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Filogenia de *Butia* (Arecaceae): um gênero de palmeiras sul-americano

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RESUMO

ELLERT-PEREIRA, Paulo Eduardo. Filogenia de *Butia* (Arecaceae): um gênero de palmeiras sul-americano. 2019. 62 f. Tese de Doutorado – Programa de Pós-graduação em Agronomia, Universidade Federal de Pelotas, Pelotas, 2019.

A classificação de *Butia* é controversa e até mesmo trabalhos recentes de natureza taxonômica não são consensuais em relação ao número de espécies reconhecidas no gênero. Tampouco as relações filogenéticas dentre as espécies estão esclarecidas. Uma sinopse nomenclatural e taxonômica abrangente para *Butia* é necessária para ajudar a esclarecer a atual sistemática do gênero. Uma sinopse taxonômica de todos os nomes publicados dentro do gênero *Butia* é apresentada. Desde a primeira descrição das espécies que hoje compõem o gênero, 97 nomes foram publicados, divididos entre os gêneros *Butia*, *Cocos* e *Syagrus*. Subordinados a *Butia*, 58 nomes foram publicados (36 espécies, quatro subespécies e 20 variedades), dos quais 21 são atualmente reconhecidos como espécies aceitas (*B. archeri, B. arenicola, B. campicola, B. capitata, B. catarinensis, B. eriospatha, B. exilata, B. exospadix, B. lallemantii, B. lepidotispatha, B. leptospatha, B. marmorii, B. matogrossensis, B. microspadix, B. odorata, B. paraguayensis, B. poni, B. pubispatha, B. purpurascens, B. witeckii* e *B. yatay*). Além disso, dois híbridos naturais entre *Butia* e *Syagrus* são reconhecidos: × *Butyagrus nabonnandii* (*B. odorata* × *Syagrus romanzoffiana*) e × *Butyagrus alegretensis* (*B. lallemantii* × *S. romanzoffiana*). Do ponto de vista filogenético, há uma escassez de regiões de DNA úteis para a pesquisa em palmeiras. Alguns estudos filogenéticos recentes utilizam com eficiência regiões do DNA nuclear como ITS e WRKY e cloroplastidial como *trn*H-*psb*A. Apesar do já confirmado monofiletismo de *Butia*, as relações filogenéticas entre as espécies pertencentes a este gênero ainda não haviam sido elucidadas. No presente estudo, após extração do DNA, síntese, purificação e sequenciamento das regiões do DNA ITS, *trn*H-*psb*A e WRKY19, confirmou-se o monofiletismo do gênero como grupo-irmão de *Jubaea*. Apesar da utilização frequente de regiões cloroplastidiais na reconstrução de filogenias, no presente estudo a região *trn*H-psbA não apresentou resolução filogenética suficiente para reconstruir a história evolutiva de *Butia* de forma congruente quando comparado com os dados nucleares de ITS e WRKY19. De modo geral, a filogenia obtida apresentou uma forte estruturação geográfica, embora as espécies do Cerrado formem um grupo parafilético. Por outro lado, as espécies do Cone Sul da América do Sul formam um grupo monofilético do qual *Butia lepidotispatha*, uma espécie do cerrado, emerge como espécie-irmã do clado composto pelas espécies do Cone Sul, encontradas tanto nos Domínios da Mata Atlântica quanto do Pampa. Do ponto de vista morfológico, é possível observar que o hábito graminiforme evoluiu independentemente várias vezes no gênero *Butia*, evidenciando a convergência evolutiva dessa característica em linhagens não proximamente relacionadas. Quando os resultados são interpretados geograficamente, é possível observar que muitas das relações filogenéticas entre as espécies do gênero seguem um padrão consistente. Da mesma forma, é possível observar diversas características morfológicas compartilhadas ao analisar-se comparativamente a morfologia de espécies-irmãs.

Palavras-chave: butiá; butiazeiros; evolução; sistemática

ABSTRACT

ELLERT-PEREIRA, Paulo Eduardo. Phylogeny of *Butia* (Arecaceae): a South American palm genus. 2019. 62 f. Ph.D. thesis – Programa de Pós-graduação em Agronomia, Universidade Federal de Pelotas, Pelotas, 2019.

Butia classification is controversial and even recent taxonomic studies are not consensual about the number of species recognized in the genus. Nor are the phylogenetic relationships among species clear. A comprehensive nomenclatural and taxonomic synopsis for *Butia* is needed to help to clarify the current genus systematics. A taxonomic synopsis of all names published within *Butia* is presented. Since the first description of species, 97 names have been published, divided between the genera *Butia*, *Cocos* and *Syagrus*. Subordinated to *Butia*, 58 names have been published (36 species, 4 subspecies and 20 varieties) of which 21 are currently recognized as accepted species *(B. archeri, B. arenicola, B. campicola, B. capitata, B. catarinensis, B. eriospatha , B. exilata, B. exospadix, B. lallemantii, B. lepidotispatha, B. leptospatha, B. marmorii, B. matogrossensis, B. microspadix, B. odorata, B. paraguayensis, B. poni, B. pubispatha, B. purpurascens, B. witeckii* and *B. yatay).* In addition, two natural hybrids between *Butia* and *Syagrus* are recognized: × *Butyagrus nabonnandii* (*B. odorata* × *Syagrus romanzoffiana*) and × *Butyagrus alegreetensis* (*B. lallemantii* × *S. romanzoffiana*). From a phylogenetic point of view, there is a constraint of DNA regions useful for palm research. Some recent phylogenetic studies have efficiently used nuclear DNA regions like ITS and WRKY and chloroplastidial like *trn*H-*psb*A. Despite *Butia*'s already confirmed monophyly, the phylogenetic relationships among species belonging to this genus had not yet been elucidated. In the present study, after DNA extraction, synthesys, purification and sequencing of the ITS, *trn*H-*psb*A, and WRKY19 regions, the monophyly of the genus was confirmed and *Jubaea* was recovered as its sister group. Despite the frequent use of chloroplast regions in the construction of phylogenies, in the present study the *trn*H-*psb*A region did not present enough phylogenetic resolution to coherently reconstruct *Butia*'s evolutionary history when compared to the ITS and WRKY19 core data. In general, the phylogeny obtained showed a strong geographical structure, although the Cerrado species form a paraphyletic group. On the other hand, species from southern South America form a monophyletic group from which *Butia lepidotispatha*, a species from the Cerrado, was recovered as the sister species of the southern clade, found in both the Atlantic Forest and Pampa regions. From the morphological point of view, it is possible to observe that the graminiform habit evolved independently several times in the genus *Butia*, evidencing the evolutionary convergence of this trait in non-closely related lineages. When the results are interpreted geographically, it is possible to observe that the species relationships follow a consistent geographic pattern of distribution. Similarly, it is possible to observe several shared morphological characteristics by comparing the morphology of sister species.

Keywords: evolution; jelly palm fruit; pindo palm; systematic

SUMÁRIO

1. INTRODUÇÃO GERAL

Arecaceae compreende 185 gêneros e 2522 nomes aceitos de espécies (THE PLANT LIST, 2019), constituindo a terceira mais importante família de plantas para uso humano (JOHNSON, 1998; HAHN, 2002). A família distribui-se nos trópicos e subtrópicos (HAHN, 2002), adaptando-se a uma variedade de climas e solos, principalmente no clima equatorial úmido, onde apresenta maior número de espécies, especialmente na Malésia, Ásia tropical e América equatorial (SOARES, 2013). No Brasil ocorrem 37 gêneros e 299 espécies (FLORA DO BRASIL ON LINE 2020 EM CONSTRUÇÃO, 2019).

A família apresenta diversos usos, além de abundância e produtividade, sendo importante dos pontos de vista alimentar, medicinal, sócio-cultural e econômico para populações locais (ZAMBRANA et al., 2007). *Phoenix dactylifera* L. (tamareira), por exemplo, é uma espécie de importante valor comercial (ZAID; deWET, 2002), que apresenta fruto mais adocicado que outras espécies cultivadas da família, além de ser a única espécie de *Phoenix* L. usada como base alimentar, sendo importante para milhões de pessoas em diferentes partes do mundo (ZAID; deWET, 2002).

A sistemática de Arecaceae baseia-se principalmente na morfologia dos estipes, folhas, flores, frutos e particularidades anatômicas dos órgãos, diferenças citológicas e histológicas, além da distribuição geográfica e estudos evolutivos da família e seus gêneros (HENDERSON et al., 1995; DRANSFIELD et al., 2008; LORENZI, 2010; SOARES et al., 2014). Entre os gêneros de Arecaceae com maior importância econômica e paisagística no Brasil, destaca-se *Butia* (Becc.) Becc., composto por palmeiras denominadas butiazeiros ou butiás (LORENZI et al., 2010), que se caracterizam por apresentar comportamento gregário, formando populações conhecidas como butiazais ou palmares (MARCATO, 2004).

Espécies de *Butia* podem ser encontradas em campos, em associações com matas com araucária, em cerrados, em restingas arbustivas, ou, mais raramente, em matas de galeria, conforme as preferências ecológicas de cada espécie (HEIDEN, 2010). As espécies de *Butia* ocorrem naturalmente em áreas das regiões Nordeste (BA), Centro-Oeste (GO, MS), Sudeste (MG, SP) e Sul (PR, SC, RS) do Brasil, no

leste do Paraguai, no nordeste da Argentina e no Uruguai (MARCATO, 2004; LORENZI et al., 2010; FLORA DO BRASIL 2020 EM CONSTRUÇÃO, 2019).

O uso dos frutos dos butiazeiros, os butiás, como alimento, remete aos primeiros habitantes do sul do Brasil: os indígenas, que consumiam tanto a polpa do fruto como as sementes (ROSSATO, 2007). No início do século XX, as folhas dos butiazeiros foram usadas para a produção de crina vegetal, um tipo de fibra utilizada para preenchimento de colchões e mobiliário estofado (BONDAR, 1964). Os ecossistemas de butiazais são fonte de informação cultural, de produção, além da importância na manutenção dos habitats nos quais encontram-se inseridos. São espécies melíferas, que durante a floração atraem grande diversidade de insetos. Seus frutos, de dispersão zoocórica, servem de recurso alimentar (com oferta de frutos por períodos prolongados) para uma série de animais frugívoros, principalmente aves e mamíferos. Essas características tornam os butiás espécies-chave nas relações ecológicas dos ecossistemas que habitam (ROSA et al., 1998).

Entre os principais argumentos sobre a importância da conservação da biodiversidade citados por Hassler (2005) estão: a contribuição econômica e o valor estético, além do direito de existir das espécies. Atualmente, além do consumo in natura, o butiá é usado para a produção de vários tipos de alimentos e bebidas tais como geleias, sorvetes, bombons, mousses, sucos e licores. As fibras das folhas e da polpa dos frutos são utilizadas no artesanato, para produção de objetos decorativos e utilitários, como cestas, chapéus, bolsas e redes. A produção de sucos, licores e geleias de butiá é uma fonte alternativa de renda em alguns lugares do Rio Grande do Sul, a qual pode ser expandida com o desenvolvimento de novos produtos (BÜTTOW et al., 2010).

A importância dos butiás na alimentação é reforçada por Fonseca (2012) que detectou altos níveis de minerais na polpa dos frutos de *Butia odorata*, especialmente ferro, manganês e potássio, além da presença de compostos bioativos com concentrações elevadas de compostos fenólicos totais, vitamina C e carotenoides. Essas palmeiras também são usadas no paisagismo rural e urbano. Além disso, a produção de óleos de boa qualidade a partir das sementes tem potencial de uso em diferentes setores da indústria, tanto alimentícia como farmacêutica e cosmética (ROSSATO, 2007).

Desde a descrição original do gênero por Beccari (1916), *Butia* apresenta histórico taxonômico complexo, com casos de equívocos na aplicação de nomes

científicos, sinonimizações e revalidações de nomes, além de inúmeras divergências entre os taxonomistas quanto ao número de espécies que o compõem, não havendo consenso nas publicações recentes sobre o total de espécies existentes. O número de espécies reconhecidas varia entre 11 (MARCATO, 2004), 18 (NOBLICK, 2010), 20 (SOARES, 2015), 21 (HEIDEN et al., 2018) e 24 (DEBLE et al., 2017). Atualmente considera-se que o gênero compreenda 21 espécies, sendo 20 encontradas no Brasil (à exceção de *B. marmorii* Noblick, exclusiva do Paraguai), distribuídas nas Regiões Nordeste, Centro-Oeste, Sudeste e Sul (HEIDEN et al., 2019) e também no leste do Paraguai, no nordeste da Argentina e no Uruguai (ESLABÃO et al., 2016; HEIDEN et al., 2019).

Desde a primeira descrição de espécie que hoje compõe o gênero [*Cocos capitata* Mart. em 1826, hoje *Butia capitata* (Mart.) Becc.], 97 nomes foram publicados, divididos entre os gêneros *Butia*, *Cocos* L. e *Syagrus* Mart.. Subordinadas a *Butia* encontram-se nomes de 36 espécies, 4 subespécies e 20 variedades das quais as 21 espécies aceitas atualmente são: *B. archeri* (Glassman) Glassman, *B. arenicola* (Barb.Rodr.) Burret, *B. campicola* (Barb.Rodr.) Noblick, *B. capitata*, *B. catarinensis* Noblick & Lorenzi, *B. eriospatha* (Mart. ex Drude) Becc., *B. exilata* Deble & Marchiori, *B. exospadix* Noblick, *B. lallemantii* Deble & Marchiori, *B. lepidotispatha* Noblick & Lorenzi, *B. leptospatha* (Burret) Lorenzi, *B. marmorii*, *B. matogrossensis* Noblick & Lorenzi, *B. microspadix* Burret, *B. odorata* (Barb.Rodr.) Noblick, *B. paraguayensis* (Barb.Rodr.) Bailey, *B. poni* (Hauman) Burret, *B. pubispatha* Noblick & Lorenzi, *B. purpurascens* Glassman, *B. witeckii* K.Soares & S.Longhi e *B. yatay* (Mart.) Becc. (HEIDEN et al., 2019). Além disso, conforme Soares et al. (2014), dois híbridos naturais entre *Butia* e *Syagrus* são reconhecidos: × *Butyagrus nabonnandii* (Prosch.) Vorster [*B. odorata* × *Syagrus romanzoffiana* (Cham.) Glassman] e × *Butyagrus alegretensis* K.Soares (*B. lallemantii* × *S. romanzoffiana*).

Dentre as espécies com maiores problemas de identificação, destaca-se *B. capitata*, espécie presente em Goiás, Bahia e Minas Gerais, cujo nome era erroneamente aplicado a populações de *B. catarinensis*, do litoral de Santa Catarina e Rio Grande do Sul, e *B. odorata*, do Rio Grande do Sul e Uruguai. Martius (1826) descreveu *C. capitata,* enquanto Barbosa Rodrigues (1903) descreveu *C. odorata*; Beccari (1916) propôs *B. capitata* var. *odorata* e posteriormente Glassman (1979), sinonimizou ambos os nomes a *B. capitata.* Desde então, muitas foram as tentativas

de validação do nome *B. odorata*, como *B. odorata* (Barb. Rodr.) Noblick & Pirani, e *B. odorata* (Barb.Rodr.) Noblick & Lorenzi, sem a publicação efetiva, até a publicação válida de *B. odorata* (Barb.Rodr.) Noblick por Noblick (2011).

Da mesma forma, outro fator que promove a variação no número de espécies reconhecidas são os casos de nomes recentemente descritos como *B. missionera* Deble & Marchiori e *B. quaraimana* Deble & Marchiori, considerados sinônimos de *B. yatay* (SOARES et al., 2014) ou dúbios, como *B. noblickii* Deble, Marchiori, F.S.Alves & A.S.Oliveira (SOARES, 2015). Também, casos como de *B. stolonifera* (Barb.Rodr.) Becc. (1916), nome que não é possível determinar a qual espécie se refere, pela falta de designação de um espécime-tipo de referência e vaga descrição no trabalho original, e *B. leiospatha* (Barb.Rodr.) Becc. (1916), considerada espécie dúbia por ter sido descrita como uma planta acaulescente, porém ilustrada como arbórea, além da ausência de material de referência em herbário, dificultam ainda mais a determinação dos limites do gênero. Citações errôneas ou equivocadas também podem ser observadas e prejudicam uma melhor compreensão das relações entre as espécies, como Sant'Anna-Santos et al. (2018), que atribuem a Heiden et al. (2018) a consideração de *B. leiospatha* sinônimo de *B. lallemantii*, fato não mencionado pelos referidos autores.

Nos últimos anos, muitas novas espécies foram descritas. De 2006 até o presente momento, 9 das 21 espécies aceitas foram descritas: *B. exospadix, B. lallemantii* e *B. marmorii* foram descritas em 2006; *B. pubispatha*, *B. catarinensis, B. lepidotispatha* e *B. matogrossensis* em 2010; *B. exilata* e *B. witeckii* em 2011 (NOBLICK, 2006; DEBLE; MARCHIORI, 2006; LORENZI et al., 2010; DEBLE; MARCHIORI, 2011; SOARES; LONGHI, 2011). Recentemente, em 2017, o nome *B. poni*, até então considerado sinônimo de *B. paraguayensis,* foi revalidado e elevado ao nível de espécie. Todas essas novas espécies não estão representadas em estudos filogenéticos (HAHN, 2002; MEEROW et al., 2009), principalmente porque foram recentemente descritas e porque há uma escassez de regiões de DNA úteis para a pesquisa filogenética em palmeiras. Baker et al. (1999) apresentaram uma filogenia de palmeiras baseada em sequências de DNA do espaçador intergênico *trn*L-*trn*F. Lewis & Doyle (2001) relataram o desenvolvimento e uso de primers para amplificação e sequenciamento de regiões do gene nuclear da malato-sintase. Hahn (2002) baseou seu estudo em dados de sequenciamento de DNA nuclear (18S SSU

rRNA) e DNA cloroplastidial (atpB e rbcL) para 65 gêneros de palmeiras. Contudo, estudos filogenéticos abrangentes de *Butia* não foram conduzidos até o momento.

Asmussen & Chase (2001) indicam que sequências de DNA plastidial são modificadas lentamente nas palmeiras, mas mostram que a família é monofilética e altamente divergente em relação a outros grandes clados de monocotiledôneas. Meerow et al*.* (2009) corroboram o monofiletismo dos gêneros pertencentes à subtribo Attaleinae, incluindo *Butia*, analisando os loci dos fatores de transcrição WRKY, que apontam um clado de espécies africanas como grupo-irmão do clado americano que inclui *Butia*. Cuenca et al*.* (2008), apontam *Butia* como grupo-irmão de *Jubaea* Kunth, que está perto de outros dois clados, compostos por *Syagrus* Mart. + *Allagoptera* Nees, e *Attalea* Kunth + *Cocos* L., enquanto Meerow et al. (2009) corroboram *Butia-Jubaea* como grupos-irmãos, e este clado relacionado a *Allagoptera*, *Parajubaea* Burret e *Polyandrococos* Barb.Rodr. Apesar do monofiletismo confirmado de *Butia*, as relações filogenéticas entre suas espécies ainda não foram elucidadas.

Outro fator que destaca *Butia* como um gênero a ser estudado mais profundamente a fim de elucidar as dúvidas na sua composição de espécies, é o fato de que duas espécies estão na Lista Mundial de Espécies Ameaçadas (IUCN, 2018), seis encontram-se ameaçadas de extinção no Brasil (MARTINELLI; MORAES, 2013), e oito estão na lista de espécies da flora ameaçadas de extinção no Rio Grande do Sul (FUNDAÇÃO ZOOBOTÂNICA DO RS, 2018). Várias dessas espécies são alvo de extrativismo em maior parte sustentável, para exploração de fibras e frutos, mas muitas vezes predatório, para a obtenção de plantas para o paisagismo (NAZARENO et al., 2011) e sobre-extrativismo de folhas para a obtenção de fibras, que podem ocasionar a morte dos indivíduos explorados inadequadamente como em *B. purpurascens* (ESLABÃO, 2017). Eslabão et al. (2019, no prelo) apontam que 20 das 21 espécies de *Butia* encontra-se em algum estado de ameaça, sendo cinco espécies (*B. exilata, B. leptospatha, B. poni, B. purpurascens* e *B. witeckii*) Criticamente Ameaçadas (CR – Critically Endangered), três (*B. exospadix, B. lallemantii* e *B. marmorii*) consideradas Em Perigo (EN – Endangered) e 11 (*B. arenicola, B. campicola, B. capitata, B. catarinensis, B. eriospatha, B. lepidotispatha, B. matogrossensis, B. microspadix, B. odorata, B. paraguayensis* e *B. yatay*) consideradas Vulneráveis (VU – Vulnerable). Somente *B.*

archeri não foi enquadrada nos critérios de ameaça apresentados, sendo considerada como Quase Ameaçada (NT – Near Threatened).

Apesar dos usos tradicionais e do grande potencial que representa para o mercado, só recentemente a comunidade científica passou a dedicar maior atenção para o butiá, os butiazeiros e os butiazais, sendo que o grupo de pesquisa da Embrapa Clima Temperado teve papel relevante nesse processo. Projetos que promovem a valorização dos butiazeiros reforçam a necessidade do melhor e maior conhecimento das espécies. Coordenada pela Embrapa Clima Temperado, com o apoio do Ministério do Meio Ambiente, além de instituições de ensino e pesquisa, ONGs e iniciativa privada, a Rota dos Butiazais é um exemplo de espaço de integração que une Brasil, Uruguai, Paraguai e Argentina, promovendo a valorização e conservação ambiental e o uso sustentável da biodiversidade associada aos butiazais, atuando onde existem remanescentes de butiazais ou onde o butiá representa importante componente da paisagem (EMBRAPA CLIMA TEMPERADO, 2018).

Dessa forma, uma sinopse nomenclatural e taxonômica abrangente e uma hipótese filogenética para *Butia* são necessárias para esclarecer a atual taxonomia e evolução do grupo, contribuindo com informações básicas necessárias para a conservação e uso sustentável dos recursos genéticos do gênero. Assim é possível entender a diversidade de espécies incluídas neste gênero e possibilitar uma melhor compreensão das conexões florísticas entre os tipos de vegetações abertas do sudeste da América do Sul, resultando em informações para subsidiar ações de conservação e uso sustentável dessas espécies e dos ecossistemas onde elas ocorrem.

2. OBJETIVOS

2.1 Objetivo geral

Prover informações sobre a nomenclatura e taxonomia e as relações filogenéticas das espécies do gênero *Butia.*

2.2 Objetivos específicos

Prover uma sinopse nomenclatural e taxonômica do gênero *Butia*, desde sua descrição e listando todos os nomes de espécies validamente publicados, incluindo espécies aceitas, sinonímias e informações atualizadas de tipo nomenclaturais, favorecendo identificações mais seguras para as espécies.

Gerar uma hipótese filogenética das relações evolutivas entre as espécies do gênero, buscando esclarecer a evolução de *Butia*.

3. A synopsis and notes for *Butia* (Arecaceae)

*Manuscrito a ser submetido ao periódico Phytotaxa (Qualis B1).

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Abstract

Butia classification is controversial and even contemporary studies of taxonomic nature are not consensual in relation to the number of species recognized in the genus. A comprehensive nomenclatural and taxonomic synopsis for *Butia* is necessary to help clarifying the current systematics of the genus. So, we herein provide a synopsis of all names published within the genus as a step towards a complete taxonomic revision of *Butia*. Since the first species description, 97 names were published, divided between the genus *Butia*, *Cocos* and *Syagrus*. Reporting to *Butia*, 58 names were published (36 species, 4 subspecies, 20 varieties), from which 21 are currently recognized as accepted species (*B. archeri*, *B. arenicola*, *B. campicola*, *B. capitata*, *B. catarinensis*, *B. eriospatha*, *B. exilata*, *B. exospadix*, *B. lallemantii*, *B. lepidotispatha*, *B. leptospatha*, *B. marmorii*, *B. matogrossensis*, *B. microspadix*, *B. odorata*, *B. paraguayensis*, *B. poni*, *B. pubispatha*, *B. purpurascens*, *B. witeckii* and *B. yatay*). In addition, two natural hybrids between *Butia* and *Syagrus* are recognized × *Butyagrus nabonnandii* (*B. odorata* × *Syagrus romanzoffiana*) and × *Butyagrus alegretensis* (*B. lallemantii* × *S. romanzoffiana*).

Keywords**:** Brazilian flora, jelly palm, Palmae, pindo palm

3.1 Introduction

Butia (Beccari 1887: 352) Beccari (1916: 489) (Arecoideae: Cocoseae: Attaleinae) comprises about 20 species in South America (Soares 2015; Flora do Brasil 2020 em construção, 2019) and following Meerow *et al.* (2009), based on 7 nuclear genes, it is a well-defined monophyletic genus. *Butia* classification is controversial and in contemporary taxonomic studies there is no agreement on the number of recognized species (Marcato 2004; Deble & Marchiori 2011; Soares *et al.* 2014; Mourelle *et al.* 2015). The taxonomical history of the genus is complex, with cases of misapplication of scientific names and there is no consensus in recent publications about the total number of recognized species, with several descriptions of new species and proposals of new synonyms (Deble & Marchiori 2011; Soares & Longhi 2011; Soares *et al.* 2014).

Meerow *et al.* (2009) supports the monophyly of the genera belonging to the subtribe Attaleinae, including *Butia*, by analyzing the loci of WRKY transcription factors, which point a clade of African species as sister to the American clade that includes *Butia*. Cuenca *et al.* (2008), point *Butia* as sister group of *Jubaea* (Kunth 1815: 308), which is close to two other clades, composed by *Syagrus* (Martius 1824: 18) plus *Allagoptera* (Nees 1821: 335), and *Attalea* (Kunth 1815: 309) plus *Cocos* (Linnaeus 1753: 1188), while Meerow *et al.* (2009) corroborate the *Butia-Jubaea* sister-relationship, and this clade relationship to *Allagoptera*, *Parajubaea* (Burret 1930: 48) and *Polyandrococos* (Barbosa Rodrigues 1901: 7). Despite the confirmed monophyly of *Butia*, the phylogenetic relationships among its species are not elucidated yet and defining how many names are accepted to the genus is a crucial step towards a comprehensive phylogenetic study.

The genus *Butia* was defined by Beccari (1916) based on the following main characteristics: stipe with bases of fallen leaves persistent or scars after the fall; visibly armed margin of pseudo-petioles; long, narrow, acuminate and double-ended leaves; peduncular

bract (spathe) glabrous or tomentose, presenting a smooth or slightly fluted surface; raquis of inflorescence with simple branching; long secondary raquis with triads of flowers in the basal part (one pistilated and two staminates) and in the rest only staminate flowers; globular, oval or conical fruits, with persistent perianth, thin exocarp and fibrous-mucilaginous mesocarp; bony, globular, oval or elliptic endocarp, with a smooth surface, containing 1-3 separate loci, each with one seed; seeds with homogeneous and oily endosperm, with more or less lateral embryo (cavity near the center of the endocarp). Recently, Marcato (2004) characterized the genus by the ascending arrangement of the leaflets in the leaves, forming a "v" in cross section, and by the presence of pores in the endocarp of the seeds.

The *Butia* classification is controversial and even contemporary studies of taxonomic nature are not consensual in relation to the number of species recognized in the genus (Mourelle et al., 2015). A comprehensive nomenclatural and taxonomic synopsis for *Butia* is here presented to help clarifying the current systematics of the genus. So, we herein provide a synopsis of all names published within the genus as a step towards a complete taxonomic revision of *Butia*.

3.2 Materials and Methods

A taxonomic survey of species were performed through consulting the databases Global Biodiversity Information Facility, International Plant Names Index, Lista de espécies da Flora do Brasil, Species Link, The Plant List, Tropicos® and specialized literature review; visit to the *Butia* collection of Jardim Botânico Plantarum (Nova Odessa, São Paulo, Brazil) and fieldworks on Brasília, Goiás and Rio Grande do Sul, Brazil. The species review were also made by consulting the herbaria BHCB, BHZB, BM, BOTU, CGMS, CEN, ECT, ESA, FLOR, HAS, HBML, HEPH, HJ, HPL, HUCS, HUFU, HURG, IAC, IBGE, ICN, JBAER, PACA, PEL, RB, SPF, UB, UFG, SPSF. The herbaria acronyms cited follow Thiers (2016).

3.3 Taxonomic history of *Butia*

The name *Butia* was first used as a subgenus of *Cocos* Linnaeus (1753: 1188) by Beccari (1887), in a preliminary study of palm trees. Barbosa Rodrigues (1903) made a subsection of *Butia* under *Cocos.* Afterwards, in a later paper, Beccari (1916) supplemented the study by a review, elevating *Butia* to generic status, in which nine distinct genera are recognized: *Barbosa* Beccari (1887: 339), *Rhyticocos* Beccari (1887: 350), *Arikury* Barbosa Rodrigues (1916: 445), *Arecastrum* (Drude 1895: 402) Beccari (1916: 446), *Syagrus* Martius (1824: 18), *Butia*, *Jubaea* Kunth (1815: 308), *Jubaeopsis* Beccari (1913: 171) and *Cocos*. *Butia* and the other considered subgenera in the previous publication [*Barbosa*, *Arecastrum* and *Glaziova* (Bureau 1868: 379)] were then raised to genera, and *Cocos* became a monotypic genus with *C. nucifera* Linnaeus (1753: 1188) as its only species.

The name *Butia* was used by Barbosa Rodrigues (1903) as a subsection of *Cocos* in "*Sertum Palmarum Brasiliensium*", recognizing the species with pseudo-petioles and jagged margin, endocarp with 1-3 seeds and homogeneous endosperm, thick and moderately high stem, including in this subsection *Cocos dyeriana* Barbosa Rodrigues (1903: 626), *C. eriospatha* Martius (1881: 424), *C. odorata* Barbosa Rodrigues (1891: 11), *C. pulposa* Barbosa Rodrigues (1891: 14), *C. stolonifera* Barbosa Rodrigues (1901: 40), *C. yatay* Martius (1844: 93) and *C. schizophylla* Martius (1826: 119), currently considered *Syagrus schizophylla* (Martius 1826: 119) Glassman (1968: 386).

When Beccari (1916) raised *Butia* to genus, seven species were recognized: *B. capitata* (Martius 1826: 78) Beccari (1916: 507) [previously *C. australis* Martius (1844: 95) and *C. capitata* Martius (1826: 114)], *B. eriospatha* (Martius ex Drude 1881: 424) Beccari (1916: 496) [previously *C. eriospatha* Martius ex Drude (1881: 424)], *B. leiospatha* (Barbosa Rodrigues 1877: 23) Beccari (1916: 520) [previously *C. lejospatha* Barbosa Rodrigues (1877: 23)], *B. yatay* (Martius 1844: 93) Beccari (1916: 498) [previously *C. yatay* Martius (1844:

93)], *B. stolonifera* (Barbosa Rodrigues 1901: 40) Beccari (1916: 492) [previously *C. stolonifera* Barbosa Rodrigues (1901: 40)], *B. bonneti* Beccari (1916: 492) [previously *C. bonneti* Linden (*nomen nudum*), *C. schizophylla* Barbosa Rodrigues, non Martius and *C. lejospatha* var. *angustifolia* (Drude 1881: 423)] and *B. pungens* Beccari (1916: 523); seven varieties of *B. capitata*: *B. capitata* var. *virescens* Beccari (1916: 495), the varieties *B. capitata* var. *elegantissima* (Chabaud 1905: 516) Beccari (1916: 157), *B. capitata* var. *erythrospatha* (Chabaud 1916: 516) Beccari (1916: 515) and *B. capitata* var. *lilaceiflora* (Chabaud 1906: 144) Beccari (1916: 518), previously described as *Cocos* by Chabaud [*C. elegantissima* Chabaud (1905: 516), *C. erythrospatha* Chabaud (1916: 516) and *C. lilaceiflora* Chabaud (1906: 144)], *B. capitata* var. *subglobosa* Beccari (1916: 513), previously *C. coronata* Chabaud, non Martius, and the varieties *B. capitata* var. *odorata* (Barbosa Rodrigues 1891: 11) Beccari (1916: 513), *B. capitata* var. *pulposa* (Barbosa Rodrigues 1891: 14) Beccari (1916: 516) and *B. yatay* var. *paraguayensis* (Barbosa Rodrigues 1899: 9) Beccari (1916: 503), previously described as *Cocos* by Barbosa Rodrigues [*C. odorata* Barbosa Rodrigues (1891: 11), *C. pulposa* Barbosa Rodrigues (1891: 14) and *C. paraguayensis* Barbosa Rodrigues (1899: 9)]. Beccari (1916) also mentions other species of *Cocos* as probably belonging to *Butia* [*C. arenicola* Barbosa Rodrigues (1903: 100), *C. amadelpha* Barbosa Rodrigues (1900: 7) and *C. wildemaniana* Barbosa Rodrigues (1903: 101)].

Nehrling (1929) relocated *C. argentea* (Engel 1865: 690), *C. nehrlingiana* (Abbott ex Nehrling 1927: 17) and *C. pulposa* (Barbosa Rodrigues 1891: 14) to *Butia.* Burret (1930) described *B. microspadix* (Burret 1929: 1050) and transferred *C. amadelpha, C. arenicola, C. poni* (Hauman 1919: 604, nom. inval.) [ICN Art. 36.1(b)] and *C. wildemaniana* to *Butia.* Bailey (1936) proposed the new combination *B. paraguayensis* (Barbosa Rodrigues 1899: 9) Bailey (1936: 47), currently accepted, and previously described by Barbosa Rodrigues

belonging to *Cocos. Butia capitata* var. *nehrlingiana* (Bailey 1930: 105) Bailey (1936: 33) and *B. capitata* var. *strictior* (Bailey 1936: 32) were also described as varieties to *B. capitata*. The name *Cocos dyerana* Barbosa Rodrigues (1903: 626) posteriorly was also recombined as *Butia dyerana* (Barbosa Rodrigues 1903: 626) Burret (1937: 696).

The difficulties of circumscribing *Butia* and *Syagrus* can be observed over time. Beccari (1916) created the combination *S. campicola* (Barbosa Rodrigues 1900: 6) Beccari (1916: 465) from *C. campicola* Barbosa Rodrigues (1900: 6); *C. amadelpha* Barbosa Rodrigues (1900: 7) and *C. arenicola* Barbosa Rodrigues (1903: 100) were recombined in *Butia* by Burret (1930) and then reallocated in *Syagrus* by Dahlgren (1936). Currently the binomials *B. arenicola* (Barbosa Rodrigues 1903: 100) Burret (1930: 1051) and *B. campicola* (Barbosa Rodrigues 1900: 6) Noblick (2004: 42) are accepted in *Butia*. Burret (1940) described *S. leptospatha* Burret (1940: 105), subsequently reallocated as *B. leptospatha* (Burret 1940: 105) Noblick (2006: 169).

Glassman (1970a; 1970b) initially considered *Butia* as a well-defined group within *Syagrus*, accepting only five species with jagged margin of pseudo-petioles [*S. arenicola* (Barbosa Rodrigues 1903: 100) Frambach ex Dahlgren (1970: 136), *S. capitata* (Martius 1826: 114) Glassman (1970: 143), *S. eriospatha* (Martius ex Drude 1881: 424) Glassman (1970: 145), *S. paraguayensis* (Barbosa Rodrigues 1899: 9) Glassman (1970: 151) and *S. yatay* (Martius 1844: 93) Glassman (1970: 157). The five species had already been included in *Butia* previously (Beccari 1916; Burret 1930). The author comments not accepting *Butia* as a genus due to the difficulty of differentiating the grooved peduncular bracts (*Syagrus*) from only striated (*Butia*) when analyzing herborized specimens.

However, Glassman (1979) restablished *Butia* again with the status of genus, describing *B. purpurascens* (Glassman 1979: 67) and transferring *S. archeri* (Glassman 1967: 235) to *Butia*. Although both species have smooth (not jagged) pseudo-petiole margins, the

species never present grooved peduncular bracts, an absolute character to distinguish *Butia* and *Syagrus*.

Throughout the study history of the genus, other varieties or subspecies were proposed, however they are invalid names or currently considered as synonyms: *B. capitata* subsp. *eucapitata* (Martius 1826: 114) Herter (1940: 148, nom. inval.), *B. capitata* subsp. *yatay* (Martius 1844: 93) Herter (1940: 148), *B. yatay* subsp. *paraguayensis* (Barbosa Rodrigues 1899: 9) Xifreda & Sanso (1996: 207), and *B. capitata* var. *purpurascens* (Glassman 1979: 67) Mattos (2008: 6, nom. inval.).

In the last two decades, the interest in the taxonomy of *Butia* was renewed mainly based on new specimens collected in previously underrepresented areas and available for studies and reevaluations of the circumscription of some previously described taxa. Many new species have been described such as *B. exospadix* Noblick (2006: 169), *B. lallemantii* Deble & Marchiori (2006: 2), *B. marmorii* Noblick (2006: 173), *B. catarinensis* Noblick & Lorenzi (in Lorenzi *et al.* 2010: 164), *B. lepidotispatha* Noblick (in Lorenzi *et al.* 2010: 170), *B. matogrossensis* Noblick & Lorenzi (in Lorenzi *et al.* 2010: 175), *B. pubispatha* Noblick & Lorenzi (in Lorenzi *et al.* 2010: 180), *B. exilata* Deble & Marchiori (2011: 5), and *B. witeckii* K. Soares e S.J. Longhi (2011: 204). However, some names recently proposed were readly synonymized such as *B. missionera* Deble & Marchiori (2011a: 5) and *B. quaraimana* Deble & Marchiori (2012: 12), or considered doubtful, for example *B. noblickii* Deble, Marchiori, F.S.Alves and A.S.Oliveira (2012: 7), which still causes divergences in the publications regarding the number of recognized species. While the new combinations *B. campicola* (Barbosa Rodrigues 1900: 6) Noblick (2004: 42) and *B. odorata* (Barbosa Rodrigues 1891: 11) Noblick (2011: 48) were proposed and Deble *et al.* (2017) revalidated the name *Butia poni* as a species.

Among the species with recurrent identification problems, we highlight *B. capitata*, a species that occurs in Bahia, Goiás and Minas Gerais, Brazil. This name was erroneously applied to populations of *B. catarinensis* from Rio Grande do Sul and Santa Catarina (Brazil) and *B. odorata* of Rio Grande do Sul and Uruguay. The validation of the name *B. odorata* had several attempts until it was proceeded by Noblick (2011) as *B. odorata* Noblick (2011: 48). *Cocos odorata* Barbosa Rodrigues (1891: 11) was transferred to *Butia* by Marcato (2004), with the combination *B. odorata* (Barbosa Rodrigues 1891: 11) Noblick ex Marcato (2004: 61), but since then, his work has never been effectively published. Lorenzi *et al*. (2004) published the name *B. odorata* (Barbosa Rodrigues 1891: 11) Noblick & Pirani (2004: 120), however missing the reference to basionym and making this proposal not valid. Lorenzi *et al.* (2010) published *B. odorata* (Noblick & Lorenzi 2010: 178), but this name presented a reference of erroneous basionym, making it illegitimate.

Based on the current knowledge of the genus, 58 names were published in *Butia*. We currently accept 21 species included in the subsequent synopsys of the genus.

3.4 A synopsys of *Butia*

In the genus, 21 species are accepted: *B. archeri*, *B. arenicola*, *B. campicola*, *B. capitata*, *B. catarinensis*, *B. eriospatha*, *B. exilata*, *B. exospadix*, *B. lallemantii*, *B. lepidotispatha*, *B. leptospatha*, *B. marmorii*, *B. matogrossensis*, *B. microspadix*, *B. odorata*, *B. paraguayensis*, *B. poni*, *B. pubispatha*, *B. purpurascens*, *B. witeckii* and *B. yatay* **(Figs. 1, 2, 3 and 4)**. Figures of *B. arenicola* can be found in Soares (2015), *B. capitata* in Lorenzi *et al.* (2010), *B. poni* in Deble *et al.* (2011) and *B. witeckiii* in Soares & Longhi (2011).

FIGURE 1. Accepted species of *Butia*. **A.** *Butia archeri*. **B.** *Butia campicola*. **C.** *Butia catarinensis*. **D.** *Butia eriospatha*.

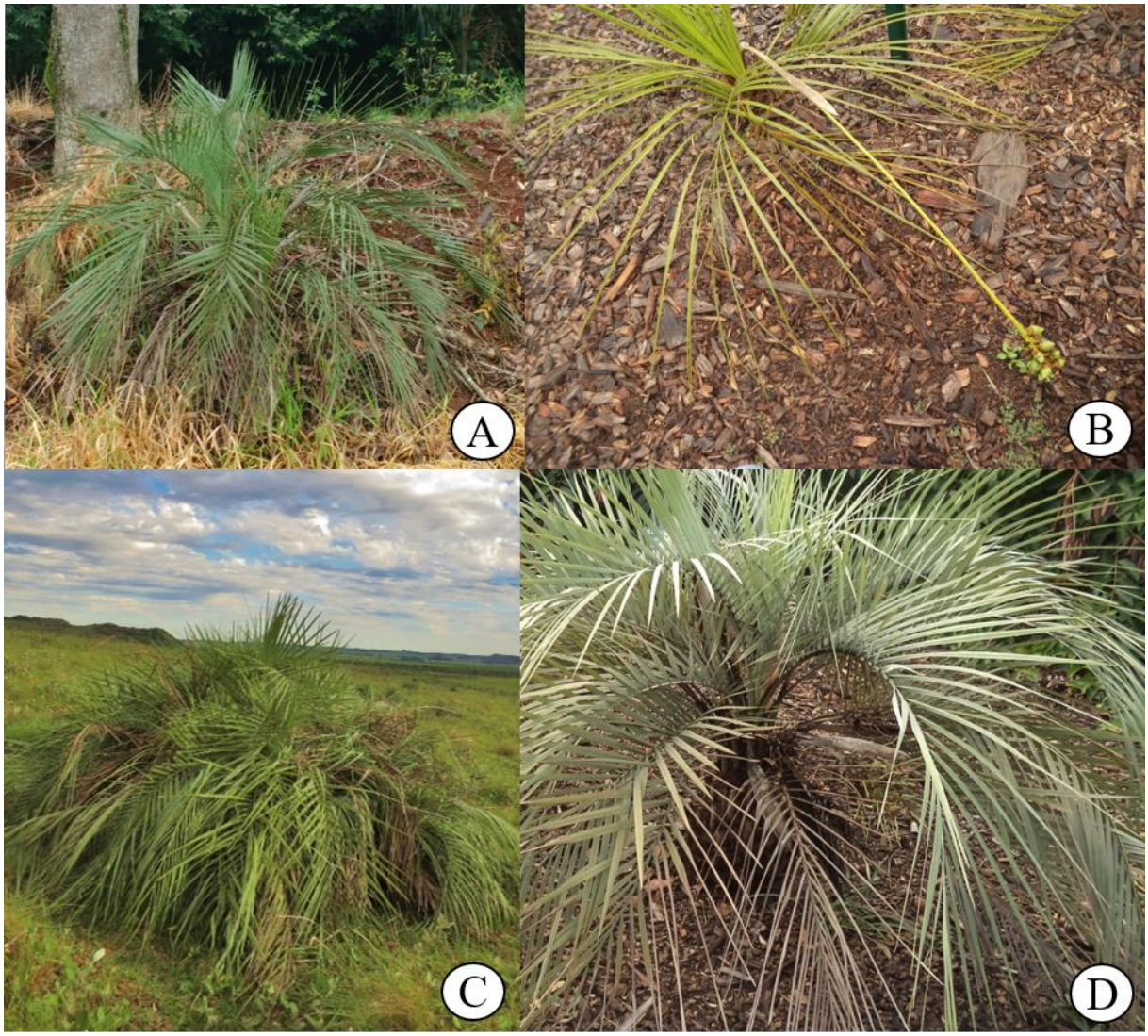

FIGURE 2. Accepted species of *Butia*. **A.** *Butia exilata*. **B.** *Butia exospadix*. **C.** *Butia lallemantii*. **D.** *Butia lepidotispatha.*

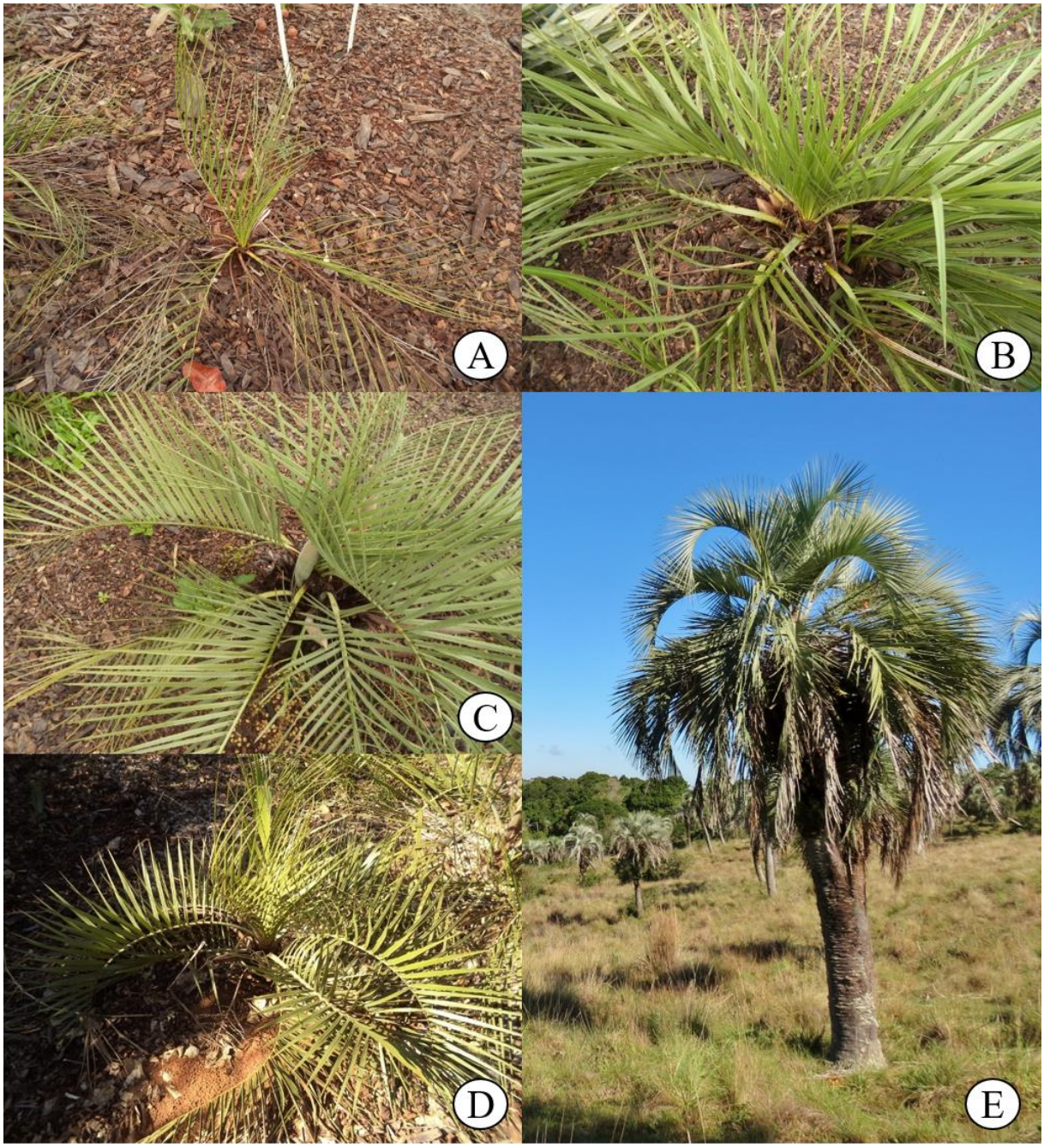

FIGURE 3. Accepted species of *Butia*. **A.** *Butia leptospatha*. **B.** *Butia marmorii*. **C.** *Butia matogrossensis*. **D.** *Butia microspadix*. **E.** *Butia odorata*.

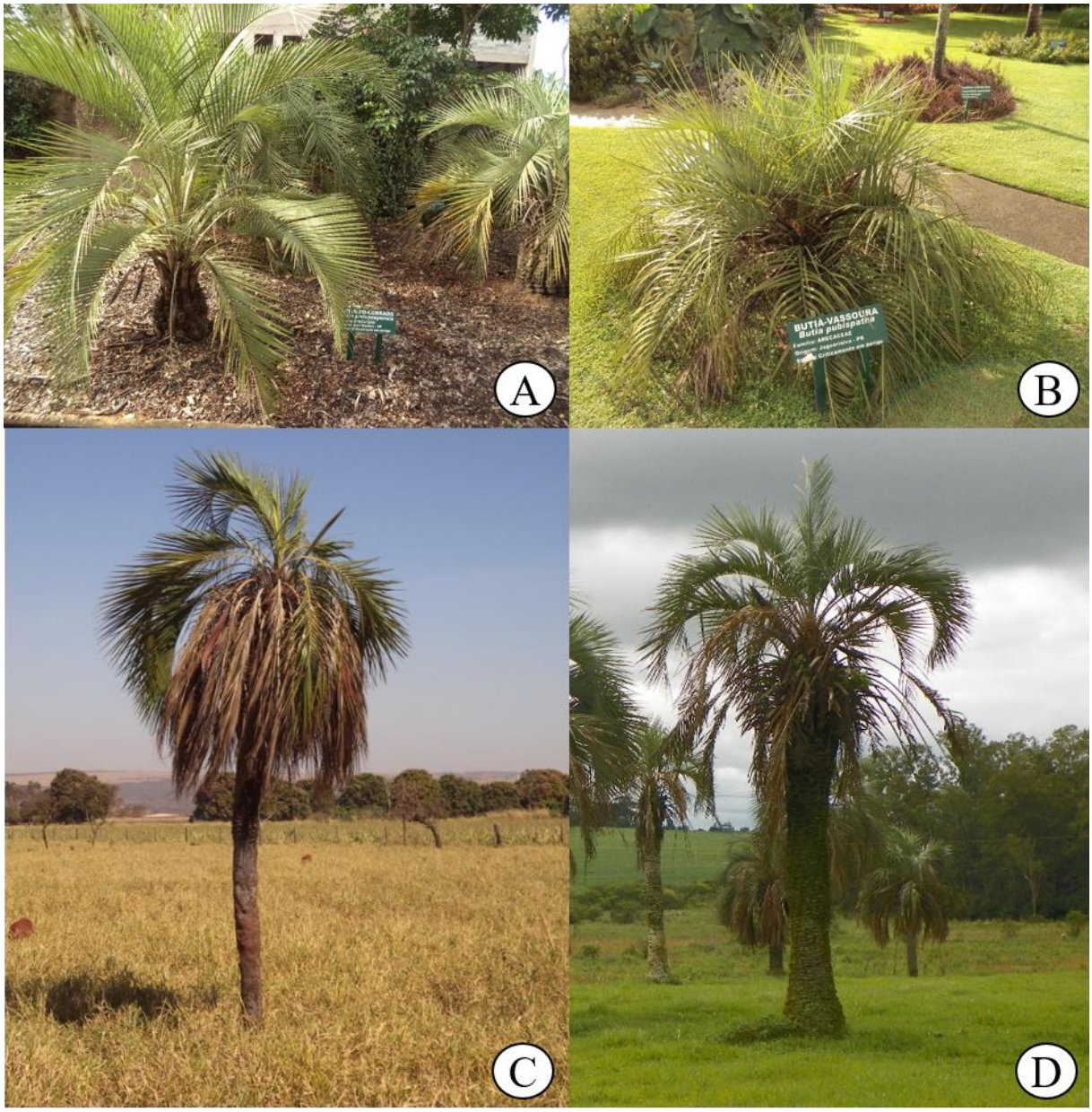

FIGURE 4. Accepted species of *Butia*. **A.** *Butia paraguayensis*. **B.** *Butia pubispatha*. **C.** *Butia purpurascens*. **D.** *Butia yatay*.

Butia (Beccari 1887: 352) Beccari (1916: 489). Type:—*Cocos capitata* Martius (1826: 114).

=*Butia capitata* (Martius 1826: 114) Beccari (1916: 507).

=*Cocos* subgen. *Butia* (Beccari 1887: 352).

=*Syagrus* sect. *Butia* (Beccari 1887: 352) Glassman (1970: 235), excluding *Syagrus vagans* (Bondar 1942: 457) A.D.Hawkes (1952: 178) and *S. schizophylla* (Martius 1826: 119) Glassman (1968: 386).

Etymology: derived from a Portuguese corruption of the vernacular name in Guarani language, *mbotiá*, said to be from *mbo* – to make, and *tiá* – those who have incurved teeth, presumably referring to the teeth on the petiole margins (Dransfield *et al.* 2008; Soares 2015).

1. ***Butia archeri*** (Glassman 1967: 235) Glassman (1979: 70). *Syagrus archeri* Glassman (1967: 235). Type:—BRAZIL. Minas Gerais: Fazenda Morro Redondo, near Lavras, in burned-over pasture, 20 Sept. 1936, *W.A. Archer 4048* (holotype A; isotype MO, barcode MO-2117278, digitized image!).

Etymology: in honor of W.A. Archer, holotype collector (Soares 2015).

Soares (2015) has described *B. archeri* var. *diamantinensis*, found in Diamantina, MG, Brazil, differentiating this variation from *B. archeri* by its width and dark green shade of the leaflets, besides being congested in the leaf rachis, wide pinnae clustered close together on the rachis, and the leaves forming an almost spherical canopy.

2. ***Butia arenicola*** (Barbosa Rodrigues 1903: 100) Burret (1930: 1051). *Cocos arenicola* Barbosa Rodrigues (1903: 100). *Syagrus arenicola* (Barbosa Rodrigues 1903: 100) Frambach ex Dahlgren (1936: 109). Type:—PARAGUAY. Cordillera de Altos: in alto planitie arenosa, s.d., *Hassler 3761* (holotype G, barcode G00039956, digitized image!).

Etymology: referring to the sandy type of soil where it grows (Soares 2015).

3. ***Butia campicola*** (Barbosa Rodrigues 1900: 6) Noblick (2004: 42). *Cocos campicola* Barbosa Rodrigues (1900: 6). *Syagrus campicola* (Barbosa Rodrigues 1900: 6) Beccari (1916: 465). Type:—PARAGUAY. Campos Ipe Hu, Sierra de Maracayu, s.d., *Hassler 5057* (holotype G, barcode G00009204, digitized image!).

Etymology: referring to the grassland habitat where the species lives (Soares 2015).

4. ***Butia capitata*** (Martius 1826: 78.) Beccari (1916: 504). *Cocos capitata* Martius (1826: 78). *Calappa capitata* (Martius 1826: 78) Kuntze (1891: 982). *Syagrus capitata* (Martius 1826: 78) Glassman (1970: 143). Type:— BRAZIL. Minas Gerais: habitat in campis, Aug., *Martius s.n.* (lectotype M, barcode M-0209405, digitized image!).

= *Butia capitata* subsp. *eucapitata* Herter (1940: 148, *nom. inval.*).

Etymology: refers to the arrangement of its leaves, which form a spherical crown, and which, according to the author, looks like a head (Soares 2015).

5. ***Butia catarinensis*** Noblick & Lorenzi (2010: 164). Type:—BRAZIL. Santa Catarina: Barra do Sul, 29 October 2009, *H. Lorenzi & K. Soares 6760* (holotype HPL!, HPL11412).

Etymology: in reference to the Brazilian state of Santa Catarina, where the species is most common (Lorenzi *et al.* 2010).

6. ***Butia eriospatha*** (Martius ex Drude 1881: 424) Beccari (1916: 496). *Cocos eriospatha* Martius ex Drude (1881: 424). *Calappa eriospatha* Martius ex Drude (1881:424) Kuntze (1891: 982). *Syagrus eriospatha* (Martius ex Drude 1881: 982) Glassman (1970: 145).

Type:—BRAZIL. Rio Grande do Sul: s.d., *A.F.M. Glaziou 8059* (holotype P, barcode P00725984, digitized image!;).

= *Butia punctata* Bomhard in H.P.Kelsey & W.A. Dayton (1942: 446, *nom. nud.*).

Etymology: from Ancient Greek *erion* = wool and Latin *spatha* = sword or spathe, referring to the lanuginose indumentum of peduncular bract (Soares 2015).

7. ***Butia exilata*** Deble & Marchiori (2011: 5). Type—BRAZIL. Rio Grande do Sul: Rondinha, 2 km do Parque Estadual de Rondinha, 22 December 2010, *L.P. Deble, A.S. Oliveira-Deble, J.N.C. Marchiori & F.S. Alves 13442* (holotype SI).

Etymology: the Latinized name means insulate, due the isolation status of the populations (Deble *et al.* 2011).

8. ***Butia exospadix*** Noblick (2006: 169). Type:—PARAGUAY. Canindeyú: Itanana, s.d., *L.R. Noblick & T. Rios Otero 5305* (holotype PY, isotypes FCQ, FTG, K, NY).

Etymology: The specific epithet is from *exo* meaning "outside" ans *spadix* referring to an "inflorescence (of palm)." Together they are translated as "outside inflorescence" or "projecting inflorescence"", referring to the elongated peduncle (in fruit) that projects the inflorescence far above and "outside" of the peduncular bract. It is not the only *Butia* to do this, but it is the one that does it in the most exaggerated manner (Noblick, 2006).

9. ***Butia lallemantii*** Deble & Marchiori (2006: 2). Type:— BRAZIL. Rio Grande do Sul: São Francisco de Assis, 12 December 2003, *L.P. Deble, A.S. Oliveira & J.N.C. Marchiori 1514* (holotype SI, barcode SI001764, digitized image!).

Etymology: tribute to the German doctor Robert Avé-Lallemant, author of the earliest literary reference related to this species (Deble & Marchiori, 2006).

10. ***Butia lepidotispatha*** Noblick & Lorenzi (2010: 170). Type:—BRAZIL. Mato Grosso do Sul: Ponta Porã, estrada para Antônio João, ca. 26 km de Ponta Porã (lado direito ao longo da antiga estrada de ferro), 22º21'54.7'' S, 55º43'59'' W, 17 November 2009, *H. Lorenzi, K. Soares & R. Campos 6767* (holotype HPL!, HPL11476).

Etymology: refers to the peduncular bract, also mentioned as spathe, covered by a lepidote indumentum (Lorenzi *et al.*, 2010).

11. ***Butia leptospatha*** (Burret 1940: 105) Noblick (2006: 169). *Syagrus leptospatha* Burret (1940: 105). Type:—BRAZIL. Mato Grosso do Sul: Campo Grande, Boliche Seco, caminho para Capão Bonito, 1936, *W.A. Archer & Gehrt 3915* (holotype SP, isotype NA, barcode 00087704, digitized image!).

Etymology: in reference to the delicate peduncular bract, that has a papyraceous consistency (Soares 2015).

12. ***Butia marmorii*** Noblick (2006: 173). Type:—PARAGUAY. Alto Paraná: Cia Laguna, s.d., *L.R. Noblick, Hazel Cropper, Tomas Ríos Otero, Marizza Quintana & Guillermo Marmori 5122* (holotype PY, isotypes FTG, K, NY, barcode NY00842225, digitized image!).

Etymology: pays tribute to the discoverer of this species, the paraguayan botanist Guillermo Caballero Marmori.

13. ***Butia matogrossensis*** Noblick & Lorenzi (2010: 175). Type:—BRAZIL. Mato Grosso do Sul: Água Clara, Nova Ponte, rodovia entre Nova Ponte e Água Clara, próximo às torres de força, 20º48'59,9'' S, 51º50'29,5'' W, 16 June 2008, *R. Tsuji, H. Lorenzi, L. Noblick & R. Ventura 2674* (holotype HPL!, HPL10301).

Etymology: refers to the State of Mato Grosso do Sul, where the palm was first collected (Lorenzi *et al.*, 2010).

14. ***Butia microspadix*** Burret (1930: 1050). Type:—BRAZIL. s. loc., s.d., *F. Sellow s.n.* [holotype B, destroyed (Lorenzi *et al.*, 2010; Soares, 2015)]. Lectotype:—BRAZIL. Rio Grande do Sul, barcode SP003016, designated by Noblick 1979: 71, digitized image!).

= *Syagrus hatschbachii* Glassman (1967: 240).

Etymology: from the Ancient Greek *micros* = small and *spadix* = spadix, in reference to the small peduncular bract (Soares 2015).

15. ***Butia odorata*** (Barbosa Rodrigues 1891: 11) Noblick (2011: 48). *Cocos odorata* Barbosa Rodrigues (1891: 11). *Butia capitata* var. *odorata* (Barbosa Rodrigues 1891: 11) Beccari (1916: 513). *Butia odorata* (Barbosa Rodrigues 1891: 11) Noblick & Pirani (2004: 120, nom. inval). *Butia odorata* (Barbosa Rodrigues 1891: 11) Noblick & Lorenzi (2010: 178, nom. inval.). Type:—BRAZIL. Rio Grande do Sul: in campis ad, cult. in Jard. Bot. Rio de Janeiro nº 64 [holotype destroyed (Lorenzi *et al.*, 2010; Soares, 2015)]. Lectotype Barbosa Rodrigues 1891. t. 4A digitized image!).

= *Cocos pulposa* Barbosa Rodrigues (1891: 14). *Butia pulposa* (Barbosa Rodrigues 1891: 14) Nehrling (1929: 1). *Butia capitata* var. *pulposa* (Barbosa Rodrigues 1891: 14) Beccari (1916: 516).

= *Cocos elegantissima* Chabaud (1906: 144, nom. illeg.).

= *Cocos erythrospatha* Chabaud (1906: 144).

= *Cocos lilaceiflora* Chabaud (1906: 144).

= *Butia capitata* var. *erythrospatha* (Chabaud 1906: 144) Beccari (1916: 515).

= *Butia capitata* var. *lilaceiflora* (Chabaud 1906: 517) Beccari (1916: 518).

= *Butia capitata* var. *elegantissima* Beccari (1916: 517).

= *B. capitata* var. *rubra* Mattos (1977: 1)

= *Butia capitata* var. *subglobosa* Beccari (1916: 513).

= *Butia capitata* var. *virescens* Beccari (1916: 519).

= *B. virescens* Beccari (1916: 519)

= *Cocos nehrlingiana* Abbott ex Nehrling (1927: 17). *Butia nehrlingiana* (Abbott ex Nehrling 1927: 17) Abbott ex Nehrling (1929: 1). *Butia nehrlingiana* L.H.Bailey (1930: 105). *Butia capitata* var. *nehrlingiana* (L.H.Bailey) L.H.Bailey (1936: 33).

= *Butia capitata* var. *strictior* L.H.Bailey (1936: 32).

= *Butia pulposa* (Barbosa Rodrigues 1891: 14) Nehrling (1929: 1). *Cocos pulposa* (Barbosa Rodrigues 1891: 1). Type:—BRAZIL. Rio Grande do Sul, em campos de São Sepé, Jaguarão e Caçapava e cult. no Jard. Bot. Rio de Jan. nº 454 (Barb. Rodr., 1903, t. 68C).

Etymology: from the Latin *odorata* = perfumed, in reference to the pleasant aroma of the fruit (Soares 2015).

Barbosa Rodrigues (1891) described *Cocos pulposa* for the region of Caçapava do Sul, São Sepé and Jaguarão without defining a type locality and based only on the analysis of fruits collected by a correspondent of the Botanical Garden of Rio de Janeiro. The (posthumous) illustration made for the Sertum Palmarum Brasiliensium shows an apparently cultivated individual, with its leaves partially removed, which is a local custom to use them in cattle feeding (Barbosa Rodrigues 1903). In the region mentioned by the author are not found native palm trees, only individuals dispersed by man or fauna along roads and in some hills (Soares, 2015).

Nehrling (1929) transferred *C. pulposa* to *B. pulposa* (Barbosa Rodrigues) Nehrling. Glassman (1979), Noblick (2010) and many other authors have maintained this binomial as a synonymy of *B. odorata*. Deble *et al*. (2011) revalidated it as a species, citing its occurrence in the restinga of the coast of Rio Grande do Sul and Uruguay, while *B. odorata* would be restricted to grassland areas from the coast to the department of Treinta y Tres in Uruguay. According to the protologues, *B. pulposa* and *B. odorata* would be separated mainly due to the characteristics of the fruits, however, these differences were not found in the *Butia* populations of these sites. It is also possible to highlight that *B. odorata* presents great morphological diversity in fruits, observing, for example, individuals from the population of Tapes – Rio Grande do Sul, being that only this character would not allow its distinction from *B. odorata*. Soares & Witeck (2009) suggest that in choosing the plants with the largest and tastiest fruits to grow in the backyards, the inhabitants of the south-central region of Rio Grande do Sul made a selection towards the domestication of the species. Thus, it is preferred to accept this taxonomic entity as a synonym of *B. odorata*.

16. ***Butia paraguayensis*** (Barbosa Rodrigues 1899: 9) Bailey (1936: 47). *Cocos paraguayensis* Barbosa Rodrigues (1899: 9). *Butia yatay* var. *paraguayensis* (Barbosa Rodrigues 1899: 9) Beccari (1916: 503 *Syagrus paraguayensis* (Barbosa Rodrigues 1899: 9) Glassman (1970: 151). *Butia yatay* subsp. *paraguayensis* (Barbosa Rodrigues 1899: 9) Xifreda & Sanso (1996: 207). Type:—PARAGUAY. “in campis in regione cursus superiores fluminis Apa”, *Hassler 896* (lectotype G, isolectotype K, barcode K000632564, designated by Glassman 1968, digitized image!).

= *Butia amadelpha* (Barbosa Rodrigues 1900: 7) Burret (1930: 1050). *Cocos amadelpha* Barbosa Rodrigues (1900: 7). *Syagrus amadelpha* (Barbosa Rodrigues 1900: 7) Frambach ex

Dahlgren (1936: 264). Type:—PARAGUAY. Capibary, *Hassler 6083* [holotype G, probably destroyed (Soares, 2015)]. ***Syn. Nov.***

= *B. dyerana* (Barbosa Rodrigues 1903: 626) Burret (1937: 696). *Cocos dyerana* Barbosa Rodrigues (1903: 626). *Syagrus dyerana* (Barbosa Rodrigues 1903: 626) Beccari (1916: 416). Type:—PARAGUAY. Campos arenosos perto de Concepción, *Hassler 7166* (Holótipo G).

Etymology: in reference to Paraguay, country where the species has been described (Soares 2015).

The holotype of this binomial is no longer in the Geneva Herbarium (G) (Soares, 2015) and probably has been destroyed (Glassman, 1979; Soares, 2015). The sample collected by Hassler was studied by Barbosa Rodrigues and probably was destroyed with its private herbarium. Description of underground stipe and pistillate flowers of 14-15 mm is reported to *B. paraguayensis*, probably of smaller size, but the description of the species is not clear about the petiole and fruits, besides not having been illustrated, making *B. amadelpha* considered an uncertain binomial (Glassman 1979; Marcato 2004; Soares 2015). When observing the original illustration of *C. amadelpha*, the inflorescence is slightly branched and the spathe is wider towards the apex, resembling a shell. In addition, the area in which the original species has been described is inserted in the distribution area of *B. paraguayensis*, according to Eslabão et al. (2016). In this way, we opted in the present work to consider *B. amadelpha* synonym of *B. paraguayensis*.

The holotype of this binomial consists only of parts of an inflorescence and a leaf (Glassman 1979). Despite being similar to *B. paraguayensis*, the absence of petiole, fruits and peduncular bract make the binomial uncertain. In addition, the sample collected by Hassler and studied by Barbosa Rodrigues was probably destroyed with the rest of its private herbarium (Soares 2015). When observing the size of the plant in the original description, this also resembles *B. paraguayensis*. In addition, the area of origin of the type is inserted in the area of *B.*

paraguayensis. Thus, in spite of the limited material in the description, it is considered in the present study *B. dyerana* synonymous of *B. paraguayensis*.

17. ***Butia poni*** Hauman ex Burret (1930: 1051). Type:—ARGENTINA. Misiones: San Ignacio, grasslands of Teyu Cuaré, 27º16'55.3''S and 55º33'35.5''W, 5 October 2015, *H. A. Keller, L. P. Deble & F. S. Alves 13022* (epitype CTES designated by Deble *et al.* 2017: 171, isoepitype SI).

Cocos poni Hauman (1919: 604, nom. inval.).

Etymology: epithet *poni* refers to the reduced habit and to the vernacular name given by Hauman 1919: 604-605. The word derives from the Tupi-Guarani expression "poñy", that means "snake", applied to plants that grow close to the soil (Deble *et al.*, 2011). Hauman (1919) uses part of the common name used in the region of Misiones "Yatai Poñi" (Soares, 2015).

18. ***Butia pubispatha*** Noblick & Lorenzi (2010: 180). Type:—BRAZIL. Paraná: Jaguariaíva, às margens da rodovia PR151 para Sengés (Km 203, lado direito), em campo de altitude, próximo ao rio das Mortes, 24º12'58,5'' S 49º39'01,5'' W. 7 November 2008, *H. Lorenzi & K. Soares 6766* (holotype HPL11475!).

Etymology: in reference to the pubescent indument that recovers the peduncular bract (Lorenzi *et al.*, 2010).

19. ***Butia purpurascens*** Glassman (1979: 67). Type:—BRAZIL. Goiás: near Jataí, s.d., *S.F. Glassman 13076* (holotype F, barcode F0092024F, digitized image!, isotype US, barcode US00344779, digitized image!).

Butia capitata var. *purpurascens* (Glassman 1979: 67) Mattos (2008: 6, nom. inval.). Etymology: from the Latin *purpurascens*, referring to the purple color of the fruits, flowers and peduncular bract (Soares 2015).

20. ***Butia witeckii*** K.Soares & S.Longhi (2011: 204). Type:—BRAZIL. Rio Grande do Sul: Quevedos, 2 km ao norte da usina de Quebra Dentes, 29º22'07,17''S, 54º00'45,31''W, 24 March 2011, *K. Soares, C. Redin & D. Brito s.n.* (holotype HDCF, isotype ICN173744, digitized image!).
Etymology: in tribute to the professor Leopoldo Witeck Neto, who discovered the population of this species (Soares & Longhi, 2011).

21. ***Butia yatay*** (Martius 1844: 93) Beccari (1916: 498). *Cocos yatay* Martius (1844: 93). *Callapa yatay* (Martius 1844: 93) Kuntze (1891: 982). *Butia capitata* subsp. *yatay* (Martius 1844: 93) Herter (1940: 148). *Syagrus yatay* (Martius 1844: 93) Glassman (1970: 157). Type:—ARGENTINA. Corrientes: Goya, Paraje Mercedes Cossio, 21 November 1970, *M.M. Arbo & V. Maruñak 553* (lectotype Martius, 1844, t. 30B, epitype CTES designated by Deble *et al.* 2013).
= *Butia missionera* Deble & Marchiori (2011: 10). Type:—BRAZIL. Rio Grande do Sul: Giruá, Campo do Butiá, 22.XII.2010, L.P. Deble, A.S. Oliveira-Deble, J.N.C. Marchiori & F.S. Alves 13418 (Holótipo SI).
= *Butia quaraimana* Deble & Marchiori (2012: 12). Type:—BRAZIL. Rio Grande do Sul: Quaraí, Palmar de Coatepe, 15 February 2011, *L.P. Deble et al. 13988* (holotype SI, barcode SI041050, digitized image!).
Etymology: from Guarani language "yatay", in reference to the small and tough fruits (Soares 2015).

3.5 Doubtful names

Butia bonneti (Linden 1878) Beccari (1916: 504). *Cocos bonneti* Linden, Kerchove de Denterghem, les Palmiers [proposed only as a valid name as specific epithet by Beccari (1916)]. Type:—FRENCH. Hyères: cultivated. No specimens cited. (lectotype Beccari t. 5, figs. 4-5, 1916).

Initially described as *Cocos bonneti* Linden in 1878, the species was transferred to *Butia* by Beccari (1916). The species presents characteristics similar to *B. catarinensis*, however, the description of this binomial is not clear and was made based on the observation of a cultivated plant without information on the collection site. There is no type citation for *B. bonneti*, preventing its correct positioning (Marcato 2004; Soares 2015).

Butia leiospatha (Barbosa Rodrigues 1877: 23) Beccari (1916: 520). *Cocos leiospatha* Barbosa Rodrigues (1877: 23). *Calappa leiospatha* (Barbosa Rodrigues 1877: 23) Kuntze (1891: 982). *Cocos capitata* var. *leiospatha* (Barbosa Rodrigues 1877: 23) Berger (1912: 87). Type:—BRAZIL. Minas Gerais: Serra do Aguapé (t. 61A, 1903).

Barbosa Rodrigues (1903) did not cite specimens in the original publication of the species, which was described as a palm with subterranean stipe or up to 1.5 x 0.15 m, while the illustration shows an individual having a high stipe (Barbosa Rodrigues 1877, fig. 7). In the description, the petioles have jagged margins, but in the ilustration the petioles margins have only fibers. Kelen (2015) reports the similarity with *B. capitata* (juvenile individuals) or with *B. matogrossensis*, while the illustration resembles an individual of *B. archeri.*

Butia noblickii Deble, Marchiori, F.S.Alves & A.S.Oliveira (2012: 7). Type:—ARGENTINA. Corrientes: Paso de los Libres, “no grupo de *Butia yatay*, 3 a 5 m de altura, flores amarelas” 1 November 1973, *A. Schinini 7828* (holotype CTES).

According to Deble *et al.* (2012), this species may be distinct from the other taxa of the *B. yatay* complex because of the smaller size of the pistillate flowers (7-9 mm vs. 10-20 mm) and the consistency of the peduncular bract (lignified-papyraceous vs. lignified). However, Soares (2015) when analyzing other exsicates belonging to *Butia* from the same region (A.G. Scultz 18543 CTES; L. Noblick, A. Schinini & R. Vanni 5406 CTES, FTG), reports that pistillate flowers can be more than 10 mm in length, and have lignified peduncular bracts, not resembling in any way a papyraceous peduncular bract (characteristic of smaller species such as *B. leptospatha* and *B. marmorii*). It is suggested that the collection of the inflorescences of the type was made when the peduncular bract was closed and the flowers immature (Soares, 2015).

Despite the existence of *B. yatay* as an accepted species, recently some species have been described as distinct from *B. yatay* and are currently considered synonymous, such as *B. missionera* and *B. quaraimana*. Deble *et al*. (2011) separated the native palm trees from the region of Giruá, Rio Grande do Sul, Brazil, then called *B. yatay* of the *B. yatay* native to the Coatepe region in Quaraí, Rio Grande do Sul, Brazil, by characters such as old leaves that touch the stipe, shorter and broader stipe with dilated base and fruit shape. Although the endocarps of Giruá *Butia* palms are generally oval and in the population of Quaraí the elongate form (turbinate) predominates, this is not an absolute character. In addition, the other differential characters are very weak to circumscribe a new species, because in any population of *Butia* can be observed individuals with more arched or erect leaves, larger or narrower stipes. In addition, Kelen (2015) reports that measurements taken on Giruá specimens showed values different from those reported in the description of the new species (Deble *et al.* 2011), such as the number of contemporary leaves: up to 31 (up to 40 in the original description) and stipe diameter: up to 42 cm, 30-50 cm above the base (between 50-60 cm in the original

description). Thus, the binomial published in 2011 is considered a synonym of *B. yatay* (Soares *et al.* 2014).

Similarly, the authors differentiates the new species *B. quaraimana*, among other examples, by being less robust, with the largest individuals measuring 8 m in height (vs. up to 16 m), with a short stipe (2,5-6,5 m vs. 6-14 m), by the smaller number of leaves and elliptical shape of fruits (vs. oval-elliptical) (Deble *et al*., 2012). Soares & Longhi (2011) analyzed 79 plants from the Coatepe region and found different measurements and qualitative traits from those described in the protologue of *B. quaraimana*, for example, individuals about 10 m height, and differences in the number of leaves and endocarp measurements. In addition, it is reported that in its wide distribution area (Argentina and Uruguay), populations of *B. yatay* present a great variation in their mean height, a fact that had previously been recognized by Deble *et al.* (2011: 21) and other authors such as Crovetto & Piccinini (1951). In this way, Soares *et al.* (2014) preferred to consider the binomial as a synonym of *B. yatay* (Soares *et al.*, 2014; Soares, 2015). The author points out those plants grown near Paso de los Libres, Argentina, do not have sufficiently differentiated characteristics, requiring a detailed *in situ* analysis to make a decision on the validity of this taxon.

Butia pungens Beccari (1916: 523). Type:—ARGENTINA. Misiones: Campina de América, II. 1907, *Spegazzini s.n*. (Fl).

According Glassman (1970b; 1979), this taxon is probably a synonym of *B. paraguayensis*, because it coincides with the general description. However, the hypothesis that this is a young individual of *B. yatay* is not rejected (Soares, 2015).

Butia stolonifera (Barbosa Rodrigues 1901: 40) Beccari (1916: 492). *Cocos stolonifera* Barbosa Rodrigues (1901: 40). Type:—URUGUAY. Pan d'Azucar, pro. Montevideu [Cult. Jard. Bot. RJ nº 2259 – destruído (Soares, 2015)].

Originally described as *Cocos stolonifera*, then transferred by Beccari to *Butia* (1916). According to the descriptions of Barbosa Rodrigues (1903), this is a cespitous to subterraneous stipe palm, an habit that refers to the species most recently described *B. lallemantii*. The flowers and fruits were not observed. The characteristics of the arrangement of the leaflets on the leaf rachis caused Beccari (1916) to transfer it from *Cocos* to *Butia*, without even observing the plant or any exsiccates. This taxon was first found by Arechavaleta in 1869 at hill Pan de Azucar (Uruguay), when two plants were removed for cultivation, one in Montevideo and another in the Botanical Garden of Rio de Janeiro, but both were lost (Glassman 1970). The species was never found again and no species of the genus shows the type of rhizomatous development described. Due to the absence of type citation and the description is not clear, there is no way to recognize the taxon (Marcato 2004; Soares 2015).

Butia wildemaniana (Barbosa Rodrigues 1903: 101) Burret (1930: 1050). *Cocos wildemaniana* (Barbosa Rodrigues 1903: 101). *Syagrus wildemaniana* (Barbosa Rodrigues 1903: 101) Frambach ex Dahlgren (1936: 270). Type:—PARAGUAY. Rio Apa, s.d., *Hassler 8554* (holotype G, probably destroyed).

The sample collected by Hassler and studied by Barbosa Rodrigues was probably destroyed with the rest of his private herbarium. The original description does not provide the size of the pistillate flowers, not allowing to define if the species belongs to the group "*capitata*" or "*yatay*" (Soares, 2015). As the type was not found, it is not possible to determine its nature.

3.6 Excluded name

Butia argentea (Engel 1865: 690) Nehrling (1929: 5). *Cocos argentea* Engel (1865: 690). *Syagrus argentea* (Engel 1865: 690) Beccari (1916: 465).

Originally described as *Cocos argentea* Engel 1965 and correctly transferred to *Syagrus sancona* H. Karst. (1857: 247). The later combinations *Syagrus argentea* (Engel) Becc.1916 and *Butia argentea* (Engel 1865: 690) Nehrling (1929: 5) are not currently accepted.

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4. A phylogenetic study of *Butia* (Arecaceae) based on nuclear and chloroplast DNA sequences

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Abstract

There is a shortage of DNA regions useful for phylogenetic research in palm trees. Some recent phylogenetic studies have efficiently used regions of nuclear DNA as ITS and WRKY and chloroplastidial DNA as *trn*H-*psb*A. Despite the confirmed monophyly of *Butia*, the phylogenetic relationships among its species had not been elucidated yet. In the present study, after sampling young leaflets of the currently accepted species, collected both in fieldwork and in the Plantarum Institute, DNA extraction, synthesis, purification and sequencing of specific regions of DNA, relationships among some *Butia* species are presented based on analysis of regions ITS, *trn*H-*psb*A and WRKY19. The results confirm *Butia* as a monophyletic genus, sister of *Jubaea.* It is possible to observe that the graminiform habit evolved independently several times in the genus, evidencing the evolutionary convergence of this trait in non closely related species. When results are geographically interpreted, it is possible to observe that the species distribution follows a consistent geographical pattern. It is possible to provide support to the clades obtained by comparatively observing the morphology of sister species, since several shared morphological characteristics can be observed.

Keywords: jelly palm fruit; pindo palm; evolution; systematic.

4.1 Introduction

Arecaceae, the family of palms, with over 252 genera and 2,600 species (Dransfield et al. 2008) is especially well represented in the Asian tropics, Pacific islands and the Americas (Lorenzi 2010). *Butia* (Becc.) Becc., the pindo palms, is a South American genus that comprises approximately 20 species, of which only *B. marmorii* Noblick is not found in Brazil. *Butia* grows in gregarious populations (*butiazais*), occurring mainly in grasslands and savannas (Marcato 2004; Lorenzi et al. 2010; Soares et al. 2014; Ellert-Pereira 2015; Flora do Brasil em construção, 2019). The species have economic and cultural importance, mainly as source of food (fruit and seeds), fibers and for landscaping (Rossato 2007), and are distributed from central and east Brazil, to north-east Argentina, east Paraguay and north-east Uruguay (Lorenzi 2010; Marcato 2004; Flora do Brasil em contrução, 2019).

Butia classification is controversial and in contemporary taxonomic works there is no agreement on the number of recognized species. The number of species varies between 11 (Marcato 2004), 18 (Noblick 2010), 20 (Soares 2015), 21 (Heiden et al. 2018) and 24 (Deble et al. 2017). The taxonomical history is complex, with cases of misapplication of scientific names and there is no consensus in recent publications about the total recognized species (Deble & Marchiori 2011; Soares & Longhi 2011; Soares et al. 2014).

Since the first species description, in 1826, 58 names were published (36 species, 4 subspecies, 20 varieties), from which only 21 are currently recognized as accepted species (*B. archeri* (Glassmann) Glassmann, *B. arenicola* (Barb.Rodr.) Burret, *B. campicola* (Barb.Rodr.) Noblick, *B. capitata* (Mart.) Becc., *B. catarinensis* Noblick & Lorenzi, *B. eriospatha* (Mart. ex Drude) Becc., *B. exilata* Deble & Marchiori, *B. exospadix* Noblick, *B. lallemantii*, *B. lepidotispatha* Noblick & Lorenzi, *B. leptospatha* (Burret) Noblick, *B. marmorii* Noblick, *B. matogrossensis* Noblick & Lorenzi, *B. microspadix* Burret, *B. odorata*, *B. paraguayensis*, *B. poni* (Haum.) Burret, *B. pubispatha* Noblick & Lorenzi, *B. purpurascens* Glassmann, *B. witeckii* K. Soares & S. Longhi and *B. yatay* (Mart.) Becc.) (Heiden et al. 2019). Aditionally, two natural intergeneric hybrids were found between *Butia* and *Syagrus*: × *Butyagrus nabonnandii* (Prosch.) Vorster [*B. odorata* × *S. romanzoffiana* (Cham.) Glassmann)] and × *Butyagrus alegretensis* K. Soares (*B. lallemantii* × *S. romanzoffiana*) (Soares et al., 2014; Soares, 2015).

Only recently the scientific community turned its attention to the pindo palm groves in Brazil, and the research group at Embrapa Temperate Climate has an important role in this process. Fonseca (2012) detected high levels of minerals in the *B. odorata* pulp and the presence of bioactive compounds. Cytogenetic analysis showed that *Butia* are diploid (2n = 32) (Correa et al. 2009). Studies of molecular characterization with ISSR markers (Rossato et al. 2007), AFLP (Büttow et al. 2010) and microssatelites (Mistura 2013) detected significant genetic variability within populations. The knowledge on the phenology of *B. odorata* (Schwartz et al. 2010) had great importance for the management and conservation of this species, as well as the work of Rivas (2013), focusing on conservation and sustainable use of pindo palm groves in the pampas.

There is a shortage of DNA regions useful for phylogenetic research in palm trees. Baker et al. (1999) present the phylogeny of palms based on DNA sequences of *trn*L-*trn*F. Lewis & Doyle (2001) reported the development and use of primers for amplification and sequencing regions of malate-synthase nuclear gene. Hahn (2002) based his study on nuclear DNA sequencing data (18S SSU rRNA) and chloroplast DNA (*atp*B and *rbc*L) to 65 genera of palms. However, comprehensive phylogenetic studies of *Butia* have not been conducted until now. Asmussen & Chase (2001) indicate that plastid DNA sequences are modified slowly in palm trees, but they show that the family is monophyletic and highly divergent relative to other major clades of monocots.

Meerow et al. (2009) supports the monophyly of the genera belonging to the subtribe Attaleinae, including *Butia*, by analyzing the loci of WRKY transcription factors, which point a clade of African species as sister of the American clade that includes *Butia*. Cuenca et al. (2008), point *Butia* as sister group of *Jubaea* Kunth, which is close to two other clades, composed by *Syagrus* Mart. plus *Allagoptera* Nees, and *Attalea* Kunth plus *Cocos* L., while Meerow et al. (2009) corroborate the *Butia*-*Jubaea* sister-relationship, and this clade relationship to *Allagoptera, Parajubaea* Burret and *Polyandrococos* Barb.Rodr. Despite the confirmed monophyly of *Butia*, the phylogenetic relationships among its species are not elucidated yet.

A phylogenetic hypothesis for *Butia* is necessary to clarify the current systematics and evolution of the group. The phylogeny of *Butia* will allow studying the diversity of species included in this genus and make possible a better understanding of the floristic connections among southeastern South American open vegetation types, resulting in informations to subsidize conservation actions and sustainable use of these species and these environments.

4.2 Materials and methods

4.2.1 Sampling

Samples from each one of the 21 recognized species were collected, preferably from young leaflets, from which DNA was extracted. Samples were collected both in fieldwork and in the Plantarum Institute. The localities from which fieldwork samples were collected are listed in table 1. The other samples were obtained through a partnership with the Plantarum Institute, a reference center for research and conservation of the Brazilian flora, located in Nova Odessa – SP. Sampling carried out covers all currently recognized species.

4.2.2 Synthesis, purification and DNA sequencing

DNA was extracted at Embrapa Clima Temperado, using the Invisorb Spin DNA Extraction Kit – Stratec, according to the manufacturer's protocol. The regions ITS, *trn*H-*psb*A, and WRKY19 were amplified and sequenced according to the protocol set previously established for these regions.

PCR amplifications of ITS, and *trn*H-*psb*A regions were carried out in 25 µL reactions, using 2,5 µL of buffer Tris HCl/KCl, 0,75 µL of 50 mM $MgCl_2$, 0,5 µL of 10 mM dNTP's, 1,0 µL of a 10 µM concentration of the forward primer, 1 µL of a 10 µM concentration of the reverse primer, 0,2 µL of Taq DNA Polymerase, 18,05 µL of DNase free sterile water and 1 µL of 40-50 ng/µL template DNA. Only for ITS region, 1 µL of D.M.S.O. was added to prevent formation of secondary DNA structure. PCR amplifications of WRKY19 region were carried out in 30 µL reactions, using using 3,0 µL of buffer Tris HCl/KCl, 1,2 µL of 50 mM $MgCl_2$, 0,6 µL of 10 mM dNTP's, 3,0 µL of a 10 mg/ml of BSA, 0,6 µL of a 10 µM concentration of the forward primer, 0,6 µL of a 10 µM concentration of the reverse primer, 0,16 µL of Taq DNA Polymerase, 19,84 µL of DNase free sterile water and 1 µL of 40-50 ng/µL template DNA.

The PCR program for ITS region followed a 5 min initial denaturation at 95°C, 30 cycles of 1 min denaturation at 95°C, 1 min annealing at 52°C, 1 min extension at 72°C, finished by a last extension of 10 min at 72°C. The PCR program for *trn*H-*psb*A region followed a 5 min initial denaturation at 95°C, 30 cycles of 30 sec denaturation at 94°C, 30 sec annealing at 56°C, 1 min extension at 72°C, finished by a last extension of 10 min at 72°C. The PCR program for WRKY19 region followed a 2 min initial denaturation at 95º, 35 cycles of 30 sec denaturation at 90°C, 1 min annealing

at 57°C, 1 min extension at 72°C, finished by a last extension of 10 min at 72°C. Ludwig Biotec, in the Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul state, Brazil, in a partnership with ACTGene Análises Moleculares – Sequenciamento de DNA, carried out the samples sequencing.

Table 1. Sampling data of *Butia* species.

Species	Origin	Collector/Collection number	Herbarium
B. archeri	Cristalina GO	Lorenzi 4937	HPL
B. archeri var. diamantinensis	Diamantina MG	Lorenzi 6800	HPL
B. arenicola	Anhanduí MS	K.Soares 22	ECT
B. campicola	Amambaí MS	Lorenzi 6771	HPL
B. capitata	Montes Claros MG	Tsuji 2705	HPL
B. catarinensis	Barra do Sul SC	Lorenzi 6760	HPL
B. eriospatha	São Bento do Sul SC	Amostra cedida pelo Instituto Plantarum	-----
B. exilata	Rondinha RS	Ellert 88	ECT
B. exospadix	Tacuru MS	Lorenzi 6772	HPL
B. lallemantii	São Francisco RS	M. Tanigushi 3	ECT
B. lepidotispatha	Ponta Porã MS	Lorenzi 6767	HPL
B. leptospatha	Ponta Porã MS	Lorenzi 6769	HPL
B. marmorii	Itakyry Pg	Lorenzi 6655	HPL
B. matogrossensis	Três Lagoas MT	Salviani 1751	HPL
B. microspadix	Ponta Grossa PR	Lorenzi 6841	HPL
B. odorata	Tapes RS	Eslabão 01 p01	ECT
B. paraguayensis	Sarandi	Ellert 89	ECT
B. poni	Ponta Porã MS	K.Soares 21	ECT
B. pubispatha	Canguçu RS	Amostra cedida por K.Soares	-----
B. purpurascens	Jataí GO	Ellert 86A	ECT
B. yatay	Giruá RS	Ellert 90A	ECT
B. witeckii	Quevedos RS	Amostra cedida por K.Soares, descritor da espécie	-----
Butyagrus nabonnandii	Canguçu RS	Ellert 91	ECT
Jubaea chilensis	-----	Heiden 2232	ECT
S. flexuosa	Canguçu RS	Amostra cedida por K.Soares	-----
S. romanzoffiana	Pelotas RS	Ellert 93	ECT

4.2.3 Data analysis

The sequences were examined, edited and aligned through using the app MAFFT Alignment with L-INS-i Algorithm in the Geneious 2019.0.4 app (http://www.geneious.com/). After that, the reconstruction of species trees was made using maximum likelihood analysis through RAxML app, also implemented in Geneious, using the Nucleotide Model GTR GAMMA and algorithm Rapid hill-climbing, under default settings.

To make the analysis more complete, sequences of the region WRKY19 of *Butia lallemantii, Butia yatay, Cocos nucifera* and *Syagrus romanzoffiana* have been downloaded from GenBank.

4.3 Results

The list of successfully sequenced samples is presented on table 2. Only sequences of WRKY19 region were found on Genbank data. The samples downloaded from GenBank are also presented on table 2. ITS region was most successfully to obtain complete sequences, and even though the *trn*H-*psb*A region had few complete sequences, it was decided to analyze the data in the same way.

Table 2. List of sequenced samples. Only forward sequence: F. Only reverse sequence: R. Both sequences: X. Samples downloaded from GenBank: G.

Espécie	ITS	*trn*H-*psb*A	WRKY19
Butia archeri			
Butia archeri var. diamantinensis	X		
Butia arenicola	R		
Butia campicola	R		
Butia capitata	X		X
Butia catarinensis	X		X
Butia eriospatha	X		R
Butia exilata	X		X
Butia exospadix	X		R
Butia lallemantii	X		G
Butia lepidotispatha	X	X	X
Butia leptospatha	R		
Butia marmorii	X	R	X
Butia matogrossensis	X	R	X
Butia microspadix			R
Butia odorata	X	R	X
Butia paraguayensis	R		X
Butia poni	R		
Butia pubispatha	X	R	
Butia purpurascens	X	F	X
Butia yatay	X	X	G
Butia witeckii	X		
Butyagrus nabonnandii			X
Cocos nucifera			G
Jubaea chilensis	X	X	X
Syagrus flexuosa			
S. romanzoffiana	X		G

The results of maximum likelyhood analysis of the regions ITS (Fig. 1), WRKY19 (Fig. 2), and *trn*H-*psb*A (Fig. 3) are presented.

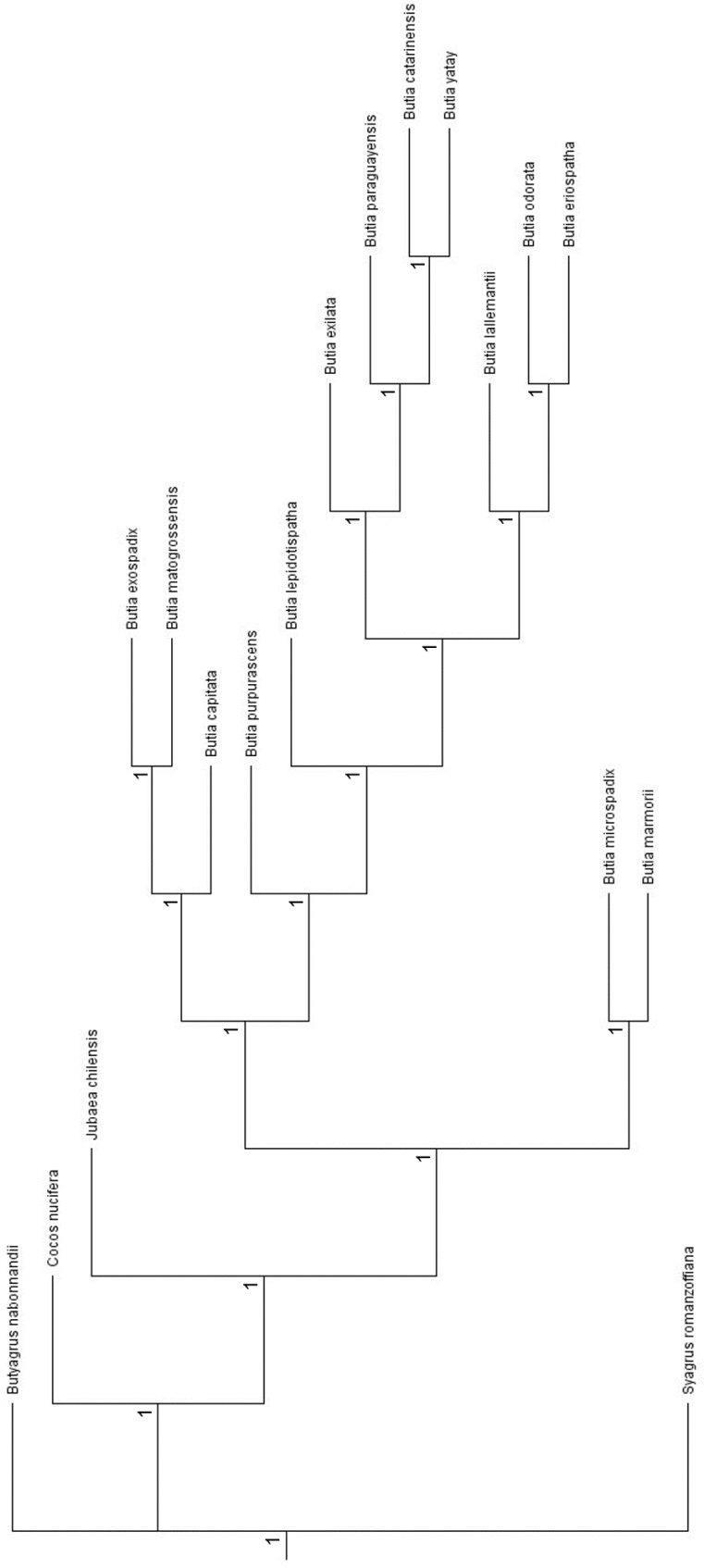

Figure 1. Phylogenetic tree of *Butia* resulting from WRKY19 region maximum likelihood analysis.

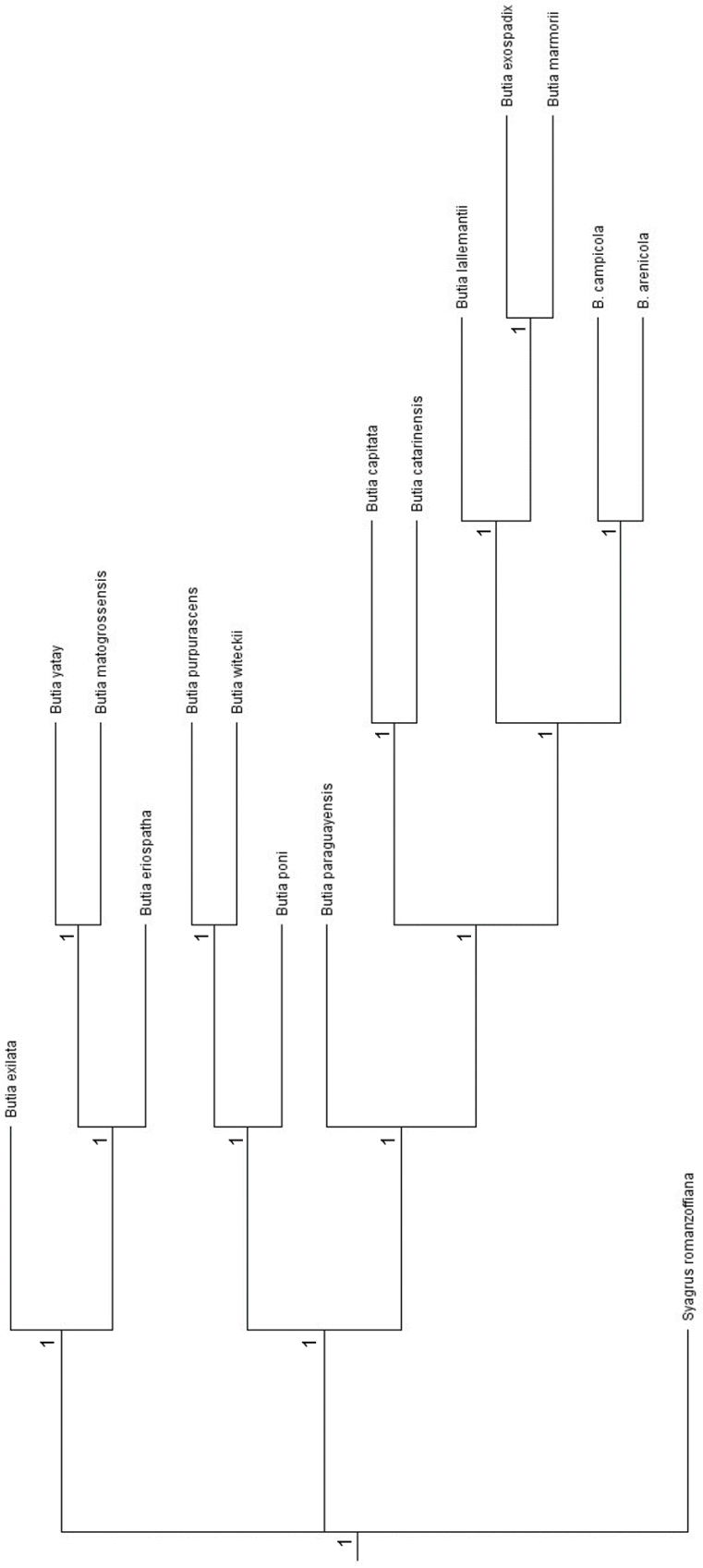

Figure 2. Phylogenetic tree of *Butia* resulting from ITS region maximum likelihood analysis.

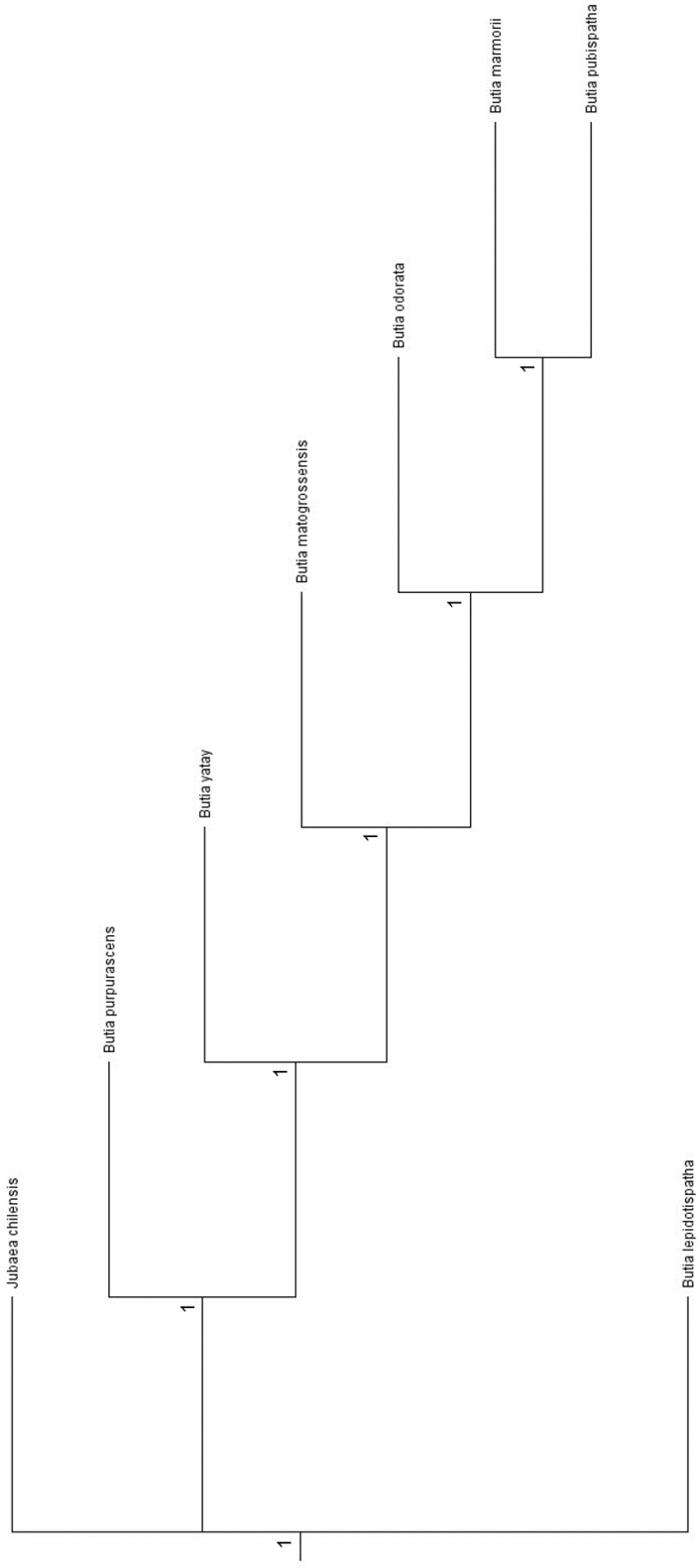

Figure 3. Phylogenetic tree of *Butia* resulting from *trn*H-*psb*A region maximum likelihood analysis.

4.4 Discussion

WRKY transcription factors are predominantly plant-specific proteins, broadly distributed across the genome (Zhang & Wang, 2005). Borrone et al. (2007) demonstrated the utility of WRKY genes for phylogenetic inference in Malvaceae. Besides that, the utility of WRKY loci for determining infraspecific relationships has been demonstrated by genetic mapping in *Theobroma cacao* L. and by differentiating individuals from one another within *T. cacao* (Borrone et al. 2004) and *C. nucifera* germplasm collections (Mauro-Herrera et al. 2006; 2007).

Meerow (2009) presents the phylogenetic relationships within the subtribe Attaleinae, using sequences of seven putatively independent, single copy of WRKY loci originally isolated from *Cocos nucifera* in order to resolve the closest extant relative of the coconut. On his study, is evidenced that the relationship between *Cocos* and *Syagrus*, resolved by the seven concatenated WRKY gene alignments is real. The closest relation between *Cocos* and *Syagrus*, previously related by Meerow (2009) can be observed in the three analysis presented in this study. However, despite the genus is present in Meerow (2009) analysis, the relations between *Butia* species and its proximity are not discussed further on his study.

Jubaea is highlighted as *Butia*'s sister group. *Butia* species found in the cerrado biome form paraphyletic clades, which evolved independently over time (Fig. 1), being *B. lepidotispatha* observed as sister group of the clade composed by the southernmost species, found in the region of Atlantic Forest and Pampa domains. Looking at the results of the phylogenetic analysis, it is possible to conclude that the species of *Butia* are distinct from *Syagrus, Cocos* and *Jubaea*, although slightly close. In addition, phylogenetic data corroborate species distribution, since geographically closer species were positioned close to each other based on phylogenetic data as well.

Noblick (2006) indicates that *B. microspadix, B. marmorii, B. exospadix, B. leptospatha* and *B. campicola* are all very small acaulescent palms referred as "grassy butia" because they tend to camouflage themselves among the grasses. In the present study, observing the results of WRKY19 and ITS analysis (Figs. 1 and 2) is possible to note the closest relashionhip of *B. marmorii* with *B. exospadix* (ITS region) and with *B. microspadix* (WRKY19 region).

Butia exospadix emerged as sister species of *B. matogrossensis* (Fig. 1). *Butia exospadix* is found in the border region between Paraguay and Brazil, being observed in both countries. In Brazilian territory, it is found in Mato Grosso do Sul state (Eslabão *et al.* 2016), same state where the type of *B. matogrossensis* was described. These are species of similar size, shrub, and close morphology, especially the short solitary stem, and *B. exospadix* may also present with underground or acaulescent stem. In addition, both species have small and ovoid fruits, ranging from purplish green to purple when ripe, a characteristic observed in other shrubby species that is distinguished from large and yellowish fruits quite common to the genus.

However, the morphological diversity of the genus can be evidenced by observing the species of the cerrado *B. capitata*, present in Goiás, Bahia and Minas Gerais, and *B. purpurascens* occurring in Goiás and Minas Gerais. Despite their geographical proximity, both are not only observed phylogenetically apart in distinct lineages, but also associated with distinct clades in the analysis (Fig. 1). Although both have arboreal size, the species have significantly different morphological characteristics, which justifies their great distance in the analysis. *Butia capitata* has pseudopetiole armed with rigid flattened fibers, similar to teeth, yellowish-green to yellow fusiform fruits, while *B. purpurascens* presents pseudopetiole with smooth to fibrous margins and purplish to slightly yellowish-green ovoid fruits. *Butia purpurascens* is a species of arboreal size, which presents defenseless petioles, without the presence of fibers, distinguishing itself from most of the other species of the genus. The similarity of the fruits is a factor that justifies the proximity of *B. capitata* with *B. catarinensis* observed in the figure 2. Both species present oblong to ovoid and yellowish fruits when ripe.

Butia lepidotispatha was recovered as the sister taxon of the clade that comprises the Southern species of *Butia.* This species is distinguished from the others by the presence of a lepidote indumentum that covers the peduncular bract, intermediate characteristic, not as prominent as in *B. eriospatha* or smooth as in most species of the genus. *Butia exilata* and *B. lallemantii* are observed emerging before other species and are not grouped in the most derived branches of the analysis (Fig. 1). Both species present a considerable degree of endemism, besides being considered endangered (FZB, 2016), being *B. exilata* found only in the region of Ronda Alta and Rondinha, in Rio Grande do Sul state and *B. lallemantii* in the region

of Santana do Livramento, Alegrete and São Francisco de Assis, in Rio Grande do Sul and in Uruguay. Both shrub-like, *B. exilata* differs from the other species of the genus by the peduncular bract, covered by a whitish or brownish indumentum and its small endocarps, whereas *B. lallemantii* has a very peculiar and easily identifiable hemispheric shape, besides being an usually cespitous palm. The distancing of *B. exilata* can also be observed in figure 2.

Although *B. exilata* did not emerge as sister species of *B. paraguayensis*, both species were positioned relatively close (Fig. 1). The similarity between these species is cited by Soares (2015), when pointing out that despite the indumentum found in the peduncular bract of *B. exilata* is deciduous, and besides being sometimes observed in other species of the genus, such as *B. paraguayensis*, the fact that *B. exilata* is geographically quite isolated would justify maintaining this species as recognized.

The proximity of *B. paraguayensis* of the clade where *B. yatay* is found is justifiable, since some botanists considered *B. paraguayensis* a dwarf variety of *B. yatay*, due to similarities in size and shape of fruits, flowers and endocarps (Fig. 1). However, their dimensions are considerably smaller than those found in *B. yatay*. On the other hand, *B. yatay*, although not belonging to the same region of *B. catarinensis*, even though part of the populations of both species are present in Rio Grande do Sul, these species have important similarities, such as arboreal size and yellow, orange or reddish-orange fruits, in addition to the ovoid to narrow-ovoid shape. However, an important character to distinguish *B. yatay* from the other species is the presence of an armed pseudopetiole with fibers, rigid as teeth (Lorenzi *et al.* 2010).

Butia odorata and *B. eriospatha*, both tree species with common location in Rio Grande do Sul, with *B. eriospatha* found further north (besides Santa Catarina and Paraná) and *B. odorata* distributed along the coast (besides Uruguay, in Rocha) (Eslabão et al. 2016) emerged as sister species (Fig. 1). These species present important morphological similarities, mainly in fruit morphology, ranging from light ovoid, slightly globous to globose, and yellow to reddish orange, being the second, most common in *B. odorata*. *Butia eriospatha* presents as main character that differentiates from the other species the peduncular bract covered by a thick reddish-brown lanuginous indument, whereas the *B. odorata* peduncular bract is smooth.

B. marmorii, a species endemic from Paraguay in a region near the border with the state of Paraná, in Brazil, is a species of shrubby habit, which according to Lorenzi (2010) does not exceed 40 cm in height. This species can be observed as sister species of *B. microspadix* (Fig. 1), found in the states of Paraná and São Paulo, Brazil, which also has a graminiform habit. The globous to slightly ovoid fruits of *B. marmorii* are similar in shape to the *B. microspadix* ellipsoid fruits, being both purplish when ripe, with those of *B. microspadix* varying to yellowish green. *Butia microspadix* has a peduncular bract covered with dense brownish-brown lanuginous tomentum, while *B. marmorii* has a papyraceous bract.

It is possible to observe that the graminiform habit evolved independently several times in the genus *Butia* (Fig. 1), evidencing the evolutionary convergence of this trait in non closely related lineages. This fact can be observed in *B. exilata*, sister species of the clade composed by *B. paraguayensis*, *B. catarinensis* and *B. yatay*, and *in B. lallemantii*, sister species of the clade composed by *B. eriospatha* and *B. odorata*.

The analysis of the tree generated by the ITS region data (Fig. 2) corroborates in many aspects the relationships observed for the WRKY region19. Clusters of graminoid plants such as *B. arenicola* and *B. campicola* emerged. The three species are found in the same region, in Mato Grosso do Sul, Brazil, and Paraguay, reinforcing their proximity, not only geographically, but also phylogenetically.

Butia lallemantii is observed as sister species of the clade composed by *B. exospadix* and *B. marmorii* (Fig. 2). The phylogenetic proximity between some species of graminiform habit previously observed in the WRKY19 region analysis is found again. Likewise, observing an important character to the identification of *Butia* species, such as fruit morphology and coloor, it is noted that the three species have ovoid fruits, and *B. lallemantii*, that has yellowish-orange fruits, emerged earlier and is pointed as sister species of the clade composed by *B. exospadix* and *B. marmorii*, both of purple fruits when ripe.

Butia poni is a recently revalidated species (Deble *et al.* 2017), which has long been considered synonymous of *B. paraguayensis* or *B. yatay* (Soares 2015, Deble *et al.* 2017), presenting intermediate characteristics between *B. arenicola* and *B. paraguayensis*. Deble *et al.* (2017) point out the main morphological differences for the recognizing of *B. poni* as species, comparing with *B. arenicola, B. exilata, B. lallemantii* and *B. paraguayensis*. In the present study (Fig. 2), *B. poni* is pointed out

emerging as sister group of two arboreous species, a similar situation to previously observed examples of graminiform species pointed as sister groups of clades composed by arboreous species. However, the geographical distance from *B. poni*, found in Argentina, to *B. purpurascens* (Goiás and Minas Gerais, Brazil), and *B. witeckii* (endemic of Rio Grande do Sul, Brazil), indicate the need for further analysis in the phylogenetic relationships of *B. poni* or an increase in sampling.

Despite the frequent use of chloroplast regions in the construction of phylogenies, in the present study the *trn*H-*psb*A region (Fig. 3) did not present enough phylogenetic resolution to explain *Butia* relatioships coherently when compared with nuclear data of ITS and WRKY19 regions.

Similarly, the clade formed by *B. marmorii* and *B. pubispatha*, morphologically similar species, can also be observed (Fig. 3). *Butia marmorii* has purple fruits and *B. pubispatha* has purple pigmented green fruits when ripe, and both present graminoid habit. *Butia pubispatha* was described after significant morphological differences were observed in a specimen initially identified as *B. microspadix* in the Instituto Plantarum collection (Lorenzi 2010), as the short pubescent peduncular bract rather than the dense woolly tomentum observed in *B. microspadix.* In the analysis of the WRKY19 region (Fig. 1) it is possible to observe the phylogenetic proximity between *B. microspadix* and *B. marmorii*, complementing the observed in the analysis of the *trn*H-*psb*A region, which points out a clade formed by *B. marmorii* and *B. pubispatha*, reinforcing the closest phylogenetic relationship of these three species.

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5. CONCLUSÕES GERAIS

Desde a primeira descrição das espécies que hoje constituem o gênero, 97 nomes foram publicados, divididos entre os gêneros *Butia, Cocos* e *Syagrus.* Pertencentes a *Butia,* 58 nomes foram publicados, incluindo 36 espécies, 4 subspécies e 20 variedades.

Atualmente são reconhecidas 21 espécies subordinadas a *Butia*: *B. archeri*, *B. arenicola, B. campicola*, *B. capitata*, *B. catarinensis*, *B. eriospatha*, *B. exilata*, *B. exospadix*, *B. lallemantii*, *B. lepidotispatha*, *B. leptospatha*, *B. marmorii*, *B. matogrossensis*, *B. microspadix*, *B. odorata*, *B. paraguayensis*, *B. poni, B. pubispatha*, *B. purpurascens*, *B. witeckii* e *B. yatay*.

Dois híbridos naturais entre *Butia* e *Syagrus* são reconhecidos: × *Butyagrus nabonnandii* (*B. odorata* × *Syagrus romanzoffiana*) e × *Butyagrus alegretensis* (*B. lallemantii* × *S. romanzoffiana*).

Apesar da utilização frequente de regiões cloroplastidiais na construção de filogenias, no presente estudo a região *trn*H-*psb*A não apresentou resolução filogenética suficiente para explicar as derivações de *Butia* de forma coerente quando comparado com os dados nucleares ITS e WRKY19.

As espécies encontradas no cerrado formam um grupo parafilético. *Butia lepidotispatha* pode ser observada como espécie-irmã do clado composto pelas espécies presentes mais ao sul, encontradas tanto na região de mata atlântica quanto pampa.

Quando os resultados são interpretados geograficamente, é possível observar que a distribuição das espécies segue um padrão geográfico consistente.

Ao avaliar-se comparativamente a morfologia das espécies-irmãs, é possível observar diversas características morfológicas compartilhadas, corroborando as relações filogenéticas com base em dados moleculares.

É possível observar que o hábito graminiforme evoluiu independentemente, algumas vezes no gênero *Butia*, evidenciando a convergência evolutiva dessa característica em linhagens não proximamente relacionadas.

Após um histórico de circunscrições por vezes controverso, *Butia* atualmente é considerado um gênero monofilético, irmão de *Jubaea*, ainda restando dúvidas quanto ao número de espécies aceitas no gênero.

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