011; Park et al., 2018; Reginato et al., 2016; Yao et al., 2019) was also recovered in *Tanaecium*. This structure is lacking in some angiosperm clades where one of the IRs were lost such as the papilionoid legumes (Palmer et al., 1987), saguaro cactus (Sanderson et al., 2015), and Geraniaceae (Blazier et al., 2016). Although structural changes have been reported for angiosperms (e.g., Fonseca and Lohmann, 2017; Park et al., 2018; Wicke et al., 2011), no rearrangement were found in *Tanaecium*.

Tanaecium plastomes have between 134 and 135 genes in total, with a gene number similar to that found in other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann, 2017; Thode and Lohmann, 2019). While genes *ycf15* and *ycf68* are lacking in some Bignoniaceae genera (Firetti et al., 2017; Fonseca and Lohmann, 2017; Thode and Lohmann, 2019), those genes were found in *Tanaecium*, as well as in *C. latifolia* (Nazareno et al., 2015), and *C. cujete* (Moreira et al., 2016). Partial *ycf15* genes were recorded in the sweet potato family (Yan et al., 2015). The complete or partial loss of genes is common in land plant (Wicke et al., 2011), including members of the Bignoniaceae (Fonseca and Lohmann, 2017).

Pseudogenization occurs in some genes in IR boundaries in *Tanaecium* and other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann, 2017; Thode and Lohmann, 2019). For

Tanaecium, the loci *ψndh*B*, ψrpl2, ψrps15*, *ψycf1*, *ψycf68* are often not functional, including gene contractions or placement within the IR boundaries. The genes *ψpet*B and *ψpet*D are not functional in *Amphilophium*, another Bignonieae (Thode and Lohmann, 2019). Even thought the gene *ycf68* has not been found in other Bignoniaceae, these genes are found in many other angiosperms, although often as pseudogenes (e.g., Huang et al., 2017; Yan et al., 2015).

The most variable genes in *Tanaecium* (i.e., *acc*D, *rpo*A, and *rps18*), are also the most variable in other plant clades. For example, while the *acc*D and *rpo*A are among the most variable genes in *Amphilophium* (Bignoniaceae), the *rpoA* was not variable in that genus (Thode and Lohmann, 2019). The *acc*D is highly variable in many other angiosperm clades such as *Artemisia* (Asteraceae) (Liu et al., 2013), and *Lamprocapnos* (Papaveraceae) (Park et al., 2018). The *rps18* gene is also highly variable in Stemonaceae (Lu et al., 2018), Bromeliaceae (Poczai and Hyvönen, 2017), and Campanulaceae (Uribe-Convers et al., 2017), among others. Interestingly, that same gene shows low evolutionary rates in *Anemopaegma*, another Bignoniaceae (Firetti et al., 2017). These variable patterns of gene variation provide additional support to the idea that plastomes are not conserved, with chloroplast genes presenting different levels of variation at different taxonomic levels.

Plastome IR boundary shifts vary among land plants (e.g., Park et al. 2018). In *Tanaecium* alone, five different boundary patterns (Fig. 2), and four main IR boundary shifts were detected (Figs. 1-2). These structural changes led to contractions of the IRs and expansions of the SSC (Fig. 1-2). *Tanaecium* IRs are 30,648 bp on average, while the SSC is 12,748 bp on average. Despite that, the IRs of *T. bilabiatum* are 24,182 bp in length, while the SSC is 26,057 bp in length. Furthermore, the IRs of *T. tetragonolobum* are 11,409 bp while the SSC is 49,868 bp, which is more than twice the average length size found in other plastomes (Tab. 2, Fig. 2). *Tanaecium tetramerum* also showed a contraction of the IRs (28,791 bp), but showed a LSC expansion (89,092 bp) due to the inclusion of genes *rpl2* and *rpl23* (Fig. 1-2). The boundaries found for *T. bilabiatum*, *T. tetragonolobum*, and *T. tetramerum* are new in the Bignoniaceae, while the more general pattern is frequent for the family, i.e,. the LSC/IRb within the *rps19* or between the *rps19* and *rpl2*, SSC between the *rps15* loci, and IRa/LSC between the duplicated gene *rpl2* and *trn*H-GUG (Firetti et al., 2017; Fonseca and Lohmann, 2017; Moreira et al., 2016; Nazareno et al., 2015; Thode and Lohmann, 2019).

Contractions and expansions of the IRs and the SSC were detected multiple times during land plant evolution, leading to exchanges of genes among regions (Zhu et al., 2015). However, changes in the IRs/LSC boundaries are more common than contractions or expansions of those regions (Raubeson et al., 2007; Wang et al., 2008). While expansions of the IRs into the LSC are common among land plants and other Bignoniaceae (Firetti et al., 2017; Fonseca and Lohmann,

2017; Thode and Lohmann, 2019), the exact opposite pattern was found in *Tanaecium*, which only shows IR contractions. Despite that, larger SSCs have been reported in other Bignoniaceae, with the inclusion of gene *ycf1* within the SSC in *C. latifolia* (Nazareno et al., 2015), and *C. cujete* (Moreira et al., 2016).

4.2. Tanaecium phylogeny

The phylogeny of *Tanaecium* reconstructed here is the most comprehensive to date, including multiple samples of 17 of the 21 recognized species in the genus (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann 2006; Pace et al., 2016), only *T. apiculatum*, *T. exitiosum*, and *T. neobrasiliense* were not sampled due to the fact that these species are only known from a few specimens from which we were unable to obtain sufficient DNA for successful amplifications. The combination of Sanger sequencing with a HTS approach, allowed us to maximize taxon and character sampling. Other authors have successfully employed a similar approach in molecular phyloegentics (e.g., Fonseca and Lohmann, 2018; Gardner et al., 2016; Uribe-Convers et al., 2017).

Our Sanger dataset was based on sequences of the *ndh*F, *rpl*32-*trn*L, and *pep*C markers, all of which have been used in earlier molecular phylogenetic studies of tribe Bignonieae (Fonseca and Lohmann, 2015; Kaehler et al., 2019, 2012; Lohmann, 2006, 2013; Medeiros and Lohmann, 2015). The topology recovered through the analysis of this dataset recovered a paraphyletic *Tanaecium*, with *F. paradoxa* emerging within the *Tanaecium* diversity (Fig. 4B). This same result was obtained in a study of *Fridericia* that used the same markers (Kaehler et al., 2019), which led to the proposal of the new combination *Tanaecium paradoxum*. Despite that, the topologies recovered based in the plastome dataset and that obtained based on the analysis of the combined plastome and Sanger dataset (Figs. 4A, 5), recovered *F. paradoxa* within *Fridericia*, supporting the maintenance of this taxon within *Fridericia*. Future studies based on multiple samples of this taxon and a more comprehensive sampling of characters, including additional nuclear markers will allow for a definition of this taxon placement with certainty.

While the topology recovered based on the analysis of the Sanger dataset allowed for an evaluation of the monophyly of various species of *Tanaecium*, and the identification of main clades, resolution among clades was low (Fig. 4B). Earlier phylogenies based on Sanger sequences of *Tanaecium* reconstructed an equally poorly resolved backbone (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann, 2006; Pace et al., 2016). Despite that, the clades recovered in this analysis were strongly supported and consistent with clades recovered through the analysis of the plastome dataset (Fig. 4A-B). On the other hand, the topology recovered

through the analysis of the plastome dataset recovered a more resolved and supported backbone for the genus, with strong support values for almost all nodes (Fig. 4A).

The topology obtained based on the analysis of the combined plastome and Sanger dataset recovered a monophyletic *Tanaecium* (Fig. 5). The main clades recovered in this topology are very similar to those recovered in the topologies that resulted from the analysis of the Sanger dataset, and the analysis of the Plastome and Sanger dataset. Despite that, the backbone is weakly supported, likely due to the high amount of missing data (see Uribe-Convers et al., 2014). Nevertheless, the topology that resulted from the analysis of the combined plastome and Sanger dataset represents the most robust phylogeny of *Tanaecium* to date. Future studies including a higher number of nuclear markers would help improve the resolution of the *Tanaecium* backbone.

The phylogenetic placement of many taxa is resolved for the first time in this study. For example, *Tanaecium tetramerum* is strongly supported as sister to *T. parviflorum*, within clade I (Fig. 5), while placed within a polytomy previously (Frazão and Lohmann, 2018; Pace et al., 2016), but. Similarly, *T. caudiculatum* appears as sister to clade that includes *T. pyramidatum* sister to *T. decorticans* plus *T. affine* (Fig. 5), but was previously reconstructed as sister to *T. bilabiatum* (Frazão and Lohmann, 2018; Lohmann, 2006), or sister to *T. pyramidatum* (Kaehler et al., 2019), or without a clear phylogenetic position within *Tanaecium* (Pace et al., 2016). *Tanaecium caudiculatum* is an intriguing species due its unique morphological features such as the campanulate corolla and presence of only two fertile anthers, contrasting to the four fertile anthers of all other Bignonieae (Gentry, 1973; Lohmann and Taylor, 2014). While the new phylogenetic placement is more strongly supported than that recovered previously (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann, 2006; Pace et al., 2016), the short branch and relatively week support for this relationship indicates that additional characters are still needed to confirm its phylogenetic placement. The phylogenetic placement of *T. bilabiatum* within clade III is also novel as this species appeared as sister to *T. caudiculatum* (Frazão and Lohmann, 2018; Lohmann, 2006), or showed a uncertain phylogenetic position (Pace et al., 2016) previously. Similarly, *T. affine* appeared as sister to *T. decorticans*, instead of sister to *T. tetragonolobum* as in previous studies (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann, 2006; Pace et al., 2016). However, it turns out that the specimen sampled as *T. affine* previously (Frazão and Lohmann, 2018; Kaehler et al., 2019; Lohmann, 2006; Pace et al., 2016) was misindentified and actually represented *T. tetragonolobum*, which explains the earlier placement.

The individual clades that emerged from the analysis of the Sanger dataset and the analysis of the plastomes dataset, also emerged in the topology that resulted from the analysis of the

plastome and Sanger combined dataset (Fig. 5), namely: (i) clade I, including *T. tetramerum* sister of *T. parviflorum*; (ii) clade IIb, including *T. tetragonolobum* sister to *T. duckei* plus *T. truncatum*; (iii) clade IIIa, including *T. cyrtanthum* sister to *T. crucigerum* plus *T. jaroba*); and, (iv) clade IVa, including *T. revillae* and multiple individuals of *T. dichotomum* (Fig. 5). The relationships among members of clade IV recovered here highlight the need of additional studies within the morphological variable *T. dichotomum.* While four different morphotypes were identified based on morphology, only one of these morphotypes, *T. dichotomum β*, appeared as monophyletic (Fig. 5). All morphotypes are diagnosable by morphological features but these morphological groupings were not supported by our molecular data. Future studies including a higher number of nuclear loci would allow further insights into the *T. dichotomum* species complex. *Tanaecium dichotomum* includes around 60 synonyms and is known for its morphological heterogeneity. Detailed molecular, morphological, and taxonomic studies are clearly needed within this group.

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Figure captions

Fig. 1. Gene maps showing the four patterns of *Tanaecium* plastomes assembled in this study. Gray shading highlights IR regions and their boundary shifts. Genes drawn below the line are transcribed in forward direction, while those drawn above the line are transcribed in reverse direction. Genes belonging to different functional groups are colored according to the legend. Asterisks (*) represent intron-containing genes.

Fig. 2. Comparison of the boundaries of the Large Single Copy (LSC), Inverted Repeat b (IRa), Small Single Copy (SSC), and Inverted Repeat a (IRb) within *Tanaecium* and among four other Bignoniaceae plastomes. The psi (*ψ)* indicates pseudogenes within the plastomes sampled. The alpha (α) and beta (β) represent different morphotypes sampled within the *Tanaecium dichotomum* species complex.

Fig. 3. Alignments of the three most variable genes encountered within *Tanaecium* plastomes before Gblocks treatment. A. *accD* gene matrix showing the poorly aligned regions. B. *rpoA* gene matrix showing the expansion between the 786 and 1,218 sites. C. *rps18* gene matrix showing an expansion with 1201 bp long. Gray shading highlights *Tanaecium* species with plastomes assembled in this study. The numbers between parentheses represent the sizes (in bp) of each expansion. Alpha (α) and beta (β) represent different morphotypes of *Tanaecium dichotomum*. Outgroups are presented in bold.

Fig. 4. Phylogenectic relationships of *Tanaecium* inferred using the Sanger dataset and the plastome dataset independently. A. Phylogeny inferred based on the Sanger dataset. Bold highlights the sample of *Fridericia paradoxa* recovered within *Tanaecium*. Gray shading highlights the species with multiple individuals sampled in the plastome dataset. B. Phylogeny inferred based on the plastome dataset. Outgroups are shown in grey. Clades recovered in both phylogenies are indicated using roman algarithms. Numbers close to nodes are bootstrap (BS) support values. Black circles indicate maximum support value (BS 100). Nodes with BS < 70 support were collapsed. Dashed lines connect species sampled in both phylogenies.

Fig. 5. Phylogeny of *Tanaecium* using the plastome and Sanger combined dataset. Samples with plastome assembled here are presented in bold. Outgroups are shown in gray. Clades recovered in both phylogenies are indicated using roman numbers. Clades A and B indicate the two clades only recovered in this topology. Numbers close to nodes represent bootstrap (BS) support values. Black circles indicate maximum support value (BS 100). Nodes with BS < 70 support were collapsed. Gray shading highlights the various accessions of *Tanaecium dichotomum* species complex sampled. The arrow highlights the placement of *Fridericia paradoxa*. The flowers shown in the right-hand side illustrates the highly diverse floral morphology of *Tanaecium*.

Table 1. Summary os datasets compiled using MEGA 7.

Datasets		Size (bp)	Parsimony informative sites (Pi)	Variable sites (V)	Proportion of variable sites in the final alignments (%)
Final datasets	Sanger	3,658	520	835	23
	NGS	101,649	6,044	13,165	12.95
	NGS-Sanger	103,058	6,501	13,765	13.35
Sanger loci	*pep*C	618	221	319	52
	*ndh*F	2,065	238	399	19.32
	*rpl*32-*trn*L	975	165	284	29
15 more variable plastome loci	*ycf*1	7,615	623	1,803	23.68
	*ycf*2	7,095	537	1,056	14.88
	*acc*D	1522	546	806	52.96
	*rpo*A	1038	406	532	51.25
	*rpo*C2	4,233	232	500	11.81
	*ndh*F	2,065	238	399	19.32
	*clp*P	761	260	382	50.20
	*rpo*B	3,228	166	354	10.97
	*rpo*C1	2,115	111	248	11.73
	*rps*18	583	151	237	40.65
	*ycf*4	714	129	209	29.27
	*mat*K	1,545	73	190	12.30
	*ndh*D	1,558	79	175	11.23
	*atp*A	1,587	80	149	9.39
	*ndh*H	1,182	50	138	11.68

Table 2. Summary of sequenced plastomes of *Tanaecium*.

Species	Voucher	Complete plastomes	No. of raw reads	No. of mapped reads	Average reads depth (x)	Plastome length (bp)	LSC length (bp)	IR length (bp)	SSC length (bp)	GC content (%)	CDS	tRNA	rRNA
T. bilabiatum	Lohmann 850		8,860,486	447,380	424	159,092	84,671	24,182	26,057	38,1	87	37	8
T. crucigerum	Lohmann 355		13,758,337	293,168	278	157,807	83,490	30,861	12,595	37,9	90	37	8
T. cyrtathum	Frazão 173	x	11,648,305	467,930	482	159,444	85,066	30,900	12,578	38	90	37	8
T. decorticans	Frazão 188	x	12,644,022	306,343	297	159,241	85,259	30,648	12,686	38,1	88	37	8
T. dichotomum 1α	Frazão 375	x	12,082,406	464,896	489	158,470	84,808	30,371	12,920	38	88	37	8
T. dichotomum 2β	Carvalho 14	x	11,994,696	470,798	679	158,718	85,054	30,412	12,840	38	88	37	8
T. duckei	Frazão 309	x	11,812,767	101,125	97	158,789	85,452	30,284	12,769	38	90	37	8
T. jaroba	Frazão 288		11,096,666	422,891	439	160,067	85,683	30,895	12,594	37,9	90	37	8
T. parviflorum	Fonseca 280		3,858,109	150,583	149	159,004	85,273	30,389	12,498	38	90	38	8
T. pyramidatum	Fonseca 321	x	12,089,468	319,715	160	160,112	85,651	30,976	12,509	38,1	88	37	8
T. revillae	Kataoka 321		10,642,085	660,086	349	159,505	84,789	30,944	12,828	37,9	88	37	8
T. selloi	Frazão 235		10,758,439	407,552	443	158,543	84,195	30,791	12,766	38	90	37	8
T. tetragonolobum	Frazão 419	x	14,350,498	189,678	85	158,851	86,165	11,409	49,868	38	86	37	8
T. tetramerum	Pace 31		5,460,117	489,472	580	159,479	89,092	28,791	12,805	38	88	38	8
T. truncatum	Frazão 340		14,079,736	612,725	216	158,634	85,072	30,489	12,584	38	90	37	8
T. xanthophyllum	Frazão 333	x	14,242,787	600,064	341	160,935	86,213	30,961	12,800	37,8	90	37	8

Table 3. Genes encoded by the *Tanaecium* plastomes. Asterisks (*) indicate genes with one intron, while double asterisks (**) indicate genes with two introns. Numbers after gene names indicate gene duplications: (1) gene duplication in the IRs, (2) gene duplication in the LSC found in *Tanaecium tetramerum* and *Tanaecium parviflorum*, (3) gene duplication in the SSC found in *Tanaecium tetragonolobum*, (4) gene duplication in the LSC found in *Tanaecium tetramerum.*

Gene function	Gene type	Gene
Self- replication	Ribossomal RNA genes	*rrn4.5*[1], *rrn55*[1], *rrn165*[1], *rrn235*[1]
	Transfer RNA genes	*trnA-UGC**[1,3], *trnC-GCA, trnD-GUC, trnE-UUC, trnF- GAA, trnfM-CAU*[2], *trnG-UCC, trnG-UCC*, trnH-GUG, trnI-CAU*[1], *trnI-GAU**[1,3], *trnK-UUU*, trnL-CAA*[1], *trnL- UAA*, trnL-UAC, trnM-CAU, trnN-GUU*[1], *trnP-UGG, trnQ-UUG, trnR-ACG*[1], *trnR-UCU, trnS-GCU, trnS-GGA, trnS-UGA, trnT-GGU, trnT-UGU, trnV-GAC*[1], *trnV-UAC*, trnW-CCA, trnY-GUA*
	Small ribosomal subunit	*rps2, rps3, rps4, rps7, rps8, rps11, rps12***[1], *rps14, rps15*[1], *rps16*, rps18, rps19*
	Large ribosomal subunit	*rpl2**[1,4], *rpl14, rpl16*, rpl20, rpl22b, rpl23*[1,4], *rpl32, rpl33, rpl36*
	RNA polymerase subunits	*rpoA, rpoB, rpoC1*, rpoC2*
Photosynthesis	Photosystem I	*psaA, psaB, psaC, psaI, psaJ*
	Assembly/stability of photosystem I	*ycf3**, *ycf4*
	Photosystem I	*psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbI, psbJ, psbK, psbL, psbM, psbN, psbT, psbZ*
	NADH dehydrogenase	*ndhA*, ndhB*[1], *ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK*
	Cytochrome b/f complex	*petA, petB*, petD*, petG, petL, petN*
	ATP synthase	*atpA, atpB, atpE, atpF*, atpH, atpI*
	Rubisco	*rbcL*
Other genes	Translational initiator factor	*infAb*
	Maturase	*matK*
	Protease	*clpP***
	Envelope membrane protein	*cemA*
	Subunit of Acetil-CoA-carboxylase	*accD*
	c-type cytochrome synthesis	*ccsA*
Pseudogenes in some species		*ψndhB*, ψrpl2*, ψrps15*, *ψycf1*, *ψycf68*
Unknown function	Hypotetical chloroplast reading frames	*ycf1, ycf 15, ycf2, ycf68*

Fig. 1

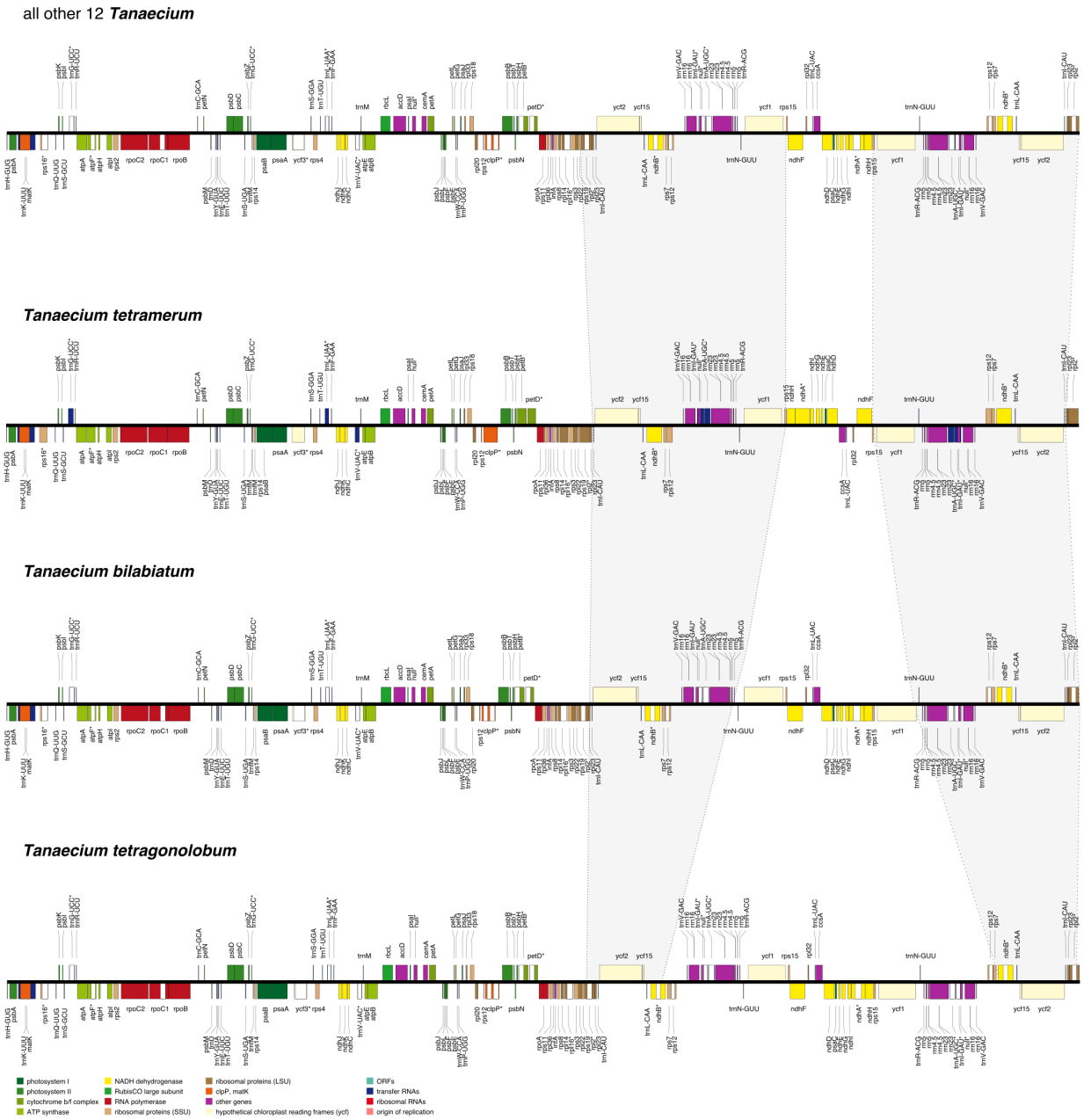
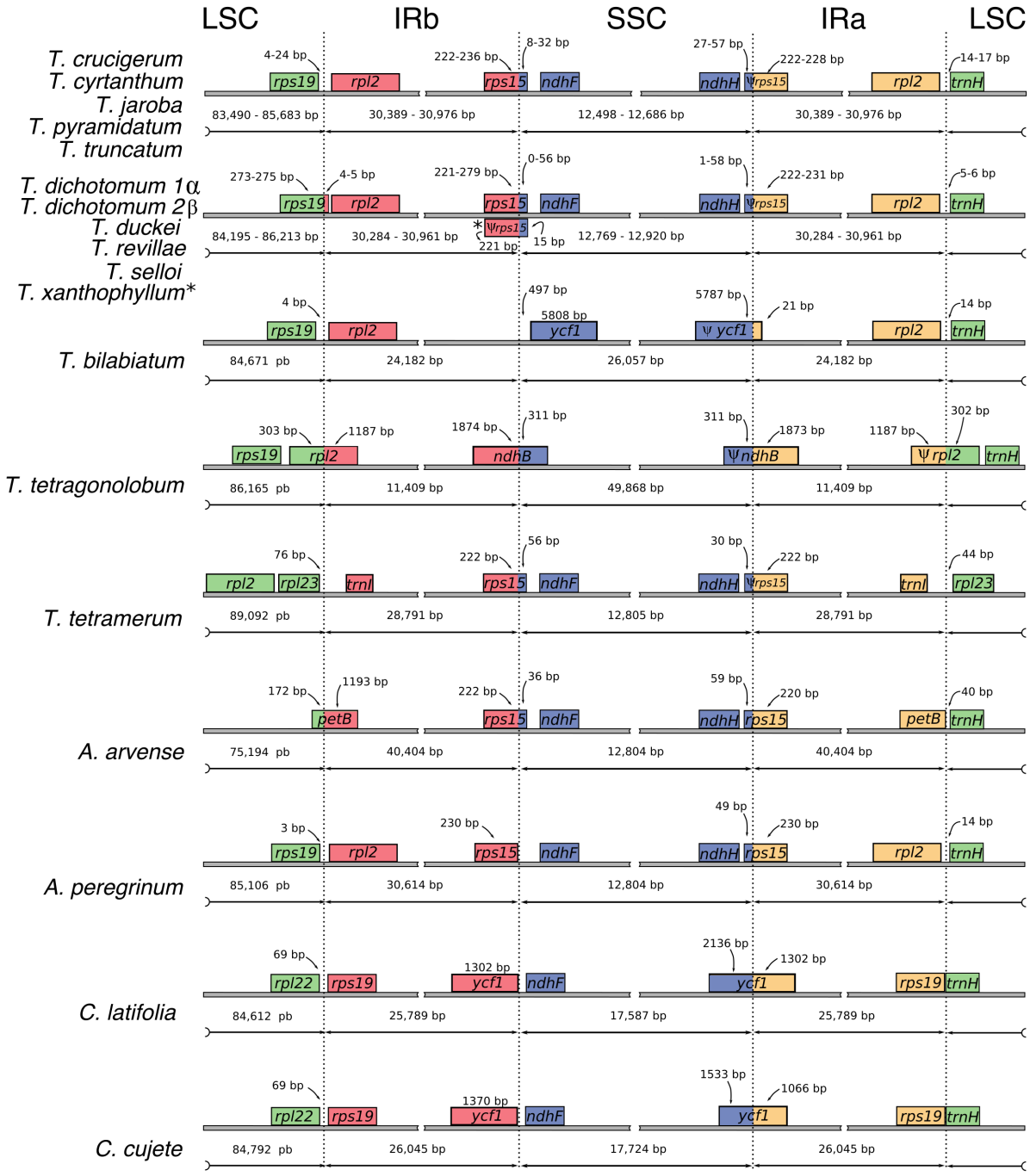

all other 12 Tanaecium
Tanaecium tetramerum
Tanaecium bilabiatum
Tanaecium tetragonolobum
photosystem I
photosystem II
cytochrome b/f complex
ATP synthase
NADH dehydrogenase
RubisCO large subunit
RNA polymerase
ribosomal proteins (SSU)
ribosomal proteins (LSU)
clpP, matK
other genes
hypothetical chloroplast reading frames (ycf)
ORFs
transfer RNAs
ribosomal RNAs
origin of replication

Fig. 2


LSC
IRb
SSC
IRa
LSC
T. crucigerum
T. cyrtanthum
T. jaroba
T. pyramidatum
T. truncatum
T. dichotomum 1α
T. dichotomum 2β
T. duckei
T. revillae
T. selloi
T. xanthophyllum*
T. bilabiatum
T. tetragonolobum
T. tetramerum
A. arvense
A. peregrinum
C. latifolia
C. cujete
rps19
rpl2
rps15
ndhF
ndhH
ψrps15
rpl2
trnH
ycf1
ψ ycf1
ndhB
ψndhB
ψrpl2
rpl23
trnI
petB
rps19
rpl22
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30,389 - 30,976 bp
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26,057 bp
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86,165 pb
11,409 bp
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12,805 bp
28,791 bp
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84,792 pb
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26,045 bp
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27-57 bp
222-228 bp
14-17 bp
273-275 bp
4-5 bp
221-279 bp
0-56 bp
1-58 bp
222-231 bp
5-6 bp
221 bp
15 bp
4 bp
497 bp
5808 bp
5787 bp
21 bp
14 bp
303 bp
1187 bp
1874 bp
311 bp
311 bp
1873 bp
1187 bp
302 bp
76 bp
222 bp
56 bp
30 bp
222 bp
44 bp
172 bp
1193 bp
222 bp
36 bp
59 bp
220 bp
40 bp
3 bp
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1302 bp
2136 bp
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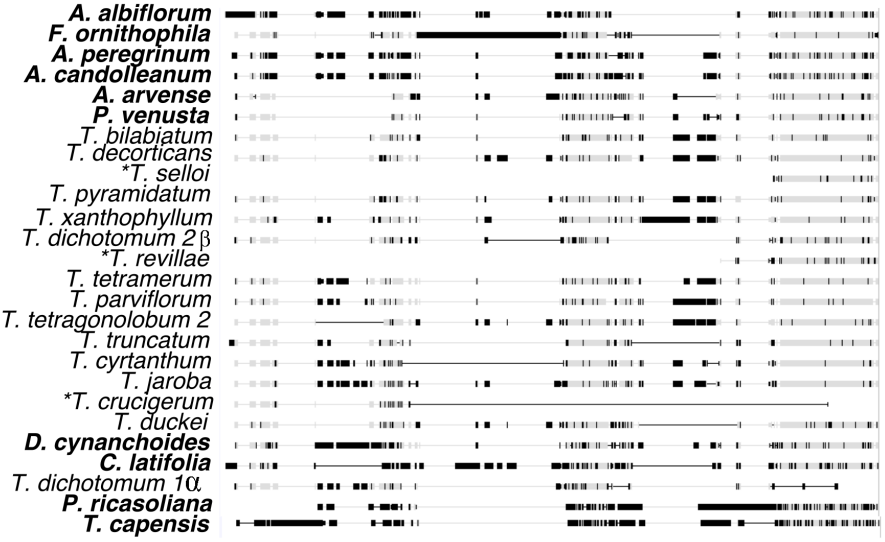
69 bp
1370 bp
1533 bp
1066 bp

Fig. 3

A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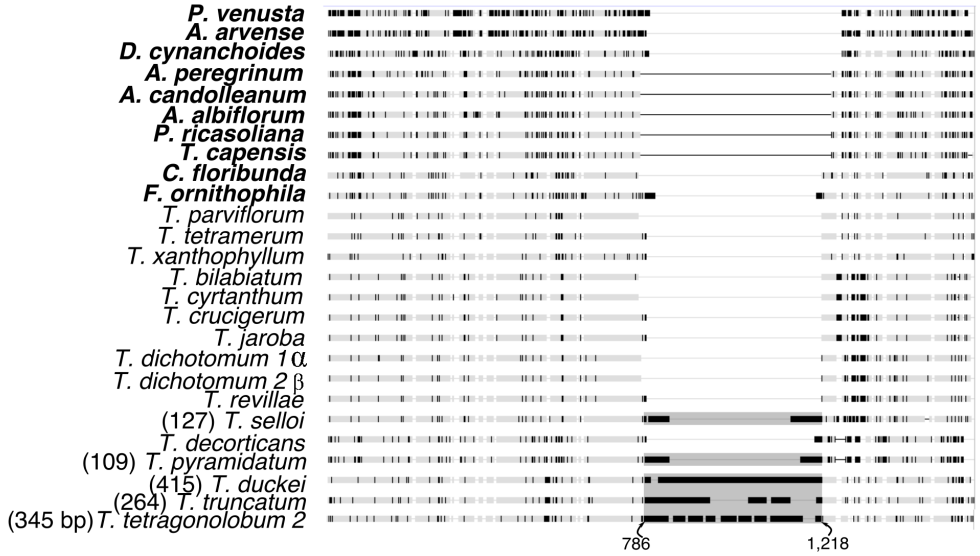
F. ornithophila
A. peregrinum
A. candolleanum
A. arvense
P. venusta
T. bilabiatum
T. decorticans
*T. selloi
T. pyramidatum
T. xanthophyllum
T. dichotomum 2 β
*T. revillae
T. tetramerum
T. parviflorum
T. tetragonolobum 2
T. truncatum
T. cyrtanthum
T. jaroba
*T. crucigerum
T. duckei
D. cynanchoides
C. latifolia
T. dichotomum 1α
P. ricasoliana
T. capensis

B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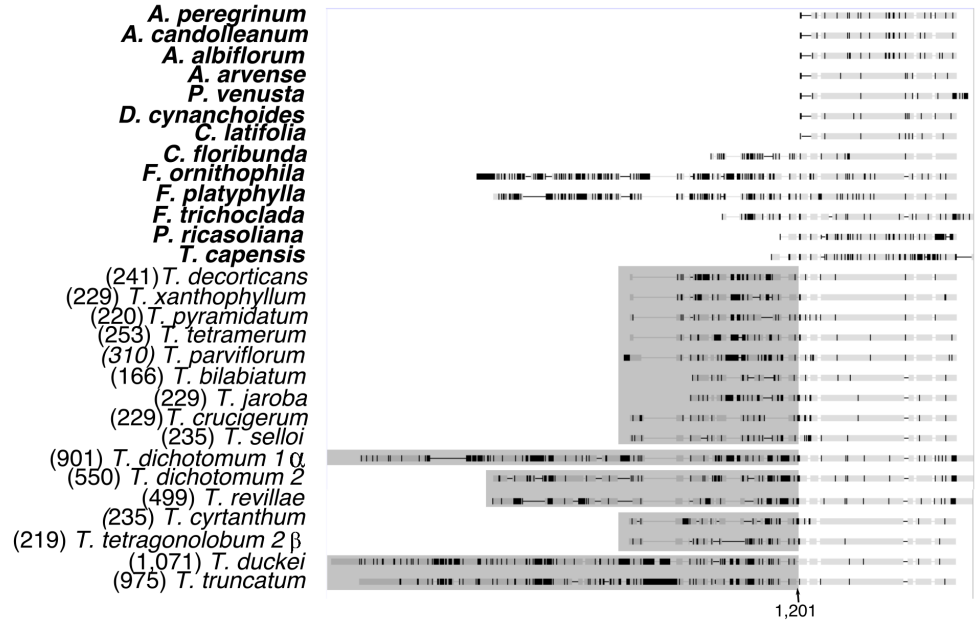
A. arvense
D. cynanchoides
A. peregrinum
A. candolleanum
A. albiflorum
P. ricasoliana
T. capensis
C. floribunda
F. ornithophila
T. parviflorum
T. tetramerum
T. xanthophyllum
T. bilabiatum
T. cyrtanthum
T. crucigerum
T. jaroba
T. dichotomum 1α
T. dichotomum 2 β
T. revillae
(127) T. selloi
T. decorticans
(109) T. pyramidatum
(415) T. duckei
(264) T. truncatum
(345 bp) T. tetragonolobum 2
786
1,218

C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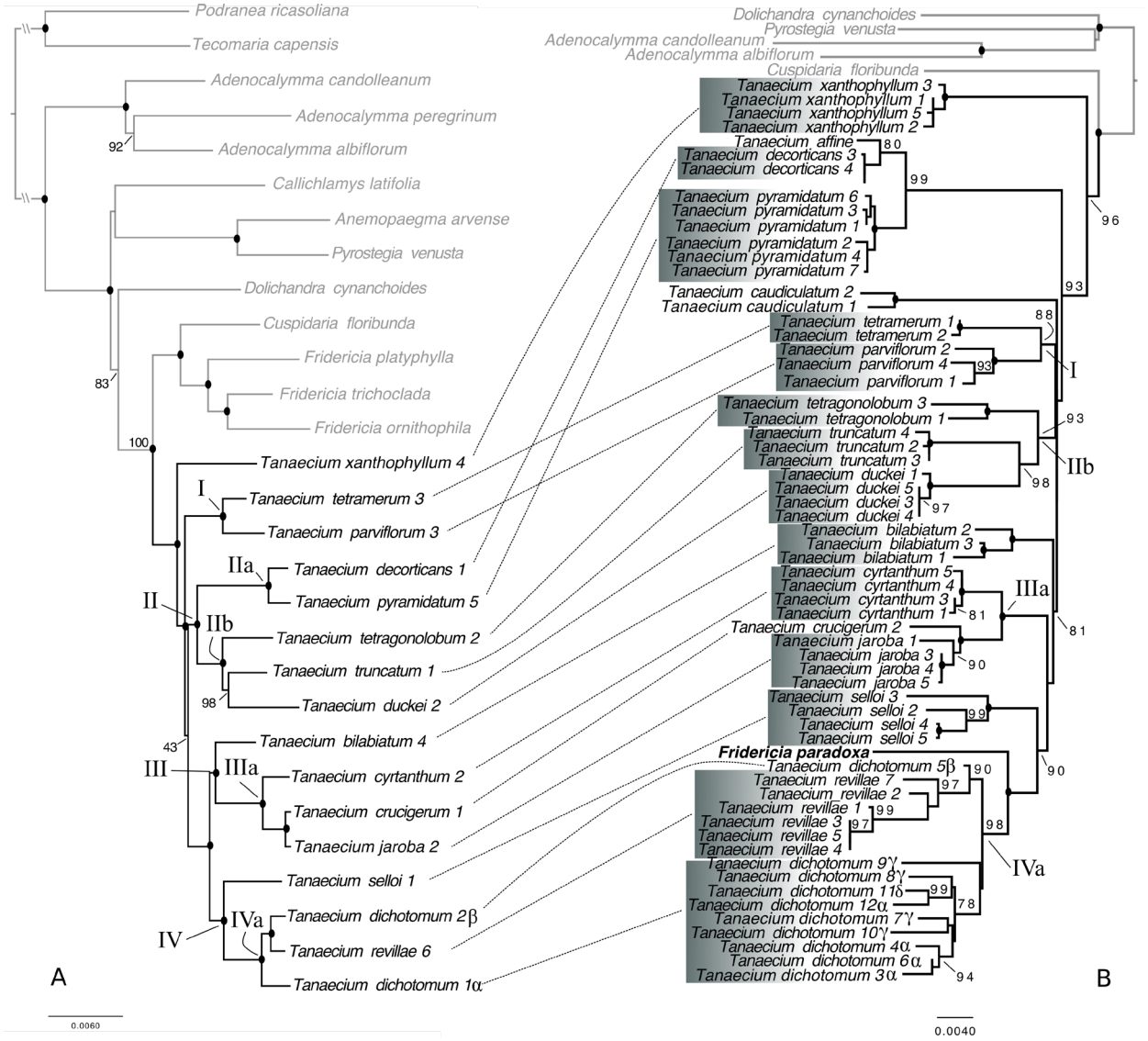
A. arvense
P. venusta
D. cynanchoides
C. latifolia
C. floribunda
F. ornithophila
F. platyphylla
F. trichoclada
P. ricasoliana
T. capensis
(241) T. decorticans
(229) T. xanthophyllum
(220) T. pyramidatum
(253) T. tetramerum
(310) T. parviflorum
(166) T. bilabiatum
(229) T. jaroba
(229) T. crucigerum
(235) T. selloi
(901) T. dichotomum 1α
(550) T. dichotomum 2
(499) T. revillae
(235) T. cyrtanthum
(219) T. tetragonolobum 2 β
(1,071) T. duckei
(975) T. truncatum
1,201

Fig. 4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Tecomaria capensis
Adenocalymma candolleanum
Adenocalymma peregrinum
Adenocalymma albiflorum
Callichlamys latifolia
Anemopaegma arvense
Pyrostegia venusta
Dolichandra cynanchoides
Cuspidaria floribunda
Fridericia platyphylla
Fridericia trichoclada
Fridericia ornithophila
Tanaecium xanthophyllum 4
Tanaecium tetramerum 3
Tanaecium parviflorum 3
Tanaecium decorticans 1
Tanaecium pyramidatum 5
Tanaecium tetragonolobum 2
Tanaecium truncatum 1
Tanaecium duckei 2
Tanaecium bilabiatum 4
Tanaecium cyrtanthum 2
Tanaecium crucigerum 1
Tanaecium jaroba 2
Tanaecium selloi 1
Tanaecium dichotomum 2β
Tanaecium revillae 6
Tanaecium dichotomum 1α
I
II
IIa
IIb
III
IIIa
IV
IVa
92
83
100
98
43
A
0.0060
Dolichandra cynanchoides
Pyrostegia venusta
Adenocalymma candolleanum
Adenocalymma albiflorum
Cuspidaria floribunda
Tanaecium xanthophyllum 3
Tanaecium xanthophyllum 1
Tanaecium xanthophyllum 5
Tanaecium xanthophyllum 2
Tanaecium affine
Tanaecium decorticans 3
Tanaecium decorticans 4
Tanaecium pyramidatum 6
Tanaecium pyramidatum 3
Tanaecium pyramidatum 1
Tanaecium pyramidatum 2
Tanaecium pyramidatum 4
Tanaecium pyramidatum 7
Tanaecium caudiculatum 2
Tanaecium caudiculatum 1
Tanaecium tetramerum 1
Tanaecium tetramerum 2
Tanaecium parviflorum 2
Tanaecium parviflorum 4
Tanaecium parviflorum 1
Tanaecium tetragonolobum 3
Tanaecium tetragonolobum 1
Tanaecium truncatum 4
Tanaecium truncatum 2
Tanaecium truncatum 3
Tanaecium duckei 1
Tanaecium duckei 5
Tanaecium duckei 3
Tanaecium duckei 4
Tanaecium bilabiatum 2
Tanaecium bilabiatum 3
Tanaecium bilabiatum 1
Tanaecium cyrtanthum 5
Tanaecium cyrtanthum 4
Tanaecium cyrtanthum 3
Tanaecium cyrtanthum 1
Tanaecium crucigerum 2
Tanaecium jaroba 1
Tanaecium jaroba 3
Tanaecium jaroba 4
Tanaecium jaroba 5
Tanaecium selloi 3
Tanaecium selloi 2
Tanaecium selloi 4
Tanaecium selloi 5
Fridericia paradoxa
Tanaecium dichotomum 5β
Tanaecium revillae 7
Tanaecium revillae 2
Tanaecium revillae 1
Tanaecium revillae 3
Tanaecium revillae 5
Tanaecium revillae 4
Tanaecium dichotomum 9γ
Tanaecium dichotomum 8γ
Tanaecium dichotomum 11δ
Tanaecium dichotomum 12α
Tanaecium dichotomum 7γ
Tanaecium dichotomum 10γ
Tanaecium dichotomum 4α
Tanaecium dichotomum 6α
Tanaecium dichotomum 3α
I
IIb
IIIa
IVa
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99
96
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99
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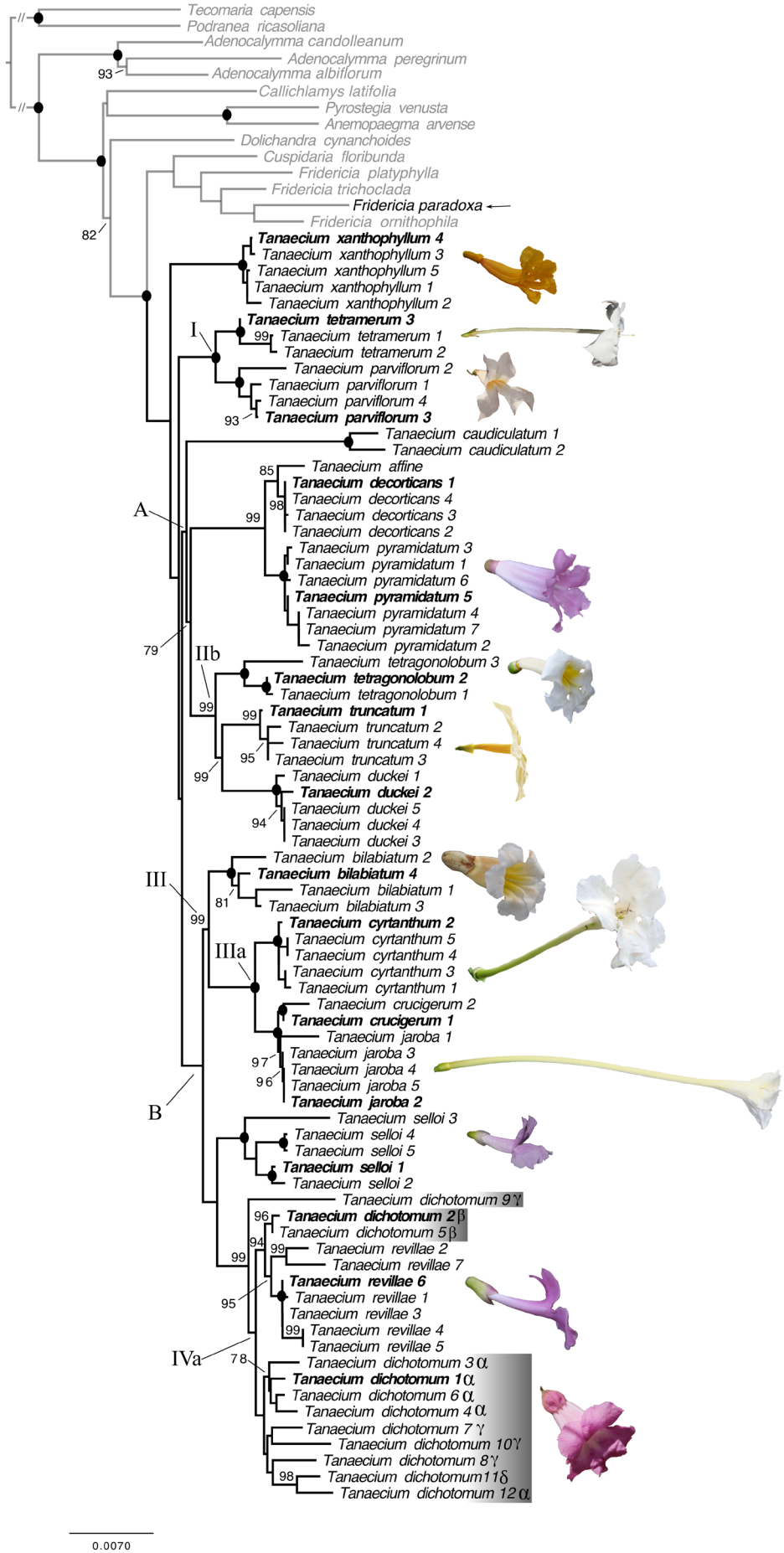
99
97
98
78
94
B
0.0040

Fig. 5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Adenocalymma candolleanum
Adenocalymma peregrinum
Adenocalymma albiflorum
Callichlamys latifolia
Pyrostegia venusta
Anemopaegma arvense
Dolichandra cynanchoides
Cuspidaria floribunda
Fridericia platyphylla
Fridericia trichoclada
Fridericia paradoxa
Fridericia ornithophila
Tanaecium xanthophyllum 4
Tanaecium xanthophyllum 3
Tanaecium xanthophyllum 5
Tanaecium xanthophyllum 1
Tanaecium xanthophyllum 2
Tanaecium tetramerum 3
Tanaecium tetramerum 1
Tanaecium tetramerum 2
Tanaecium parviflorum 2
Tanaecium parviflorum 1
Tanaecium parviflorum 4
Tanaecium parviflorum 3
Tanaecium caudiculatum 1
Tanaecium caudiculatum 2
Tanaecium affine
Tanaecium decorticans 1
Tanaecium decorticans 4
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Tanaecium pyramidatum 6
Tanaecium pyramidatum 5
Tanaecium pyramidatum 4
Tanaecium pyramidatum 7
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Tanaecium tetragonolobum 2
Tanaecium tetragonolobum 1
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Tanaecium truncatum 2
Tanaecium truncatum 4
Tanaecium truncatum 3
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Tanaecium duckei 2
Tanaecium duckei 5
Tanaecium duckei 4
Tanaecium duckei 3
Tanaecium bilabiatum 2
Tanaecium bilabiatum 4
Tanaecium bilabiatum 1
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Tanaecium cyrtanthum 2
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Tanaecium cyrtanthum 4
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Tanaecium cyrtanthum 1
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Tanaecium jaroba 4
Tanaecium jaroba 5
Tanaecium jaroba 2
Tanaecium selloi 3
Tanaecium selloi 4
Tanaecium selloi 5
Tanaecium selloi 1
Tanaecium selloi 2
Tanaecium dichotomum 9γ
Tanaecium dichotomum 2β
Tanaecium dichotomum 5β
Tanaecium revillae 2
Tanaecium revillae 7
Tanaecium revillae 6
Tanaecium revillae 1
Tanaecium revillae 3
Tanaecium revillae 4
Tanaecium revillae 5
Tanaecium dichotomum 3α
Tanaecium dichotomum 1α
Tanaecium dichotomum 6α
Tanaecium dichotomum 4α
Tanaecium dichotomum 7γ
Tanaecium dichotomum 10γ
Tanaecium dichotomum 8γ
Tanaecium dichotomum11δ
Tanaecium dichotomum 12α
A
B
I
IIb
III
IIIa
IVa
0.0070

Supplementary material

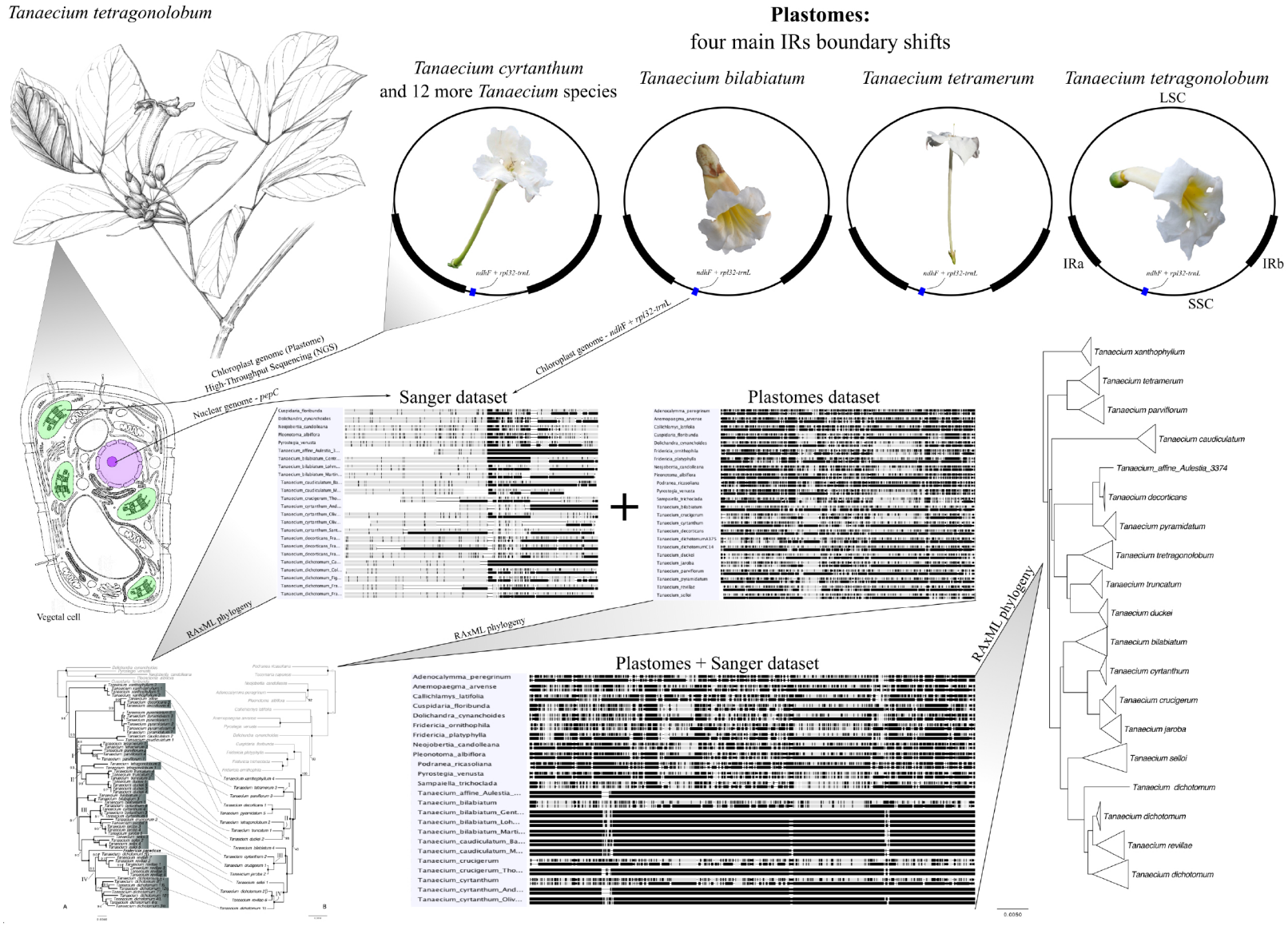
Table A.1: Taxa sampled in the molecular phylogeny of *Tanaecium* Sw. emend L.G. Lohmann. Gray cells represent sequences obtained using Sanger sequencing for the *ndh*F, *rpl*32-*trn*L, and *Pep*C. Samples with plastomes sequenced using high-throughput sequencing (HTS) approach are in bold. Asterisk (*) indicates outgroups, while the symbol "$" indicates *pep*C sequences assembled from the HTS data. The Greek letter at the end of the *Tanaecium dichotomum* samples indicate different morphological groups.

Taxa	Voucher	Localidade	ndhF	rpl32-trnL	PepC
Adenocalymma peregrinum	Fonseca 444 (SPF)	Brazil, Goiás, São Jorge da Chapada	MG008314	MG008314	
Anemopaegma arvense	Fonseca s.n. (SPF)	Brazil, Goiás, Cristalina	MG831872	MG831872	
Callichlamys latifolia	Lohmann 619 (MO)	Peru, Madre de Dios, Manu National Park	KR534325	KR534325	
Cuspidaria convolute	Lohmann 418 (MO, SPF)	Brazil, São Paulo, Cult. Instituto Plantarum	MG831873	MG831873	DQ222711
Dolichandra cynanchoides	Galleto 1019 (MO)	Argentina, Buenos Aires, Buenos Aires	MG831874	MG831874	DQ222728
Fridericia ornithophila	Frazão 330 (SPF)	Brazil, Mato Grosso, Paranaíta			
Fridericia paradoxa	Nascimento 262 (RB)	Brazil, Bahia, Remanso			
Fridericia platyphylla	Lorenzi 709 (MO)	Peru, Madre de Dios	MG831875	MG831875	
Neojobertia candolleana	Lohmann 363 (SPF)	Brazil, Bahia, Mucugê	MG008316	MG008316	DQ222778
Pleonotoma albiflora	Matos 1733 (SPF)	Brazil: Bahia, Porto Seguro	MG831876	MG831876	DQ222791
Podranea ricasoliana	Fonseca 304 (SPF)	Cultivated	MG831877	MG831877	
Pyrostegia venusta	Lorenzi 718 (SPF)	Brazil, São Paulo, Campinas	MG831878	MG831878	DQ222803
Sampaiella trichoclada	Leoni 5933 (SPF)	Brazil: Espírito Santo, Pinheiros	MG831879	MG831879	DQ222807
Tecomaria capensis	Fonseca 305 (SPF)	Cultivated	MG831880	MG831880	
Tanaecium affine	Aulestia 3374 (QCNE, MO)	Ecuador, Napo, Aguarico			
Tanaecium bilabiatum 1	Lohmann 846 (SPF)	Brazil, Amazonas, Novo Airão			
Tanaecium bilabiatum 2	Martino 143 (NY)	Venezuela, Apure, Muñoz			
Tanaecium bilabiatum 3	Gentry 10707 (MO)	Venezuela, Bolívar, Anacoco			
***Tanaecium bilabiatum* 4**	**Lohmann 850 (SPF)**	**Brazil, Amazonas, Anavilhanas**			
Tanaecium caudiculatum 1	Balick 2631 (NY)	Belize, Stann Creek District, Cockscomb Basin.	Kaehler et al. (2019)		Kaehler et al. (2019
Tanaecium caudiculatum 2	Meave 1299 (MO)	Belize, Cayo			
***Tanaecium crucigerum* 1**	**Lohmann 355 (MO)**	**USA, Missouri, Cult. Missouri Botanical Garden**			**DQ222811**
Tanaecium crucigerum 2	Thomas 3522 (NY)	Venezuela, Cojedes			
Tanaecium cyrtanthum 1	Santo 104 (SPF, VASF)	Brazil, Bahia, Jaguarari			
***Tanaecium cyrtanthum* 2**	**Frazão 173 (SPF)**	**Brazil, Ceará, Aiuaba,**			
Tanaecium cyrtanthum 3	Oliveira 1102 (IBGE, K)	Brazil, Goiás, São Domingos	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium cyrtanthum 4	Oliveira 4030 (SPF, VASF)	Brazil, Ceará, Mauriti			
Tanaecium cyrtanthum 5	Andrade 282 (EAC)	Brazil, Ceará, Aiuaba			
***Tanaecium decorticans* 1**	**Frazão 188 (SPF)**	**Brazil, Pará, Belterra**			**MH765565**

Tanaecium decorticans 2	Frazão 197 (SPF)	Brazil, Pará, Santarém	MH790867		MH765568
Tanaecium decorticans 3	Frazão 210 (SPF)	Brazil, Pará, Belterra	MH790869		MH765566
Tanaecium decorticans 4	Frazão 220 (SPF)	Brazil, Pará, Óbidos	MH790873		MH765567
[$]***Tanaecium dichotomum* 1α**	**Frazão 375 (SPF)**	**Brazil, Mato Grosso, Peixoto de Azevedo**			
[$]***Tanaecium dichotomum* 2β**	**Carvalho 14 (SPF)**	**Brazil, Mato Grosso do Sul, Porto Murtinho**			
Tanaecium dichotomum 3α	Frazão 329 (SPF)	Brazil, Mato Grosso, Paranaíta			
Tanaecium dichotomum 4α	Frazão 416 (SPF)	Brazil, Acre, Rio Antimary			
Tanaecium dichotomum 5β	Carvalho 18 (SPF)	Brazil, Mato Grosso do Sul, Aquidauana			
Tanaecium dichotomum 6α	Frazão 247 (SPF)	Brazil, Goiás, Colinas do Sul			
Tanaecium dichotomum 7γ	Nogueira 321 (SPF)	Brazil, Bahia, Jussiape	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium dichotomum 8γ	Paula-Souza 10975 (RB)	Brazil, Ceará, Santa Quitéria		Kaehler et al. (2019	Kaehler et al. (2019
Tanaecium dichotomum 9γ	Figueiredo 233 (SPF)	Brazil, Pernambuco, Buíque	Kaehler et al. (2019		
Tanaecium dichotomum 10γ	Colombo 26 (UFRN)	Brazil, Rio Grande do Norte, Bento Fernandes	Kaehler et al. (2019	Kaehler et al. (2019	Kaehler et al. (2019
Tanaecium dichotomum 11δ	Labiak 2765 (SPF, UPCB)	Bolívia, Santa Cruz, Puerto Soares	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium dichotomum 12α	Lohmann 549 (SPF, NY)	Brazil, Acre, Xapuri	Kaehler et al. (2019	Kaehler et al. (2019	Kaehler et al. (2019
Tanaecium duckei 1	Frazão 409 (SPF)	Brazil, Acre, Bujari			
***Tanaecium duckei* 2**	**Frazão 309 (SPF)**	**Brazil, Amazonas, Reserva Florestal Ducke**			
Tanaecium duckei 3	Frazão 339 (SPF)	Brazil, Mato Grosso, Cotriguaçu			
Tanaecium duckei 4	Frazão 205 (SPF)	Brazil, Pará, Belterra			
Tanaecium duckei 5	Frazão 219 (SPF)	Brazil, Pará, Óbidos			
Tanaecium jaroba 1	Pace 585 (SPF)	Brazil, Mato Grosso do Sul, Corumbá			
***Tanaecium jaroba* 2**	**Frazão 288 (SPF)**	**Brazil, Roraima, Caracaraí**			
Tanaecium jaroba 3	Gomes 598 (SPF)	Brazil, Amazonas, Novo Airão			
Tanaecium jaroba 4	Gomes 642 (SPF)	Brazil, Roraima, Rorainópolis			
Tanaecium jaroba 5	Frazão 145 (SPF)	Brazil, Roraima, Rorainópolis			
Tanaecium parviflorum 1	Siniscalchi 624 (SPF)	Brazil, Bahia, Gentio de Ouro			
Tanaecium parviflorum 2	Fonseca 263 (SPF)	Brazil, Minas Gerais, Itaobim	Kaehler et al. (2019		Kaehler et al. (2019
***Tanaecium parviflorum* 3**	**Fonseca 280 (SPF)**	**Brazil, Bahia, Itaberaba**			**Kaehler et al. (2019**
Tanaecium parviflorum 4	Farias-Fonseca 77 (RB)	Brazil, Pernambuco, Tupanatinga	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium pyramidatum 1	Silva 1 (HUFU)	Brazil, Minas Gerais, Delfinópolis	MH790864		MH765564
Tanaecium pyramidatum 2	Lohmann 274 (SPF)	Brazil, Amazonas, Rio Solimões	DQ222618		DQ222782

Tanaecium pyramidatum 3	Lohmann 264 (SPF)	Brazil, Minas Gerais, Uberlândia	MH790866		
Tanaecium pyramidatum 4	Forzza 6785 (RB)	Brazil, Roraima, Caracaraí	MH790865		
[$]***Tanaecium pyramidatum* 5**	**Fonseca 321 (SPF)**	**Amazonas, Novo Airão, Parque Nacional de Anavilhanas**			
Tanaecium pyramidatum 6	Fonseca 315 (SPF)	Amazonas, Novo Airão			MH765569
Tanaecium pyramidatum 7	Francisco 44 (SPF)	Brazil, Roraima, Caracaraí	MH790871		MH765570
Tanaecium revillae 1	Frazão 298 (SPF)	Brazil, Roraima, Caracaraí			
Tanaecium revillae 2	Fonseca 310 (SPF)	Brazil, Amazonas, Novo Airão, Parque Nacional de Anavilhanas	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium revillae 3	Fonseca 320 (SPF)	Brazil, Amazonas, Novo Airão			
Tanaecium revillae 4	Frazão 275 (SPF)	Brazil, Roraima, Caracaraí			
Tanaecium revillae 5	Frazão 276 (SPF)	Brazil, Roraima, Caracaraí			
[$]***Tanaecium revillae* 6**	**Kataoka 321 (SPF)**	**Brazil, Roraima, Caracaraí**			
Tanaecium revillae 7	Gomes 597 (SPF)	Brazil, Amazonas, Novo Airão, Parque Nacional de Anavilhanas	Kaehler et al. (2019		Kaehler et al. (2019
[$]***Tanaecium selloi* 1**	**Frazão 235 (SPF)**	**Brazil, Rio de Janeiro, Engenheiro Paulo de Frontin**			
Tanaecium selloi 2	Frazão 435 (SPF)	Brazil, Rio de Janeiro, Vassouras			
Tanaecium selloi 3	Lohmann 702 (SPF)	Brazil, Paraíba, Guarabira	DQ222560		DQ222696
Tanaecium selloi 4	Kaehler 415 (UPCB)	Brazil, Paraná, Iretama			
Tanaecium selloi 5	Kaehler 420 (UPCB)	Brazil, Paraná, Campo Mourão			
Tanaecium tetragonolobum 1	Frazão 357 (SPF)	Brazil, Mato Grosso, Cotriguaçu			
***Tanaecium tetragonolobum* 2**	**Frazão 419 (SPF)**	**Brazil, Acre, Bujari**			
Tanaecium tetragonolobum 3	Lohmann 619 (MO)	Peru, Madre de Dios, Manu National Park	DQ222568		DQ222707
***Tanaecium tetragonolobum* 4**	**Lohmann 619 (MO)**	**Peru, Madre de Dios, Manu National Park**	KR534325	KR534325	
Tanaecium tetramerum 1	Antezana-Valera 1327 (BOLV, MO)	Bolívia, Cochabamba, Campero	KU757040		KU757043
Tanaecium tetramerum 2	Pace 32 (SPF)	Bolívia, Santa Cruz, Valle Grande	KU757039		KU757041
[$]***Tanaecium tetramerum* 3**	**Pace 31 (SPF)**	**Bolívia, Santa Cruz, Valle Grande**			
***Tanaecium truncatum* 1**	**Frazão 340 (SPF)**	**Brazil, Mato Grosso, Cotriguaçu**			
Tanaecium truncatum 2	Frazão 311 (SPF)	Brazil, Amazonas, Manaus			
Tanaecium truncatum 3	Fonseca 307 (SPF)	Brazil, Amazonas, Novo Airão			
Tanaecium truncatum 4	Fonseca 308 (SPF)	Brazil, Amazonas, Novo Airão			
Tanaecium xanthophyllum 1	Vásquez 22631 (MO)	Peru, Amazonas, Condorcanqui			
Tanaecium xanthophyllum 2	Udulutsch 2779 (SPF)	Brazil, Mato Grosso, Nova Lacerda	Kaehler et al. (2019		Kaehler et al. (2019
Tanaecium xanthophyllum 3	Ribeiro s.n. (HERBAM)	Brazil, Mato Grosso, Nova Bandeirantes			
[$]***Tanaecium xanthophyllum* 4**	**Frazão 333 (SPF)**	**Brazil, Mato Grosso, Paranaíta**			
Tanaecium xanthophyllum 5	Frazão 422 (SPF)	Brazil, Acre, Bujari			

Graphical abstract



- Uma espécie nova apresentada nesta tese [i.e. *Tanaecium decorticans* Frazão & L.G.Lohamnn].
- Uma nova combinação foi proposta e *Tanaecium mutabile* (Bureau & K.Schum.) L.G. Lohmann foi transferido para o gênero *Fridericia* [=*F. mutabilis* (Bureau & K.Schum.) L.G.Lohmann].
- A tipificação do gênero foi revisada e um epítipo foi designado.
- Duas lectotipificações foram propostas para os seguintes nomes: (1) *Arrabidaea muehlbergiana* Hassl. [= *F. mutabilis*] e (2) *Tanaecium crucigerum* Seem.
- Apresentamos uma sinopse atualizada para *Tanaecium*, o qual contém, ao final deste estudo, 21 espécies, incluindo a nova combinação de *Spathicalyx kuhlmannii* J.C.Gomes em *Tanaecium kuhlmannii* (J.C.Gomes) Frazão & L.G.Lohmann.
- Apresentamos a montagem de 16 genomas de cloroplasto (=plastomas) para 15 espécies de *Tanaecium* (duas amostras de *Tanaecium dichotomum* (Jacq.) Kaehler & L.G.Lohmann, morfotipos α e β), sendo oito com plastoma completo e oito com plastoma quase completo.
- Os plastomas obtidos para *Tanaecium* variam entre 157,807 pb (*T. crucigerum*) até 160,935 pb (*Tanaecium xanthophyllum* (DC.) L.G.Lohmann).
- Quatro principais padrões referentes às mudanças dos limites das IRs foram detectadas, onde as SSC (variando de 12,498 pb a 49,868 pb de comprimento) e LSC (variando de 83,490 pb a 89,092 pb) apresentaram expansões associadas e contrações em diferentes graus das IRs (variando de 11,409 pb a 30,961 pb).
- Combinamos os dados dos plastomas e sequências geradas pelo método Sanger em uma supermatriz somando um total de 92 espécimens representando 17 espécies de *Tanaecium* mais 14 representantes do grupo-externo.
- A filogenia de *Tanaecium* reconstruída aqui é a mais robusta já realizada até o momento, incluindo múltiplos acessos para 17 das 21 espécies reconhecidas no gênero.
- A combinação do conjunto de dados gerados por sequenciamento Sanger e sequenciamento em grande escala (HTS) permitiu maximizar a amostragem de taxa e caráteres para a reconstrução da filogenia de *Tanaecium*.
- *Tanaecium* é um gênero monofilético.
- Os diferentes morfotipos amostrados para *Tanaecium dichotomum* emergiram em diferentes linhagens, sendo que apenas o morfotipo β emergiu como monofilético.

- Estudos moleculares, morfológicos e taxonômicos são necessários para *T. dichotomum* objetivando a revisão da delimitação desta espécie.
- Futuros estudos incluindo um alto número de marcadores nucleares serão importantes no que diz respeito ao aumento de resolução do arcabouço filogenético de *Tanaecium*.
- Esta tese destaca a importância de estudos aprofundados de linhagens individuais, incluindo estudos detalhados em taxonomia, distribuição e relações evolutivas, para o entendimento da composição de biotas de regiões megadiversas tais como o Neotrópico.