



UNIVERSIDADE FEDERAL DE PERNAMBUCO

CENTRO DE BIOCÊNCIAS

PROGRAMA DE PÓS-GRADUAÇÃO EM BIOLOGIA VEGETAL

DÉBORA MARIA CAVALCANTI FERREIRA

**SISTEMÁTICA E EVOLUÇÃO DE *CRYPTANTHUS* Otto & A. Dietr.
(BROMELIOIDEAE, BROMELIACEAE)**

Recife

2021

DÉBORA MARIA CAVALCANTI FERREIRA

**SISTEMÁTICA E EVOLUÇÃO DE *CRYPTANTHUS* Otto & A. Dietr.
(BROMELIOIDEAE, BROMELIACEAE)**

Tese apresentada ao Programa de Pós-Graduação
em Biologia Vegetal do Centro de Biociências
da Universidade Federal de Pernambuco como
parte dos requisitos obrigatórios para obtenção
do título de Doutora em Biologia Vegetal.

Área de concentração: Sistemática e Evolução

Orientador: Prof^o. Dr. Rafael Batista Louzada

Coorientador: Prof^o. Dr. Santelmo Vasconcelos

Recife

2021

Catálogo na fonte:
Bibliotecária Claudina Queiroz, CRB4/1752

Ferreira, Débora Maria Cavalcanti

Sistemática e evolução de *Cryptanthus* Otto & A. Dietr.
(Bromelioideae, Bromeliaceae) / Débora Maria Cavalcanti Ferreira -
2021.

265 folhas: il., fig., tab.

Orientador: Rafael Batista Louzada

Coorientador: Santelmo Vasconcelos

Tese (doutorado) – Universidade Federal de Pernambuco. Centro
de Biociências. Programa de Pós-Graduação em Biologia Vegetal.
Recife, 2021.

Inclui referências e apêndices.

1. Cloroplasto 2. Filogenia 3. Filogenômica

I. Louzada, Rafael Batista (Orientador) II. Vasconcelos, Santelmo
(Coorientador) III. Título

584.85

CDD (22.ed.)

UFPE/CB-2021-347

DÉBORA MARIA CAVALCANTI FERREIRA

**SISTEMÁTICA E EVOLUÇÃO DE *CRYPTANTHUS* Otto & A. Dietr.
(BROMELIOIDEAE, BROMELIACEAE)**

Tese apresentada ao Programa de Pós-Graduação em Biologia Vegetal do Centro de Biociências da Universidade Federal de Pernambuco como parte dos requisitos obrigatórios para obtenção do título de Doutora em Biologia Vegetal.

DATA DE APROVAÇÃO: 29/07/2021

BANCA EXAMINADORA

Profº. Dr. Rafael Batista Louzada (Orientador)

Universidade Federal de Pernambuco

Profª Drª. Clarisse Palma da Silva (Titular)

Universidade Estadual de Campinas

Profº. Dr. Geyner Alves dos Santos Cruz (Titular)

Universidade de Pernambuco

Profº. Dr. Jefferson Rodrigues Maciel (Titular)

Jardim Botânico do Recife

Drª. Beatriz Neves Ferreira da Silva (Titular)
Universidade Federal do Rio de Janeiro - Museu Nacional
Recife

2021

Aos meus pais José Ferreira e Maria Marceli,

Dedico

AGRADECIMENTOS

Agradeço aos meus familiares por todo apoio, incentivo e carinho. Aos meus avôs Maria José Gonçalves Ferreira, Onerides Leite Ferreira (em memória), Maria da Conceição Carneiro Cavalcanti (em memória) e Pedro Primo Cavalcanti (em memória) por todo o ensinamento que me proporcionaram. Aos meus pais, José Ferreira Gomes Neto e Maria Marcelli Cavalcanti Ferreira por todo o esforço que fizeram para me proporcionar uma boa formação profissional, por todo suporte e amor. Aos meus irmãos Diego, Diogo e Jéssica, por todo carinho.

Aos órgãos de fomento que proporcionaram a realização dessa pesquisa, ao CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) pela bolsa concedida e a FACEPE (Fundação de Amparo a Ciência e Tecnologia de Pernambuco) pelo Auxílio Mobilidade Discente.

Ao meu orientador, Dr. Rafael Louzada, por todo ensinamento, ajuda, confiança, amizade e parceria ao longo desses seis anos de pós-graduação. Ao meu coorientador Dr. Santelmo Vasconcelos pela amizade, parceria e ensinamento.

A todos do laboratório de Morfo-Taxonomia Vegetal pelas conversas e ajuda. À Rayssa Valentin, pelo carinho, por ter sempre me ajudado no cultivo das plantas. À querida Dra. Danielly Lucena, por toda ajuda e conselhos. À Dra. Aline Melo e ao Dr. Thales Coutinho por toda ajuda. À Camila pelas fotos das exsicatas dos tipos do Herbário Bradeanum. À Regina Carvalho e ao Felipe Martins pelas ilustrações belíssimas. Ao professor Dr. Benoît pela disponibilização de bibliografias taxonômicas e conversas taxonômicas. À todos do laboratório de Citogenética Vegetal pela ajuda. À professora Dr. Andrea Pedrosa, pela ajuda quando eu tinha dúvida. Ao Dr. Tiago Ribeiro, por ter me ensinado o protocolo de extração. Ao Dr. Tiago Espósito pela amizade e por ter me ensinado vários procedimentos da

molecular. Ao Dr. Geadelande Delgado pela ajuda com o programa geneious, pelo incentivo, amizade e momentos de descontração. Ao Erton Mendonça, pela parceria, pelas coletas de *Cryptanthus*, pelas conversas e momentos de descontração.

A todos do Instituto Tecnológico Vale em especial ao Dr. Eder Pires e à Dra. Gisele Lopes, pela empatia acadêmica, por terem me ajudado mesmo com o instituto fechado devido à pandemia, serei eternamente grata. Ainda a Dra. Gisele e as suas gatinhas Maya Malia e Lilica por terem sido a minha família em Belém durante três meses de estágio na pandemia, por todo carinho e amizade.

A todas as pessoas que me ajudaram nas coletas. Ao Felipe Martins pelas coletas no Rio Grande do Norte e Paraíba. Ao Lukas Daneu pelas coletas na Bahia e pela coleta da espécie nova no período da pandemia. Em especial a Álvaro Nepomuceno pela imensa ajuda nas coletas do Espírito Santo, muito obrigada mesmo. Ao Manoel (ex-técnico do herbário VIES) pela imensa ajuda na coleta no Parque Estadual Paulo César Vinha. Ao Túlio Pena pela ajuda na coleta no Espírito Santo. Aos meus amigos Monique, Japa e Natália que perderam um dia de trabalho para me ajudar na coleta em Sergipe. À Nicole e ao Gabriel pela ajuda na coleta em Itacaré. À Elania e seu companheiro pela ajuda na coleta em Pirambu. Ao gestor da APA de Goiapaba-Açú, David Casarin, pela ajuda na coleta e boas risadas. Ao Dr. Anderson Alves-Araújo, pela ajuda no Espírito Santo e ajuda no pedido do auxílio para visita dos herbários do Espírito Santo mas que infelizmente não foi aceito.

Ao Dr. Leonardo Felix, a Dra. Lidyanne Aona-Pinheiro e ao Dr. Geyner Alves pela doação de amostras de *Cryptanthus*.

Ao Andy Siekkinen pela correção do inglês do artigo de espécie nova.

Aos avaliadores da disciplina de projetos e seminários integrados: Dr. Benoit Loeuille, Dr. Leonardo Versieux, Dr. Geyner Alves, Dr. Jefferson Maciel e Dr. Diego Sotero, pelas

sugestões.

À Dra. Rafaela Forzza por ter me ajudado no pedido de auxílio para a visita ao herbário RB, mas que infelizmente não foi aprovado.

Ao Elton Leme pelo envio dos protótipos e ajuda com informações para a coleta das amostras de *Cryptanthus*.

Ao Dr. Eric Gouda pelo envio de protótipos.

À Dra. Ana Maria Benko Iseppon pela articulação para que eu conseguisse o hormônio de florescimento de bromélia.

Ao INMA pela doação de amostras vivas de Bromeliaceae. Em especial a Josy que mesmo com o herbário fechado devido ao feriado se disponibilizou a trabalhar para que eu pudesse analisar a coleção.

Ao Dr. Ricardo Pessoa de Queiroz responsável pelo Jardim Botânico da Usina Arte pela doação de amostras das espécies novas.

Ao Felipe e à Soraya da secretaria da pós, pela ajuda com a parte burocrática.

À Wanessa pelas conversas e pelas caronas até UFPE.

As minhas queridas amigas da pós-graduação, Isabelle, Rafaella e Carolina, por todo carinho e incentivo.

RESUMO

Cryptanthus é um gênero da família Bromeliaceae que apresenta 64 espécies que estão distribuídas na parte leste do Brasil nas regiões nordeste e sudeste, ocorrendo nos domínios fitogeográficos da Floresta Atlântica e Caatinga. As relações filogenéticas do gênero não são completamente entendidas e os estudos taxonômicos feitos para o gênero estão desatualizados visto que nos últimos anos houve um grande incremento de espécies novas publicadas. Assim, o objetivo geral desta tese foi realizar o estudo sistemático e evolutivo de *Cryptanthus*. Para a reconstrução filogenética foram usados 44 acessos pertencentes a 29 espécies, sendo 23 do gênero *Cryptanthus*. As análises foram realizadas utilizando 69 genes codificantes de proteína do cloroplasto. O estudo mostrou que *Cryptanthus* é monofilético e que os clados foram formados pela proximidade geográfica das espécies. Os clados não estão de acordo com a classificação infragenérica anteriormente proposta para o gênero. As reconstruções de estado de caráter ancestral mostraram que a presença de pecíolos e que a coloração das pétalas alvas com ápice verde ou esverdeado surgiram múltiplas vezes na história evolutiva do gênero. Na parte taxonômica, cinco espécies novas foram descritas para o gênero: *Cryptanthus apiculatantherus*, *C. brevibracteatus*, *C. cinereus*, *C. pirambuensis* e *C. vinosibracteatus*. Uma sinopse taxonômica de *Cryptanthus* para a região nordeste do Brasil é apresentada e inclui 39 espécies. O estudo contou com uma chave de identificação do gênero para a região e inclui ilustrações e fotografias, bem como mapas de distribuição geográfica e análise do status de conservação das espécies. Além disso, dois complexos de espécies foram reconhecidos para *Cryptanthus*, o complexo *Cryptanthus pickelii* que engloba as espécies *Cryptanthus alagoanus* e *Cryptanthus pickelii*, e o complexo *Cryptanthus zonatus* que inclui as espécies *Cryptanthus diana*, *Cryptanthus reptans* e *Cryptanthus zonatus*. Uma nova sinonimização foi proposta onde *C. heimenii* foi sinonimizado em *C. bahianus*. Além disso, a flora do estado de Alagoas foi apresentada e inclui seis espécies: *C. alagoanus*, *C. bahianus*, *C. cinereus*, *C. diana*, *C. felixii* e *C. zonatus*. O estudo contou com chave de identificação das espécies para o estado, descrição das espécies, dados sobre distribuição e comentários taxonômicos. Por fim, um guia de campo incluindo fotografias é apresentado para facilitar a identificação das espécies do gênero.

Palavras-chave: cloroplasto; filogenia; filogenômica; NGS; sinopse; taxonomia.

ABSTRACT

Cryptanthus is a genus of the family Bromeliaceae that has 64 species and is distributed in the eastern part of Brazil in the northeast and southeast regions, occurring in the phytogeographic domains of the Atlantic Forest and Caatinga. Phylogenetic relationships of the genus are not completely understood and the taxonomic studies for the genus are outdated, since in recent years there has been a large increase in new published species. Thus, the general objective of the thesis was to carry out the systematic and evolutionary study of the genus *Cryptanthus*. For phylogenetic reconstruction, 44 accessions of 29 species, being 23 of the *Cryptanthus* genus, were used. The analyzes were performed using 69 protein-coding genes of the chloroplast. The study reveals that *Cryptanthus* is monophyletic and that the clades were formed by the proximity of the species. The clades are not in accordance with the infra-generic classification previously proposed. The ancestral character state reconstructions suggests that the presence of petioles and that the petal color white, except for the green or greenish apex arisen multiple times in the evolutionary history of the genus. In the taxonomic part, five new species are described for the genus: *Cryptanthus apiculatantherus*, *C. brevibracteatus*, *C. cinereus*, *C. pirambuensis* and *C. vinosibracteatus*. A taxonomic synopsis of *Cryptanthus* in the Northeastern region from Brazil is presented and it includes 39 species. The study has an identification key of genus for the region and it includes illustrations and photos, as well as geographical distribution maps and analysis of the conservation status of the species. In addition, two species complexes are described for *Cryptanthus*, the *Cryptanthus pickelii* complex which includes *Cryptanthus alagoanus* and *Cryptanthus pickelii* species, and the *Cryptanthus zonatus* complex which includes *Cryptanthus diana*, *Cryptanthus reptans* and *Cryptanthus zonatus* species. A new synonymization is proposed where *C. heimenii* is synonymized in *C. bahianus*. In addition, the flora of the state of Alagoas is presented and includes six species: *C. alagoanus*, *C. bahianus*, *C. cinereus*, *C. diana*, *C. felixii* and *C. zonatus*. The study has a species identification key for the state, description of the species, data about distribution and taxonomic comments. Finally, a field guide including images is presented to facilitate an identification of the genus species.

Keywords: chloroplast; phylogeny; phylogenomics; NGS; synopsis; taxonomy.

LISTA DE FIGURAS

REFERENCIAL TEÓRICO

- Figura 1 — Distribuição agrupada de indivíduos do gênero *Cryptanthus* Otto & A. Dietr. A. *Cryptanthus dorotheae* Leme. B. *Cryptanthus zonatus* (Vis.) Vis. 30
- Figura 2 — Estudos filogenéticos com o clado Cryptanthoid. A. Estudo de Silvestro, Zizka e Schulte (2013). B. Estudo de Louzada et al. (2014). C. Estudo de Cruz et al. (2017). D. Estudo de Leme et al. (2017). Valores acima dos ramos representam as probabilidades posteriores e abaixo dos ramos são os valores de bootstrap. 32
- Figura 3 — Tipos de reprodução assexuada em *Cryptanthus*. A. Brotos emitidos diretamente do rizoma em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada. B. Estolões que partem do rizoma em *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. C. Brotos axilares em *Cryptanthus zonatus* (Vis.) Vis. 36
- Figura 4 — Hábitos em *Cryptanthus*. A. Terrícola em *Cryptanthus teretifolius* Leme. B. Rupícola em *Cryptanthus bahianus* L.B. Sm. (Foto: J. Maciel). 37
- Figura 5 — Indivíduo de *Cryptanthus apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada evidenciando o rizoma, o caule e a raque. 37
- Figura 6 — Formato das folhas em *Cryptanthus*. A. Peciolas em *Cryptanthus walkerianus* Leme & L. Kollmann. B. Estreitas na base em *Cryptanthus pickelii* L. B. Sm.. C. Mais larga na base em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada. 38
- Figura 7 — Inflorescência do tipo espiga de glomérulos em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada evidenciando o glomérulo apical e os glomérulos laterais da inflorescência. 39

- Figura 8 — Raque da inflorescência de *Cryptanthus walkerianus* Leme & L. Kollmann evidenciada em branco. 39
- Figura 9 — Flores de *Cryptanthus robsonianus* Leme, a estaminada com tamanho menor (lado esquerdo) e a perfeita com tamanho maior (lado direito). 40
- Figura 10 — Flores de *Cryptanthus diana*e Leme. A. Com número usual de três pétalas. B. Com número incomum de quatro pétalas. 41
- Figura 11 — Corte longitudinal da flor de *Cryptanthus pickelii* L.B.Sm. evidenciando em preto o tubo epigínico. 41
- Figura 12 — Frutos de *Cryptanthus pickelii* L.B.Sm.. A. Frutos. B. Fruto alvo na base (parte que fica escondida) e verde no ápice (parte exposta). 42

ARTIGO 1 - PHYLOGENY AND CHARACTER EVOLUTION IN THE GENUS *CRYPTANTHUS* OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) USING NEXT-GENERATION SEQUENCING DATA

- Figura 1 — Species of *Cryptanthus* included in the study. A. *C. alagoanus*. B. *C. bahianus* (Photo: J. Maciel). C. *C. beuckeri*. D. *C. boanovens*is. E. *C. capitellatus*. F. *C. cinereus* (Photo: A. Melo). G. *C. diana*e. H. *C. crassifolius*. I. *C. reptans*. J. *C. robsonianus*. K. *C. sergipensis*. L. *C. teretifolius*. M. *C. venecianus* (Photo: A. Nepomuceno). N. *C. viridipetalus*. O. *C. walkerianus*. P. *C. zonatus*. 79
- Figura 2 — Phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae. Numbers above the branches represent posterior probabilities values. The colors of the branches are in accordance with the colors of the geographic distribution of the species. Sections of the *Cryptanthus* proposed by Ramírez-Morillo (1996) are indicated in symbols on the left side. The horizontal bar indicates the mutation rates. 80

Figura 3 — Phylogram of the majority-rule consensus tree from the Maximum-likelihood analyses based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae. Numbers above the branches represent bootstrap values. The colors of the branches are in accordance with the colors of the geographic distribution of the species. Sections of the *Cryptanthus* proposed by Ramírez-Morillo (1996) are indicated in symbols on the left. The horizontal bar indicates the mutation rates.

81

Figura 4 — Ancestral character state reconstruction for petioles plotted on phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae.

82

Figura 5 — Ancestral character state reconstruction for petals color plotted on phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae.

83

ARTIGO 2 - TWO NEW SPECIES OF *CRYPTANTHUS* (BROMELIOIDEAE, BROMELIACEAE) FROM ATLANTIC FOREST OF NORTHEASTERN BRAZIL

Figura 1 — Geographical distribution of *Cryptanthus pirambuensis* and *Cryptanthus vinosibracteatus* in the Atlantic Forest of northeastern Brazil.

102

Figura 2 — *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. A. Habit. B. Leaf sheath (adaxial surface). C. Leaf (adaxial surface). D. Staminate flower. E. Perfect flower. F. Bract of the staminate flower. G. Bract of perfect flower. H. Sepals of the staminate flower. I. Sepals of the perfect flower. J. Petals and stamens of the staminate flower. K. Petals and stamens of the perfect flower. L. Anther of the staminate flower. M. Anther of the perfect flower. N. Style and stigma. O. Ovary and epigynous tube of staminate flower. P. Ovary and epigynous tube of perfect flower.

103

Figura 3 — *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. A. Habitat. B. Individual in nature. C. Flowering individual in cultivation. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Apical glomerule of the inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of the staminate flower. K. Bract of perfect flower. L. Anther. M. Staminate flower. N. Perfect flower. 104

Figura 4 — *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. A. Habit. B. Leaf sheath (adaxial surface). C. Leaf (adaxial surface). D. Floral bract of staminate flower (abaxial surface). E. Floral bract of staminate flower (adaxial surface). F. Staminate flower with the floral bract. G. Sepals of staminate flower. H. Petals and stamens of staminate flower. I. Detail of conspicuous callosities on the petals of staminate flower. J. Anther of the staminate flower. K. Ovary of the staminate flower. 105

Figura 5 — *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. A. Habit. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf (abaxial surface). E. Leaf (adaxial surface). F. Inflorescence. G. Staminate flower with the floral bract. H. Floral bract of staminate flower (adaxial surface). I. Anther of the staminate flower. 106

ARTIGO 3 - A TAXONOMIC SYNOPSIS OF THE GENUS *CRYPTANTHUS* OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) IN THE NORTHEASTERN REGION FROM BRAZIL

Figura 1 — Distribution map of the genus *Cryptanthus* in South America showing the Northeastern region from Brazil in grey. 177

Figura 2 — Geographical distribution of *Cryptanthus* species from Northeastern Brazil. A. *Cryptanthus alagoanus*, *C. apiculatantherus*, *C. arelii*, *C. argyrophyllus* and *C. bahianus*; B. *C. beuckeri*, *C. bibarrensensis* and *C. boanovensensis*; C. *C. brevibracteatus*, *C. cinereus*, *C. colnagoi*, *C. crassifolius* and *C. cruzalmensis*; D. *C. diamantinensis*, *C. diana*, *C. sp.*, *C. felixii* and *C. ilhanus*. 178

Figura 3 — Geographical distribution of *Cryptanthus* species from Northeastern Brazil.

A. *Cryptanthus lacerdae* (without precise locality), *C. lyman-smithii*, *C. osiris* (without precise locality), *C. pickelii* and *C. pirambuensis*; B. *C. pseudopetiolatus*, *C. reisii*, *C. reptans*, *C. robsonianus* and *C. ruthiae*; C. *C. santateresinhensis*, *C. seidelianus*, *C. sergipensis*, *C. teretifolius* and *C. ubairensis*; D. *C. vexatus*, *C. vinosibracteatus*, *C. viridovinosus*, *C. walkerianus*, *C. warren-loosei* and *C. zonatus*.

179

Figura 4 — Species of *Cryptanthus*. A-B. *Cryptanthus alagoanus* (D. Cavalcanti et al.

906). A. Leaf blade linear-oblongate. B. Staminate flower evidencing the epigynous tube. C-D. *Cryptanthus apiculatantherus* (E. M. Almeida 3246). C. Leaf blade linear triangular. D. Anther apiculate. E. *Cryptanthus arelii* (R.L.Frasier, E.M.C. Leme & J. Kent s.n.) - Leaf blade lanceolate. F. *Cryptanthus argyrophyllus* (E. Leme 4872)- Leaf blade oblongate. G-J. *Cryptanthus bahianus*. G. Floral bract of the staminate flower. H. Petals obtuse and stamens. I. Anther emarginate. J. Ovary. K-M. *Cryptanthus beuckeri* (D. Cavalcanti et al. 726). K. Leaf with petiole. L. Portion of the adaxial surface of the canaliculate petiole with revolute margins. M. Portion of the abaxial surface of the canaliculate petiole with revolute margins.

180

Figura 5 — Species of *Cryptanthus*. A. *Cryptanthus boanovensensis* (D. Cavalcanti et al.

838) - Petals acute and stamens. B. *Cryptanthus colnagoi* (E. Colnago s.n.) - abaxial surface of the leaf blade with revolute margins. C. *Cryptanthus diamantinensis* (E. Leme 3812) - Plant short caulescent. D. *Cryptanthus lacerdae* (E.M.C. Leme 200) - adaxial surface of the leaf blade with three longitudinal lines of lepidote trichomes. E. *Cryptanthus osiris* (Amanda et Michael Bleher 125) - sepals connate for 2 mm long. F. *Cryptanthus sergipensis* (D. Cavalcanti & N. Souza 902) - ovary. G. *Cryptanthus ubairensis* (T. R. Soderstrom 2175) - Plants long caulescent. H-J. *Cryptanthus walkerianus* (D. Cavalcanti & L. Dane 884). H. Leaf with petiole. I. Portion of the abaxial surface of the canaliculate petiole with revolute margins. J. Portion of the adaxial surface of the canaliculate petiole with revolute margins.

181

- Figura 6 — *Cryptanthus alagoanus* Leme & J.A.Siqueira. A. Habitat - Atlantic Forest (semideciduous seasonal forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Floral bract of staminate flower. K. Floral bract of perfect flower. L. Staminate flower. M. Perfect flower. N. Anther. 182
- Figura 7 — *Cryptanthus apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada. A. Population in nature (Photo: E. Mendonça). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G-H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Bract of perfect flower. L. Staminate flower. M. Perfect flower. N. Detail of two conspicuous callosities. O. Anther apiculate. P. Fruits. O. Seed. 183
- Figura 8 — *Cryptanthus bahianus* L.B.Sm. A. Habitat - Brejo de altitude (Photo: E. Mendonça). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical glomerule of the inflorescence. K. Lateral glomerule of the inflorescence. L. Floral bract of staminate flower. M. Staminate flower. N. Anther. O. Perfect flower. P. Ovary of perfect flower. Q. Fruit. R. Seeds. 184
- Figura 9 — *Cryptanthus beuckeri* E. Morren. A. Habitat - Atlantic Forest (Lowland Tropical Moist Forest). B. individual in nature. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Inflorescence. F. Sepal lobe. G. Anther. 185
- Figura 10 — *Cryptanthus boanovenssis* Leme. A. Habitat - transition area between Atlantic Forest and Caatinga with vegetation type called as Mata de Cipó. B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Top view of the rosette showing the inflorescence. I. Lateral glomerule of the inflorescence. J. Staminate

flower. K. Bract of perfect flower. L. Perfect flower. M. Sepal lobe. N. Anther.

186

Figura 11 — *Cryptanthus brevibracteatus* D.M.C. Ferreira & Louzada. A. Habitat - transition area between Atlantic Forest and Caatinga with vegetation type called as Mata de Cipó. B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Bract of staminate flower. J. Staminate flower K. Bract of perfect flower. L. Perfect flower.

187

Figura 12 — *Cryptanthus cinereus* D. M. C. Ferreira & Louzada. A. Habitat - Atlantic Forest (rocky outcrop). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence. H. Apical glomerule of the inflorescence. I. Bract of staminate flower. J. Staminate flower. K. Anther. L. Fruits. M. Seed.

188

Figura 13 — *Cryptanthus crassifolius* Leme. A. Habitat - Caatinga (rock outcrops along of the Mato Grosso river valley). B. Population in nature. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence. H. Lateral glomerule of the inflorescence. I. Staminate flower. J. Perfect flower. K. Anther.

189

Figura 14 — *Cryptanthus cruzalmensis* Leme & E.H.Souza. A. Individual. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf (abaxial surface). E. Leaf (adaxial surface).

190

Figura 15 — *Cryptanthus diana* Leme. A. Habitat - (Atlantic Forest) Submontane Tropical Moist Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf blades (adaxial surface). G. Inflorescence. H. Lateral glomerule of the inflorescence. I. Staminate flower. J. Perfect flower. K. Anther.

191

Figura 16 — *Cryptanthus* sp.. A. Population in nature (Photo: E. Mendonça). B. Individual in nature (Photo: E. Mendonça). C. Leaf sheath (abaxial

surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence (Photo: E. Mendonça). H. Bract of staminate flower. I. Staminate flower. 192

Figura 17 — *Cryptanthus felixii* J.A.Siqueira & Leme. A. Individual. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf (abaxial surface). E. Leaf (adaxial surface). 193

Figura 18 — *Cryptanthus pickelii* L.B.Sm.. A. Habitat - Atlatic Forest (semideciduous seasonal forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical glomerule of the inflorescence. K. Lateral glomerule of the inflorescence. L. Bract of staminate flower. M. Staminate flower. N. Bract of perfect flower. O. Perfect flower. P. Anther. Q. Fruit. R. Seed. 194

Figura 19 — *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. A. Habitat - Atlatic Forest (semideciduous seasonal forest). B. Individual in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Apical glomerule of the inflorescence. J. Lateral glomerule of the inflorescence. K. Bract of staminate flower. L. Staminate flower. M. Bract of perfect flower. N. Perfect flower. O. Sepal lobe. P-Q. Anther. 195

Figura 20 — *Cryptanthus pseudopetiolatus* Philcox. A. Habitat - Atlantic Forest (Lowland Tropical Moist Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Staminate flower. K. Floral bract of staminate flower (abaxial surface). L. Floral bract of staminate flower (adaxial surface). 196

Figura 21 — *Cryptanthus reisii* Leme. A. Population in nature (Photo: L. Daneu). B. Individual. C. Plant in longitudinal section showing the rachis, stem and

rhizome. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Staminate flower. L. Bract of perfect flower. M. Perfect flower. N. Anther apex rounded. O. Anther apex emarginate. 197

Figura 22 — *Cryptanthus reptans* Leme & J.A.Siqueira. A. Population in nature. B. Individual. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Floral bract of staminate flower. J. Staminate flower. K. Sepal lobe. L. Anther. 198

Figura 23 — *Cryptanthus robsonianus* Leme. A. Habitat - Atlantic Forest (Restinga Forest). B. Individual in nature with adaxial surface of the leaf blades with crossbars of lepidote trichomes. C. Individual. D. Inflorescence. E. Lateral glomerule of the inflorescence. F. Bract of staminate flower. G. Staminate flower. H. Perfect flower. I. Sepal lobe. J. Anther. K. Fruits. 199

Figura 24 — *Cryptanthus ruthiae* Philcox. A. Individual in nature (Photo: G. Alves). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Apical glomerule of the inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Staminate flower. L. Bract of perfect flower. M. Perfect flower. 200

Figura 25 — *Cryptanthus sergipensis* I.Ramírez. A. Habitat - Atlantic Forest (Restinga Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical glomerule of the inflorescence. K. Portion of the rachis. L. Lateral glomerule of the inflorescence. M. Floral bract of staminate flower. N. Staminate flower. O. Floral bract of perfect flower. P. Perfect flower. Q. Anther. R. Ovary of perfect flower. S. Fruit. 201

Figura 26 — *Cryptanthus teretifolius* Leme. A. Habitat - Atlantic Forest (Submontane Tropical Moist Forest). B. Individual in nature. C. Leaf sheath (abaxial

surface). D. Leaf sheath (abaxial surface). E. Leaf (adaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Inflorescence in longitudinal section showing the rachis. I. Floral bract of staminate flower. J. Anther. K. Staminate flower. 202

Figura 27 — A-B. *Cryptanthus vexatus* Leme. A. Population in nature. B. Individual in nature. C-K. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Floral bract of staminate flower (abaxial surface). J. Floral bract of staminate flower (adaxial surface). K. Staminate flower. 203

Figura 28 — *Cryptanthus walkerianus* Leme & L.Kollmann. A. Habitat - Atlantic Forest (Submontane Tropical Moist Forest). B. Individuals in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Inflorescence. H. Lateral glomerule of the inflorescence. I. Anther. J. Floral bract of staminate flower. K. Staminate flower. L. Floral bract of perfect flower. M. Perfect flower. 204

Figura 29 — *Cryptanthus warren-loosei* Leme. A. Population in nature (Photo: R. Valentin). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Floral bract of staminate flower. I. Staminate flower. K. Staminate flower. J. Floral bract of perfect flower. K. Perfect flower. L. Sepal lobe. M. Anther. 205

Figura 30 — *Cryptanthus zonatus* (Vis.) Vis.. A-C. Population in nature. D. Individual. E. Leaf sheath (abaxial surface). F. Leaf sheath (adaxial surface). G. Leaf (abaxial surface). H. Leaf (adaxial surface of the leaf blades with crossbars of lepidote trichomes). I-J. Inflorescence. K. Lateral glomerule of the inflorescence. L. Floral bract of staminate flower. M. Staminate flower. N. Floral bract of perfect flower. O. Perfect flower. P-Q. Anther. R. Fruit. S. Seeds. 206

CAPÍTULO DE LIVRO 1 - FLORA DE ALAGOAS: *CRYPTANTHUS*

Figura 1 — *Cryptanthus* de Alagoas. A. *Cryptanthus alagoanus* Leme & J. A. Siqueira. B. *Cryptanthus bahianus* L. B. Sm. (Foto: J. R. Maciel). C. *Cryptanthus cinereus* D.M.C. Ferreira & Louzada. D. *Cryptanthus diana* Leme. E. *Cryptanthus felixii* J. A. Siqueira & Leme (Foto: R. Pontes). F. *Cryptanthus zonatus* (Vis.) Vis.

LISTA DE TABELAS

REFERENCIAL TEÓRICO

Tabela 1 — Espécies novas do gênero <i>Cryptanthus</i> publicadas após a última revisão taxonômica realizada por Ramirez-Morillo (1996).	35
--	----

ARTIGO 1 - PHYLOGENY AND CHARACTER EVOLUTION IN THE GENUS *CRYPTANTHUS* OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) USING NEXT-GENERATION SEQUENCING DATA

Tabela 1 — Studied material with locality, DNA No. and Voucher (all deposited in Herbarium Geraldo Mariz of Universidade Federal de Pernambuco). Abbreviations: AL: Alagoas; BA: Bahia; PE: Pernambuco; PB: Paraíba; RN: Rio Grande do Norte; SE: Sergipe; ES: Espírito Santo. *living collection of the Museu de Biologia Prof. Mello Leitão, in Santa Teresa, Espírito Santo	73
Tabela 2 — Matrix allignment statistics	75
Tabela S1 — Accessions and morphological characters with their respective character states coded used for ancestral character state reconstruction. Codification: Subpetiole= 0-absent, 1-present; Petals color= 1-white, 2-white with green or greenish apex, 3-greenish, 4-pink, 5-purple, 6-blue.	77

ARTIGO 2 - TWO NEW SPECIES OF *CRYPTANTHUS* (BROMELIOIDEAE, BROMELIACEAE) FROM ATLANTIC FOREST OF NORTHEASTERN BRAZIL

Tabela 1 — Comparison of characters and geographic distribution of <i>Cryptanthus pirambuensis</i> and morphologically similar species	100
Tabela 2 — Comparison of characters of <i>Cryptanthus vinosibracteatus</i> and morphologically similar species	101

LISTA DE SIGLAS

AFLP - Amplified Fragment Length Polymorphism

AOO - Area of Occupancy

CR - Critically Endangered

DD - Data Deficient

EN - Endangered

EOO - Extent of Occurrence

LN - Least Concern

NGS - Next-Generation Sequencing

SUMÁRIO

1	INTRODUÇÃO	25
2	REFERENCIAL TEÓRICO	26
2.1	A família Bromeliaceae Juss.	26
2.2	O gênero <i>Cryptanthus</i> Otto & A. Dietr.	28
2.2.1	Posicionamento filogenético e mudanças taxonômicas	28
2.2.2	Etimologia, distribuição geográfica, status de ameaça e importância econômica	30
2.2.3	Reconstruções filogenéticas e biogeografia	31
2.2.4	Número cromossômico e tamanho genômico	33
2.2.5	Estudos de genética de populações	33
2.2.6	Estudos taxonômicos	34
2.2.7	Morfologia e biologia reprodutiva	36
3	OBJETIVOS	42
3.1	Objetivo geral	42
3.2	Objetivos específicos	42
4	RESULTADOS	44
4.1	ARTIGO 1 - PHYLOGENY AND CHARACTER EVOLUTION IN THE GENUS <i>CRYPTANTHUS</i> OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) USING NEXT-GENERATION SEQUENCING DATA	44
4.2	ARTIGO 2 - TWO NEW SPECIES OF <i>CRYPTANTHUS</i> (BROMELIOIDEAE, BROMELIACEAE) FROM ATLANTIC FOREST OF NORTHEASTERN BRAZIL	84

4.3	ARTIGO 3 - A TAXONOMIC SYNOPSIS OF THE GENUS <i>CRYPTANTHUS</i> OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) IN THE NORTHEASTERN REGION FROM BRAZIL	107
4.4	CAPÍTULO DE LIVRO 1 - FLORA DE ALAGOAS: <i>CRYPTANTHUS</i>	207
4.5	GUIA DE CAMPO 1 - THE GENUS <i>CRYPTANTHUS</i> OTTO & A. DIETR. (BROMELIACEAE). ENDEMIC GENUS TO BRAZIL	220
5	CONCLUSÃO	237
	REFERÊNCIAS	238
	APÊNDICE A - A NEW SPECIES OF <i>CRYPTANTHUS</i> (BROMELIACEAE, BROMELIOIDEAE) IN THE BRAZILIAN ATLANTIC FOREST NORTH OF THE SÃO FRANCISCO RIVER, AND ITS CONTRIBUTION TO THE TAXONOMY OF THE GENUS	247
	APÊNDICE B - TWO NEW SPECIES OF <i>CRYPTANTHUS</i> (BROMELIOIDEAE, BROMELIACEAE) FROM NORTHEASTERN BRAZIL	254

1 INTRODUÇÃO

Cryptanthus é um gênero endêmico do Brasil que conta com 64 espécies distribuídas nas regiões Nordeste e Sudeste. As relações filogenéticas do gênero não são completamente entendidas e os estudos taxonômicos realizados com o gênero estão desatualizados visto que muitas espécies foram descobertas e descritas recentemente. O objetivo geral desta tese foi realizar o estudo sistemático e evolutivo do gênero *Cryptanthus* Otto & A. Dietr.

Esta tese está dividida em fundamentação teórica, três artigos científicos que ainda serão publicados, um capítulo de livro e um guia de campo. Além disso, a tese inclui dois apêndices referentes a dois artigos publicados. O referencial teórico conta com informações sobre a família Bromeliaceae e sobre o gênero *Cryptanthus*.

O primeiro artigo trata da análise filogenética do gênero *Cryptanthus* que foi realizada utilizando dados de Sequenciamento de Nova Geração (NGS). Para a análise, 44 amostras de 29 espécies foram utilizadas, sendo 23 do gênero *Cryptanthus*. Um total de 69 genes codificantes de proteínas do cloroplasto foi isolado para cada espécie e depois foram concatenados para análise de Máxima Verossimilhança e Inferência Bayesiana. O estudo mostrou que *Cryptanthus* é monofilético e que os clados foram formados pela proximidade geográfica das espécies. Os clados não estão de acordo com a classificação infragenérica anteriormente proposta para o gênero. As reconstruções de estado de caráter ancestral indicaram que a presença de pecíolos e a coloração das pétalas alvas com ápice verde ou esverdeado surgiram múltiplas vezes na história evolutiva do gênero.

O segundo artigo inclui a descrição de duas espécies novas de *Cryptanthus* na Floresta Atlântica do Nordeste do Brasil: *C. pirambuensis* e *C. vinosibracteatus*. A primeira espécie ocorre em Sergipe e a segunda ocorre na Bahia. São apresentadas ilustrações para os táxons, bem como fotografias, mapas de ocorrência e comentários taxonômicos.

O terceiro artigo inclui uma sinopse taxonômica do gênero *Cryptanthus* na região nordeste do Brasil. O estudo inclui 39 espécies das quais 36 são endêmicas para o nordeste e apenas três ocorrem no nordeste e sudeste do Brasil. Das 39 espécies encontradas no nordeste, 19 são conhecidas apenas para uma única localidade. O estudo conta com uma chave de identificação para a região com ilustrações dos caracteres mais importantes para a identificação dos táxons, fotografias, comentários taxonômicos, e para cada espécie é avaliado

o status de conservação e apresentado o mapa de distribuição. Uma nova sinonimização foi proposta onde *C. heimenii* foi sinonimizado em *C. bahianus*.

O capítulo de livro é referente à Flora de Alagoas para o gênero *Cryptanthus* e inclui seis espécies: *Cryptanthus alagoanus*, *C. bahianus*, *C. cinereus*, *C. diana*, *C. felixii* e *C. zonatus*. O estudo conta com chave de identificação das espécies para o estado, descrição detalhada de cada espécie, dados sobre distribuição e comentários taxonômicos.

O guia de campo é referente a fotografias das espécies de *Cryptanthus* para a rápida identificação das espécies do gênero. O guia de campo inclui fotos de 29 espécies do gênero. As fotos são do hábito, bainha foliar, folha, inflorescência, bráctea da flor estaminada e perfeita, flor estaminada e perfeita, frutos e sementes.

Por fim, o apêndice A trata de um artigo de espécie nova que foi publicado na Systematic Botany. O artigo conta com a descrição da espécie nova, *Cryptanthus cinereus*, e inclui ilustração, fotografias, mapa de distribuição, chave de identificação das espécies que ocorrem na Floresta Atlântica ao norte do Rio São Francisco e a descrição de dois complexos de espécies: o complexo *Cryptanthus pickelii* que engloba as espécies *Cryptanthus alagoanus* e *Cryptanthus pickelii*, e o complexo *Cryptanthus zonatus* que inclui as espécies *Cryptanthus diana*, *Cryptanthus reptans* e *Cryptanthus zonatus*. E o apêndice B corresponde a um artigo publicado na Phytotaxa que conta com a descrição de duas espécies novas de *Cryptanthus* que ocorrem no estado da Bahia: *C. apiculatantherus* e *C. brevibracteatus*. São apresentadas ilustrações para os táxons, bem como fotografias, mapa e comentários taxonômicos.

2 REFERENCIAL TEÓRICO

2.1 A família Bromeliaceae Juss.

Bromeliaceae Juss. pertence à ordem Poales (APG IV, 2016). Apresenta 3692 espécies, pertencentes a 79 gêneros (GOUDA; BUTCHER; GOUDA, continuamente atualizado), sendo o Brasil representado por 1379 espécies distribuídas em 56 gêneros (FORZZA et al., 2020). A família ocorre nas regiões tropicais e subtropicais das Américas (GIVNISH et al., 2011), e uma única espécie, *Pitcairnia feliciana* (A. Chev.) Harms &

Mildbr., ocorre na costa oeste da África e teria chegado no continente africano através de uma dispersão à longa distância (GIVNISH et al., 2004).

Bromeliaceae surgiu a aproximadamente 130 milhões de anos atrás (GIVNISH et al., 2018). De acordo com Zizka et al. (2020), os centros de diversidade e endemismo da família são a América Central, as encostas dos Andes, o Planalto das Guianas e o leste do Brasil (Mata Atlântica). A família é um excelente exemplo de radiação adaptativa (CRAYN; WINTER; SMITH, 2014). Os representantes da família são ervas perenes apresentam hábito terrícola, rupícola ou epífita (WANDERLEY et al., 2007). O caule é geralmente curto encoberto pelas bainhas foliares que estão dispostas em roseta ou, mais raramente, o caule é desenvolvido e alongado (WANDERLEY et al., 2007). As folhas são alternas, espiraladas, polísticas, raramente dísticas, formando ou não um “tanque” (WANDERLEY et al., 2007). As inflorescências são simples ou compostas, com flores sésseis ou pediceladas, trímeras (WANDERLEY et al., 2007). O ovário é súpero, semi-ífero ou ífero, o fruto é baga, ou cápsula, em geral septicida, ou fruto composto (WANDERLEY et al., 2007).

Anteriormente a família era dividida em três subfamílias que foram delimitadas com base em caracteres morfológicos: Bromelioideae, Pitcairnioideae e Tillandsioideae (MEZ, 1935; SMITH, 1955; SMITH; DOWNS 1974, 1977, 1979; GIVNISH et al., 2007). Sendo Bromelioideae caracterizada por apresentar frutos do tipo baga e sementes inapendiculadas, Pitcairnioideae por apresentar fruto cápsula e sementes aladas (ou raramente sem apêndices) e Tillandsioideae por possuir fruto cápsula e sementes com apêndices plumosos (SMITH; DOWNS 1974, 1977, 1979; GIVNISH et al., 2007).

Contudo, reconstruções filogenéticas têm mostrado que Bromelioideae e Tillandsioideae são monofiléticas enquanto que Pitcairnioideae é parafilética (TERRY et al., 1997; GIVNISH et al. 2007, 2011). Assim, as espécies de Pitcairnioideae foram reorganizadas em quatro novas subfamílias (Brocchinioideae, Hechtioideae, Lindmanioideae e Puyoideae) e em Pitcairnioideae que foi recircunscrita (GIVNISH et al., 2007). Além disso, Navioideae também foi recircunscrita (GIVNISH et al., 2007), essa subfamília já havia sido descrita por Harms (1930 apud TERRY et al., 1997), porém, Smith e Downs (1974) a tratava como Pitcairnioideae. Portanto, atualmente a família Bromeliaceae está dividida em oito subfamílias: Brocchinioideae, Bromelioideae, Hechtioideae, Lindmanioideae, Pitcairnioideae, Puyoideae, Navioideae e Tillandsioideae (GIVNISH et al., 2007). Entretanto, o monofiletismo

do gênero *Puya* (subfamília Puyoideae) ainda é controverso, já que o gênero aparece como parafilético na análise de Givnish et al. (2011).

Quanto aos estudos filogenéticos inter e infragenéricos em Bromeliaceae, importantes contribuições vêm sendo publicadas, ampliando o conhecimento da família (ver estudos em PALMA-SILVA et al., 2016). E recentemente, com o avanço tecnológico, tem sido empregado o uso sequenciamento de nova geração com o uso do plastoma inteiro (PAULE et al., 2020) ou parcial (MACHADO et al., 2020) para análises filogenéticas mais robustas.

Bromeliaceae possui importância alimentícia com os frutos do abacaxi (*Ananas comosus* (L.) Merril) e grande importância ornamental com vários gêneros sendo utilizados em cultivo como exemplo *Aechmea* Ruiz & Pav., *Billbergia* Thunb., *Bromelia* L., *Guzmania* Ruiz & Pav., *Neoregelia* L.B. Sm., *Pitcairnia* L'Hér., *Tillandsia* L., e *Vriesea* Lindl. (JUDD, 2009). Devido a retirada de espécies da natureza para cultivo como ornamental, e principalmente devido a perda de habitats, muitas espécies do gênero estão presentes em lista de espécies ameaçadas, sendo 202 espécies classificadas como ameaçadas pelo Livro Vermelho da Flora do Brasil (FORZZA et al., 2013) e pelo MMA (2014).

Importantes contribuições taxonômicas foram realizadas para a família com as seguintes publicações: Die familie der Bromeliaceen (BEER, 1857), Flora brasiliensis (MEZ, 1892), Monographiae Phanerogamarum (MEZ, 1896), Das Pflanzenreich (MEZ, 1934-1935) e Flora Neotropica (SMITH; DOWNS, 1974, 1977, 1979). Recentes revisões taxonômicas têm sido publicadas a nível genérico (e.g. ZIZKA; TRUMPLER; ZÖLLNER, 2002; FORZZA, 2005; LOUZADA; WANDERLEY, 2010; VERSIEUX; WANDERLEY, 2015) ampliando o conhecimento taxonômico da família.

2.2 O gênero *Cryptanthus* Otto & A. Dietr.

2.2.1 Posicionamento filogenético e mudanças taxonômicas

Cryptanthus Otto & A. Dietr. pertence à subfamília Bromelioideae. Nessa subfamília o gênero emerge como a primeira linhagem divergente em um clado denominado eubromelioids (SCHULTE; BARFUSS; ZIZKA, 2009). O gênero pertence ao clado

Cryptanthoid que era conhecido como “complexo Cryptanthoid” devido ao não monofiletismo de alguns gêneros, porém, recentes estudos filogenéticos resolveram este complexo (LOUZADA et al., 2014; LEME et al., 2017) com a criação de novos gêneros (*Forzzaea* Leme & S. Heller, *Lapanthus* Louzada & Versieux, *Rokautskyia* Leme) e reestabelecimento de gêneros (*Hoplocryptanthus* (Mez) Leme, S. Heller & Zizka e *Sincoraea* Ule) (LOUZADA; VERSIEUX, 2010; LOUZADA; WANDERLEY, 2016; LEME et al., 2017).

Anteriormente, *Cryptanthus* apresentava 78 espécies (CHRISTENHUSZ; FAY; CHASE, 2017). E era dividido em dois subgêneros propostos por Mez (1892), o *Cryptanthus* subg. *Cryptanthus* Mez (originalmente *Eucryptanthus*) foi caracterizado pelas folhas geralmente contraídas na base, margens onduladas, aculeada-serreada e menos óvulos, enquanto que *Cryptanthus* subg. *Hoplocryptanthus* Mez foi caracterizado pelas folhas não contraídas na base (acima das bainhas foliares), acúleos espinhosos e muitos óvulos. Ramírez-Morillo (1996) aceita a classificação de Mez (1892) e inclui novos caracteres morfológicos para separar os subgêneros. O subgênero *Cryptanthus* é diferenciado do subgênero *Hoplocryptanthus* principalmente pela plantas hermafroditas (vs. plantas andromonóicas), inflorescência nidular (vs. inflorescência geralmente escaposa, raramente nidular), estigma com três lobos livres geralmente recurvados (vs. estigma com três lobos quase conados, retos, nunca recurvados). Além disso, para cada subgênero Ramírez-Morillo (1996) propôs seções, sendo cinco seções para o subgênero *Cryptanthus* (Bahianae, Beuckeriae, *Cryptanthus*, Lacerdae and Zonatae) e quatro seções para o subgênero *Hoplocryptanthus* (*Hoplocryptanthus*, Mesophyticae, Schwackeanus and Xerophyticae).

Os estudos filogenéticos indicam que o subgênero *Cryptanthus* é monofilético, enquanto que *Hoplocryptanthus* não é monofilético (SILVESTRO; ZIZKA; SCHULTE, 2013; LOUZADA et al., 2014; CRUZ et al., 2017; LEME et al., 2017). Assim, o estudo de Leme et al. (2017) separa as espécies que eram do subgênero *Hoplocryptanthus* em três gêneros, sendo dois novos gêneros (*Forzzaea* e *Rokautskyia*) e propõe um novo status genérico para *Hoplocryptanthus*.

Atualmente o gênero *Cryptanthus* inclui apenas as espécies do antigo subgênero *Cryptanthus*, sendo diferenciado dos gêneros *Forzzaea*, *Hoplocryptanthus* e *Rokautskyia* principalmente pelas plantas andromonóicas (vs. homógamas), estigma conduplicado-patente (vs. cilíndrico, simples-ereto ou simples-imbricado) (LEME et al., 2017).

2.2.2 Etimologia, distribuição geográfica, status de ameaça e importância econômica

O nome do gênero é derivado do grego, onde “cryptos” significa escondido ou coberto, e “anthos” significa flor, em referência à inflorescência (RAMÍREZ-MORILLO, 1996).

Atualmente, *Cryptanthus* apresenta 62 espécies (GOUDA; BUTCHER ; GOUDA, continuamente atualizado) que são endêmicas do Brasil e estão distribuídas nas regiões Nordeste (Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe e Bahia) e Sudeste (Minas Gerais, Espírito Santo e Rio de Janeiro) (LEME et al., 2017). Ocorrendo principalmente na Floresta Atlântica com algumas espécies sendo encontradas na Caatinga (LEME et al., 2017). Além disso, ocorrem tanto em áreas abertas como em áreas fechadas de floresta (RAMÍREZ-MORILLO, 1996).

Muitas espécies do gênero têm distribuição restrita sendo consideradas microendêmicas (CRUZ, 2013). Mesmo nos fragmentos florestais onde ocorrem, as espécies têm distribuição restrita com indivíduos ocorrendo de forma agrupada (Figura 1), tornando desafiador encontrá-las em campo sem dados precisos de coordenadas geográficas.



Figura 1- Distribuição agrupada de indivíduos do gênero *Cryptanthus* Otto & A. Dietr. A. *Cryptanthus dorothyae* Leme. B. *Cryptanthus zonatus* (Vis.) Vis.

Seis espécies do gênero (*Cryptanthus capitatus* Leme, *C. coriaceus* Leme, *C. dorothyae* Leme, *C. maritimus* L.B. Sm., *C. minarum* L.B. Sm., e *C. zonatus* (Vis.) Vis.)

estão classificadas com ameaçadas pelo Livro Vermelho da Flora do Brasil (FORZZA et al., 2013) e pelo MMA (2014).

As espécies de *Cryptanthus* são conhecidas popularmente como “estrelas-da-terra” e tem grande importância ornamental (STEENS, 2007; VERSIEUX; MAGALHÃES; CALVENTE, 2013), como exemplo *C. zonatus*, que é difundida em cultivo há mais de um século (LEME; SIQUEIRA-FILHO, 2006). As espécies do gênero atraem diversos colecionadores que estão reunidos na *Cryptanthus* Society (STEENS, 2007; VERSIEUX; MAGALHÃES; CALVENTE, 2013) onde através do *Cryptanthus* Society Journal houve publicações periódicas de descrições de espécies novas e informações sobre cultivo do gênero.

2.2.3 Reconstruções filogenéticas e biogeografia

As relações intergenéricas em *Cryptanthus* ainda permanecem incertas. A maioria dos estudos desenvolvidos até o momento não englobam a totalidade dos gêneros do clado Cryptanthoid (SILVESTRO; ZIZKA; SCHULTE, 2013; LOUZADA et al., 2014; CRUZ et al., 2017) na atual circunscrição de Leme et al. (2017).

A seguir serão apresentadas as relações inter e infragenéricas de *Cryptanthus* utilizando a circunscrição atual proposta por Leme et al. (2017). A primeira reconstrução filogenética em *Cryptanthus* foi baseada em 23 caracteres morfológicos com o intuito de indicar quem representava o grupo irmão de *Cryptanthus* (RAMÍREZ-MORILLO, 1996). Na análise, *Cryptanthus* emerge como grupo irmão de *Hoplocryptanthus*.

Posteriormente, Silvestro, Zizka e Schulte (2013) apresentaram uma filogenia baseada em marcadores plastidiais (*atpB-rbcL*, *trnL-trnF*, *trnL* e *matK* com parte do adjacente intron 3'trnK) e nuclear (*PHYC*) utilizando cinco espécies do gênero (*C. bahianus*, *C. bromelioides*, *C. colnagoi*, *C. diamantinensis* e *C. warren-loosei*). Neste estudo, *Cryptanthus* apresenta como grupo irmão, a linhagem formada pelos gêneros *Hoplocryptanthus*, *Lapanthus*, *Orthophytum*, *Rokautskyia* e *Sincoraea* (Figura 2A).

Posteriormente, Louzada et al. (2014) realizaram um estudo utilizando dados combinados de sequência de duas regiões plastidiais (*trnL-trnF* e *trnH-psbA*) e uma região nuclear (*PHYC*) utilizando cinco espécies de *Cryptanthus* (*C. bahianus*, *C. colnagoi*, *C.*

diamantinensis, *C. warren-loosei* e *C. zonatus*), onde *Cryptanthus* aparece como grupo irmão do gênero *Hoplocryptanthus* (Figura 2B). Depois deste estudo, Cruz et al. (2017) realizaram um estudo filogenético utilizando Amplified Fragment Length Polymorphism (AFLP), com uma ampla amostragem de espécies do gênero *Cryptanthus* (40 espécies), no estudo *Cryptanthus* apresenta como grupo irmão o gênero *Forzzaea* (Figura 2 C).

E por fim, Leme et al. (2017) apresentam uma filogenia baseada em marcadores plastidiais (*matK*, *trnH-psbA* e *ycf1*) e nucleares (AGT1 exon, AGT1 intron, ETS e PHYC) utilizando 14 espécies de *Cryptanthus* (*C. acaulis*, *C. bahianus*, *C. beuckeri*, *C. bromelioides*, *C. burle-marxii*, *C. colnagoi*, *C. diamantinensis*, *C. diana*, *C. dorothyae*, *C. maritimus*, *C. ruthiae*, *C. teretifolius*, *C. warren-loosei* e *C. zonatus*). Neste estudo, *Cryptanthus* emerge em uma politomia, não sendo possível inferir quem é o clado irmão do gênero (Figura 2D).

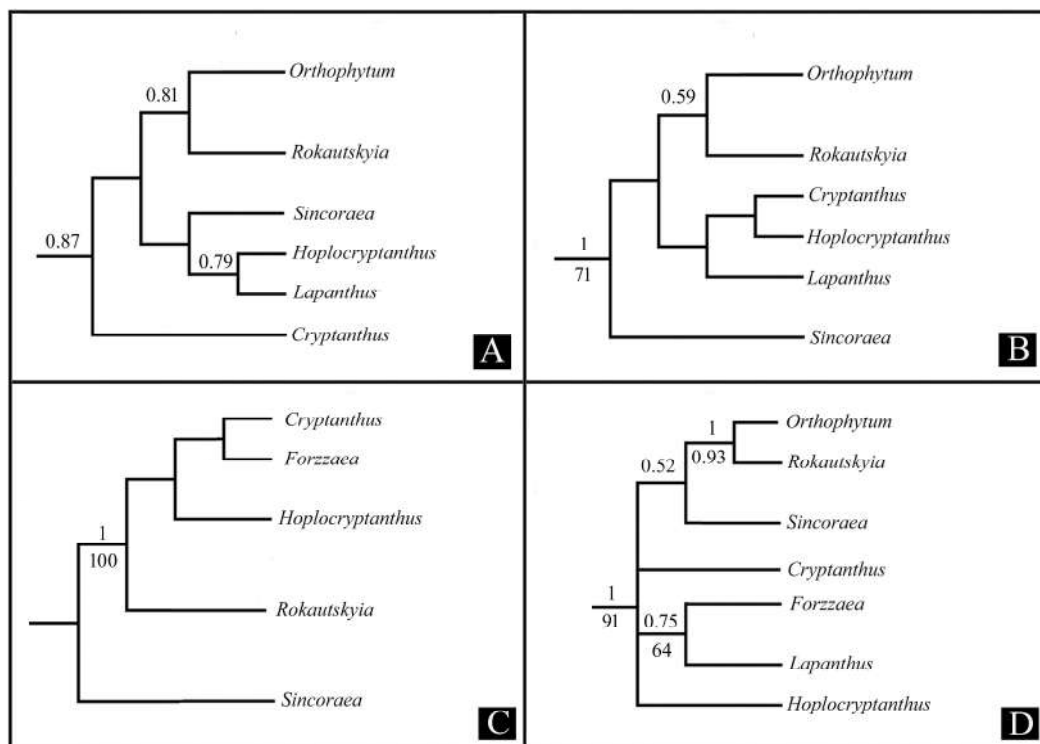


Figura 2 - Estudos filogenéticos com o clado Cryptanthoid. A. Estudo de Silvestro, Zizka e Schulte (2013). B. Estudo de Louzada et al. (2014). C. Estudo de Cruz et al. (2017). D. Estudo de Leme et al. (2017). Valores acima dos ramos representam as probabilidades posteriores e abaixo dos ramos são os valores de bootstrap.

Quanto às relações infragenéricas, as relações de parentesco em *Cryptanthus* s.s. são ainda preliminares. Os estudos têm baixa amostragem em termos de número de espécies com 5, 5 e 14 espécies, respectivamente (SILVESTRO; ZIZKA; SCHULTE, 2013; LOUZADA et

al., 2014; LEME et al., 2017) que representam apenas 25% das espécies do gênero, ou tem ampla amostragem (CRUZ et al., 2017), porém, não há uma boa resolução.

Quanto aos estudos de evolução de caráter morfológico, até o momento as reconstruções foram realizadas apenas com caracteres que não apresentam variação a nível infragenérico, tais como mecanismo fotossintético (CAM) e evolução do hábito tanque (não forma tanque) em Silvestro, Zizka e Schulte (2013), sistema sexual (andromonoiccia) em Cruz et al. (2017). Além disso, foram usadas conação das pétalas (conadas), forma das lâminas das pétalas (sublinear-lanceolada ou amplamente espatulada) e tamanho das sementes (>3 mm de comprimento) em Leme et al. (2017).

Quanto as reconstruções de áreas ancestrais, até o momento Cruz et al. (2017) indicam que provavelmente a linhagem do gênero *Forzzaea* que ocorre em cerrados e campos rupestres é irmã da linhagem do gênero *Cryptanthus* que teria surgido na Floresta Atlântica e se mantido nesse ambiente, com uma única espécie (*C. bahianus* L.B.Sm.) migrando para a Caatinga e uma outra espécie (*C. arelli* H. Luther) migrando para Cerrados e campos rupestres. Já Leme et al. (2017) mostram que a linhagem formada por *C. bahianus* L.B.Sm. que ocorre na Caatinga e *C. warren-loosei* Leme que ocorre em Floresta Atlântica é irmã das demais espécies de *Cryptanthus* que teriam se mantido na Floresta Atlântica. Mas o estudo conta uma baixa amostragem de espécies.

Diante do exposto, é importante que haja a realização de uma nova reconstrução filogenética para a obtenção de uma hipótese robusta acerca das relações filogenéticas em *Cryptanthus*, e a realização de uma reconstrução de estados de caráter ancestral utilizando estados de caráter com variação infragenérica para entender a evolução do gênero.

2.2.4 Número cromossômico e tamanho genômico

Cryptanthus apresenta número cromossomos distinto de outros gêneros de Bromeliaceae com $2n = 34, 36$ ou 54 , enquanto que a maioria dos outros gêneros tem $2n = 50$ (RAMÍREZ-MORILLO; BROWN, 2001). O tamanho do genoma (conteúdo de DNA nuclear) varia de $2C = 0.76$ pg a $2C = 1.66$ pg (CRUZ et al., 2020).

2.2.5 Estudos de genética de populações

Estudos de transferabilidade de marcadores microssatélites já foram desenvolvidos com o gênero tanto com microssatélites nucleares (FERREIRA et al., 2017) quanto com plastidiais (KRAPP et al., 2013). E um de estudo genética de populações e delimitação de espécies usando dados de microssatélites nucleares foi desenvolvido com o complexo *Cryptanthus zonatus* (Vis.) Vis. que inclui as espécies *Cryptanthus burle-marxii* Leme e *C. zonatus* (FERREIRA et al., 2021). Ambas espécies são diferenciadas por Leme (1990) pelo tipo de propagação vegetativa, espaçamento dos tricomas transversais nas lâminas foliares, comprimento das sépalas e conação das pétalas. No estudo, a análise de estrutura genética foi feita com o $K=2$ (número de agrupamentos mais provável) e indicou que *C. burle-marxii* e *C. zonatus* são a mesma espécie já que pertencem a um mesmo agrupamento genético (FERREIRA, 2016; FERREIRA et al., 2021). Assim, *C. burle-marxii* foi sinonimizado em *C. zonatus* (FERREIRA et al., 2021). Os agrupamentos genéticos tiveram um padrão geográfico, formando um agrupamento ao norte e outro ao sul da distribuição e entre os agrupamentos há uma possível barreira histórico-geográfica na depressão do Abiaí que foi responsável pela divisão dos dois agrupamentos (FERREIRA et al., 2021). Além disso, o estudo indicou que provavelmente no Último Máximo Glacial, a espécie ocupou áreas que atualmente estão submersas pelo mar (FERREIRA et al., 2021).

2.2.6 Estudos taxonômicos

Cryptanthus é um nome conservado e foi originalmente descrito em 1836 por Friedrich Otto e Albert Dietrich (OTTO; DIETRICH, 1836). Alguns estudos taxonômicos já foram desenvolvidos com *Cryptanthus*, tais como estudos de flora: Flora brasiliensis (MEZ, 1892: que inclui oito táxons no tratamento taxonômico), Flora Neotropica (SMITH; DOWNS, 1979: 15 táxons), Flora do estado de Alagoas e Pernambuco (LEME; SIQUEIRA-FILHO, 2007: 8 táxons) e Flora do estado de Sergipe (FERREIRA; LOUZADA, 2015: 2 táxons). Também já foram realizadas sinopses (SMITH; DOWNS, 1955: 15 táxons) e revisões taxonômicas (BAKER, 1889: 12 táxons; RAMÍREZ-MORILLO, 1996: 21 táxons).

Embora existam os citados estudos taxonômicos, o conhecimento de *Cryptanthus* ainda é incipiente, uma vez que o estudo mais completo até o momento é a última revisão taxonômica de Ramírez-Morillo (1996), que inclui menos da metade (21 espécies) das espécies atualmente aceitas (LEME et al., 2017).

Desde a última revisão de Ramirez-Morillo (1996) até os dias atuais, houve um grande incremento de espécies novas descritas para o gênero que totalizam 34 táxons (Tabela 1), dos quais 22 têm ocorrência na região nordeste.

Além disso, Martinelli et al. (2008) enfatizam a importância da realização de um estudo taxonômico do gênero com esforços intensivos de coleta, uma vez que o gênero apresenta um grande número de espécimes indeterminados ou com identificações imprecisas nos herbários.

Tabela 1 - Espécies novas do gênero *Cryptanthus* publicadas após a última revisão taxonômica realizada por Ramirez-Morillo (1996).

Obras	Espécies
Leme (1996)	<i>C. dorothyae</i> Leme
Ramírez-Morillo (1998)	<i>C. lutherianus</i> I. Ramírez, <i>C. sergipensis</i> I. Ramírez, <i>C. ubairensis</i> I. Ramírez
Luther (1999a)	<i>C. grazielae</i> H. Luther
Luther (1999b)	<i>C. arelii</i> H. Luther
Leme (1999)	<i>C. diamantinensis</i> Leme, <i>C. lyman-smithii</i> Leme
Leme e Siqueira-Filho (2001)	<i>C. alagoanus</i> Leme & J. A. Siqueira
Leme (2001)	<i>C. argyrphyllus</i> Leme
Leme (2002a)	<i>C. bibarrensensis</i> Leme, <i>C. reisii</i> Leme
Leme (2002b)	<i>C. teretifolius</i> Leme
Leme e Siqueira-Filho (2007)	<i>C. felixii</i> J. A. Siqueira & Leme, <i>C. reptans</i> Leme & J. A. Siqueira
Leme et al. (2008)	<i>C. crassifolius</i> Leme, <i>C. giganteus</i> Leme & A. P. Fontana
Leme (2010)	<i>C. brevifolius</i> Leme
Leme et al. (2010)	<i>C. capitellatus</i> Leme & L. Kollmann, <i>C. venecianus</i> Leme & L. Kollmann, <i>C. viridovinosus</i> Leme
Leme e Kollmann (2013)	<i>C. ilhanus</i> Leme, <i>C. rigidifolius</i> Leme, <i>C. tabuleiricola</i> Leme & L. Kollmann, <i>C. viridipetalus</i> Leme & L. Kollmann
Leme et al. (2014)	<i>C. walkerianus</i> Leme & L. Kollmann
Leme (2014)	<i>C. robsonianus</i> Leme
Leme (2015)	<i>C. boanovensensis</i> Leme
Braun e Brito (2019)	<i>C. heimenii</i> P. J. Braun & Gonçalves Brito
Leme et al. (2020)	<i>C. cruzalmensis</i> Leme & E.H.Souza, <i>C. guanduensis</i> Leme & L.Kollmann, <i>C. santateresinhensis</i> Leme, <i>C. univittatus</i> Leme
Ferreira e Louzada (2020)	<i>C. cinereus</i> D.M.C. Ferreira & Louzada
Ferreira, Almeida e Louzada (2021)	<i>Cryptanthus apiculatantherus</i> D.M.C. Ferreira, E.M. Almeida & Louzada, <i>Cryptanthus brevibracteatus</i> D.M.C. Ferreira & Louzada

2.2.7 Morfologia e biologia reprodutiva

A reprodução assexuada é realizada através da emissão brotos pelo rizoma (Figura 3A), ou por estolões que são emitidos pelo rizoma (Figura 3B) ou ainda por brotos axilares que surgem nas axilas das folhas (Figura 3C). Estudo realizado por Ferreira et al. (2021a) mostra que populações de *C. zonatus* têm alta produção de clone.



Figura 3 – Tipos de reprodução assexuada em *Cryptanthus*. A. Brotos emitidos diretamente do rizoma em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada. B. Estolões que partem do rizoma em *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. C. Brotos axilares em *Cryptanthus zonatus* (Vis.) Vis.

Os hábitos das espécies do gênero (Figura 1) são terrícolas ou rupícolas (LEME et al., 2017), curto caulescente ou longo caulescente (FERREIRA; LOUZADA 2020; FERREIRA; ALMEIDA; LOUZADA, 2021). O caule (Figura 5) é definido como a porção da base planta (acima das raízes) até as primeiras flores dos glomérulos laterais (FERREIRA; LOUZADA 2020), já que há dificuldade em diferenciar caule e pedúnculo.

A face adaxial das folhas pode variar de glabra a densamente lepidota (FERREIRA; LOUZADA 2020) e a face abaxial das folhas é densamente coberta por tricomas. As margens das folhas são aculeadas (RAMÍREZ-MORILLO, 1996).



Figura 4- Hábitos em *Cryptanthus*. A. Terrícola em *Cryptanthus teretifolius* Leme. B. Rupícola em *Cryptanthus bahianus* L.B. Sm. (Foto: J. Maciel).

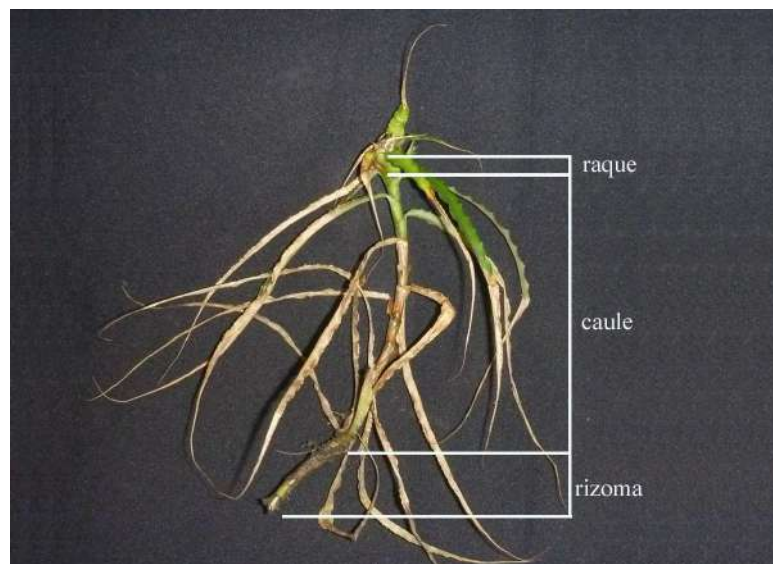


Figura 5- Indivíduo de *Cryptanthus apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada evidenciando o rizoma, o caule e a raque.

As folhas podem ter pecíolos (Figura 6A) como em *Cryptanthus beuckeri* E. Morren (MORREN, 1880), *C. capitellatus* Leme & L. Kollmann (LEME et al., 2010), *Cryptanthus teretifolius* Leme (LEME, 2002b) e *C. walkerianus* Leme & L. Kollmann (LEME et al., 2014). Ou podem ser sésseis (não ter pecíolos) e ser estreitas na base, acima das bainhas (Figura 6B) como exemplo em *Cryptanthus vexatus* Leme (LEME et al., 1995). Ou podem ser mais largas na base, acima das bainhas (Figura 6C) como em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada (FERREIRA; LOUZADA 2020).

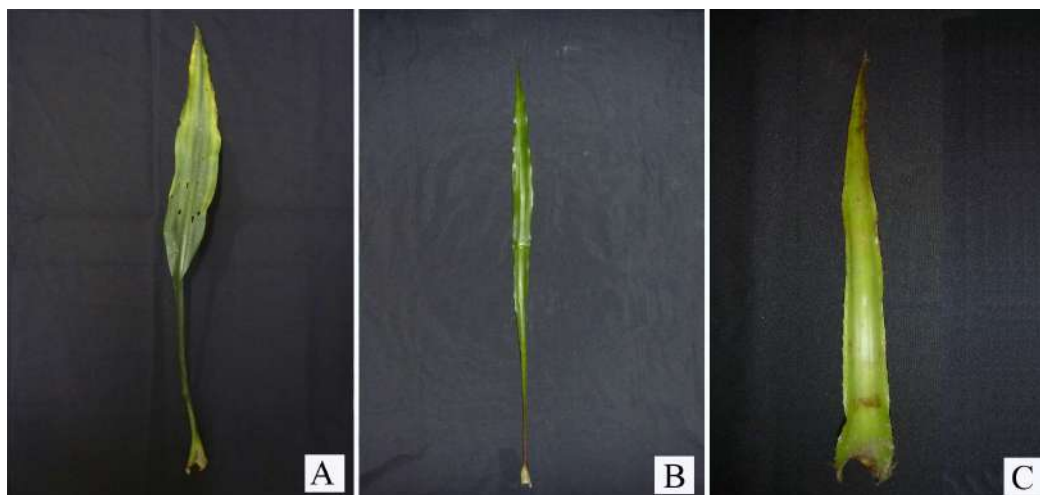


Figura 6 – Formato das folhas em *Cryptanthus*. A. Pecioladas em *Cryptanthus walkerianus* Leme & L. Kollmann. B. Estreitadas na base em *Cryptanthus pickelii* L. B. Sm.. C. Mais largas na base em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada.

Algumas espécies apresentam variação na coloração das folhas como exemplo em *Cryptanthus zonatus* que dentro de uma mesma população há plantas com coloração verdes ou marrons (FERREIRA et al., 2021).

A inflorescência (Figura 7) é uma espiga de glomérulos (FERREIRA; LOUZADA, 2020). Geralmente o glomérulo apical da inflorescência tem uma quantidade maior de flores do que os glomérulos laterais (FERREIRA; LOUZADA, 2020). As brácteas primárias são similares às folhas (FERREIRA; LOUZADA, 2020). A raque da inflorescência fica encoberta pelas brácteas primárias e flores (Figura 8). As plantas são andromonóicas apresentam flores estaminadas e perfeitas em um mesmo indivíduo (LEME et al. 2017; FERREIRA; LOUZADA, 2020; FERREIRA; ALMEIDA; LOUZADA, 2021). As flores estaminadas geralmente são menores e as flores perfeitas são maiores (Figura 9) como exemplo em *C. apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada e *C. brevibracteatus* D.M.C. Ferreira & Louzada (FERREIRA; ALMEIDA; LOUZADA, 2021).

Além disso, foi registrado tanto em *Cryptanthus diana* quanto em *C. zonatus* que há uma produção maior de flores estaminadas do que perfeitas e que ambas as espécies apresentam odor floral (imperceptível aos humanos) evidenciado no teste de vermelho neutro (SIQUEIRA-FILHO; MACHADO, 2008; OLIVEIRA-JÚNIOR, 2015).

As flores em *Cryptanthus* são trímeras, apresentam três sépalas, três pétalas e seis estames (Figura 10) que estão dispostos em duas séries, sendo três antepétalos e três antesépalos. Os estames são parcialmente adnados às pétalas e a adnação às vezes tem o mesmo comprimento dos antesépalos e antepétalos ou eles podem variar de tamanho (FERREIRA; LOUZADA, 2020; FERREIRA; ALMEIDA; LOUZADA, 2021). As anteras variam no formato do ápice entre as espécies (FERREIRA; ALMEIDA; LOUZADA, 2021).

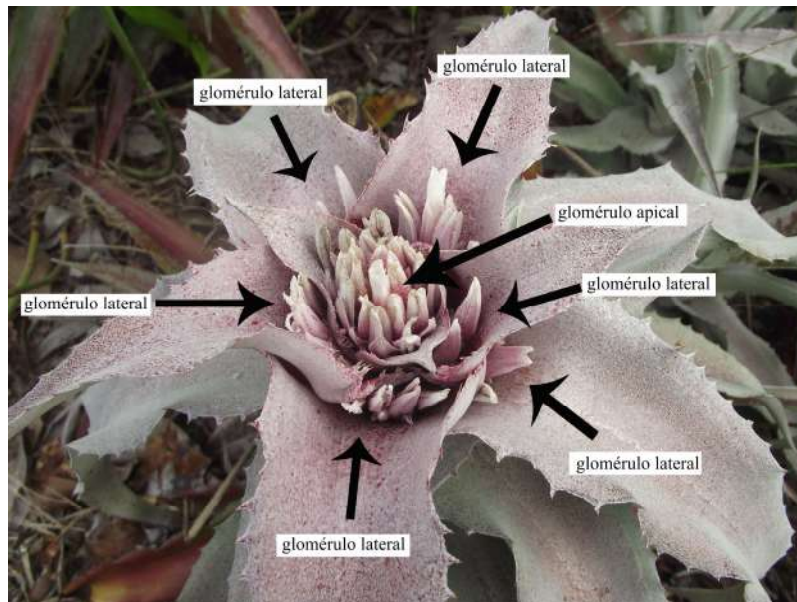


Figura 7- Inflorescência do tipo espiga de glomérulos em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada evidenciando o glomérulo apical e os glomérulos laterais da inflorescência.



Figura 8– Raque da inflorescência de *Cryptanthus walkerianus* Leme & L. Kollmann evidenciada em branco.



Figura 9- Flores de *Cryptanthus robsonianus* Leme, a estaminada com tamanho menor (lado esquerdo) e a perfeita com tamanho maior (lado direito).

Algumas anormalidades já foram encontradas em algumas flores de *C. diana* Leme, como a variação da quantidade de pétalas e estames (Figura 10), que também já foram relatadas por Siqueira-Filho e Machado (2008).

Algumas espécies de *Cryptanthus* têm um tubo epigínico bem evidente (Figura 11) como em *Cryptanthus cinereus* D.M.C. Ferreira & Louzada (FERREIRA; LOUZADA 2020) e outras têm o tubo muito pequeno ou inconspícuo como em *Cryptanthus vexatus* Leme (LEME et al., 1995). De acordo com Ramírez-Morillo (1996) o tubo epigínico consiste em um tubo que circunda a base do estilete e está localizado entre a porção que fica acima do ovário até a inserção das sépalas e das pétalas (Figura 11).

O estigma em *Cryptanthus* é do tipo conduplicado-patente sendo importante na diferenciação dos gêneros relacionados (LEME et al., 2017) e o grão de pólen é do tipo reticulado, levemente reticulado ou fosulado (RAMÍREZ-MORILLO, 1996). O ovário é ínfero (RAMÍREZ-MORILLO, 1996).

A reprodução sexuada também pode ocorrer em *Cryptanthus* levando a formação de sementes. Em experimentos realizados com *C. zonatus* (Vis.) Vis., Oliveira-Júnior (2015) indica que a espécie realiza polinização cruzada, mas que também pode ocorrer a autopolinização.



Figura 10- Flores de *Cryptanthus dianae* Leme. A. Com número usual de três pétalas. B. Com número incomum de quatro pétalas.

Apesar de haver registro da visita de diferentes animais (beija-flores, moscas, mariposas diurnas, borboletas e abelhas) nas flores de algumas espécies do gênero (SIQUEIRA-FILHO; MACHADO, 2008; OLIVEIRA-JÚNIOR, 2015), a polinização é realizada principalmente por beija-flor (*Phaetornis ruber*) e abelha (*Eulaema nigrata*) em *Cryptanthus zonatus* (OLIVEIRA-JÚNIOR, 2015; MILET-PINHEIRO et al., 2021), e por abelha (machos de *Euglossa cordata*) em *Cryptanthus dianae* Leme (SIQUEIRA-FILHO; MACHADO, 2008). As flores de *Cryptanthus zonatus* produzem néctar que atraem beija-flor e emitem compostos florais semivoláteis que atraem as abelhas (machos de *Eulaema nigrata*) que fazem a raspagem das pétalas (MILET-PINHEIRO et al., 2021).



Figura 11- Corte longitudinal da flor de *Cryptanthus pickelii* L.B.Sm. evidenciando em preto o tubo epigínico.

Os frutos são bagas (RAMÍREZ-MORILLO, 1996) e ficam parcialmente escondidos e protegidos pelas brácteas primárias (Figura 12), a parte escondida tem coloração alva e a parte exposta tem coloração verde (ex: *Cryptanthus pickelii* L.B.Sm.) ou vermelha (ex: *C. sergipensis* I. Ramírez), ou ainda de acordo com Ferreira, Almeida e Louzada (2021) pode ser completamente alvo como em *C. apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada. Ainda não há estudos sobre dispersores de sementes de *Cryptanthus*.



Figura 12- Frutos de *Cryptanthus pickelii* L.B.Sm.. A. Frutos. B. Fruto alvo na base (parte que fica escondida) e verde no ápice (parte exposta).

3 OBJETIVOS

3.1 Objetivo Geral

Realizar o estudo sistemático e evolutivo do gênero *Cryptanthus* Otto & A. Dietr.

3.2 Objetivos específicos

- Reconstruir a filogenia de *Cryptanthus* a partir de marcadores plastidiais para melhorar o entendimento das relações infragenéricas do gênero e reconstruir a evolução de caracteres-chave para o gênero, como a presença de pecíolos e coloração das pétalas;

- Indicar os genes plastidiais mais informativos para o gênero *Cryptanthus*;
- Realizar uma sinopse taxonômica das espécies do gênero *Cryptanthus* que ocorrem na região nordeste, bem como, ilustrar e indicar o status de conservação das mesmas;
- Realizar o tratamento taxonômico das espécies do gênero *Cryptanthus* que ocorrem no estado de Alagoas;
- Elaborar um guia de campo com fotos das espécies de *Cryptanthus* para facilitar a identificação das espécies do gênero;

4 RESULTADOS

4.1 ARTIGO 1- PHYLOGENY AND CHARACTER EVOLUTION IN THE GENUS *CRYPTANTHUS* OTTO & A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) USING NEXT-GENERATION SEQUENCING DATA

Phylogeny and character evolution in the genus *Cryptanthus* Otto & A. Dietr. (Bromelioideae, Bromeliaceae) using Next-Generation Sequencing data

Débora Maria Cavalcanti Ferreira^{1*}, Santelmo Vasconcelos², Gisele Lopes Nunes², Eder Soares Pires², Guilherme Oliveira², Rafael Batista Louzada³

¹Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, Recife, Pernambuco, CEP 50670-901, Brazil

² Instituto Tecnológico Vale, Rua Boaventura da Silva, 955, Belém, Pará, CEP 66055-090, Brazil

³Departamento de Botânica, Universidade Federal de Pernambuco, Recife, Pernambuco, CEP 50670-901, Brazil

*Corresponding author: deboracavalcantif@hotmail.com

Running Title: Phylogeny and character evolution in the genus *Cryptanthus*

ABSTRACT

The genus *Cryptanthus* had a recent new circumscription and currently comprises 62 species that are restricted to the northeastern and southeastern regions of Brazil. However, the infra-generic phylogenetic relationships of the genus are not completely understood. Here, we present the phylogenetic reconstruction of *Cryptanthus* using a genome skimming approach of next-generation sequencing (NGS), aiming: 1) to improve understanding of the infra-generic relationships of *Cryptanthus*; 2) to test the infra-generic classification of *Cryptanthus*; 3) to reconstruct the evolution of petioles and petals color; and 4) to indicate the most informative genes of the chloroplast DNA. A total of 44 accessions were used for the phylogenetic reconstruction including 23 species of *Cryptanthus*. Maximum-likelihood and Bayesian inference analyses were performed using 69 protein-coding genes of chloroplast DNA, with a total alignment length of concatenated genes of 61,981 bp. The results show that *Cryptanthus* is monophyletic, however, the phylogenetic relationships of the genus with *Orthophytum* and *Rokautskyia* are not supported. Two main clades were obtained for the genus, however, there is no morphological support. The infra-generic relationships of *Cryptanthus* are better understood with the clades being formed by the geographic proximity of the species. The species *Cryptanthus alagoanus*, *Cryptanthus diana*, *Cryptanthus pickelii* and *Cryptanthus zonatus* emerged as non-monophyletic. Besides, one specimen *Cryptanthus pickelii* emerged as sister of *Cryptanthus zonatus* due to a possible hybridization. The ancestral character state reconstruction of petiole and petals color indicate that the presence of petioles and petals color white with green or greenish apices had multiple origins in evolution of the genus. The most informative genes of the chloroplast DNA are indicated and they can be used in future studies with the genus.

ADDITIONAL KEYWORDS: Brazil, chloroplast, Cryptanthoid, NGS, phylogeny

INTRODUCTION

Bromeliaceae comprises 79 genera and 3692 species (Gouda *et al.*, cont. updated) and has a Neotropical distribution (Givnish *et al.*, 2011), with the exception of one species that occurs in west Africa (Givnish *et al.*, 2004). Currently, the family includes eight subfamilies with Bromelioideae arising as most recent subfamily of Bromeliaceae (Givnish *et al.*, 2011). Bromelioideae is characterized by the presence of berry-type fruits and inapendiculate seeds (Smith & Downs, 1974, 1977, 1979; Givnish *et al.*, 2007). Into this subfamily, the species either lack (“basal bromelioids” clade and basal species of the “eu-bromelioids” clade) or present (derived species of the “eu-bromelioids” clade that belong to the “core-bromelioids” clade) the tank habit (Schulte *et al.*, 2009).

Cryptanthus Otto & A. Dietr., described by Otto & Dietrich (1836), is a genus included in Bromelioideae and, belonging to the group that lacks the tank habit (Schulte *et al.*, 2009). Within the subfamily, *Cryptanthus* and *Orthophytum* Beer arise as the first divergent lineage in the “eu-bromelioids” clade (Schulte *et al.*, 2009). *Cryptanthus* is related to genera *Forzzaea* Leme, S. Heller, *Hoplocryptanthus* (Mez) Leme, S. Heller & Zizka, *Lapanthus* Louzada & Versieux, *Orthophytum*, *Rokautskyia* Leme, S. Heller & Zizka and *Sincoraea* Ule, which together form the Cryptanthoid clade (Louzada *et al.*, 2014; Leme *et al.*, 2017).

The Cryptanthoid clade was known as the “Cryptanthoid complex” because some genera were polyphyletic, but recent phylogenetic studies have elucidated this complex (Louzada *et al.*, 2014; Leme *et al.*, 2017) with the description of the new genera, and with the reestablishment of the genera within this clade (Louzada & Versieux, 2010; Louzada & Wanderley, 2016; Leme *et al.*, 2017).

Cryptanthus had 78 species (Christenhusz *et al.*, 2017) that were divided into two subgenera that were proposed by Mez (1891) in *Flora brasiliensis*, the subgenus *Hoplocryptanthus* was characterized by its leaf blades not contracted at base (above leaf

sheaths), spinose margins and many ovules, and the subgenus *Eucryptanthus* was characterized by its leaf blades generally contracted at the base, margins undulate, minutely serrate-aculeate and less ovules. This classification was accepted by Ramírez-Morillo (1996) that added new morphological characters to separate them such as plants andromonoecious, inflorescences nidular, stigma with three free lobes, usually recurving in subgenus *Cryptanthus* (*Eucryptanthus*) vs. plants hermaphrodite, inflorescences usually scapose, rarely nidular, stigma with three almost connate or straight stigmatic lobes, never recurved in subgenus *Hoplocryptanthus*.

In addition, Ramírez-Morillo (1996) proposed sections that were based on morphological evidence being five sections for subgenus *Cryptanthus* (*Bahianae*, *Beuckeriae*, *Cryptanthus*, *Lacerdae* and *Zonatae*) and four for subgenus *Hoplocryptanthus* (*Hoplocryptanthus*, *Mesophyticae*, *Schwackeanus* and *Xerophyticae*).

However, recent phylogenetic studies indicated that the subgenus *Cryptanthus* is monophyletic, whereas *Hoplocryptanthus* is not monophyletic (Silvestro *et al.*, 2013; Louzada *et al.*, 2014; Cruz *et al.*, 2017; Leme *et al.*, 2017). Thus, the study by Leme *et al.* (2017) separated subgenus *Hoplocryptanthus* species into three genera, being two new genera *Forzzaea* and *Rokautskyia* and proposes a new generic status for *Hoplocryptanthus*. Therefore, currently the genus *Cryptanthus* includes only the species of the subgenus *Cryptanthus* which shows as synapomorphy an andromonoid condition in the species (Leme *et al.*, 2017).

Cryptanthus includes 62 species (Gouda *et al.*, cont. updated) that are distributed in the Northeastern and Southeastern regions of Brazil occurring in the Atlantic Forest and Caatinga (Leme *et al.*, 2017). *Cryptanthus* species have restricted distribution (Cruz *et al.*, 2017) and six species are in the Livro Vermelho da Flora do Brasil (Red List of Brazilian Flora; Forzza *et al.*, 2013). The species of the genus are popularly known as “earth stars” and

have an ornamental importance (Steens, 2007; Versieux *et al.*, 2013). The chromosome numbers of the genus varies from $2n = 32$ to 36 (Gitaí *et al.*, 2014; Cruz *et al.*, 2020) and the nuclear DNA content varies from $2C = 0.76$ pg to $2C = 1.66$ pg (Cruz *et al.*, 2020).

The infra-generic phylogenetic relationships in *Cryptanthus* are still preliminary (Silvestro *et al.*, 2013; Louzada *et al.*, 2014; Leme *et al.*, 2017), with the studies using few molecular markers and presenting a low sampling of species of *Cryptanthus*. On the other hand, Cruz *et al.* (2017) used a more comprehensive sampling with Amplified Fragment Length Polymorphism (AFLP) markers, however, the relationships are not well understood due to poor resolution among clades. In addition, Schulte *et al.* (2009) indicated that studies developed with Bromelioideae have low variation in plastid DNA sequences and the resolutions of studies using few regions have remained poor.

Thus, the use of next generation sequencing (NGS) can solve this problem and help to obtain a robust hypothesis about phylogenetic relationships. This technique specifically using genome skimming generates large amounts of plastid genome data, overcoming the limitations that Sanger sequencing has (Nauheimer *et al.*, 2019). Recent phylogenetic studies in Bromeliaceae with the genus *Fascicularia* and *Ochagavia* of Bromelioideae (Paule *et al.*, 2020) and *Vriesea* of the subfamily Tillandsioideae (Machado *et al.*, 2020) have used the NGS approach.

Here, we reconstruct a phylogeny based in 69 protein-coding genes of the plastome to: 1) to improve understanding of the infra-generic relationships of *Cryptanthus*; 2) to test the sections of the infra-generic classification of *Cryptanthus* proposed by Ramírez-Morillo (1996); 3) to reconstruct the evolution of petioles and petals color; and 4) to indicate the most informative genes of the chloroplast DNA that can be used in future studies with the genus.

MATERIALS AND METHODS

PLANT MATERIAL AND DNA EXTRACTION

A total of 40 samples of 29 species of the Cryptanthoid clade (including 23 species of *Cryptanthus* (ca. 36% of the known diversity of the genus; Fig. 1), three of *Orthophytum*, two *Sincoraea*, and one of *Rokautskyia*) was collected in field and only one sample was collected in a living collection (Museu de Biologia Prof. Mello Leitão), as indicated in Table 1. The sampling of *Cryptanthus* covers a good geographical range including species that occur in varied environments with different morphologies. Vouchers were deposited in the UFP (Geraldo Mariz) herbarium. In addition, sequences of four species of Bromeliaceae were obtained from GenBank and they were included in the analyses: *Ananas comosus* (NCBI number NC_026220), *Fascicularia bicolor* (NCBI number MN563795), *Ochagavia elegans* (NCBI number NC_045385) and *Puya mirabilis* (NCBI number NC_045380). *Puya mirabilis* was chosen as the outgroup.

The collected samples were stored in silica-gel and total genomic DNA was extracted from fresh young leaves following the protocol described by Ferreira & Grattapaglia (1998). DNA extractions were checked on 1% agarose gel stained with GelRed. DNA quantifications were performed in a NanoDrop Spectrophotometer (Thermo Scientific, Waltham, MA, USA) and Eon (BioTek) spectrophotometer. Qubit 3 (Invitrogen Life Technologies) fluorometer also was used with dsDNA BR Assay Kit (Invitrogen Life Technologies) and dsDNA HS Assay Kit (Invitrogen Life Technologies).

LIBRARY PREPARATION AND GENOME SKIMMING SEQUENCING

For the preparation of the shotgun libraries, ca. 50 ng of the total genomic DNA were used, using the kit SureSelectQXT (Agilent Technologies), following the manufacturer's instructions. DNA quantity and quality of the indexed libraries were accessed in a 4200

TapeStation system (Agilent Technologies) using a High Sensitivity D1000 Screen Tape. The paired-end libraries (2x 150bp) were sequenced in the Illumina NextSeq 500 platform, using the NextSeq 500/550 High Output Reagent Cartridge v2.

DNA QUALITY, ASSEMBLY AND ALIGNMENT

The samples were demultiplexed and the FASTQ files were used in the software FASTQC (<https://www.bioinformatics.babraham.ac.uk/projects/fastqc/>) to check the quality of the reads. The reads were trimmed using AdapterRemoval v2 (Schubert et al., 2016). The trimming was performed to remove adapter and low-quality bases from the beginning and end of the reads using a Phred quality score ≥ 20 in a 10-bp window. Besides, reads with less than 70 bases of length were removed.

The sequences of the plastid DNA were assembled with NovoPlasty v.2.6.7 (Dierckxsens et al., 2017) using the sequence of the chloroplast gene *rbcL* (NCBI number MN719165.1) of the species *C. warren-loosei* Leme (Hermida-Carrera *et al.*, 2020) as seed, generating either complete or partial plastomes, depending on the species. The genes of the species with a complete plastome were used as seed to assemble the sequences of the closely related species. The plastome sequences were annotated in CHLOROBX (<https://chlorobox.mpimp-golm.mpg.de/index.html>). The annotations were adjusted by comparison with reference genome of *Ananas comosus* (NCBI number NC_026220) using Geneious Prime version 2020.1.2 (Kearse et al., 2012). A total of 69 protein-coding genes (*accD*, *atpA*, *atpB*, *atpE*, *atpH*, *atpI*, *ccsA*, *cemA*, *infA*, *matK*, *ndhB*, *ndhC*, *ndhD*, *ndhE*, *ndhF*, *ndhG*, *ndhH*, *ndhI*, *ndhJ*, *petA*, *petD*, *petG*, *petL*, *petN*, *psaA*, *psaB*, *psaC*, *psaI*, *psaJ*, *psbA*, *psbB*, *psbD*, *psbE*, *psbF*, *psbH*, *psbI*, *psbJ*, *psbK*, *psbM*, *psbN*, *psbT*, *psbZ*, *rbcL*, *rpl2*, *rpl14*, *rpl16*, *rpl20*, *rpl22*, *rpl23*, *rpl32*, *rpl33*, *rpoA*, *rpoB*, *rpoC1*, *rpoC2*, *rps2*, *rps3*, *rps4*, *rps7*, *rps8*, *rps11*, *rps14*, *rps15*, *rps16*, *rps18*, *rps19*, *ycf2*, *ycf3* and *ycf4*) was isolated for each sample (Table 2).

Each gene was aligned separately using MAFFT version 7.450 with auto algorithm (Kato & Standley, 2013) that was implemented in Geneious Prime version 2020.1.2 (Kearse *et al.*, 2012). The 69 protein-coding genes were concatenated for the phylogenetic analyses.

PHYLOGENETIC RECONSTRUCTION

Maximum-likelihood (ML) analyses were carried out in RAxML v.8.2.12 (Stamatakis, 2014) using the GTRGAMMA model with 1000 bootstrap replicates. And Bayesian inference (BI) analyses were performed in MrBayes v.3.2.7a (Ronquist *et al.*, 2012) using the GTRGAMMA model with the parameters for four simultaneous Markov Chain Monte Carlo (MCMC) in the option of 10,000,000 generations, with sampling every 1000 generations and burnin fraction of 25% of the trees. All these analyses were conducted on the CIPRES Science Gateway (<http://www.phylo.org/>). The phylogenetic trees were visualized using the FigTree v1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree/>).

ANCESTRAL CHARACTER STATE RECONSTRUCTION

The analyses were performed RStudio program (<https://rstudio.com/>) integrated into R program (v. 3.5.2; <https://r-project.org>) using the package Phytools (Revell, 2012). Two characters were chosen for ancestral character state reconstruction (Supporting Information, Table S1): petioles (character states coded as [0] absent and [1] present) and petals color (character states coded as = [1] white, [2] white with green or greenish apex, [3] greenish, [4] pink, [5] purple and [6] blue). The determination of character states was based on observation of the samples collected in field and on the literature data (Table S1) for the following species: *Ananas comosus* (Monteiro 2020), *Cryptanthus capitellatus* (Leme *et al.*, 2010), *C. rigidifolius* (Leme & Kollmann, 2013), *C. venecianus* (Leme *et al.*, 2010), *Fascicularia bicolor* (Zizka *et al.*, 1999), *Ochagania elegans* (Zizka *et al.*, 2002) and *Puya mirabilis*

(Jabaily & Sytsma 2010). The re-rooting method (Yang *et al.*, 1995) was used with the equal rates (ER) model. The analyses were performed separately for the two characters. The character states of each character were plotted separately on tree of the Bayesian inference.

RESULTS

SEQUENCES DATA OF THE CHLOROPLAST DNA

The total alignment length of the concatenated matrix for 69 protein-coding genes of chloroplast DNA was 61,981 bp and the number of variable sites was 1858 that represents ca. 3% of variation (Table 2). Specifically for species of *Cryptanthus*, the number of variable sites was 1006 representing 0.61% of variation (Table 2). The number of recovered sequences was 2749 being 2137 specifically for the genus *Cryptanthus*, not all sequences of the 69 protein-coding genes could be recovered for all taxa (Table 2). Some protein-coding genes (*atpF*, *clpP*, *ndhA*, *ndhK*, *petB*, *psbC*, *rlp36*, *rps12*, *ycf1*) were not used in the analyzes due to the low number of samples recovered or the possible presence of pseudogenes. The ten most informative genes (Table 2) were *rpl22* (10.7% of variation), *rps16* (9.7%), *psbN* (8.3%), *rpoA* (7.0%), *rpl32* (6.8%), *ndhF* (6.6%), *matK* (5.4%), *ccsA* (5.4%), *ycf3* (4.9%) and *petN* (4.4%). Specifically for the species of the genus *Cryptanthus*, the ten most informative genes (Table 2) were *rpl22* (8.5% of variation), *psbN* (8.3%), *rps16* (6.5%), *rpoA* (5.3%), *ycf3* (3.3%), *ndhF* (3.1%), *psbI* (2.7%), *matK* (2.6%), *ycf2* (2.5%) and *ccsA* (2.3%).

PHYLOGENETIC RELATIONSHIPS

The ML and BI analyses of the 69 protein-coding genes resulted in similar topologies (Fig. 2 and 3). The few differences between them are presented below. The first clade that diverged from outgroup (PP 1) included two lineages (Fig. 2 and 3), one with the species

Fascicularia bicolor subsp *bicolor* and *Ochagavia elegans* (PP 1, BS 100), and another with the remaining species of the study. *Ananas comosus* emerged as sister to the Cryptanthoid clade with high support (PP 1, BS 95). The two species of the genus *Sincoraea* was recovered as the first divergent lineage of the Cryptanthoid clade with high support values (PP 1, BS 95).

The *Cryptanthus* comprises a monophyletic group (PP 1, BS 100), however, the phylogenetic relationship of the genus with *Orthophytum* and *Rokautskyia* was not supported (PP 0.53, BS 36). *Cryptanthus* emerged as sister to the clade containing members of the genus *Orthophytum* (*Orthophytum foliosum*, *Orthophytum triunfense* and *Orthophytum jabrense*) and *Rokautskyia* (*Rokautskyia sanctaluciae*), and the relationships in this clade are highly supported in BI (PP 1) and poorly supported in ML (BS 67).

Two main clades emerged in *Cryptanthus* (clades A and B). The clade A (PP 1, BS 100) includes species that are distributed in the northern range of the distribution of *Cryptanthus* (Paraíba, Pernambuco, Alagoas and Sergipe States). The clade A included the *pickelii* clade (PP 1, BS 100), composed of species that occur in the phytogeographic domain of Atlantic Forest (*Cryptanthus alagoanus*, *Cryptanthus cinereus*, *Cryptanthus pickelii* and *Cryptanthus pirambuensis*) and the *bahianus* clade (PP 1, BS 100), with two specimens of *Cryptanthus bahianus* that occur in the phytogeographic domain of the *Caatinga* (a seasonally dry forest from brazilian semi-arid region). In the *pickelii* clade, four specimens of *Cryptanthus pickelii* that occur in Paraíba and Pernambuco States formed a lineage highly supported (P 1, BS 100). Besides, one specimen of *Cryptanthus pickelii* emerges in the *zonatus* clade that belongs to clade B. The other lineage of the *pickelii* clade (P 1, BS 100) includes species that occur in Sergipe State (*Cryptanthus pirambuensis*) and Alagoas State (*Cryptanthus alagoanus* and *Cryptanthus cinereus*).

The clade B (PP 1, BS 100) appeared as the sister lineage to the clade A (Fig. 2), presenting a trichotomy composed of clades 1 and 2, and *Cryptanthus sergipensis*. The clade 1 (PP 1, BS 100) also presented a trichotomy and included the following clades: zonatus clade, walkerianus clade and ruthiae clade. The zonatus clade (PP 1, BS 100) contained species that occur in the northern range of the distribution of *Cryptanthus* in the Atlantic Forest. The first diverging lineage (PP 1, BS 100) in this clade was composed of two specimens of *Cryptanthus zonatus* with the northernmost distribution (Rio Grande do Norte State) of the genus. The other lineage (PP 1, BS 68) was composed of the remaining species (Pernambuco State) of the zonatus clade. In the remaining species, a branch (P 1, BS 90) containing two specimens of different sympatric species (*Cryptanthus pickelii* and *Cryptanthus zonatus*). The species *Cryptanthus diana*, *Cryptanthus reptans* and *Cryptanthus zonatus* formed a politomy in an internal node (P 1, BS 71) of the zonatus clade. *Cryptanthus diana* and *Cryptanthus zonatus* were recovered as non-monophyletic and *Cryptanthus reptans* was unresolved. The walkerianus clade and the ruthiae clade are composed by species that occur in the Atlantic Forest in the Bahia State. The walkerianus clade (PP 1, BS 99) includes three species: *Cryptanthus robsonianus*, *Cryptanthus teretifolius* and *Cryptanthus walkerianus*. And the ruthiae clade (PP 1, BS 94) is composed by species *Cryptanthus apiculatantherus*, *Cryptanthus ruthiae* and *Cryptanthus vinosibracteatus*.

The clade 2 was formed by a trichotomy being composed of the the warren-loosei clade, capixaba clade and the *Cryptanthus beuckeri* species (Fig. 2 and 3). The warren-loosei clade (PP 1, BS 1) included the species *Cryptanthus boanovens*, that occurs in a transition area between Atlantic Forest and Caatinga, and *Cryptanthus crassifolius* and *Cryptanthus warren-loosei* that occur in the phytogeographic domain of the *Caatinga*. And the capixaba clade (PP 0,95, BS 47) contained the species with the southernmost distribution of the genus

that occur in the Atlantic Forest: *Cryptanthus capitellatus*, *Cryptanthus rigidifolius*, *Cryptanthus venecianus* and *Cryptanthus viridipetalus*.

ANCESTRAL CHARACTER STATE RECONSTRUCTION

The ancestral state reconstruction for petioles shows that the absence of petioles was ancestral character state of *Cryptanthus* (Fig. 4). The presence of petioles had multiple origins in evolution of the genus, evolving three times independently. The petioles are present in the species *Cryptanthus beuckeri*, *C. capitellatus* (capixaba clade), *C. teretifolius* and *C. walkerianus* (both are sister and are included in the walkerianus clade).

For petals color, the ancestral state reconstruction shows the character state white petals as ancestral character state in *Cryptanthus* and it prevailed in most clades (Fig. 5). The character state white with green or greenish apex petals had multiple origins in evolution of the genus appearing three times independently. This petals color is present in species *C. apiculatantherus* (ruthiae clade), *C. robsonianus* (walkerianus clade) and in all species of the capixaba clade (*C. capitellatus*, *C. rigidifolius*, *C. venecianus* and *C. viridipetalus*).

DISCUSSION

The phylogenetic reconstructions with a comprehensive sampling of the plastome genes show a robust phylogenetic hypothesis for *Cryptanthus* with the most of the clades being well supported. The infra-generic relationships are better understood with the clades being formed by the geographic proximity of the species. The taxonomic complexes described by Ferreira & Louzada (2020) are confirmed with species of the complexes emerging as non-monophyletic. The infra-generic classification proposed by Ramírez-Morillo (1996) is not supported. A hybridization hypothesis between *C. pickelii* and *C. zonatus* is proposed. The

presence of petioles and petals color white with green or greenish apex petals had multiple origins in evolution of the genus. The study reveals low variation in protein-coding genes and indicate the most informative genes of the chloroplast DNA for *Cryptanthus* that can be used in future studies.

PHYLOGENETIC RELATIONSHIPS AND SPECIES COMPLEXES IN *CRYPTANTHUS*

The study recovered the two species of *Sincoraea* as the first divergent lineage in Cryptanthoid clade with high support values (PP 1, BS 95), and this phylogenetic relationship is in accordance with the study of Louzada et al. (2014). In the cited study, the species of *Sincoraea* were included as *Orthophytum* in the amoenum clade. The genus *Sincoraea* was re-established by Louzada & Wanderley (2016) after of the study Louzada et al. (2014). Leme (2017) also inferred the phylogenetic relationship of the genera in the Cryptanthoid clade. However, the relationships were unresolved, resulting in a polytomy (PP 1, BS 91) composed of four main clades: clade I (*Hoplocryptanthus*), clade II (*Lapanthus* and *Forzzaea*), clade III (*Cryptanthus*), and clade IV (*Sincoraea*, *Orthophytum* and *Rokautskyia*).

We recovered *Cryptanthus* as sister to the clade containing members of the genus *Orthophytum* and *Rokautskyia*. In Louzada et al. (2014), the genus *Cryptanthus* emerged as sister to the recently described genus *Hoplocryptanthus* (in the study represented by *Cryptanthus tiradentesensis* Leme), whereas in Cruz et al. (2017), it was recovered as sister to the recently described *Forzzaea* (accessions included in the study as *Cryptanthus leopoldo-horstii* Rauh and *Cryptanthus micrus* Louzada, Wand. & Versieux). The sister lineage to *Cryptanthus* could not be confirmed in the present study due to the lack of sampling of the genera of the Cryptanthoid clade: *Lapanthus*, *Forzzaea* and *Hoplocryptanthus*.

The phylogenetic reconstructions recovered the genus *Cryptanthus* as monophyletic and it is in accordance with the current classification proposed by Leme et al. (2017). The clades of the genus *Cryptanthus* were consistent with the geographical distribution of the species (Figs 2 and 3). The geographic pattern of clades was also found in study carried out with *Dyckia* species by Pinangé et al. (2017).

The infra-generic relationships in *Cryptanthus* showed significant differences when compared to previous studies (Silvestro et al., 2013; Louzada et al., 2014; Cruz et al., 2017; Leme et al., 2017). *Cryptanthus bahianus* and *C. warren-loosei* were recovered as closely related in phylogenetic reconstructions (Silvestro et al., 2013; Louzada et al., 2014; Leme et al., 2017). Both species occur in dry environments, in the phytogeographic domain of the *Caatinga*. However, in the present study, these species emerged in different clades. *Cryptanthus beuckeri* and *Cryptanthus teretifolius*, species with petiolate leaves, are indicated as sister (Leme et al., 2017), but both species also emerge in different clades in the present study.

Some species of *Cryptanthus* have overlapping morphological characters and compose two different species complexes described by Ferreira & Louzada (2020). These complexes are confirmed in this study. The *Cryptanthus pickelii* L. B. Sm. complex includes the species *C. alagoanus* and *C. pickelii*. For identification of sampled specimens of the *Cryptanthus pickelii* L. B. Sm. complex, we used the material examined by Leme & Siqueira-Filho (2007) since it is difficult to distinguish the two species due to overlapping of characters. These authors are the same who described the species *C. alagoanus*. According to the material examined of Leme & Siqueira-Filho (2007), the specimens (DNA N° 30553 and N° 30554) can be identified as *C. alagoanus*. And the specimen (DNA N° 30570) can be identified as *C. pickelii*. In addition, according to protologue of *C. alagoanus* (Leme & Siqueira-Filho, 2001) the holotype is from the municipality of Paripueira, Alagoas State. Thus, the specimen (DNA

N° 30555) also can be identified as *C. alagoanus*. In this way, the species *C. alagoanus* and *C. pickelii* emerges as non-monophyletic. In the *pickelii* clade, one lineage includes the specimens that occur in Pernambuco and Paraiba States and another lineage includes the species that occur in Alagoas and Sergipe States. Thus, we decided to consider the lineage that occurs in Pernambuco and Paraiba States as the species *C. pickelii*. And we only consider the lineage that occur in Alagoas State as *C. alagoanus*.

The other species complex called *Cryptanthus zonatus* (Vis.) Vis. complex contains the species *C. diana*, *C. reptans* and *C. zonatus* (Ferreira & Louzada, 2020). *Cryptanthus zonatus* is also shown as non-monophyletic and it is included in the *zonatus* clade with the species *Cryptanthus pickelii*, *Cryptanthus diana* and *Cryptanthus reptans*. The morphological similarities between *Cryptanthus diana*, *Cryptanthus reptans* and *Cryptanthus zonatus* were presented by Ferreira & Louzada (2020). Another species, *Cryptanthus burle-marxii*, is treated as a synonym of *Cryptanthus zonatus* by Ferreira et al. (2021), and this classification was adopted here.

In the *zonatus* clade, two lineages were formed confirming the north-south pattern obtained by Ferreira et al. (2021). The specimens of *Cryptanthus zonatus* with northern distribution (Rio Grande do Norte State) formed the first diverging lineage (DNA N° 30591 and 30592) and the remaining specimens (DNA N° 30589, 30590, 30588, 30593) formed the other lineage with distribution to the south (Pernambuco State). The last-mentioned lineage also included *Cryptanthus pickelii*, *Cryptanthus diana* and *Cryptanthus reptans*, although these species were not included in the study of Ferreira et al. (2021). The genetic differentiation between the two genetic clusters formed in the study of Ferreira et al. (2021) with the *Cryptanthus zonatus* complex (species *C. burle-marxii* and *C. zonatus*) was low ($F_{CT} = 0.054$, $P = 0.005$) to consider the northern and southern clusters as different species in *Cryptanthus zonatus*. The results here suggest that possibly *Cryptanthus diana*, *Cryptanthus*

reptans and *Cryptanthus zonatus* could be considered the same species. However, population genetic studies are recommended for the resolution of these complexes.

INFRA-GENERIC CLASSIFICATION OF *CRYPTANTHUS* AND ANCESTRAL CHARACTER STATE RECONSTRUCTION

Ramírez-Morillo (1996) proposed five sections based on morphological evidence for the subgenus *Cryptanthus* (current genus *Cryptanthus*): *Bahianae*, *Beuckeriae*, *Cryptanthus*, *Lacerae* and *Zonatae* (unpublished data) that are tested in this study. The clades of the present study (Figs 2 and 3) are not in accordance with the infra-generic classification proposed by Ramírez-Morillo (1996). None of five morphological sections proposed for *Cryptanthus* was supported (except section *Lacerae*, that was not sampled here, however this section is monospecific). Cruz et al. (2017) also did not support this classification of the sections with data AFLP.

The section *Bahianae* is characterized by their very succulent and thick leaf blades with pungent spines and apex and includes the species *C. bahianus* L.B.Sm., *C. seidelianus* W. Weber, *C. sergipensis* I. Ramirez and *C. warren-loosei* Leme (Ramírez-Morillo, 1996). The species of this sections emerged in bahianus and warren-loosei clades showing that this section is not monophyletic.

The section *Beuckeriae* is mainly characterized by petiolate leaves and it includes only the *C. beuckeri* E. Morren (Ramírez-Morillo, 1996). When Ramírez-Morillo (1996) defined this sections there is only one species with petiolate leaves, however, later new species with petioles leaves were discovered such as *C. capitellatus*, *C. teretifolius* and *C. walkerianus* described by Leme et al. (2010), Leme (2002) and Leme et al. (2014), respectively. The presence of petioles had multiple origins in evolution of the genus appearing three times independently (Fig. 4). Therefore, this section is non-monophyletic.

The section *Cryptanthus* includes most species of *Cryptanthus* totaling 14 species with highly variable morphological characters (Ramírez-Morillo, 1996). In total three species from this section were sampled in the present study: *C. pickelii*, *C. diana* and *C. ruthiae*. In the study of Ramírez-Morillo (1996), the author synonymized *C. pickelii* under *C. maritimus* L.B.Sm. and *C. ruthiae* under *C. pseudopetiolatus* Philcox. However, in this study we consider *C. pickelii* and *C. ruthiae* as different species. The species of this section emerged in different clades: *pickelii*, *ruthiae* and *zonatus* showing that this section is not monophyletic. The section *Lacerdae* was the only section not sampled in this study. It is characterized by three longitudinal gray bands formed by trichomes on adaxial leaf blades and includes only one species *C. lacerdae* Antoine (Ramírez-Morillo 1996).

The section *Zonatae* is characterized by transversal lepidote bands on the adaxial leaf blades and includes the species: *C. burle-marxii*, *C. fosterianus* and *C. zonatus* (Ramírez-Morillo, 1996). After the study of Ramírez-Morillo (1996), Alves & Marcucci (2015) synonymized *C. fosterianus* under *C. zonatus* based on morphological evidence and Ferreira *et al.* (2021) synonymized *C. burle-marxii* under *C. zonatus* based on morphological evidence and genetic structure data. In the present study, the species *C. zonatus* emerged as non-monophyletic showing that this section is not monophyletic.

The proposal of an infra-generic classification for the genus has been a challenge due to the presence of homoplasy for morphological characters in the genus. This study shows that presence of petioles had multiple origins in evolution of the genus evolving three times independently. The petioles have a distinct morphology with *C. beuckeri* presenting canaliculate petioles with revolute margins while *C. capitellatus*, *C. teretifolius* and *C. walkerianus* have canaliculate petioles with straight margins.

For petals color, the character state white with green or greenish apex petals had multiple origins in evolution of the genus evolving three times independently. Therefore, this character also is labile and can not be used to propose an infra-generic classification for the genus.

HYBRIDIZATION HYPOTHESIS

The specimen (DNA N° 30553) belongs to a population that is identified by Leme & Siqueira-Filho (2007) as *Cryptanthus alagoanus* although the authors indicate that the population has morphological traits discordant of *C. alagoanus*. In fact, this population is similar to the *C. pickelii* complex populations despite having some discordant traits. Here, we consider this specimen as *C. pickelii* because of the closest proximity to the holotype. The specimen (DNA N° 30553) was expected to be nested in the *pickelii* clade however the specimen emerged as sister to *C. zonatus* (DNA N° 30589) in the *zonatus* clade.

Both specimens are sympatric in “Mata do Cupe”, have simultaneous flowering in part of the reproductive cycle and share the same pollinators (Oliveira-Júnior, 2015). Oliveira-Júnior (2015) indicated a possible hybridization between these species because there was fruit formation in 30.8% of the analyzed samples (n = 26) of *C. zonatus* in a manual interspecific crossing experiment carried out *in situ* with average formation of 6,75 ($\pm 0,6$, n = 8) seeds/fruit (Oliveira-Júnior, 2015). The molecular data of the present study corroborates the results of Oliveira-Júnior (2015), suggesting that hybridization between *Cryptanthus pickelii* and *Cryptanthus zonatus* is possibly occurring in nature, since both have been nested together. Despite the formation of fruits from interespecific experiments, Oliveira (2015) indicates that there was the formation of a greater amount of fruit in monospecific outcrossing of *C. zonatus* (88,9%; n = 27) suggesting that there is some mechanism for decreasing reproductive success when there is interspecific outcrossing between species.

Cases of natural hybridization in Bromeliaceae have been shown in the literature (Wendt *et al.*, 2001; Wendt *et al.*, 2002; Gonçalves & Azevedo-Gonçalves, 2019; Schulte *et*

al., 2010; Palma-Silva *et al.*, 2011; Versieux *et al.*, 2012; Zanella *et al.*, 2016; Neri *et al.*, 2017, 2018; Mota *et al.*, 2019). Study of hybridization between *Vriesea scalaris* and *V. simplex* shows that morphological and genetic integrity of these species are maintained by the combination of prezygotic and postzygotic barriers (Neri *et al.*, 2017, 2018). It would be important to investigate prezygotic and postzygotic barriers of *C. pickelii* and *C. zonatus* and check whether this also occurs in these sympatric populations.

A population genetics study also is recommended to detect hybrid zones between sympatric populations of *C. pickelii* and *C. zonatus* and test the integrity of these species. In fact, the population identified as *Cryptanthus pickelii* has a discordant morphology from the *C. alagoanus*, *C. pickelii* and *C. zonatus*. This population may be accumulating genetic variation and may be in process of hybrid speciation. However, studies are needed to confirm this.

INFORMATIVE GENES OF THE CHLOROPLAST DNA FOR *CRYPTANTHUS*

The initial idea of the study was to carry out the phylogenetic analyzes with the complete plastome, however, we were able to assemble the complete plastome only for less than ¼ of the species sampled. Machado *et al.* (2019) also had the assembly problem of the plastome in *Vriesea* species. The authors indicate that the assembly problem can be explained by rigorous quality filtering. Thus, the study of Machado *et al.* (2019) used a partial portion of the plastome to do the phylogenetic analyzes instead of the complete plastome.

Here, we choose to use the protein-coding genes (total alignment length = 61,981 bp) to do the phylogenetic analyzes that represent about 39% of the plastome (if we compare with *C. pickelii* species that we obtained the complete plastome with total size = 159,481 bp - unpublished data). The study reveals low variation in protein-coding genes with the number of variable sites = 1006 representing 0.61% of variation for *Cryptanthus* that can be related to

the recent origin of the genus estimated by Silvestro et al. (2014) in 5-7.5 Ma years ago. The low variation of the chloroplast DNA is known for Bromeliaceae (e.g. Schulte, Horres and Zizka, 2005; Schulte *et al.*, 2009).

The ten most informative genes for the genus *Cryptanthus* are presented (*rpl22*, *psbN*, *rps16*, *rpoA*, *ycf3*, *ndhF*, *psbI*, *matK*, *ycf2* and *ccsA*) and they can be used in future studies with the genus such as phylogenetic positioning of new species since new species have been recently described for the genus.

CONCLUSION

This study shows a robust hypothesis about phylogenetic relationships within of *Cryptanthus*. The genus is monophyletic and the clades of the genus *Cryptanthus* were consistent with the geographical distribution of the species. However, they were not in accordance with the infra-generic classification based on morphology proposed by Ramírez-Morillo (1996). The infra-generic relationships in genus showed significant differences when compared to previous studies. *Cryptanthus alagoanus*, *Cryptanthus diana*, *Cryptanthus pickelli*, *Cryptanthus zonatus* emerged as non-monophyletic and the current circumscription of these species needs to be revised. Besides, the molecular data show a possible hybridization between *Cryptanthus alagoanus* and *Cryptanthus zonatus*. Some morphological characteristics of *Cryptanthus* were shown as homoplastic, such as leaves petiolate and coloring of the petals white except for the green or greenish apex. The ten most informative genes were indicated to be used in future studies with the genus.

ACKNOWLEDGEMENTS

This study is part of the Ph.D. research of the first author conducted at the Programa de Pós-Graduação em Biologia Vegetal (PPGBV) from Universidade Federal de Pernambuco

under the supervision of RBL. The first author thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco (FACEPE) for financial support. RBL thanks CNPq for the financial support (grants no. 310871/2014-0 and 449686/2014-0). DMCF thanks the A. Nepomuceno, L. Daneu, D. Casarin, T. Pena, F. Guedes and E. M. Almeida for assistance with field work.

REFERENCES

- Alves M, Marcucci R. 2015.** Nomenclatural correction in *Cryptanthus* Otto & A. Dietrich. (Bromeliaceae - Bromelioideae). *Rodriguésia* **66**: 661-664.
- Christenhusz MJM, Fay MF, Chase MW. 2017.** Bromeliaceae. In: Christenhusz MJ ., Fay MF, Chase MW, eds. *Plants of the world: an illustrated encyclopedia of vascular plants*. Chicago: The University of Chicago Press, 194-196.
- Cruz GAS, Zizka G, Silvestro D, Leme EMC, Schulte K, Benko-Iseppon AM. 2017.** Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). *Molecular Phylogenetics and Evolution* **107**: 152–165.
- Cruz GAS, Filho JRM, Vasconcelos S, Gitaí J, Campos JMS, Viccini LF, Zizka G, Leme EMC, Brasileiro-Vidal AC, Benko-Iseppon AM. 2020.** Genome size evolution and chromosome numbers of species of the cryptanthoid complex (Bromelioideae, Bromeliaceae) in a phylogenetic framework. *Botanical Journal of the Linnean Society* **192**: 887–899.
- Dierckxsens N, Mardulyn P, Smits G. 2017.** NOVOPlasty: *de novo* assembly of organelle genomes from whole genome data. *Nucleic Acids Research* **45**: e18.

- Ferreira ME, Grattapaglia D. 1998.** *Introdução ao uso de marcadores moleculares em análise genética*. Brasília: Embrapa-CENARGEN.
- Ferreira DMC, Louzada RB. 2020.** A new species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in Brazilian Atlantic Forest north of the São Francisco River, and its contribution to the taxonomy of the genus. *Systematic Botany* **45**: 460-465.
- Ferreira DMC, Palma-Silva C, Néri J, Medeiros MCP de, Pinangé DS, Benko-Iseppon, Louzada RB. 2021.** Population genetic structure and species delimitation in the *Cryptanthus zonatus* complex (Bromeliaceae). *Botanical Journal of the Linnean Society* **196**: 123–140.
- Forzza RC, Costa AF, Leme EMC, Versieux LM, Wanderley MGL, Louzada RB, Monteiro RF, Judice DM, Fernandez EP, Borges RAX, Penedo TSA, Monteiro NP, Moraes MA. 2013.** Bromeliaceae. Martinelli G, Moraes MA, eds. *Livro Vermelho da Flora do Brasil*. Rio de Janeiro: Andrea Jakobsson. 315-396.
- Gitaí J, Paule J, Zizka G, Schulte K, Benko-Iseppon AM. 2014.** Chromosome numbers and DNA content in Bromeliaceae: additional data and critical review. *Botanical Journal of the Linnean Society* **176**: 349–368.
- Givnish TJ, Millam KC, Evans TM, Hall JC, Pires JC, Berry PE, Sytsma KJ. 2004.** Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and south american–african disjunctions in Rapateaceae and Bromeliaceae based on *ndhF* sequence data. *International Journal of Plant Sciences* **165**: 35–S54.
- Givnish TJ, Milliam KC, Berry PE, Sytsma KJ. 2007.** Phylogeny, adaptive radiation, and historical biogeography of Bromeliaceae inferred from *ndhF* sequence data. *Aliso* **23**: 3–26.
- Givnish TJ, Barfuss MHJ, Van Ee B, Riina R, Schulte K, Horres R, Gonsiska PA, Jabaily RS, Crayn DM, Smith JAC, Winter K, Brown GK, Evans TM, Holst BK,**

- Luther H, Till W, Zizka G, Berry PE, Sytsma KJ. 2011.** Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. *American Journal of Botany* **98**: 872–895.
- Gouda EJ, Butcher D, Gouda K. cont. updated.** Encyclopaedia of bromeliads, Version 4. University Utrecht Botanic Gardens. Available at: <http://bromeliad.nl/encyclopedia/>
- Gonçalves CN, Azevedo-Gonçalves CF de. 2019.** A New Hybrid Bromeliad from Southernmost Brazil, *Tillandsia ×baptistana*. *NOVON* **19**: 353–356.
- Hermida-Carrera C, Fares MA, Font-Carrascosa M, Kapralov MV, Koch MA, Mir A, Molins A, Ribas-Carbó M, Rocha J, Galmés J. 2020.** Exploring molecular evolution of Rubisco in C3 and CAM Orchidaceae and Bromeliaceae. *BMC Evolutionary Biology* **20**: 11.
- Jabaily RS, Sytsma KJ. 2010.** Phylogenetics of *Puya* (Bromeliaceae): placement, major lineages, and evolution of chilean species. *American Journal of Botany* **97**: 337–356.
- Katoh K, Standley DM. 2013.** MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Molecular Biology and Evolution* **30**: 772–780.
- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Meintjes P, Drummond A. 2012.** Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* **28**: 1647–1649.
- Leme EMC. 2002.** *Cryptanthus teretifolius*, a new species from the coastal zone of Espírito Santo State. *The Cryptanthus Society Journal* **17**: 15–16.
- Leme EMC, Kollmann LJC. 2013.** Miscellaneous New species of Brazilian Bromeliaceae. *Phytotaxa* **108**: 1–40.

- Leme EMC, Siqueira-Filho JA. 2001.** Studies in Bromeliaceae of Northeastern Brazil. I. *Selbyana* 22: 146-154.
- Leme EMC, Siqueira-Filho JA. 2007.** Bromeliad taxonomy in Atlantic Forest fragments of Pernambuco and Alagoas. In: Siqueira-Filho JA, Leme EMC, eds. *Fragments of the Atlantic Forest of Northeast Brazil. Biodiversity, conservation and the bromeliads*. Rio de Janeiro: Andrea Jakobsson Estúdio, 190–381.
- Leme EMC, de Fraga CN, Kollmann LJC, Brown GK, Till W, Ribeiro OBC, Machado MC, Monteiro FJS, Fontana AP. 2010.** Miscellaneous new species in the Brazilian Bromeliaceae. *Rodriguésia* 61: 021-067.
- Leme EMC, Till W, Kollmann LJC, Moura RL de, Ribeiro OBC. 2014.** Miscellaneous New Species of Brazilian Bromeliaceae – III. *Phytotaxa* 177: 061-100.
- Leme EMC, Heller S, Zizka G, Halbritter H. 2017.** New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318: 001-008.
- Louzada RB, Versieux LM. 2010.** *Lapanthus* (Bromeliaceae, Bromelioideae): A new genus from the southern Espinhaço Range, Brazil. *Systematic Botany* 35: 497–503.
- Louzada RB, Schulte K, Wanderley MGL, Silvestro D, Zizka G, Barfuss MHJ, Palma-Silva C. 2014.** Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (Bromelioideae, Bromeliaceae) and its implications on morphological character evolution. *Molecular Phylogenetics and Evolution* 77: 54–64.
- Louzada RB, Wanderley MGL. 2016.** Re-establishment of *Sincoraea* (Bromeliaceae). *Journal of the Bromeliad Society* 66: 6–19.
- Machado TM, Loiseau O, Paris M, Weigand A, Versieux LM, Stehmann JR, Lexer C, Salamin N. 2020.** Systematics of *Vriesea* (Bromeliaceae): phylogenetic relationships

- based on nuclear gene and partial plastome sequences. *Botanical Journal of the Linnean Society* **192**: 656-674.
- Maciel JR, Louzada RB, Benko-iseppon AM, Zizka G, Alves M. 2018.** Polyphyly and morphological convergence in Atlantic Forest species of *Aechmea* subgenus *Chevaliera* (Bromeliaceae). *Botanical Journal of the Linnean Society* **188**: 281-295.
- Mez C. 1896.** Bromeliaceae. In: De Candolle C, ed. *Monographiae Phanerogamarum*. Paris: Sumptibus Masson, 1-144.
- Monteiro RF. 2020.** *Ananas* in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Available at: <<http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB16574>>.
- Mota MR, Pinheiro F, Leal BSS, Wendt T, Palma-Silva C. 2019.** The role of hybridization and introgression in maintaining species integrity and cohesion in naturally isolated inselberg bromeliad populations. *Plant Biology* **21**: 122-132.
- Nauheimer L, Cui L, Clarke C, Crayn DM, Bourke G, Nargar K. 2019.** Genome skimming provides well resolved plastid and nuclear phylogenies, showing patterns of deep reticulate evolution in the tropical carnivorous plant genus *Nepenthes* (Caryophyllales). *Australian Systematic Botany* **32**: 243–254.
- Neri J, Wendt T, Palma-Silva C. 2018.** Natural hybridization and genetic and morphological variation between two epiphytic bromeliads. *AoB PLANTS* **10**: plx061.
- Neri J, Wendt T, Leles B, Santos MF dos, Palma-Silva. 2017.** Variation in reproductive systems facilitates species boundaries of sympatric *Vriesea* (Bromeliaceae). *Botanical Journal of the Linnean Society* **184**: 272–279.
- Oliveira-Júnior JB. 2015.** *Fenologia da floração e ecologia reprodutiva da Bromeliaceae ameaçada *Cryptanthus burle-marxii* Leme e simpatria com *Cryptanthus alagoanus* Leme & J.A.* Unpublished M.S. Thesis, Universidade Federal de Pernambuco.

- Otto F, Dietrich A. 1836.** Eine neue gattung aus der familie der Bromeliaceae. *Allgemeine Gartenzeitung* **38**: 297–299.
- Palma-Silva C, Wendt T, Pinheiro F, Barbará T, Fay MF, Cozzolino S, Lexer C. 2011.** Sympatric bromeliad species (*Pitcairnia* spp.) facilitate tests of mechanisms involved in species cohesion and reproductive isolation in Neotropical inselbergs. *Molecular Ecology* **20**: 3185–3201.
- Paule P, Schmickl R, Fér T, Matuszak-Renger S, Halbritter H, Zizka G. 2020.** Phylogenomic insights into the *Fascicularia-Ochagavia* group (Bromelioideae, Bromeliaceae). *Botanical Journal of the Linnean Society* **192**: 642–655.
- Paradis E, Claude J, Strimmer K. 2004.** APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**: 289–290.
- Pinangé DSB, Krapp F, Zizka G, Silvestro D, Leme EMC, Weising K, Benko-Iseppon AM. 2017.** Molecular phylogenetics, historical biogeography and character evolution in *Dyckia* (Bromeliaceae, Pitcairnioideae). *Botanical Journal of the Linnean Society* **183**: 39–56.
- Ramírez-Morillo I. 1996.** *Systematics, Phylogeny and Chromosome Number Evolution in Cryptanthus (Bromeliaceae)*. Unpublished D. Phil. Thesis, University of Missouri.
- Revell LJ. 2012.** Phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* **3**: 217–223.
- Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012.** MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61**: 539–542.
- Schubert M, Lindgreen S, Orlando L. 2016.** AdapterRemoval v2: rapid adapter trimming, identification, and read merging. *BMC Research Notes* **9**: 88.

- Schulte K, Barfuss MHJ, Zizka G. 2009.** Phylogeny of Bromelioideae (Bromeliaceae) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molecular Phylogenetics and Evolution* **51**: 327–339.
- Schulte K, Silvestro D, Kiehlmann E, Vesely S, Novoa P, Zizka G. 2010.** Detection of recent hybridization between sympatric Chilean *Puya* species (Bromeliaceae) using AFLP markers and reconstruction of complex relationships. *Molecular Phylogenetics and Evolution* **57**: 1105–1119.
- Schulte K, Horres R, Zizka G. 2005.** Molecular phylogeny of Bromelioideae and its implications on biogeography and the evolution of CAM in the family (Poales, Bromeliaceae). *Senckenbergiana biologica* **85**: 1–13.
- Silvestro D, Zizka G, Schulte K. 2014.** Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). *Evolution* **68**: 163–175.
- Smith LB. 1955.** The Bromeliaceae of Brazil. *Smithsonian Miscellaneous Collections* **126**: 1–290.
- Smith LB, Downs RJ. 1974.** Pitcairnioideae (Bromeliaceae). *Flora Neotropica Monograph* **14**: 1–662.
- Smith LB, Downs RJ. 1977.** Tillandsioideae (Bromeliaceae). *Flora Neotropica Monograph* **14**: 663–1492.
- Stamatakis A. 2014.** RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313.
- Steens A. 2007.** *Bromeliads, the connoisseur's guide*. Glebe: Florilegium.
- Versieux LM, Barbará T, Wanderley MGL, Calvente A, Fay MF, Lexer C. 2012.** Molecular phylogenetics of the Brazilian giant bromeliads (*Alcantarea*, Bromeliaceae): implications for morphological evolution and biogeography. *Molecular Phylogenetics and Evolution* **64**: 177–189.

- Versieux LM, Magalhães R, Calvente A. 2013.** Extension of the *Cryptanthus* range in Northeastern Brazil with new findings in the phenotypic variation including changes in the trichome's distribution, thus enhancing the understanding of the *Cryptanthus zonatus* complex (Bromeliaceae). *Phytotaxa* **109**: 54-60.
- Yang Z, Kumar S, Nei M. 1995.** A new method of inference of ancestral nucleotide and amino acid sequences. *Genetics* **141**: 1641–1650.
- Zanella CM, Palma-Silva C, Goetze M, Bered F. 2016.** Hybridization between two sister species of Bromeliaceae: *Vriesea carinata* and *V. incurvata*. *Botanical Journal of the Linnean Society* **181**: 491–504.
- Zizka G, Horres R, Nelson EC, Weising K. 1999.** Revision of the genus *Fascicularia* Mez (Bromeliaceae). *Botanical Journal of the Linnean Society* **129**: 315-332.
- Zizka G, Trumpler K, Zöllner O. 2002.** Revision of the genus *Ochagavia* (Bromeliaceae, Bromelioideae). *Willdenowia* **32**: 331-350.
- Wendt T, Canela MBF, De Faria APG, Rios RI. 2001.** Reproductive biology and natural hybridization between two endemic species of *Pitcairnia* (Bromeliaceae). *American Journal of Botany* **88**: 1760–1767.
- Wendt T, Canela MBF, Klein DE, Rios RI. 2002.** Selfing facilitates reproductive isolation among three sympatric species of *Pitcairnia* (Bromeliaceae). *Plant Systematics and Evolution* **232**: 201–212.

Table 1. Studied material with locality, DNA No. and Voucher (all deposited in Herbarium Geraldo Mariz of Universidade Federal de Pernambuco). Abbreviations: AL: Alagoas; BA: Bahia; PE: Pernambuco; PB: Paraíba; RN: Rio Grande do Norte; SE: Sergipe; ES: Espírito Santo. *living collection of the Museu de Biologia Prof. Mello Leitão, in Santa Teresa, Espírito Santo

Species	Locality	DNA No.	Voucher
<i>Cryptanthus alagoanus</i> Leme & J.A. Siqueira	AL, Paripueira	30555	<i>D. Cavalcanti et al.</i> 906
<i>Cryptanthus apiculatantherus</i> D.M.C. Ferreira, E.M. Almeida & Louzada	BA, Itacaré	30580	<i>E.M. Almeida</i> 2757
<i>Cryptanthus bahianus</i> L. B. Smith	PB, Areia	30558	<i>E. M. Almeida</i> 2857
	PE, Caruaru	30557	<i>D. Cavalcanti et al.</i> 900
<i>Cryptanthus beuckeri</i> E. Morren	BA, Una	30559	<i>D. Cavalcanti et al.</i> 726
<i>Cryptanthus boanovensensis</i> Leme			<i>D. Cavalcanti & L. Daneu</i> 838
	BA, Boa Nova	30560	
<i>Cryptanthus capitellatus</i> Leme & L. Kollmann	ES, Santa Teresa	30561	Photographic Register
<i>Cryptanthus cinereus</i> D.M.C. Ferreira & Louzada	AL, Ibateguara	30562	<i>D. Cavalcanti et al.</i> 921
<i>Cryptanthus crassifolius</i> Leme			<i>D. Cavalcanti & L. Daneu</i> 848
	BA, Ituaçu	30563	
<i>Cryptanthus diana</i> Leme	PE, Jaqueira	30564	<i>D. Cavalcanti et al.</i> 799
	PE, São Vicente Ferrer	30565	<i>D. Cavalcanti et al.</i> 771
<i>Cryptanthus pickelii</i> L. B. Sm.	PE, Camaragibe	30552	<i>D. Cavalcanti & V. Aya</i> 782
	PE, Gravata	30569	<i>D. Cavalcanti et al.</i> 730
	PE, Ipojuca	30553	<i>D. Cavalcanti et al.</i> 766
	PB, Mamanguape	30554	<i>D. Cavalcanti & F. M. Guedes</i> 827
	PE, Paulista	30570	<i>D. Cavalcanti & J. Oliveira-Júnior</i> 773
<i>Cryptanthus pirambuensis</i> D.M.C. Ferreira & Louzada	SE, Pirambu	30551	<i>D. Cavalcanti & E. Ferreira</i> 829
<i>Cryptanthus reptans</i> Leme & J.A.Siqueira			<i>D. Cavalcanti et al.</i> 910
	PE, Água Preta	30573	<i>D. Cavalcanti & D. V. Casarin</i> 938
<i>Cryptanthus rigidifolius</i> Leme	ES, Fundão	30574	
<i>Cryptanthus robsonianus</i> Leme	BA, Maraú	30576	<i>D. Cavalcanti et al.</i> 703
<i>Cryptanthus ruthiae</i> Philcox	BA, Maraú	30577	Photographic Register
<i>Cryptanthus sergipensis</i> I.	SE, Santa Luzia	30578	<i>D. Cavalcanti & N. Sousa</i>

Ramírez	do Itanhi	828	
<i>Cryptanthus teretifolius</i> Leme	BA, Ubaíra	30582	<i>D. Cavalcanti & L. Daneu</i> 852
<i>Cryptanthus venecianus</i> Leme & L. Kollmann	ES, Nova Venécia	30583	<i>D. Cavalcanti et al.</i> 924
<i>Cryptanthus vinosibracteatus</i> D.M.C. Ferreira & Louzada	BA, Itapetinga	30556	<i>D. Cavalcanti et al.</i> 834
<i>Cryptanthus viridipetalus</i> Leme & L. Kollmann	ES, Boa Esperança	30585	<i>D. Cavalcanti & A. Nepomuceno</i> 922
<i>Cryptanthus walkerianus</i> Leme & L. Kollmann	BA, Camamu	30586	<i>D. Cavalcanti & L. Daneu</i> 884
<i>Cryptanthus warren-loosei</i> Leme	BA, Morro do Chapéu	30587	<i>D. Cavalcanti & R. B. Louzada</i> 901
<i>Cryptanthus zonatus</i> (Vis.) Vis.	RN, Natal	30591	Photographic Register
	RN, Baía Formosa	30592	<i>D. Cavalcanti & R. B. Louzada</i> 763
	PE, Paulista	30593	Photographic Register
	PE, Igarassu	30588	<i>D. Cavalcanti & R. B. Louzada</i> 897
	PE, Gravata	30590	<i>D. Cavalcanti et al.</i> 784
	PE, Ipojuca	30589	<i>D. Cavalcanti et al.</i> 764
<i>Orthophytum foliosum</i> L.B.Sm.	ES, Nova Venécia	30594	<i>D. Cavalcanti et al.</i> 925
<i>Orthophytum jabrense</i> G.S.Baracho & J.A.Siqueira	PB, Maturéia	30596	<i>D. Cavalcanti et al.</i> 942
<i>Orthophytum triunfense</i> J.A.Siqueira & Leme	PE, Triunfo	30597	<i>D. Cavalcanti et al.</i> 943
<i>Rokautskyia sanctaluciae</i> (Leme & L. Kollmann) Leme, S. Heller & Zizka*	ES, Santa Leopoldina	30598	<i>D. Cavalcanti</i> 940
<i>Sincoraea burle-marxii</i> (L.B. Sm. & Read) Louzada & Wand.	BA, Palmeiras	30599	<i>D. Cavalcanti et al.</i> 944
<i>Sincoraea ophiuroides</i> (Louzada & Wand.) Louzada & Wand.	BA, Lençóis	30600	<i>D. Cavalcanti et al.</i> 945

Table 2. Matrix alignment statistics

Genes	Raw sequence length of alignment (without gaps)	Aligned bases (with gaps)	N° recovered sequences	N° of variable sites	N° recovered sequences (<i>Cryptanthus</i>)	N° of variable sites (<i>Cryptanthus</i>)
<i>accD</i>	1467-1539	1473*	39	42	31	34
<i>atpA</i>	1524	1524	41	29	32	16
<i>atpB</i>	1497	1497	39	22	30	6
<i>atpE</i>	405	405	39	13	30	3
<i>atpH</i>	246	246	41	1	32	0
<i>atpI</i>	744	744	41	16	32	4
<i>ccsA</i>	948-960	961	42	52	32	23
<i>cemA</i>	690	690	39	16	30	4
<i>infA</i>	234	234	37	7	29	5
<i>matK</i>	1527-1548	1548	40	85	31	41
<i>ndhB</i>	2224-2233	2233	44	21	34	13
<i>ndhC</i>	363	363	35	8	28	3
<i>ndhD</i>	1506	1506	44	42	34	13
<i>ndhE</i>	306	306	44	7	34	3
<i>ndhF</i>	1950-2050	2214*	41	148	32	70
<i>ndhG</i>	531	531	44	17	34	8
<i>ndhH</i>	1182	1182	38	25	29	8
<i>ndhI</i>	543	543	44	10	34	4
<i>ndhJ</i>	480	480	38	12	29	5
<i>petA</i>	963	963	39	28	30	16
<i>petD</i>	564	564	38	20	30	7
<i>petG</i>	114	114	38	1	29	0
<i>petL</i>	96	96	38	1	30	0
<i>petN</i>	90	90	40	4	31	2
<i>psaA</i>	2253	2253	41	36	32	10
<i>psaB</i>	2205	2205	41	43	32	18
<i>psaC</i>	246	246	44	4	34	2
<i>psaI</i>	111	111	39	1	29	0
<i>psaJ</i>	135	135	38	2	29	1
<i>psbA</i>	1062	1062	41	15	32	7
<i>psbB</i>	1527	1527	38	23	29	7
<i>psbD</i>	1062	1062	40	21	31	9
<i>psbE</i>	252	252	39	2	30	1
<i>psbF</i>	120	120	40	0	31	0
<i>psbH</i>	222	222	39	6	30	0
<i>psbI</i>	111	111	39	3	30	3
<i>psbJ</i>	123	123	39	1	30	1
<i>psbK</i>	186	186	41	6	32	2

Table S1. Accessions and morphological characters with their respective character states coded used for ancestral character state reconstruction. Codification: Subpetiole= 0-absent, 1-present; Petals color= 1-white, 2-white with green or greenish apex, 3-greenish, 4-pink, 5-purple, 6-blue.

Accessions	Subpetiole	Petals color
NC_026220_Ananas_comosus	0	5
30551_Cryptanthus_alagoanus	0	1
30552_Cryptanthus_alagoanus	0	1
30553_Cryptanthus_alagoanus	0	1
30554_Cryptanthus_alagoanus	0	1
30555_Cryptanthus_alagoanus	0	1
30580_Cryptanthus_apiculatantherus	0	2
30557_Cryptanthus_bahianus	0	1
30558_Cryptanthus_bahianus	0	1
30559_Cryptanthus_beuckeri	1	1
30560_Cryptanthus_boanovenssis	0	1
30561_Cryptanthus_capitellatus	1	2
30562_Cryptanthus_cinereus	0	1
30563_Cryptanthus_crassifolius	0	1
30564_Cryptanthus_dianae	0	1
30565_Cryptanthus_dianae	0	1
30569_Cryptanthus_pickelii	0	1
30570_Cryptanthus_pickelii	0	1
30573_Cryptanthus_reptans	0	1
30574_Cryptanthus_rigidifolius	0	2
30576_Cryptanthus_robsonianus	0	2
30577_Cryptanthus_ruthiae	0	1
30578_Cryptanthus_sergipensis	0	1
30582_Cryptanthus_teretifolius	1	1
30583_Cryptanthus_venecianus	0	2
30556_Cryptanthus_vinosibracteatus	0	1
30585_Cryptanthus_viridipetalus	0	2
30586_Cryptanthus_walkerianus	1	1
30587_Cryptanthus_warren-loosei	0	1
30588_Cryptanthus_zonatus	0	1
30589_Cryptanthus_zonatus	0	1
30590_Cryptanthus_zonatus	0	1
30591_Cryptanthus_zonatus	0	1
30592_Cryptanthus_zonatus	0	1
30593_Cryptanthus_zonatus	0	1
MN563795_Fascicularia_bicolor_subsp_bicolor	0	6
NC_045385_Ochagavia_elegans	0	4
30594_Orthophytum_foliosum	0	1

30596_Orthophytum_jabrense	0	1
30597_Orthophytum_triunfense	0	3
30598_Rokautskyia_sanctaluciae	0	1
30599_Sincoraea_burlemarxii	0	1
30600_Sincoraea_ophiuroides	0	1
NC_045380_Puya_mirabilis	0	3

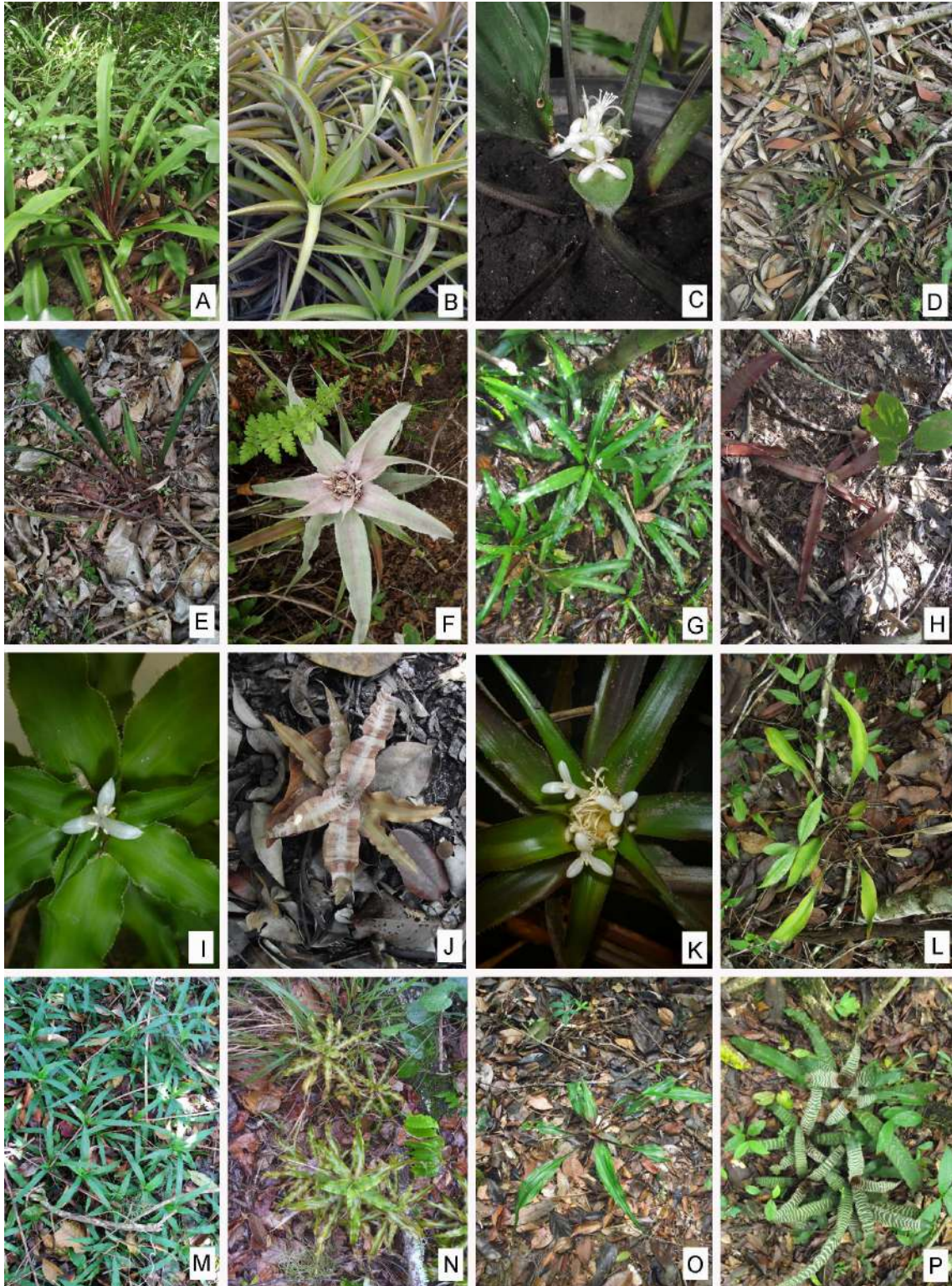


Figure 1. Species of *Cryptanthus* included in the study. A. *C. alagoanus*. B. *C. bahianus* (Photo: J. Maciel). C. *C. beuckeri*. D. *C. boanovenssis*. E. *C. capitellatus*. F. *C. cinereus* (Photo: A. Melo). G. *C. diana*. H. *C. crassifolius*. I. *C. reptans*. J. *C. robsonianus*. K. *C. sergipensis*. L. *C. teretifolius*. M. *C. venecianus* (Photo: A. Nepomuceno). N. *C. viridipetalus*. O. *C. walkerianus*. P. *C. zonatus*.

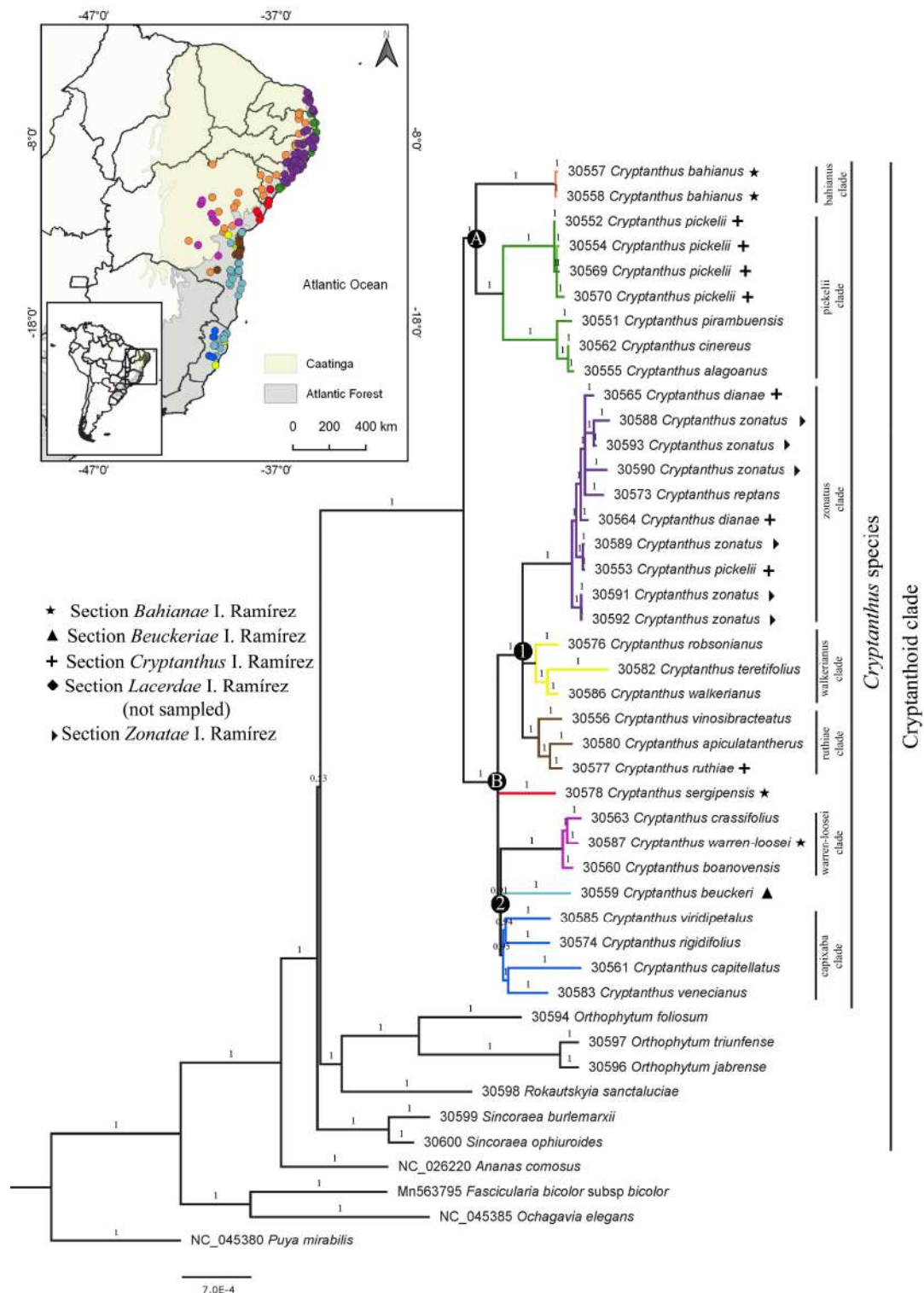


Figure 2. Phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae. Numbers above the branches represent posterior probabilities values. The colors of the branches are in accordance with the colors of the geographic distribution of the species. Sections of the *Cryptanthus* proposed by Ramírez-Morillo (1996) are indicated in symbols on the left side. The horizontal bar indicates the mutation rates.

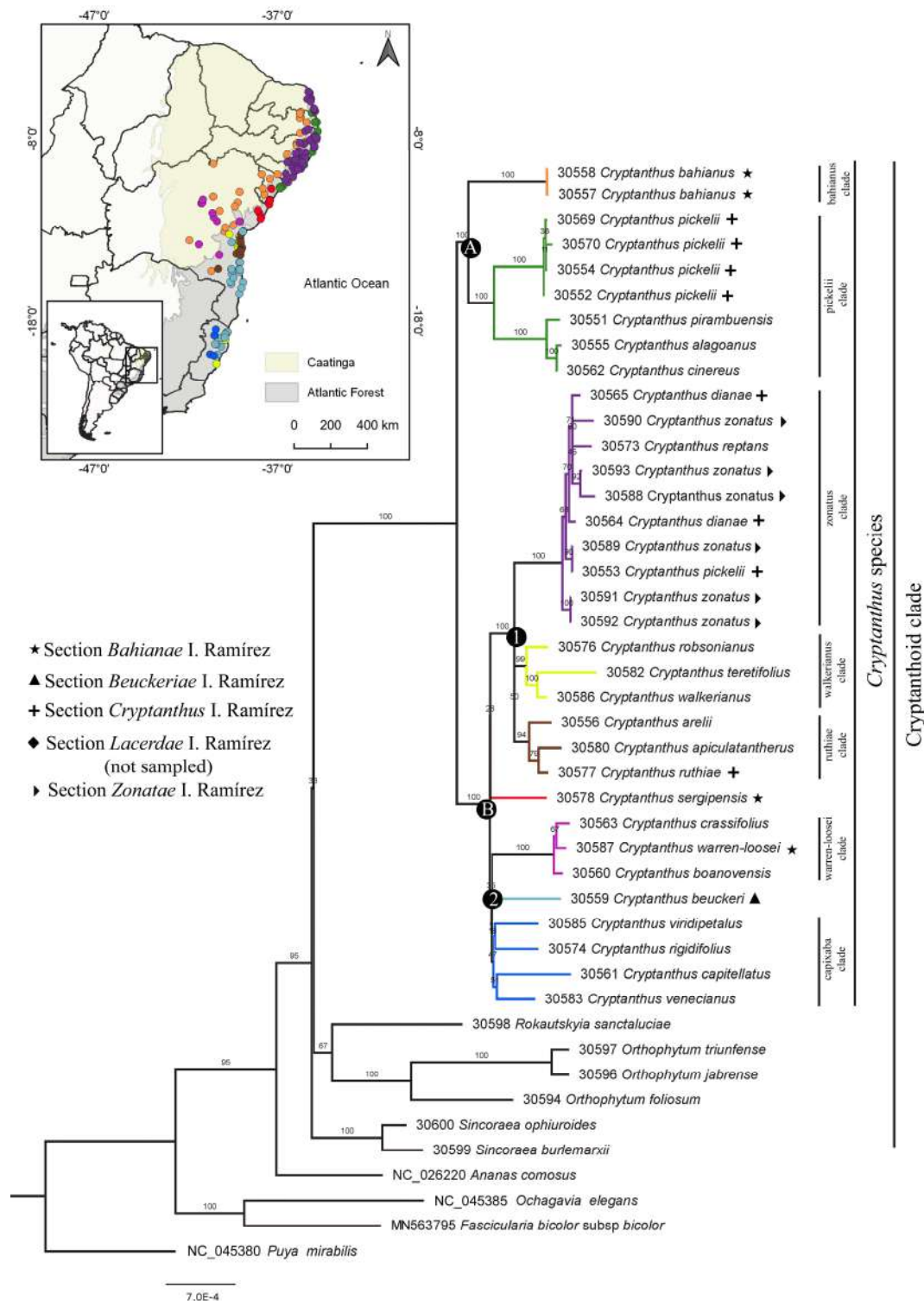


Figure 3. Phylogram of the majority-rule consensus tree from the Maximum-likelihood analyses based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae. Numbers above the branches represent bootstrap values. The colors of the branches are in accordance with the colors of the geographic distribution of the species. Sections of the *Cryptanthus* proposed by Ramírez-Morillo (1996) are indicated in symbols on the left. The horizontal bar indicates the mutation rates.

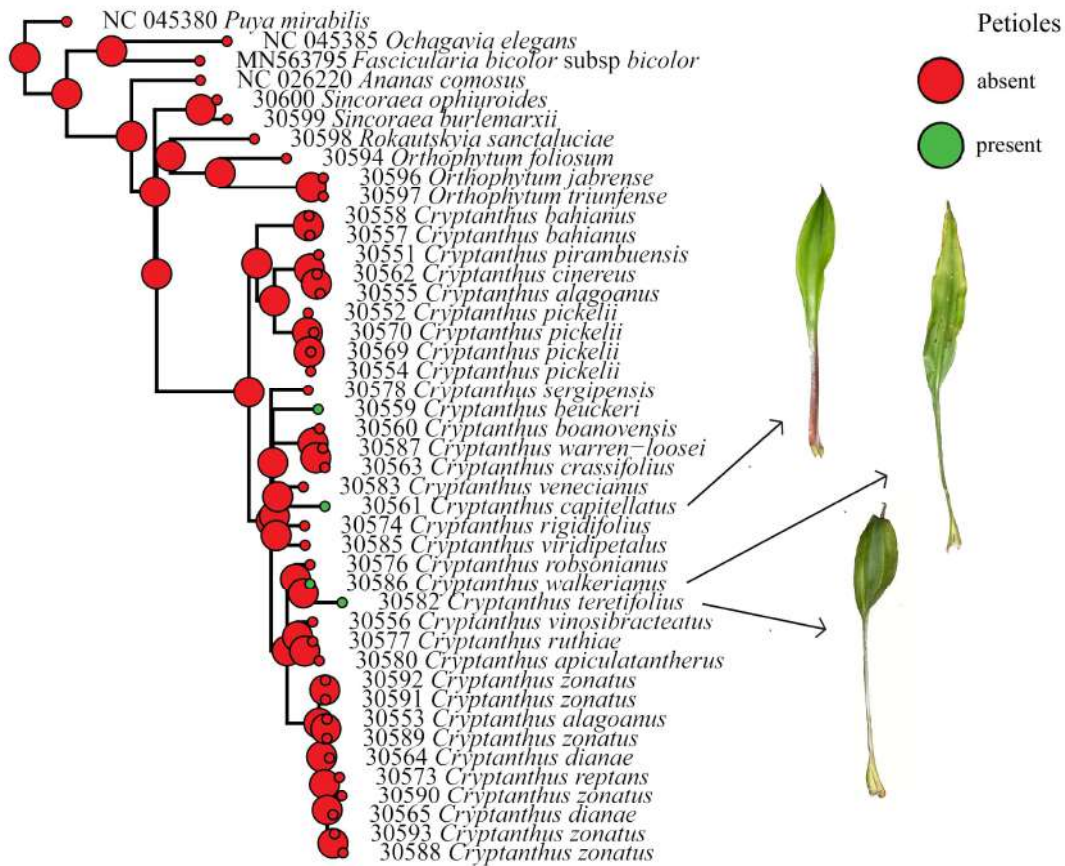


Figure 4. Ancestral character state reconstruction for petioles plotted on phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae.

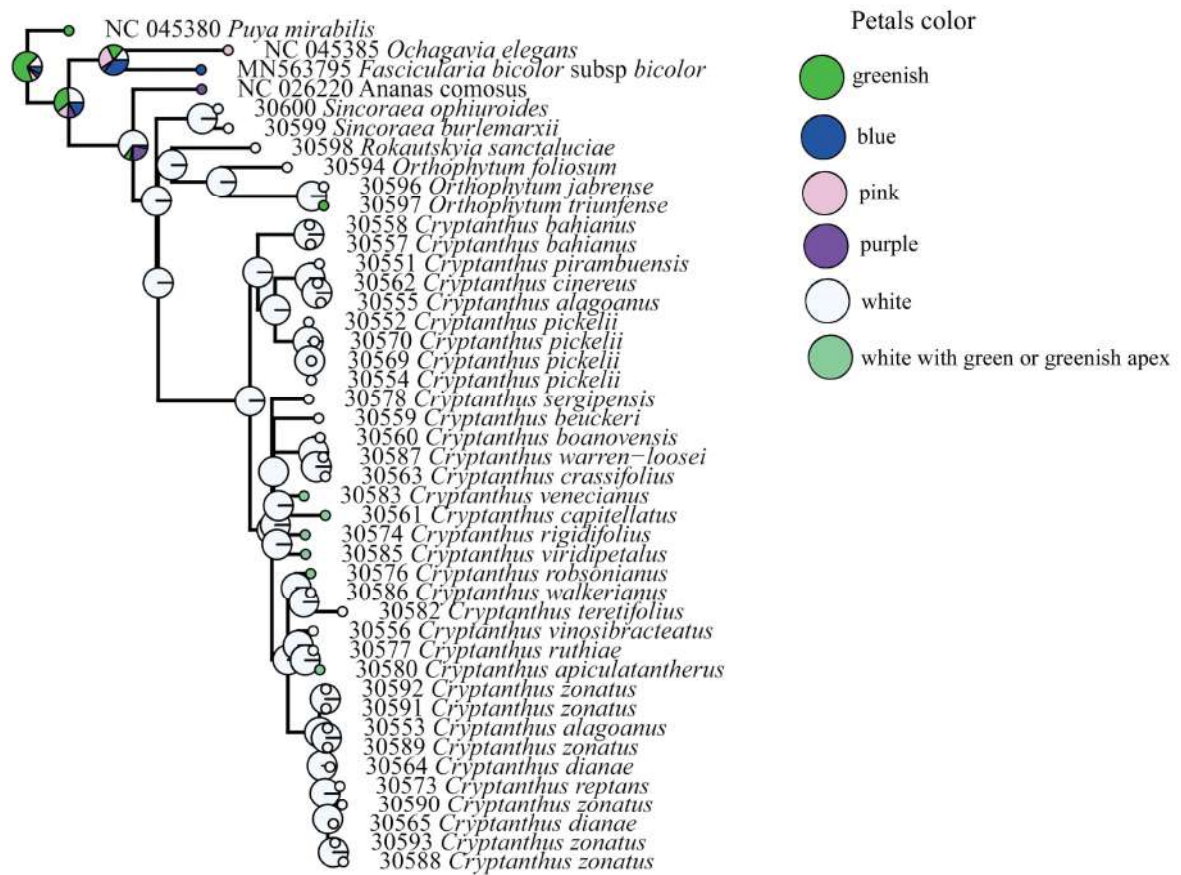


Figure 5. Ancestral character state reconstruction for petals color plotted on phylogram of the majority-rule consensus tree from the Bayesian Inference based on the alignment of 69 protein-coding genes of chloroplast DNA (total alignment length = 61,981 bp) for 44 accessions of Bromeliaceae.

4.2 ARTIGO 2 - TWO NEW SPECIES OF *CRYPTANTHUS* (BROMELIOIDEAE,
BROMELIACEAE) FROM ATLANTIC FOREST OF
NORTHEASTERN BRAZIL

Original Article

**Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from Atlantic
Forest of Northeastern Brazil**

Débora Maria Cavalcanti Ferreira^{1*} and Rafael Batista Louzada²

¹ Universidade Federal de Pernambuco, Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, 50670-901, Recife, Pernambuco, Brazil.

² Universidade Federal de Pernambuco, Departamento de Botânica, 50670-901, Recife, Pernambuco, Brazil

* Corresponding author: deboracavalcantif@hotmail.com

Abstract

Two new species of genus *Cryptanthus* from Atlantic Forest of Northeastern Brazil are described and illustrated. *Cryptanthus pirambuensis* occurs in Sergipe State and it is compared to *C. alagoanus* and *C. pickelii*, from which it differs by the number of flowers in the apical glomerule of the inflorescence. *Cryptanthus vinosibracteatus* was discovered in Bahia state and is morphologically similar to *C. arelli*, but it can be differentiated by the absence of trichomes on the adaxial surface of the leaf blades, length and color of the floral bracts, length and color of the sepals, and length and connation of the petals. The study includes data on geographic distribution with a map of species occurrence. In addition, photographs and comments on the new species are provided.

Keywords: Bahia, Bromeliad, Poales, Sergipe, taxonomy.

Introduction

Cryptanthus Otto & A. Dietr. is a tropical genus of bromeliad restricted to Brazil and includes 60 species (Gouda *et al.* cont. updated) that occurs mainly in the phytogeographic domain of the Atlantic Forest and few are found in the Caatinga (Maciel 2020). A recent phylogenetic study has shown a new relationship between *Cryptanthus* and allied genera resulting in a new circumscription for the genus with the transference of some species of *Cryptanthus* to new genera (Leme *et al.* 2017). It is characterized mainly by the habit terricolous or rupicolous, petioles present or absent, flowers staminate and perfect (plants andromonoecious), sepals and petals partially connate and petals white or white with green or greenish apices and stigma conduplicate-patent (Ramírez-Morillo 1996; Leme *et al.* 2017).

The last taxonomic revision of the genus was carried out by Ramírez-Morillo (1996) and it included 21 species of the genus (considering the new circumscription of the genus - Leme *et al.* 2017). After this revision, 33 new species were described for the genus of which 22 occur in the northeastern Brazil (Leme 1996; 1999; 2001; 2002a; 2002b; 2010; 2014; 2015; Leme & Siqueira-Filho 2001; Luther 1999a; 1999b; Leme & Siqueira-Filho 2007; Leme *et al.* 2008; 2010; 2014; 2020 Leme & Kollmann 2013; Braun & Brito 2019; Ferreira & Louzada 2020; Ferreira *et al.* 2021). However, the currently existing species of *Cryptanthus* in the region is not fully cataloged.

In order to improve the knowledge on the taxonomy of *Cryptanthus*, herein we describe two new species from of Atlantic Forest of Northeastern Brazil: *Cryptanthus pirambuensis* and *Cryptanthus vinosibracteatus*. *Cryptanthus pirambuensis* is compared to *C. alagoanus* and *C. pickelii* due to similarities in leaf blade shape. And *Cryptanthus vinosibracteatus* is compared to *C. arelii* due to similarities in leaf blade shape and color.

Distribution map, draw line illustrations and photographs of new species are also provided. In addition, taxonomic comments and tables with comparison of characters of morphologically similar species are included.

Materials and methods

Samples of the new species of *Cryptanthus* genus were collected in the Bahia and Sergipe States. The areas were georeferenced and the specimens were photographed. The specimens were herborized and deposited in the UFP herbarium and duplicates were sent to ASE and RB. In addition, the following herbarium specimens were analyzed for complementation of information and comparison with other morphologically similar species: ALCB, ASE, CEPEC, HB**, HUEFS, HURB*, IPA, JPB, MAC, NY*, RB*, UFP, UESC, US* (*photos of the online collection; **photos). All acronyms are according to *Index Herbariorum* (<http://sweetgum.nybg.org/ih/>).

For morphological terminology, Radford *et al.* (1974) and Harris & Harris (2001) were used. Except for the stem length and the type of stigma that follow Ferreira & Louzada (2020) and Leme *et al.* (2017), respectively.

The morphological information of *Cryptanthus arelii* H. Luther, morphologically similar species, was taken from the protologue in Luther (1999b).

Results and discussion

Taxonomic treatment

1. *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada, *sp. nov.*

Type: BRAZIL. Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 18 April 2018, fl., *D. Cavalcanti & E. Ferreira 904* (UFP!). (Fig. 2 and 3).

Cryptanthus pirambuensis differs from *C. alagoanus* Leme & J.A.Siqueira by the number of flowers in apical glomerule of the inflorescence with 17-24 flowers (vs. ca. 8 flowers), number of flowers in lateral glomerule of the inflorescence with 9-10 flowers (vs. 5-6 flowers), floral bracts basally white or white-greenish with vinaceous apices (vs. white with brown or greenish apices), sepals lobes narrowly elliptic or elliptic (vs. lanceolate or ovate) and stigma 6-7.2 mm long (vs. 5-5.5 mm long). *Cryptanthus pirambuensis* differs from *C. pickelii* by its number of flowers in apical glomerule of the inflorescence with 17-24 flowers (vs. ca. 5-11 flowers), number of flowers in lateral glomerule of the inflorescence with 9-10 flowers (vs. 3-6 flowers), ovary 15-17 ovules per locule in the perfect flowers (vs. 7-13 ovules per locule in the perfect flowers).

Herbs terrecolous, andromonoecious, propagation by stolon, rhizomes 1-8 cm long, 0.7-0.8 cm in diameter. Stems 2.2-3.8 cm, 0.7-1 cm in diameter, erect. Leaves 7-9 in number; leaf sheaths 2.6-2.7 x 2.1-4.2 cm, very widely ovate, abaxial surface densely lepidote, white-greenish on the base and vinaceous on the apices, adaxial surface glabrous except on the apices densely lepidote, white-greenish, prickles 0.2-0.3 mm long, 0.2-1 mm apart, generally antrorse; leaf blades 21.8-70.1 x 0.9-3.4 cm, linear-oblongate, oblongate or narrowly elliptic, green except on the base vinaceous, abaxial surface densely lepidote, adaxial surface glabrous except on the base densely lepidote, margins slightly undulate, prickles 0.2-0.7 mm long, 0.6-5.6 mm apart, antrorse, apices acuminate or cirrhose. Inflorescences spikes of glomerules, with staminate and perfect flowers; spike with 6-7 lateral glomerules; each glomerule with 9-10 flowers, apical glomerule of the inflorescence with 17-23 flowers; rachis 2.3-2.5 cm long, primary bracts 8-11 in number, 2-7.4 x 1-4.8 cm, foliaceous, linear-

oblanceolate, oblanceolate, lanceolate or narrowly triangular, green except on the base vinaceous, abaxial surface densely lepidote, adaxial surface glabrous except on the base densely lepidote, margins slightly undulate, prickles 0.2-0.6 mm long, 1-4.6 mm apart, apices acuminate or cirrhose. **Staminate flowers:** floral bracts 31-34 x 8-15 mm, narrowly elliptic or elliptic, white or white-greenish on the base and vinaceous on the apices, abaxial surface glabrous except on the apices densely lepidote, adaxial surface glabrous except on the apices sparsely lepidote, apices mucronate; flowers 44-50 mm long; sepals 20 mm long, connate 7.3-9.5 mm, white on the base and vinaceous or green on the apices, lobes 10.8-12.1 x 3.5-4 mm, narrowly elliptic, mucronate; petals 29.2-40 x 3.8-4 mm, oblanceolate, acute or obtuse, connate for 12-22 mm, white, with 2 callosities bearing inconspicuous capitate trichomes, callosities appearing 12.5-22 mm distant from the base, stamens 6, in two whorls of three, filaments 18-30 mm long, first whorl of three antepetalous, adnate 9.5-19 mm to the petal blades, second whorl of three antesepalous, adnate 9.8-22 mm to the petal blades, anthers 5-6.7 mm long, subbasifixed, dehiscence longitudinal, bases cordate, apices mucronulate or emarginate; ovary trigonous, 7.2 x 3-4.6 mm, placentation axial, ovules 0 per locule, epigynous tube 3.8-8 mm, styles 0.3 mm, atrophied, stigma 0.6 mm, atrophied. **Perfect flowers:** floral bracts 27.5-32 x 15.2-20 mm, ovate-falcate, white on the base and vinaceous on the apices, abaxial surface glabrous except on the apices densely lepidote, adaxial surface glabrous except on the apices sparsely lepidote, apices mucronate; flowers 55-61 mm long; sepals 21-22.5 mm long, connate 7.5-9.5 mm, white on the base and vinaceous or green on the apices, lobes 12.5-13.6 x 4.8-5.5 mm, narrowly elliptic or elliptic, mucronate; petals 36-39.6 x 5-6.2 mm, oblanceolate, acute, connate for 13 mm, white, with 2 callosities bearing inconspicuous capitate trichomes, callosities appearing 14-16.2 mm distant from the base, stamens 6, in two whorls of three, filaments 24-26 mm long, first whorl of three antepetalous, the antepetalous ones adnate 12.3-15 mm to the petal blades, second whorl of three

antesepalous, the antesepalous ones adnate 14.5-15 mm to the petal blades, anthers 5.3-6.8 mm long, subbasifixed, dehiscence longitudinal, bases cordate, apices mucronulate; ovary trigonous, 11.5-12 x 5.5 mm, placentation axial, ovules 15-17 per locule, epigynous tube 6.5-8.5 mm, styles 28-32 mm, stigma 6-7.2 mm, conduplicate-patent.

Distribution and habitat— *Cryptanthus pirambuensis* is known from two locations in the municipality of Pirambu, Sergipe State, Brazil, at 41 m elevation (Fig. 1). It occurs in the phytogeographic domain of the Atlantic Forest, on the vegetation types Lowland Semideciduous Seasonal Forest and Restinga Forest (see vegetation types in Thomas & Barbosa 2008). The individuals grow on clayey or sandy soils of closed forest with tree ca. 5 m tall. The area is included in the biogeographical sub-region of Bahia (see biogeographical sub-region in Silva & Casteleti 2005; Ribeiro *et al.* 2009).

Etymology— The specific epithet refers to the municipality of Pirambu where the type specimen was collected.

Phenology— Flowering in nature has been registered in May and in cultivation in January and April.

Conservation status— *Cryptanthus pirambuensis* is only known from two locations that are about 10 km apart from each other. One of them is on a private property and the other is inside a conservation unit named Reserva Biológica de Santa Isabel. In the type locality it was seen that some trees were cut down. This can cause a decline in the area of occupancy of the species. Thus, we suggest that *C. pirambuensis* can be classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Comments— In herbarium specimens, *C. pirambuensis* was identified as *Cryptanthus alagoanus*. *C. alagoanus* was described only with specimens of the municipality of Paripueira, Alagoas State (Leme & Siqueira-Filho 2001). In fact, *C. pirambuensis* is

morphologically similar to *C. alagoanus* due its elongated leaf blades but differs mainly by the number of flowers in apical glomerule of the inflorescence with 17-24 flowers (vs. ca. 8 flowers) and number of flowers in lateral glomerule of the inflorescence with 9-10 flowers (vs. 5-6 flowers), sepals lobes narrowly elliptic or elliptic (vs. lanceolate or ovate) (Table 1). *Cryptanthus pirambuensis* is also morphologically similar to *C. pickelii*, *C. pseudopetiolatus* and *C. ruthiae* due to leaf blade shape and color. *C. pirambuensis* can be differentiated from *C. pickelii* mainly by number of flowers in apical glomerule of the inflorescence with 17-24 flowers (vs. ca. 5-11 flowers) and number of ovules per locule in the ovary of the perfect flowers with 15-17 ovules (vs. 7-13 ovules) (Table 1). *C. pirambuensis* differs from *C. pseudopetiolatus* and *C. ruthiae* mainly by the number of ovules per locule in the ovary of the perfect flowers with 15-17 ovules (vs. 2-9 ovules) (Table 1).

Additional specimens examined (Paratypes)— BRAZIL. Sergipe: Pirambu, Margem esquerda da estrada no bosque, 46 m, 10°36'52.40"S, 36°42'25.90"W, 19 October 2012, sterile, *J.A. Siqueira-Filho* 2866 (HURB); Pirambu, Mata de Sambaíba, 40 m, 10°39'22.20"S, 36°51'48.50"W, 02 July 2010, fl. cult. 19 January 2013, fl., *J. A. Siqueira-Filho et al.* 2896 (HURB); Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 28 June 2018, *D. Cavalcanti & E. Ferreira* 829 (RB!); Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 11 April 2018, fl., *D. Cavalcanti & E. Ferreira* 903 (ASE); Pirambu, Reserva Biológica de Sta Isabel, September 1994, sterile, *M. Landim* 732 (ASE); Pirambu, Reserva Biológica de Santa Isabel, 0-50 m, 10°41'17"S, 36°47'75"W, fl., 06 May 1999, *G. Martinelli & T. Barbará* 15349 (CEPEC, RB).

2. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada, *sp. nov.*

Type: BRAZIL. Bahia: Itapetinga, Fazenda Santa Cruz, antiga propriedade de Salvador, atualmente de Vardão, 308 m, 15°07'48.9"S, 40°14'38.9"W, 19 March 2018, fl. cult. 17 July 2019, *D. Cavalcanti & L. Daneu 834* (Fig. 4 and 5)

Cryptanthus vinosibracteatus differs from *C. arelii* H. Luther by its leaf blades adaxial surface glabrous (vs. glabrous except for a few bands of pale trichomes toward the base), floral bracts 25-26 mm long (vs. 18-22 mm long), white-greenish on the base and vinaceous on the apices (vs. cream or pale green), sepals 13.5-14.5 mm long (vs. 18-20 mm long), white on the base, and castaneous on lobes (vs. cream to pale green), petals 32.5-34.3 mm long (vs. 40-45 mm long), connate for 15-15.5 mm (vs. 10 mm).

Herbs terricolous, andromonoecious, rhizomes ca. 1 cm long, ca. 0.6 cm in diameter. Stems ca. 2 cm, ca. 0.6 cm in diameter, erect. Leaves 7 in number; leaf sheaths 1.5-2.4 × 1.8-3 cm, very widely ovate, abaxial surface white on base and brown on apices, densely lepidote, adaxial surface white-greenish on base and greenish on apices, glabrous, prickles 0.3-1 mm long, 0.1-0.4 mm apart, antrorse and retrorse; leaf blades 11-4.5 × 1.9-3.2 cm, narrowly elliptic, oblanceolate or lanceolate, brown-reddish, brown or brown and green, abaxial surface densely lepidote, adaxial surface glabrous, margins undulate, prickles 0.2-1.5 mm, 0.3-2.5 mm apart, antrorse, acuminate. Inflorescences spikes of glomerules, rachis ca. 1 cm long; primary bracts 3 in number, 2.2-6.5 × 0.8-1.1 cm, foliaceous, lanceolate, brown-reddish or brown, abaxial surface densely lepidote, adaxial surface glabrous, margins undulate, prickles 0.1-0.5 mm long, 0.1-1 mm apart, antrorse, apices acuminate. **Staminate flowers:** floral bracts 25-26.2 × 13-13.5 mm, triangular-cymbiform, white-greenish on the base and vinaceous on the apices, abaxial surface glabrous except on the apices densely lepidote, adaxial surface glabrate except on the apices sparsely lepidote, apices mucronate; flowers 40.5-41 mm long; sepals 13.5-14.5 mm long, connate 7-8.6 mm, white on the base, and castaneous on lobes, lobes 5.4-6.3 × 2.5-2.6 mm, elliptic, mucronate; petals 32.5-34.3 × 4-4.5

mm, oblanceolate, acute or rounded, connate for 15-15.5 mm, white, with 2 callosities bearing inconspicuous capitate trichomes, callosities appearing 15-16 mm distant from the base, stamens 6, in two whorls of three, filaments 27.5 mm long, first whorl of three antepetalous, adnate 14.5-15.3 to the petal blades, second whorl of three antesepalous, adnate 15-15.5 mm to the petal blades, anthers 3.5-4.5 mm long, subbasifixed, dehiscence longitudinal, bases cordate, apices rounded; ovary botuliform, 6.5-7 x 4.6-5 mm, placentation axial, ovules 0 per locule, epigynous tube 0.5 mm, styles 0.3 mm, atrophied, stigma 0.8 mm, atrophied. **Perfect flowers** unknown. Fruits unknown.

Distribution and habitat— *Cryptanthus vinosibracteatus* is known from one locality in the municipality of Itapetinga, Bahia State, Brazil, at 308 m elevation (Fig. 1). It occurs in the phytogeographic domain of the Atlantic Forest and according to map of the Area of Application of Law number 11 428 of the year 2006 of the Brazilian Atlantic Forest the vegetation type is Deciduous Seasonal Forest. The individuals grows on partially closed forest with trees with about 4 m high. The population is small with less than ten individuals. The area is included in the biogeographical sub-region of Diamantina (see biogeographical sub-region in Silva & Casteleti 2005; Ribeiro *et al.* 2009).

Etymology— The specific epithet is a combination of words “vinosos” and “bracteatus” and it refers to vinaceous color of the floral bracts.

Phenology— Flowering in cultivation has been registered in July.

Conservation status— *Cryptanthus vinosibracteatus* is only known for one location on a private property. Perhaps the species also occurs in the municipality of Jequié (*W. W. Thomas et al.* 12599-[NY]), Bahia State, Brazil. However, this specimen is sterile and does not allow its correct identification. It is similar to *C. vinosibracteatus* due to leaf blades shape. The record of Jequié is about 150 km from type locality. *Cryptanthus vinosibracteatus* is probably

threatened due to the few number of occurrence locations (one or maybe two), few individuals in the typical population, furthermore, the vegetation of the municipality of Itapetinga is very fragmented due to cattle raising. Thus, this species can be classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Comments— *Cryptanthus vinosibracteatus* is morphologically similar to *C. arelii* due to similarities in leaf blade shape and color, but differs by the leaf blades adaxial surface glabrous (vs. glabrous except for a few bands of pale trichomes towards the base), floral bracts 25-26 mm long (vs. 18-22 mm long), white-greenish on the base and vinaceous on the apices (vs. cream or pale green), sepals 13.5-14.5 mm long (vs. 18-20 mm long), white on the base, and castaneous on lobes (vs. cream to pale green) and petals 32.5-34.3 mm long (vs. 40-45 mm long), connate for 15-15.5 mm (vs. 10 mm) (Table 2). *C. vinosibracteatus* can be confused with *C. diana* Leme due to leaf blades shape but differs by the sepals 13.5-14.5 mm long (vs. 16.5-21 mm long), white on the base, and castaneous on lobes (vs. white on the base, and green on lobes) (Table 2). *C. vinosibracteatus* is also morphologically similar to *C. zonatus* due to leaf blades shape but differs by the floral bracts 25-26 mm long (vs. 14-20.5 mm long), white-greenish on the base and vinaceous on the apices (vs. white on the base, and green-pink, pink or castaneous on apices), sepals 13.5-14.5 mm long (vs. 16.7-20.5 mm long) and petals 32.5-34.3 mm long (vs. 35-40.5 mm long) (Table 2).

Acknowledgements

This study is part Ph.D. dissertation of the first author that is supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico). The study was conducted at the Programa de Pós-Graduação em Biologia Vegetal at the Universidade Federal de Pernambuco. This research was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES, Finance Code 001). The second author thanks

CNPq for the financial support (grants no. 310871/2014-0 and 449686/2014-0). The authors thank Dr. Benoit Loeuille for helping with the nomenclature, and the scientific illustrator Felipe Martins.

References

- Gouda EJ, Butcher D, Gouda CS. cont. updated. Encyclopaedia of Bromeliads, Version 4. Utrecht, University Botanic Gardens. <https://bromeliad.nl/encyclopedia/>. 16 Nov. 2021.
- Braun P, Brito BG. 2019. Xeromorphe Bromelien aus Brasilien (III): *Cryptanthus heimenii*, eine neue Art aus Sergipe. Xeromorphic Bromeliads from Brazil (III): *Cryptanthus heimenii*, a New Species from Sergipe. Die Bromelie 2: 54-61.
- Ferreira DMC, Louzada RB. 2020. A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus. Systematic Botany 45: 460–465.
- Ferreira DMC, Almeida EM de, Louzada RB. 2021. Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from northeastern Brazil. Phytotaxa 523: 099–109.
- Harris JG, Harris MW. 2001. Plant identification terminology - an illustrated glossary. 2nd. ed. Payson, Spring Lake Publishing.
- Leme EMC. 1996. Two new *Cryptanthus* species from Brazil. Cryptanthus Society Journal 11: 6-8.
- Leme EMC. 1999. New species of Brazilian Bromeliaceae: A tribute to Lyman B. Smith. Harvard Papers in Botany 4: 135-168.
- Leme EMC. 2001. New *Cryptanthus* species from Espírito Santo, Brazil. Cryptanthus Society Journal 16: 12-13.

- Leme EMC. 2002a. Two New sympatric *Cryptanthus* species. *Cryptanthus Society Journal* 17: 86-89.
- Leme EMC. 2002b. *Cryptanthus teretifolius*, a new species from the coastal zone of Espírito Santo State. *Cryptanthus Society Journal* 17: 15-16.
- Leme EMC. 2010. Describing *Cryptanthus* 'Bello # 2'. *Cryptanthus Society Journal* 25: 79-82.
- Leme EMC. 2014. A New Species of *Cryptanthus* from Espírito Santo, Brazil. *Journal of the Bromeliad Society* 64: 150-155.
- Leme EMC. 2015. Two new bromelioid species from Brazil. *Journal of the Bromeliad Society* 65: 87-99.
- Leme EMC, Siqueira-Filho JA. 2001. Studies in Bromeliaceae of Northeastern Brazil. I. *Selbyana* 22: 146-154.
- Leme EMC, Siqueira-Filho JA. 2007. Taxonomia das bromélias dos fragmentos de mata atlântica de Pernambuco e Alagoas. In: Siqueira-Filho JA, Leme, EMC. (eds.) *Fragmentos de mata atlântica do Nordeste – biodiversidade, conservação e suas bromélias*. Rio de Janeiro, Andrea Jakobsson Estúdio. p. 190-381.
- Leme EMC, Heller S, Zizka G, Halbritter H. 2017. New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318: 001-008.
- Leme EMC, Kollmann LJC, Fontana AP. 2008. Three New *Cryptanthus* Species from Espírito Santo and Bahia, Brazil. *Journal of the Bromeliad Society* 58: 12-19.

- Leme EMC, Kollmann LJC. 2013. Miscellaneous new species of Brazilian Bromeliaceae. *Phytotaxa* 108: 1-40.
- Leme EMC, Fraga CN de, Kollmann LJC, Brown GK, Till W, Ribeiro OBC, Machado MC, Monteiro FJS, Fontana AP. 2010. Miscellaneous new species in the Brazilian Bromeliaceae Miscellaneous new species in the Brazilian Bromeliaceae. *Rodriguésia* 61: 021-067.
- Leme EMC, Till W, Kollmann LJC, Moura RL de, Ribeiro OBC. 2014. Miscellaneous New Species of Brazilian Bromeliaceae – III. *Phytotaxa* 177: 061–100.
- Leme EMC, Ribeiro OBC, Souza FVD, Souza EH de, Kollmann LJC, Fontana AP. 2020. Miscellaneous new species in the “Cryptanthoid complex” (Bromeliaceae: Bromelioideae) from Eastern Brazil. *Phytotaxa* 430: 157-202.
- Luther HE. 1999a. New *Cryptanthus* species from Espírito Santo, Brazil. *Cryptanthus Society Journal* 13: 12-13.
- Luther HE. 1999b. *Cryptanthus arelii*, an "Old" New species from Bahia, Brazil. *The Cryptanthus Society Journal* 14: 54-55.
- Maciel JR. 2020. *Cryptanthus* in Flora do Brasil 2020. Rio de Janeiro, Jardim Botânico do Rio de Janeiro, Brazil. <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB5991>. 12 Apr. 2021.
- Silva JMC, Casteleti CHM. 2005. Estado da biodiversidade da Mata Atlântica brasileira. In: Galindo-Leal C, Câmara IG (eds.) *Mata Atlântica: biodiversidade, ameaças e perspectivas*. Belo Horizonte, Fundação SOS Mata Atlântica and Conservação Internacional. p. 43-59.

- Radford AE, Dickison WC, Massey JR, Bell CR. 1974. Vascular Plant Systematics. New York, Harper and Row.
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation . *Biological Conservation* 142: 1141–1153.
- Thomas WW, Barbosa RV. 2008. Natural vegetation types in the Atlantic Coastal Forest of Northeastern Brazil. In: Thomas WW (ed.) *Atlantic Coastal Forest of Northeastern Brazil*. New York, The New York Botanical Garden Press. p. 6-20.

Tables and Figure

Table 1. Comparison of characters and geographic distribution of *Cryptanthus pirambuensis* and morphologically similar species

Characters and geographic distribution	<i>C. alagoanus</i>	<i>C. pickelii</i>	<i>C. pirambuensis</i>	<i>C. pseudopetiolatus</i>	<i>C. ruthiae</i>
Number of flowers in the apical glomerule of the inflorescence	ca. 8	5-11	17-23	--	ca. 32
Number of flowers in the lateral glomerule of the inflorescence	5-6	3-6	9-10	4-10	4-5
Length of the lobes of the sepals (mm)	11-13.7	6.5-12	10.8-13.6	9-10	3.5-7.5
Length of the lobes of the stigma (mm)	5-5.5	3-7.7	6-7.2	3.2	2.6-3
Length of the ovary (mm)	8.8-12	6-12	7.2-12	4.5-6.5	4.5-9
Length of epigynous tube (mm)	4.5-9.3	2.8-9	3.8-8.5	2.5-4	1-2.5
Number of ovules per locule in the perfect flowers	12-16	7-13	15-17	8-9	ca. 2
Geographic distribution (States)	Alagoas	Paraiba and Pernambuco	Sergipe	Bahia	Bahia

Table 2. Comparison of characters of *Cryptanthus vinosibracteatus* and morphologically similar species

Characters/Species	<i>C. arelii</i>	<i>C. diana</i>	<i>C. vinosibracteatus</i>	<i>C. zonatus</i>
Leaf blades adaxial surface	Glabrous except for a few bands of pale trichomes toward the base	Glabrous to densely lepidote base	Glabrous	With crossbars of lepidote trichome, glabrous, or glabrous with base densely lepidote
Length of the floral bracts (mm)	18-22	19.5-26.2	25-26	14-20.5
Floral bracts color	Cream or pale green	White on the base, and green or vinaceous on apices	White-greenish on base and vinaceous on apices	White on the base, and green-pink, pink or castaneous on apices
Length of the sepals (mm)	18-20	16.5-21	13.5-14.5	16.7-20.5
Sepals color	Cream to pale Green	White on the base, and green on lobes	White on the base, and castaneous on lobes	White on the base, and green or greenish on lobes
Length of the petals (mm)	40-45	33-42.5	32.5-34.3	35-40.5
Connation of the petals (mm)	10	5.5-15	15-15.5	4-14

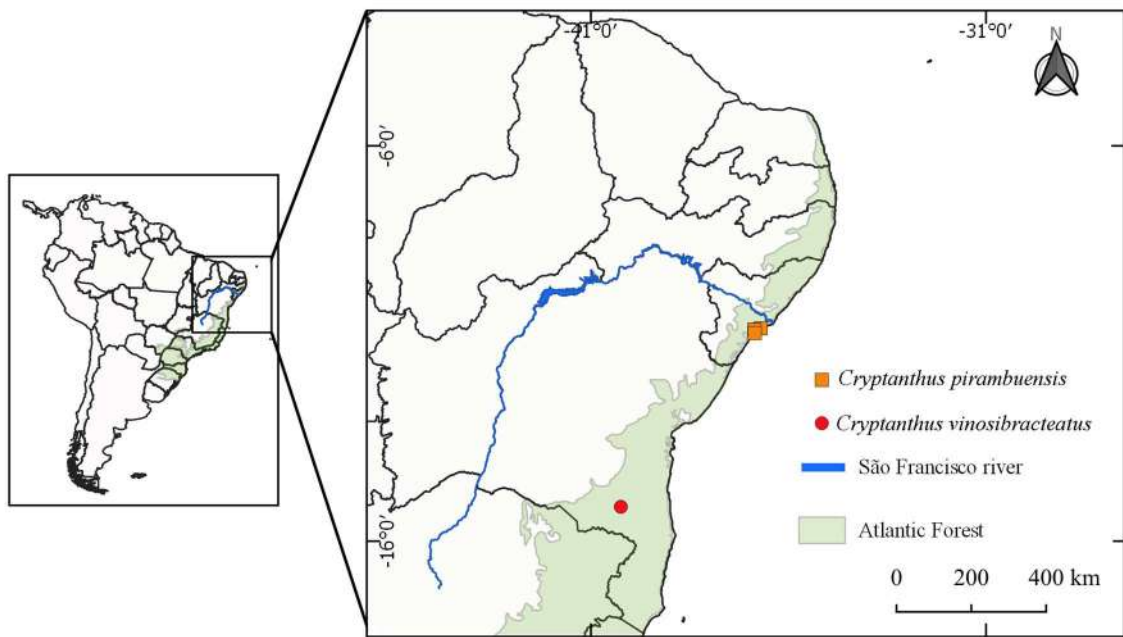


Figure 1. Geographical distribution of *Cryptanthus pirambuensis* and *Cryptanthus vinosibracteatus* in the Atlantic Forest of northeastern Brazil.

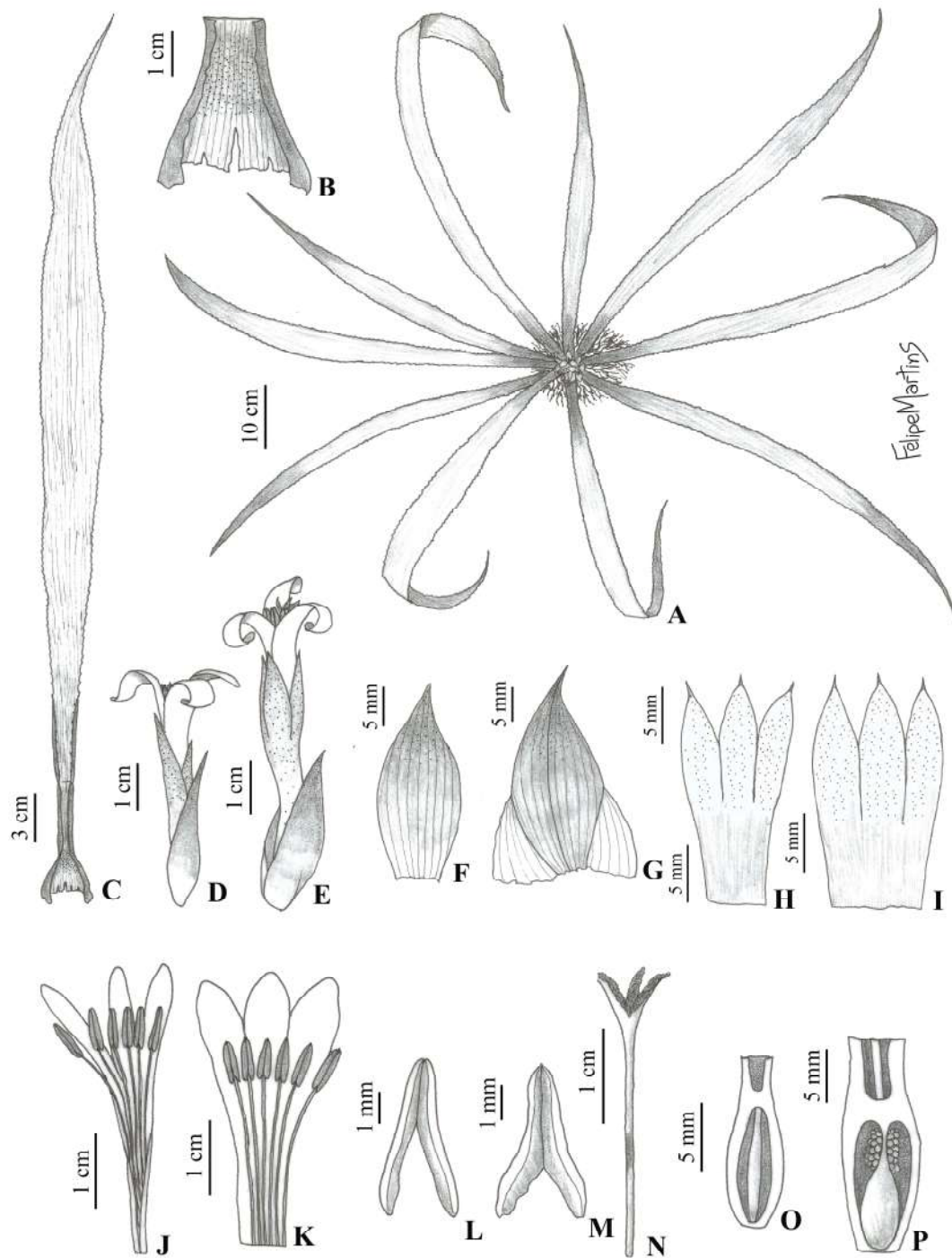


Figure 2. *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. **A.** Habit. **B.** Leaf sheath (adaxial surface). **C.** Leaf (adaxial surface). **D.** Staminate flower. **E.** Perfect flower. **F.** Bract of the staminate flower. **G.** Bract of perfect flower. **H.** Sepals of the staminate flower. **I.** Sepals of the perfect flower. **J.** Petals and stamens of the staminate flower. **K.** Petals and stamens of the perfect flower. **L.** Anther of the staminate flower. **M.** Anther of the perfect flower. **N.** Style and stigma. **O.** Ovary and epigynous tube of staminate flower. **P.** Ovary and epigynous tube of perfect flower.

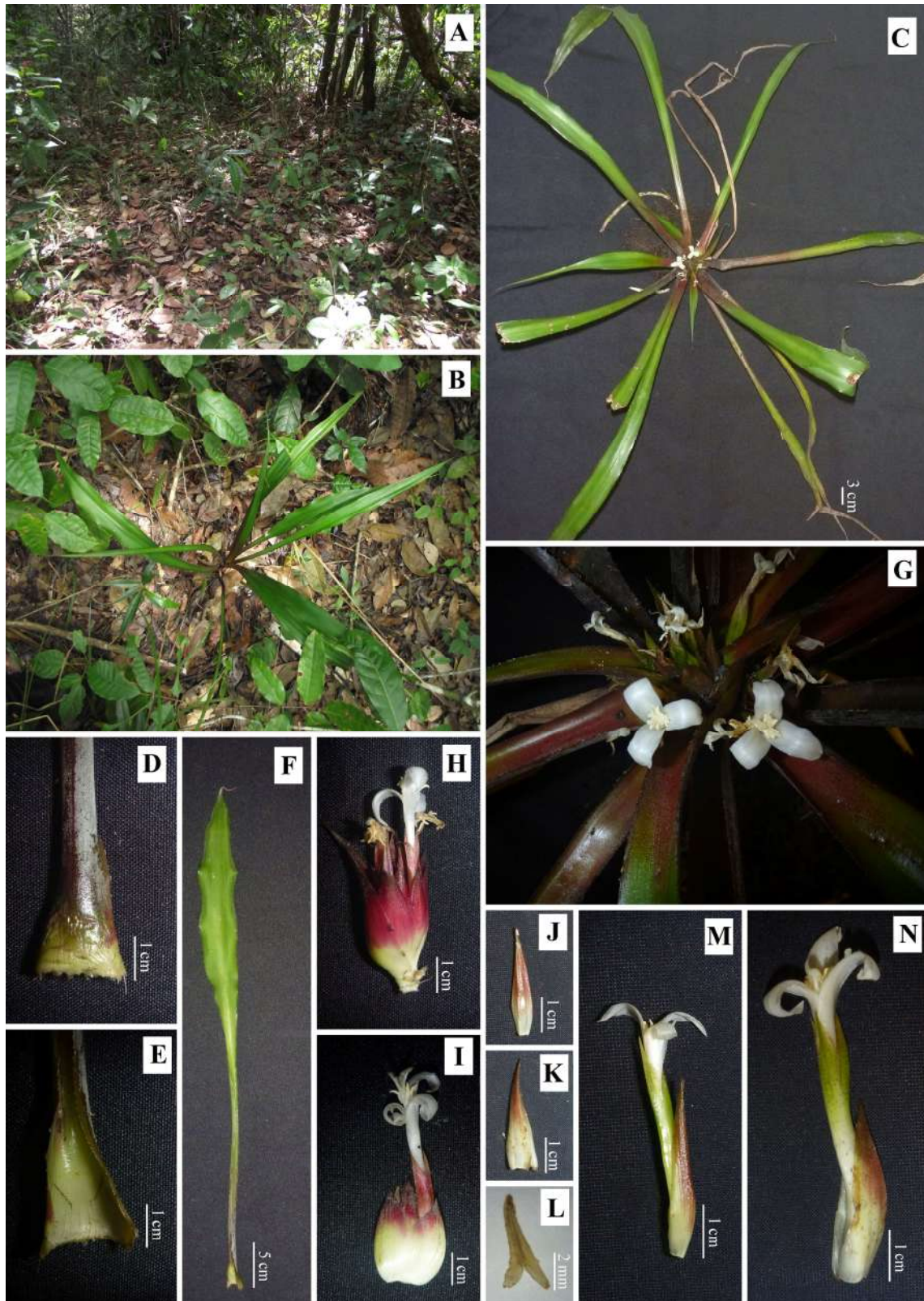


Figure 3. *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. **A.** Habitat. **B.** Individual in nature. **C.** Flowering individual in cultivation. **D.** Leaf sheath (abaxial surface). **E.** Leaf sheath (adaxial surface). **F.** Leaf (adaxial surface). **G.** Inflorescence. **H.** Apical glomerule of the inflorescence. **I.** Lateral glomerule of the inflorescence. **J.** Bract of the staminate flower. **K.** Bract of perfect flower. **L.** Anther. **M.** Staminate flower. **N.** Perfect flower.

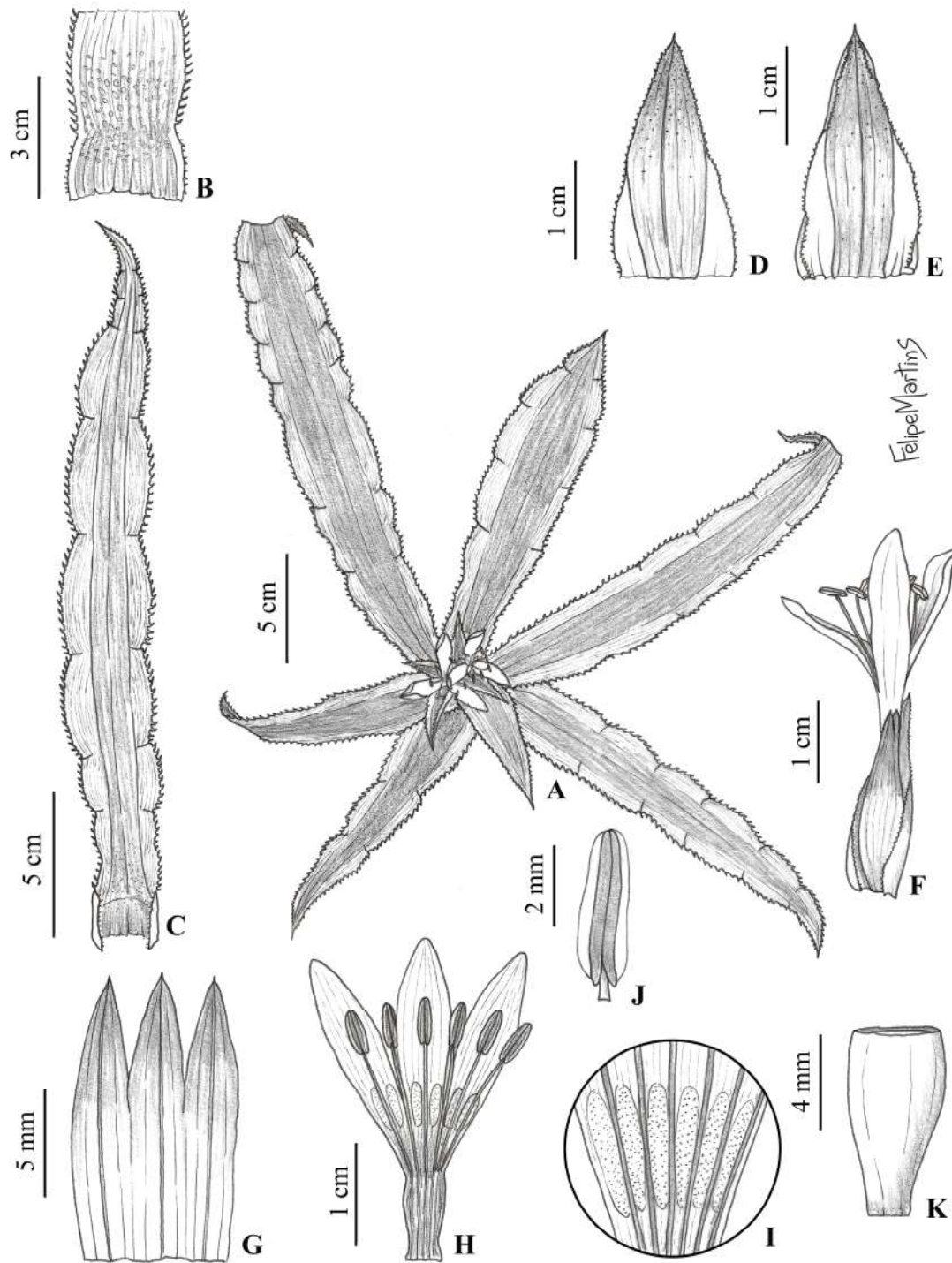


Figure 4. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. **A.** Habit. **B.** Leaf sheath (adaxial surface). **C.** Leaf (adaxial surface). **D.** Floral bract of staminate flower (abaxial surface). **E.** Floral bract of staminate flower (adaxial surface). **F.** Staminate flower with the floral bract. **G.** Sepals of staminate flower. **H.** Petals and stamens of staminate flower. **I.** Detail of conspicuous callosities on the petals of staminate flower. **J.** Anther of the staminate flower. **K.** Ovary of the staminate flower.

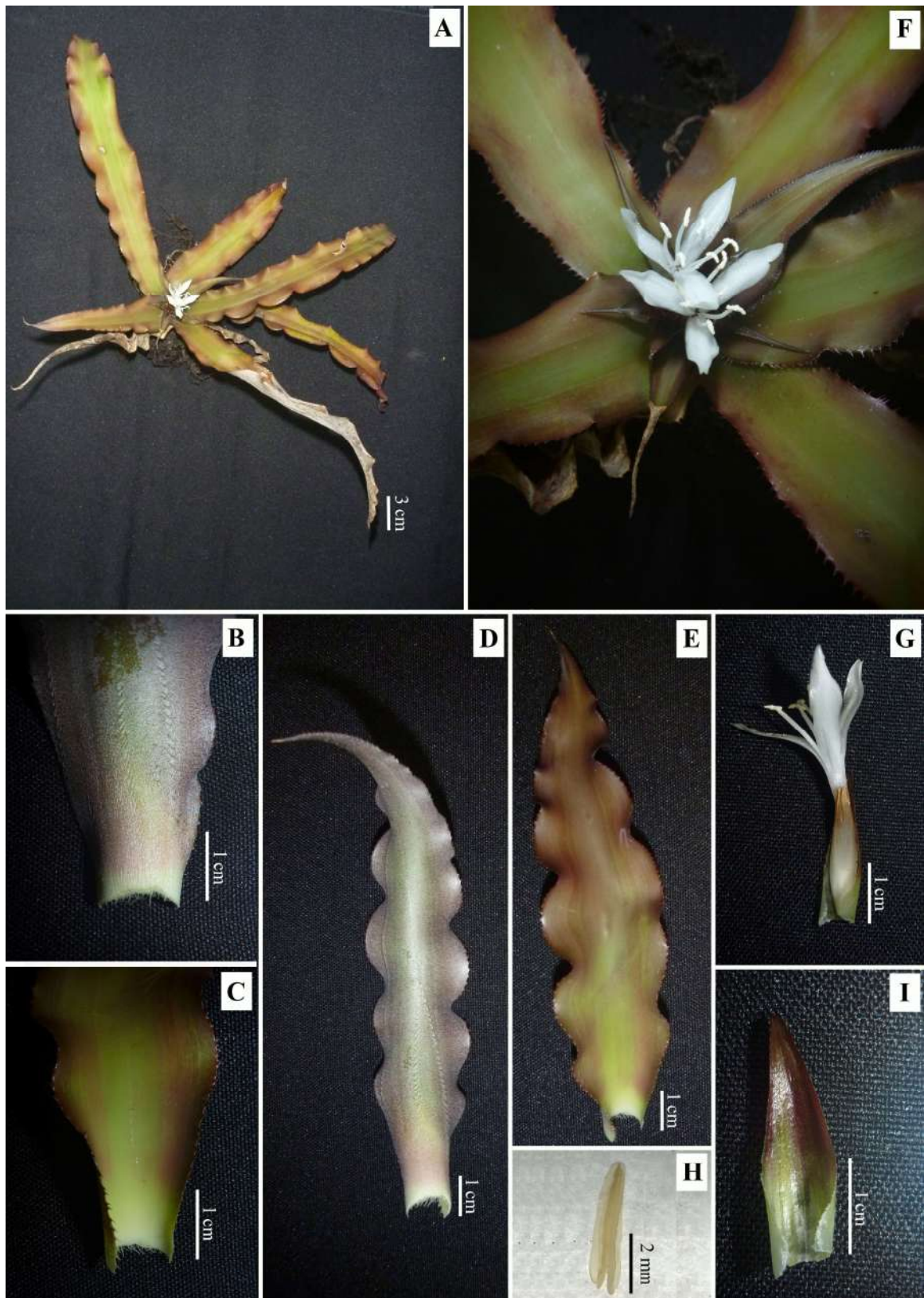


Figure 5. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. **A.** Habit. **B.** Leaf sheath (abaxial surface). **C.** Leaf sheath (adaxial surface). **D.** Leaf (abaxial surface). **E.** Leaf (adaxial surface). **F.** Inflorescence. **G.** Staminate flower with the floral bract. **H.** Floral bract of staminate flower (adaxial surface). **I.** Anther of the staminate flower.

4.3 ARTIGO 3 - A TAXONOMIC SYNOPSIS OF THE GENUS *CRYPTANTHUS* OTTO &
A. DIETR. (BROMELIOIDEAE, BROMELIACEAE) IN THE
NORTHEASTERN REGION FROM BRAZIL

A taxonomic synopsis of the genus *Cryptanthus* Otto & A. Dietr. (Bromelioideae, Bromeliaceae) in the Northeastern region from Brazil

DÉBORA MARIA CAVALCANTI FERREIRA¹ & RAFAEL BATISTA LOUZADA²

¹*Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil. E-mail: deboracavalcantif@hotmail.com*

²*Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil. E-mail: rafael.louzada@ufpe.br*

Author for correspondence: deboracavalcantif@hotmail.com

Abstract

Cryptanthus is a genus that occurs in the northeastern and southeastern region from Brazil. In the Northeastern region, taxonomic studies are incipient and many new species were recently discovered and described making it a challenge to identify the species of the genus in the region. In this study, a taxonomic synopsis of *Cryptanthus* in the Northeastern region from Brazil is presented with taxonomic key, illustrations, photos and taxonomic comments for the taxa. In addition, conservation status of the species were evaluated and maps of geographic distribution are provided. For this study, samples of species of the genus were collected during field expeditions between 2014 to 2020 in the following northeastern states of Brazil: Alagoas, Bahia, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe. Specimens of 28 herbaria were analyzed. A total of 39 species is found in northeastern Brazil, being 33 in Atlantic Forest (with three occurring in transition area between Atlantic Forest and *Caatinga*) and six in *Caatinga*. All species are endemic to the northeastern except *C. beuckeri*, *C. teretifolius* and *C. robsonianus*. In general the species have a restricted distribution and 19 species are known only from the type locality. One new synonymization is proposed where *Cryptanthus heimenii* is synonymized in *Cryptanthus bahianus*.

Key words: bromeliad, conservation status, endemism, taxonomy.

Introduction

Bromeliaceae is within the order Poales (APG IV 2016). The family occurs along the tropics and subtropics of the America (Givnish *et al.* 2011), except for *Pitcairnia feliciana* (A. Chev.) Harms & Mildbr. that is native to Africa (Givnish *et al.* 2011). Bromeliaceae includes 3692 species and 79 genera (Gouda *et al.*, cont. updated), being 1179 species and 24 genera endemic to Brazil (Forzza *et al.* 2020). Currently, the family is classified into eight subfamilies: Brocchinioideae, Bromelioideae, Hechtioideae, Lindmanioideae, Pitcairnioideae, Puyoideae, Navioideae e Tillandsioideae (Givnish *et al.* 2007).

Cryptanthus Otto & A. Dietr. (1836: 297) nom. cons. is a genus endemic to Brazil where it occurs in the northeastern (Alagoas, Bahia, Paraíba, Pernambuco, Rio Grande do Norte and Sergipe States) and southeastern (Espírito Santo, Minas Gerais and Rio de Janeiro States) regions in the phytogeographic domains of the Atlantic Forest and Caatinga (Leme *et al.* 2017). The genus is included in the subfamily Bromelioideae in the eu-bromelioids clade (Schulte *et al.* 2009).

Phylogenetic studies including *Cryptanthus* species have been conducted (e.g. Silvestro *et al.* 2013; Louzada *et al.* 2014; Cruz *et al.* 2017; Leme *et al.* 2017; Ferreira *et al.* Artigo 1). In order to the genus become monophyletic, Leme *et al.* (2017) proposes a new circumscription for *Cryptanthus* segregating twenty-five homogamous species that were part of the genus into the following genera: *Forzzaea* Leme, S. Heller & Zizka, *Hoplocryptanthus* (Mez) Leme, S. Heller & Zizka and *Rokautskyia* Leme, S. Heller & Zizka. *Cryptanthus* is mainly differentiated from *Forzzaea*, *Hoplocryptanthus* and *Rokautskyia* by andromonoecy and stigma conduplicate-patent (Leme *et al.* 2017).

Subsequently, Ferreira *et al.* (Artigo 1) carried out a phylogenetic study with extensive sampling of plastid genes where they show that the presence of petioles and petal color white, except for the green or greenish apex evolved multiple times in the evolutionary history of the genus. The species of the genus are included in seven clades that are consistent with the geographical distribution: bahianus clade (*C. bahianus* L.B. Smith), pickelii clade (*C. alagoanus* Leme & J.A. Siqueira, *C. cinereus* D.M.C. Ferreira & Louzada, *C. pickelii* L.B. Sm., *C. pirambuensis* D.M.C. Ferreira & Louzada, warren-loosei clade (*C. boanovenssis* Leme, *C. crassifolius* Leme, *C. warren-loosei* Leme), capixaba clade (*C. capitellatus* Leme & L. Kollmann, *C. venecianus* Leme & L. Kollmann, *C. viridipetalus* Leme & L. Kollmann, *C. rigidifolius* Leme), walkerianus clade (*C. teretifolius* Leme, *C. robsonianus* Leme, *C. walkerianus* Leme & L. Kollmann) ruthiae clade (*C. apiculatantherus* D.M.C. Ferreira, E.M.

Almeida & Louzada, *C. ruthiae* Philcox, *C. vinosibracteatus* D.M.C. Ferreira & Louzada), zonatus clade (*C. diana* Leme, *C. reptans* Leme & J.A. Siqueira, *C. zonatus* (Vis.) Vis.) (Ferreira *et al.* Artigo 1). In addition, Ferreira *et al.* (Artigo 1) show that the infra-generic classification proposed by Ramírez-Morillo (1996) is not in accordance with the formed clades. The clades were formed based on the geographic distribution of the species (Ferreira *et al.* Artigo 1).

Taxonomic studies for *Cryptanthus* are incipient (e.g. Baker 1889; Mez 1891; Smith 1955; Smith & Downs 1979; Ramírez-Morillo 1996). A recent study of Maciel (2020) was done but does not have illustrations and photographs, which makes it difficult to identify the species. In northeastern Brazil, the taxonomic studies include few species and are restricted to the northern part of the Atlantic Forest: Leme & Siqueira-Filho (2007), Ferreira & Louzada (2015, 2020, Capítulo de livro 1). The studies do not include the state of Bahia and, according to Maciel (2020), this is richest in number of species. Moreover, after the last taxonomic revision of the genus made by Ramírez-Morillo (1996), twenty-four new species were discovered and described for the genus in the northeastern region (e.g., Luther 1999; Leme 1999, 2001, 2002a, 2002b, 2014, 2015, Leme & Siqueira-Filho 2007, Leme *et al.* 2008, 2010, 2014, 2020, Leme & Siqueira-Filho 2001, Leme & Kollmann 2013, Braun & Brito 2019, Ferreira & Louzada 2020, Ferreira *et al.* 2021a, Ferreira & Louzada Artigo 2), making it a challenge to identify the species of the genus in the region.

Thus, we aim to contribute to the taxonomic knowledge of *Cryptanthus* in northeastern Brazil. Here we provide a taxonomic synopsis of *Cryptanthus* to the Brazilian northeastern region with an identification key, illustrations, photos, and taxonomic comments for the taxa. Besides we evaluate the conservation status, provide maps of geographic distribution of each species and, in addition, we propose a new synonymization.

Materials and Methods

Samples of the genus *Cryptanthus* were collected during field work between 2014 to 2020 in the following northeastern states of Brazil: Rio Grande do Norte, Paraíba, Pernambuco, Alagoas, Sergipe and Bahia. The samples were georeferenced, photographed, and herbarium specimens were prepared according to Peixoto & Maia (2013) and were deposited at UFP herbarium. The duplicates were sent to RB herbarium.

The morphological observations were carried out based on samples collected in the field and herbarium specimens deposited at ALCB, ASE, CEPEC, EAC, MBML, VIES, HST

(Herbário Sérgio Tavares), IPA, JPB, MAC, UFP, UFRN, UESC, PEUFR and SAMES. In addition, online collections and photos of the BM*, CEN*, F*, GH*, HB**, HUNEB**, HURB*, K*, MBM*, NY*, P*, RB* SP*, UEC* and US* were accessed (*digital image; **photos). The online collections were accessed using specific collection sites or using specieslink (<http://www.splink.org.br/>). All the herbarium acronyms are listed according to *Index Herbariorum*: <http://sweetgum.nybg.org/ih/> except HST. The reproductive morphological characters of some species were taken from the protologue: *Cryptanthus arelii* H. Luther (Luther 1999), *C. argyrophyllus* Leme (Leme 2001), *C. bibarrensensis* Leme (Leme 2002a), *C. cruzalmensis* Leme & E.H.Souza (Leme *et al.* 2020), *C. diamantinensis* Leme (Leme 1999), *C. felixii* J.A.Siqueira & Leme (Leme & Siqueira-Filho 2007), *C. lyman-smithii* Leme (Leme 1999), *C. santateresinhensis* Leme (Leme *et al.* 2020), *C. seidelianus* W.Weber (Weber 1986), *C. ubairensis* I.Ramírez (Ramírez M. 1998), *C. viridovinosus* Leme (Leme *et al.* 2010) and *C. vexatus* Leme (Leme 1995). In addition, the information about the leaf color of the species *C. arelii* H. Luther and *C. ilhanus* Leme, and the trichomes of the leaves of *C. argyrophyllus* Leme were also taken from the protologue in Luther (1999), Leme & Kollmann (2013) and Leme (2001), respectively. And the information petal color of *C. lacerdae* Antoine was taken in Ramírez-Morillo (1996). The information of the stem and leaves of *C. santateresinhensis* Leme was taken in Leme *et al.* (2020) by observing the photos and measurements. Morphological terminology followed Radford *et al.* (1974) and Harris and Harris (2001). For stem length, we followed Ferreira and Louzada (2020) and the morphology of stigma followed Leme *et al.* (2017). Barcodes of the type specimens examined are included in square brackets.

The vegetation types in the phytogeographic domain of the Atlantic Forest were classified according to Thomas & Barbosa (2008). For conservation status analysis, the categories and criteria followed the IUCN (2019). The extent of occurrence (EOO) and the area of occupancy (AOO) were measured using GeoCAT (Geospatial Conservation Assessment Tool – Bachman *et al.* 2011). The EOO and AOO were measured using the geographic coordinates indicated on the exsiccate labels. The geographic coordinates were converted of graus-min-seg to graus decimais using the Specieslink tool (<http://splink.cria.org.br/conversor>). When the labels had no indication of the geographic coordinates or when the geographic coordinates were invalid, the municipal coordinates were used. The distribution maps were produced using QGis3.

Results

Cryptanthus Otto & A. Dietr., *Allg. Gartenzeit.* 4: 297. 1836. **Type:**— *Cryptanthus bromelioides* Otto & A. Dietr. (1836: 298) (neotype and isoneotypes designated by Ramírez M. 1998): BRAZIL. Rio de Janeiro: Matas do Jardim Botânico, *Pereira 5637* (neotype: HB; isoneotypes: B digital image! [B 10 0244058], MBM digital image! [MBM 022530]). *nom. cons.*, non *Cryptanthus* Osbeck, *Dagb. Ostind. Resa*: 215. 1757.

Herbs terricolous or rupicolous, andromonoecious, propagating by rhizome, stolons and/or axillary shoots. Stems erect and/or decumbent, short and/or long caulescent. Leaves not contracted at the base, contracted at the base or wider at the base; sessile or petiolate, canaliculate petioles with revolute or straight margins. Leaf blades linear, linear triangular, narrowly triangular, triangular, linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic, with longitudinal colored lines along the margins in the living plant or absent, margin aculeate. Inflorescences in spikes of glomerules; apical glomerule with 4–82 flowers, lateral glomerule with 1–10 flowers. Primary bracts foliaceous. Rachis covered by the primary bracts and the flowers. Flowers staminate and perfect, sessile; in general staminate flowers shorter than the perfect ones. Sepals partially connate, 3-lobed. Petals partially connate, 3-lobed, white or white with green or greenish apices, with 2 inconspicuous or conspicuous callosities bearing inconspicuous capitate trichomes. Stamens 6, in two whorls of three, first whorl antepetalous, second whorl antesepalous. Filaments partially adnate to the petals. Anthers, subbasifixed, dehiscence longitudinal, apices apiculate, mucronulate, acute, emarginate or rounded. Stigma 3-lobed, conduplicate-patent; ovary inferior, 3-locular, trigonous, ovules 0–29 per locule, placentation axial, epigynous tube present or absent. Fruits berry, trigonous. Seeds asymmetrical.

Number of Species, Distribution, and Habitat- *Cryptanthus* includes 64 species that occur in Northeastern and Southeastern Brazil (Figure 1). In Northeastern 39 species are found (Figures 2, 3 and 4), being 33 in Atlantic Forest (three occurring in transition area between Atlantic Forest and *Caatinga*) and six in *Caatinga*. Of the 39 species found in the region, 36 are endemic to the Northeastern and three (*C. beuckeri* E. Morren, *C. teretifolius* Leme and *C. robsonianus* Leme) occur in the Northeastern and Southeastern regions from Brazil. The most species occur in shaded areas of forest and few species occur in sun-exposed areas. In general the species have a restricted distribution and 19 species are known only from the type locality. The State with the richest in number of species is Bahia with 31 species followed by

Pernambuco (8 spp.), Alagoas (6 spp.), Paraíba (4 spp.), Sergipe (4 spp.) and Rio Grande do Norte (1 spp.).

Artificial Key to the Species of *Cryptanthus* from northeastern Brazil

1. Adaxial surface of the leaf blades with three longitudinal lines of lepidote trichomes or with crossbars of lepidote trichomes.....2
 - Adaxial surface of the leaf blades densely lepidote, glabrous with base and/or apices densely lepidote, sparsely lepidote or glabrous.....4
2. Adaxial surface of the leaf blades with three longitudinal lines of lepidote trichomes.....*Cryptanthus lacerdae*
 - Adaxial surface of the leaf blades with crossbars of lepidote trichomes.....3
3. Petals white with apices greenish.....*Cryptanthus robsonianus*
 - Petals white.....*Cryptanthus zonatus*
4. Leaves petiolate.....5
 - Leaves sessile, contracted at the base above the leaf sheaths or not contracted at the base.....8
5. Canaliculate petioles with revolute margins.....*Cryptanthus beuckeri*
 - Canaliculate petioles with straight margins.....6
6. Petals white except for slightly greenish apex.....*Cryptanthus lyman-smithii*
 - Petals white.....7
7. Floral bracts of staminate flower 21–22 mm long; filaments of the staminate flower 24–27 mm long.....*Cryptanthus teretifolius*
 - Floral bracts of staminate flower 26–32 mm long; filaments of the staminate flower 20 mm long.....*Cryptanthus walkerianus*
8. Adaxial surface of the leaf blades entirely densely lepidote in the older leaves (the younger ones can be glabrous).....9
 - Adaxial surface of the leaf blades glabrous with base and/or apices densely lepidote, or glabrous in the older and younger leaves.....15
9. Plants with leaf blades 1.1–1.5 cm wide.....*Cryptanthus crassifolius*
 - Plants with leaf blades >2 cm wide.....10
10. Leaf blades narrowly triangular; wider at the base.....*Cryptanthus cinereus*
 - Leaf blades oblanceolate, narrowly elliptic or elliptic; contracted at base.....11

11. Sepals 12–14 mm long; filaments adnate to the petals for 20 mm.....*Cryptanthus cruzalmensis*
- Sepals 15.5–21.2 mm long; filaments adnate to the petals for 5–15 mm.....12
12. Petals white with apices green or greenish.....13
- Petals white.....14
13. Floral bracts 15 mm long; Sepals connate for 10 mm, lobes 8–9 mm long; Petals 6 mm wide; Epigynous tube absent.....*Cryptanthus argyrophyllus*
- Floral bracts 17.5–28.2 mm long; Sepals connate for 6–7.5 mm, lobes 11–14 mm long; Petals 2–4.5 mm wide; Epigynous tube present 2.5–3 mm long.....*Cryptanthus robsonianus*
14. Petals 33–42.5 mm long; styles 26.2–36 mm long; Epigynous tube 1–1.2 mm long.....*Cryptanthus diana*
- Petals 24.5–29.5 mm long; styles ca. 24.5 mm long; Epigynous tube 2.3–4 mm long.....*Cryptanthus pseudopetiolatus*
15. Petals white with apices green or greenish.....16
- Petals white.....20
16. Plants with leaf blades that never exceed 7.5 cm long.....*Cryptanthus lacerdae*
- Plants with leaf blades that exceed 7.5 cm long in the adult leaf blades.....17
17. Plants long caulescent, stem ≥ 8 cm; leaf blades linear triangular or narrowly triangular in the young leaves; Anthers apices apiculate.....*Cryptanthus apiculatantherus*
- Plants short caulescent, stem < 8 cm; leaf blades oblanceolate, lanceolate, narrowly elliptic or elliptic; Anthers apices obtuse or obtuse and inconspicuously apiculate.....18
18. Floral bracts white on the base and vinaceous or greenish on the apex; sepals 17–21.2 mm long; lobes 14–17 mm long, lanceolate; petals connate for 6.5–9.3 mm long.....*Cryptanthus robsonianus*
- Floral bracts castaneous or castaneous-hyaline; sepals 12–15 mm long; lobes 5–6 mm long, ovate or oblong-elliptic; petals connate for 16–17 mm long.....19
19. Flowers 40 mm long; sepals 12–13 mm long, connate for 6–7 mm; lobes oblong-elliptic; petals 30–33 mm long.....*Cryptanthus viridovinosus*
- Flowers 44 mm long; sepals 15 mm long, connate for 10 mm; lobes ovate; petals 35 mm long.....*Cryptanthus santateresinhensis*

20. Leaf blades with longitudinal colored lines along the margins in the living plant.....*Cryptanthus ilhanus*
- Leaf blades without longitudinal colored lines along the margins in the living plant.....21
21. Leaf blades linear, linear triangular, narrowly triangular or triangular.....22
- Leaf blades linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic.....32
22. Leaf blades with revolute margin.....*Cryptanthus colnagoi*
- Leaf blades with straight margin.....23
23. Plants long caulescent, stem ≥ 8 cm.....24
- Plants short caulescent, stem < 8 cm.....26
24. Ovary 14 mm long.....*Cryptanthus bibarrensii*
- Ovary 4.7–10.5 mm long.....25
25. Apical glomerule of the inflorescence with 13–33 flowers; ovary with 22–29 ovules per locule in the perfect flowers.....*Cryptanthus bahianus*
- Apical glomerule of the inflorescence with ca. 82 flowers; ovary with 9–13 ovules per locule in the perfect flowers.....*Cryptanthus sergipensis*
26. Floral bracts 9 mm long; anthers apices apiculate.....*Cryptanthus diamantinensis*
- Floral bracts 10–31 mm long; anthers apices emarginate, rounded, acute.....27
27. Petals apices acuminate.....*Cryptanthus seidelianus*
- Petals apices rounded, obtuse, mucronulate or acute.....28
28. Ovary with 22–29 ovules per locule in the perfect flowers.....*Cryptanthus bahianus*
- Ovary with 3–13 ovules per locule in the perfect flowers.....29
29. Apical glomerule of the inflorescence with ca. 82 flowers.....*Cryptanthus sergipensis*
- Apical glomerule of the inflorescence with < 29 flowers.....30
30. Petals connate for 3–5 mm long; filaments 15.2–19.8 mm long; Anther apices acute.....*Cryptanthus warren-loosei*
- Petals connate for 7–13 mm long; filaments 22–32 mm long; Anther apices rounded or emarginate.....31
31. Plants with leaf blades that never exceed 1.2 cm wide; Apical glomerule of the inflorescence with ca. 4 flowers; Ovary with 7–9 ovules per locule in the perfect flowers.....*Cryptanthus boanovensii*

- Plants with leaf blades that exceed 1.2 cm long in the adult leaf blades; Apical glomerule of the inflorescence with 15–29 flowers; Ovary with 6 ovules per locule in the perfect flowers.....*Cryptanthus reisii*
- 32. Plants long caulescent, stem ≥ 8 cm.....33
- Plants short caulescent, stem < 8 cm.....36
- 33. Ovary 15–20 mm long.....*Cryptanthus felixii*
- Ovary 2.5–10.5 mm long.....34
- 34. Sepal lobes 4×2 –2.5 mm; Ovary 5 mm long.....*Cryptanthus ubairensis*
- Sepal lobes 6.4 – 10×3 –6 mm; Ovary 7–11.2 mm long.....35
- 35. Sepals connate for 4–5 mm long; petals 25 mm long; filaments 13 mm long.....*Cryptanthus vexatus*
- Sepals connate for 8.2–11 mm long; petals 29.2–45 mm long; filaments 22–36 mm long*Cryptanthus zonatus* complex (including *Cryptanthus diana*e and *Cryptanthus reptans*)
- 36. Floral bracts 9.2 – 10×3.2 mm.....*Cryptanthus brevibracteatus*
- Floral bracts 11 – 28×4.7 –22.1 mm37
- 37. Sepals connate for 2 mm long.....*Cryptanthus osiris*
- Sepals connate for 4–16 mm.....38
- 38. Epigynous tube absent.....39
- Epigynous tube present.....40
- 39. Sepal lobes 4×2 –2.5 mm; Ovary 5 mm long.....*Cryptanthus ubairensis*
- Sepal lobes 5 – 6×5 mm; Ovary 7 mm long.....*Cryptanthus cruzalmensis*
- 40. Adaxial surface of the leaf blades reddish-brown or olive-brown to reddish-brown.....41
- Adaxial surface of the leaf blades green, green except for the red, brown or purple base, brown or purple.....43
- 41. Floral bracts 25–26 mm long; floral bracts white-greenish on the base and vinaceous on the apices.....*Cryptanthus vinosibracteatus*
- Floral bracts 12.2–22.5 mm long; floral bracts white, cream or pale green.....42
- 42. Apical glomerule of the inflorescence with ca. 14 flowers; floral bracts white*Cryptanthus* sp.

- Apical glomerule of the inflorescence with 8–10 flowers; floral bracts cream or pale green.....*Cryptanthus arelii*
- 43. Floral bracts white.....*Cryptanthus sp.*
- Floral bracts white with brown, vinaceous or green apex.....44
- 44. Each lateral glomerule of the inflorescence with 9–10 flowers.....45
- Each lateral glomerule of the inflorescence with 2–8 flowers.....46
- 45. Floral bracts 19–23 mm long; flowers 29.5–37 mm long; sepals 15.5–17.5 mm long; sepals lobes ovate or lanceolate; petals connate for 3.2–6 mm long; Callosities of the petals appearing 4–5 mm distant from the base; stigma lobes 3.2 mm long in the perfect flowers; ovary with 8–9 ovules per locule in the perfect flowers.....*Cryptanthus pseudopetiolaris*
- Floral bracts 27.5–34 mm long; flowers 44–61 mm long; sepals 20–22.5 mm long; sepals lobes narrowly elliptic or elliptic; petals connate for 12–22 mm; Callosities of the petals appearing 12.5–22 mm distant from the base; stigma lobes 6–7.2 mm in the perfect flowers; ovary with 15–17 ovules per locule in the perfect flowers.....*Cryptanthus pirambuensis*
- 46. Apical glomerule of the inflorescence with 15–32 flowers.....47
- Apical glomerule of the inflorescence with 5–12 flowers.....48
- 47. Styles 26 mm long.....*Cryptanthus reisii*
- Styles 30 mm long.....*Cryptanthus ruthiae*
- 48. Leaf blades predominantly linear-oblongate or oblongate..... *Cryptanthus pickelii* L. B. Sm. complex.....(including *Cryptanthus alagoanus* and *Cryptanthus pickelii*)
- Leaf blades predominantly narrowly elliptic..*Cryptanthus zonatus* (Vis.) Vis. complex(including *Cryptanthus diana*, *Cryptanthus reptans*, *Cryptanthus zonatus*)

Taxonomic Treatment

1. *Cryptanthus alagoanus* Leme & J.A.Siqueira, *Selbyana* 22(2): 151 (2001). [Figs. 2A, 4A–B, 6].

Type:—BRAZIL. Alagoas: Paripueira, 17 January 2009, *Artur Frassy s.n.*, fl. cult. February 2001, *E. Leme 5085* (Holotype: HB photo! [HB 89558]).

Etymology:—It refers to the Alagoas State where the specimen type was collected.

Distribution and Habitat:— *Cryptanthus alagoanus* is known from the Alagoas State (municipality of Paripueira). It occurs in the phytogeographic domain of the Atlantic Forest, at 50 m elevation. It is terricolous and grows on clay soil in semideciduous seasonal forest.

Phenology:—Flowering in nature in January and in cultivation in February and July. Fruiting in nature in August.

Conservation status:—*C. alagoanus* is known from one location in a conservation unit: RPPN Placas (O Sabiá). Currently, the species is included in the *Cryptanthus pickelii* L. B. Sm. complex by Ferreira & Louzada (2020). Thus, this species is classified as Data Deficient (DD).

Taxonomic affinities:—*C. alagoanus* is phylogenetically related to *C. pickelii* L.B.Sm, *C. cinereus* D.M.C. Ferreira & Louzada and *C. pirambuensis* D.M.C. Ferreira & Louzada that together are included in the *pickelii* clade. Ferreira & Louzada (2020) include *C. alagoanus* and *C. pickelii* in *Cryptanthus pickelii* L. B. Sm. complex due to their morphological overlap. In the phylogenetic study of Ferreira *et al.* (Artigo 1), the authors confirm the complex and recommend population genetic studies to resolve this complex.

Specimens examined:—BRAZIL. **Alagoas:** Paripueira, RPPN Placas (O Sabiá), 50 m, 09°26'17"S, 35°36'07"W, 01 October 2017, fl. cult. 18 July 2018, *D. Cavalcanti et al. 906* (UFP); Paripueira, RPPN Sabiá, 29 August 2009, fr., *Chagas-Mota & V. G. Ramalho 5258* (MAC); Paripueira, RPPN Placas, 09°27'49"S, 35°33'83"W, 11 January 2010, fl., *R. P. Lyra-Lemos 12861* (MAC); Paripueira, 17 January 2009, *Artur Frassy s.n.*, fl. cult. February 2001, *E. Leme 5085* (HB).

2. *Cryptanthus apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada, *Phytotaxa* 523(1): 100 (2021a). [Figs. 2A, 4CD, 7].

Type:—BRAZIL. Bahia: Itacaré, Serra dos Vinháticos, 124 m elev., 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, fr. cult. 22 November 2019, *E. M. Almeida 2757* (holotype: UFP!)

Etymology:—It refers to the apices apiculate of the anthers (Ferreira *et al.* 2021a).

Distribution and habitat:—*Cryptanthus apiculatantherus* is known from the Bahia State (municipality of Itacaré). It occurs in the phytogeographic domain of the Atlantic Forest, at 124 m elevation in the vegetation type submontane tropical moist forest. It is terricolous and grows on dense litter layer of clayey soil inside closed forest with tree ca. 5 m tall on the border of a rocky outcrop known as Serra dos Vinháticos (Ferreira *et al.* 2021a).

Phenology:—Flowering in cultivation in January and March and fruiting in nature in January.

Conservation status:—The conservation status of *C. apiculatantherus* was recently evaluated by Ferreira *et al.* (2021a). This species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii) due to the species occurs in only one location and also due to possible decline of the area of occupancy (Ferreira *et al.* 2021a).

Taxonomic affinities:—*C. apiculatantherus* is phylogenetically related to *C. ruthiae* Philcox and *C. vinosibracteatus* D. M. C. Ferreira & Louzada that together are included in the *ruthiae* clade. *C. apiculatantherus* is easily differentiated from these species by the long stem ≥ 8 cm (vs. < 8 cm) and petals white with apices green or greenish (vs. petals white). *C. apiculatantherus* is morphologically related to the group of species with leaves sessile, contracted at base above the leaf sheaths or not contracted at base, adaxial surface of the leaf blades glabrous with base and/or apices densely lepidote, or glabrous in the older and younger leaves and petals white with apices green or greenish. Among these species, *C. apiculatantherus* is distinguished by the long stem ≥ 8 cm (vs. short stem 8 cm), leaf blades linear triangular or narrowly triangular in the young leaves (vs. leaf blades oblanceolate, lanceolate, narrowly elliptic or elliptic) and apices anthers apiculate (vs. obtuse or obtuse and inconspicuously apiculate).

Specimens examined:—BRAZIL. **Bahia:** Itacaré, Serra dos Vinháticos, 124 m, 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, fl. and fr., *E. M. Almeida* 2757 (UFP); Itacaré, Serra dos Vinháticos, 124 m, 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, fl. cult. 27 August 2019, *E. M. Almeida* 3246 (CEPEC); Itacaré, Serra dos Vinháticos, 124 m, 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, fl. cult. 28 January 2021, *E. M. Almeida* 3318 (RB).

3. *Cryptanthus arelii* H. Luther, *Cryptanthus Soc. J.* 14(2): 54 (1999). [Figs. 2A, 4E]

Type:—BRAZIL. Bahia: Palmeiras, Coll. 5 km south of Palmeiras on Hwy 24, 11 February 1997, *H.B. Luther s.n.*, fl. cult. January 1982, fl., *R.L.Frasier, E.M.C. Leme & J. Kent s.n.* (Holotype: HB photo! [HB 92703]; Isotypes: SEL digital image! [SEL 076727], US digital image! [US 3392313])

Etymology:—It is not indicated in Luther (1999).

Distribution and Habitat:—*Cryptanthus arelii* is only known from the Bahia State (municipality of Palmeiras). It occurs in the phytogeographic domain of the Caatinga. It is terricolous and grows under bushes of the Chapada Diamantina.

Phenology:— Flowering in cultivation in January.

Conservation status:—*C. arelii* is known only from the type locality (one location). It occurs in the Chapada Diamantina that is a touristic area where it can be collected for use as ornamental plant which causes a decline of the population. This, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—The information about reproductive characteres of *C. arelii* was taken from Luther (1999) for comparison with the close species. *Cryptanthus arelii* can be confused with *C. vinosibracteatus* D.M.C. Ferreira & Louzada by the leaf blades color but *C. arelii* differs from *C. vinosibracteatus* by length of floral bracts 18–22 mm long (vs. 25–26 mm long) and floral bracts color cream or pale green (vs. white-greenish on the base and vinaceous on the apice). *Cryptanthus arelii* is also morphologically similar to *C. sp.*, both occur in Chapada Diamantina. However, *C. arelii* can be differentiated from *C. sp.* by the number of flowers in the apical glomerule of the inflorescence (8–10 flowers vs. 14 flowers) and the floral bract cream or pale green (vs. white).

Specimens examined:— BRAZIL. **Bahia:** Palmeiras, Coll. 5 km south of Palmeiras on Hwy 24, 11 February 1997, *H.B. Luther s.n.*, fl. cult. January 1982, fl., *R.L.Frasier, E.M.C. Leme & J. Kent s.n.* (HB, SEL, US).

4. *Cryptanthus argyrophyllus* Leme, *Cryptanthus Soc. J.* 16(1): 12 (2001). [Figs. 2A, 4F].

Type:—BRAZIL. Bahia: Santa Cruz da Vitória, *E. Colnago s.n.*, fl. cult. December 2000, fl., *E. Leme 4872* (Holotype: HB image! [HB 89568])

Etymology:—It refers to typical silver color of the dense silver-lepidote trichomes on both surfaces of the leaf blades (Leme 2001).

Distribution and Habitat—According to the holotype, *Cryptanthus argyrophyllus* occurs in the Bahia State (municipality of Santa Cruz da Vitória). However, the title of the study of Leme (2001) indicate that it is a new species from Espírito Santo State. This species is only known by its type material and there is no more information about where the species was found (Leme 2001). The municipality of Santa Cruz da Vitória is included in the phytogeographic domain of the Atlantic Forest.

Phenology:—Flowering in cultivation in December.

Conservation status:—*C. argyrophyllus* is known only from the type locality (one location) in the Atlantic Forest that is severely fragmented. Since its discovery (nineteen years ago), no other samples have been collected. The species is classified as Data Deficient (DD) due to the confused collection site.

Taxonomic affinities:—The information about morphological characters of *C. argyrophyllus* was taken from Leme (2001) for comparison with the close species. *C. argyrophyllus* is morphologically related to *C. robsonianus* Leme by the abaxial surface of the leaf blades entirely densely lepidote and petals white with apices greenish but *C. argyrophyllus* differs from *C. robsonianus* by the floral bracts 15 mm long (vs. 15.5–28.2 mm long), sepals connate for 10 mm (vs. 6–7.5 mm long), lobes 8–9 mm long (vs. 11–14 mm long), petals 6 mm wide (vs. 2–4.5 mm wide) and epigynous tube absent (vs. present 2.5–3 mm long). *C. argyrophyllus* is not included in the study of Maciel (2020) of the “Flora do Brasil 2020”.

Specimens examined:—BRAZIL. **Bahia**: Santa Cruz da Vitória, *E. Colnago s.n.*, fl. cult. December 2000, fl., *E. Leme 4872* (HB).

5. *Cryptanthus bahianus* L.B.Sm., *Arq. Bot. Estado São Paulo* 1 (6): 106 (1944). [Figs. 2A, 4G–J, 8].

Type:—BRAZIL. Bahia: Jacobina, 18 June 1939, *M.B. & R. Foster 98* (Holotype: GH digital image! [00032943])

= *Cryptanthus heimenii* P.J.Braun & Gonç. Brito (2019: 55) *syn. nov.*

TYPE:— BRAZIL. Sergipe: Simão Dias, 350m, 15 September 2018, *B. Gonçalves Brito 3* (Holotype: HBR [HBR 57550], Isotype: SP, JOI, HAL [HAL 146711])

Etymology:—It refers to the Bahia state where the specimen type was collected.

Distribution and Habitat:— *Cryptanthus bahianus* is known from the Alagoas (municipality of Traipu), Bahia (Baixa Grande, Brejões, Castro Alves, Conceição do Coité, Itambé,

Jacobina, Milagres, Quijingue, Riachão do Jacuípe, Senhor do Bonfim and Rio de Contas), Paraíba (municipality of Arara, Araruna, Areia, Cacimba de Dentro and Gurinhém), Pernambuco (Caruaru, Garanhuns, Gravatá and Vitória) and Sergipe (Nossa Senhora da Glória, Poço Redondo, Riachão do Dantas and Simão Dias) States. It occurs in the phytogeographic domain of the Caatinga, at 250 to 882 m elevation with the exception of an area that the species occurs in Atlantic Forest in Brejo de Altiude in municipality of Areia, Paraíba State. *Cryptanthus bahianus* is terricolous or rupicolous and occurs in areas exposed to the sun or it grows under bushes.

Phenology:—Flowering in nature in January, February, March, April, May, June, August, November and in cultivation in March, April, May and June. Fruiting in nature in August.

Conservation status:—*C. bahianus* is the species with the greatest geographical distribution of the genus. It occurs in 33 locations. One population occurs in a protected area called of Parque Estadual da Pedra da Boca, municipality of Araruna, in Paraíba State. The species is versatile. It occurs in areas exposed to the sun and in shaded areas. The extent of occurrence (EOO) is 284,213.569 km² and the area of occupancy (AOO) is 112 km². Thus, the species is classified as Least Concern (LC) due to wide extent of occurrence and species versatility.

Taxonomic Notes:—The species was first described by Smith (1937-8) as *Cryptanthus glaziovii* L. B. Smith, however, this specific epithet had already been used by Mez (1891) in another species of *Cryptanthus* in Flora brasiliensis that currently belongs to the genus *Hoplocryptanthus* (Leme *et al.* 2017) making the name illegitimate. Another synonymous name, *Cryptanthus heimenii* P. J. Braun & Gonç. Brito, for *C. bahianus* was published by Braun & Brito (2019). The species was compared to *Cryptanthus crassifolius* Leme (2008: 17) and *Cryptanthus sergipensis* (1998: 219) (Braun & Brito 2019). However, it was not compared to *C. bahianus*. Clearly *C. heimenii* is synonymous to *C. bahianus*.

Taxonomic affinities:—*C. bahianus* is included in the bahianus clade (Ferreira *et al.* Artigo 1). *Cryptanthus bahianus* is morphologically similar to *C. sergipensis* I. Ramírez due to the leaf blades linear triangular or narrowly triangular but *C. bahianus* differs from *C. sergipensis* by the apical glomerule of the inflorescence with 13–33 flowers (*vs.* ca. 82 flowers) and ovary with 22–29 ovules per locule in the perfect flowers (*vs.* 9–13 ovules per locule in the perfect flowers). *Cryptanthus bahianus* can be confused with *C. seidelianus* W. Weber due to the leaf blades linear triangular or narrowly triangular but *C. bahianus* differs from *C. seidelianus* by the apices of the petals obtuse (*vs.* acuminate). The information about apex of petals of *C. seidelianus* was taken from Weber (1986) for comparison with the *C. bahianus*.

Specimens examined:—BRAZIL. **Alagoas:** Traipu, Serra da Mão, 18 May 2011, fl., *A. Costa* 510 (MAC). **Bahia:** Baixa Grande, February 1996, fl., *A. L. Coticio* s.n. (ALCB 028397); Brejões, Faz. Lagoa do Morro, 882 m, 13°5'59"S, 39°54'7"W, 11 November 2007, fl., *F.M. Ferreira et al.* 1860 (CEPEC); Castro Alves, BR 342, Km 30, 11 May 1985, sterile, *A. L. Costa* s.n. (ALCB 15888); Conceição do Coité, Serra do Mucambo, no topo da Serra, 11°30'S, 39°11'W, 11 May 2013, fl., *D. N. Carvalho & A. O. Matos* 2013 (HUEFS); Itambé, Rodovia BA-265, km 8 do trecho BR-415 (cruzamento)/ Caatiba e a 15 km NW de Itapetinga em linha reta, próx. a Faz. São João, 400 m, 03 March 1978, fl., *S.A. Mori et al.* 9381 (CEPEC); Jacobina, 18 June 1939, fl., *M.B. & R. Foster* 98 (US); Jacobina, ca. 25 km na estrada Jacobina/Morro do Chapéu, 15 March 1991, fl., *A. M. de Carvalho et al.* 4555 (CEPEC); Jacobina, Itaitu, 26 June 1905, fl. cult. 13 June 2014, fl., *O. Ribeiro* 4 (RB); Milagres, Serra do Jatobá, 20 January 2019, fl., *A.J.A. Carvalho et al.* PE0054 (HURB); Quijingue, Proa da Serra das Candeias, a ca. de 5 km W do Povoado Quixaba do Mandacaru, 10°55'39"S, 39°04'51"W, 15 May 2005, fl., *D. Cardoso & T. M. de Santana* 544 (HUEFS); Riachão do Jacuípe, 250 m, 11°42'47"S, 39°19'38"W, 04 June 2009, fl., *E. Melo et al.* 6243 (HUEFS); Rio de Contas, 13 Km E of Rio de Contas on road to Abaíba, 22 June 1978, fl., *Storr* 200 (K); Salvador, Região Metropolitana de Salvador, May 2007, fl., *A. L. Cotias* s.n. (ALCB 78158); Senhor do Bonfim-Petrolina, 13-25 May 1974, fl., *A. Lima* 74-7631 (IPA); without precise location, Vicinity of Monte do Cruzeiro, 24-25 June 1915, fl., *J. N. Rose & P. G. Russel* 20030 (US). **Paraíba:** Arára, 30 May 1959, fl., *J. C. de Moraes* 2167 (EAN); Arára, 30 May 1959, fl., *J. C. de Moraes* 2168 (EAN); Araruna, Parque Estadual da Pedra da Boca, trilha para o Gemedouro, 28 October 2004, fl., *R. A. Pontes & P. C. Gadelha-Neto* 137 (JPB); Araruna, Parque Estadual da Pedra da Boca, trilha para o Gemedouro, 28 October 2004, *R. A. Pontes & P. C. Gadelha-Neto* 138 (JPB); Araruna, Parque Estadual da Pedra da Boca, 28 October 2005, fl. cult. 08 May 2006, fl., *R. A. Pontes & P. C. Gadelha-Neto* 359 (JPB); Areia, Engenho Cipó, 513 m, 07°41'45"S, 35°45'59"W, 13 August 2018, fr. cult. 28 August 2019, *E. M. Almeida* 2857 (UFP); Areia, Mata do Junco, 550 m, 6°53'15"S, 35°47'48"W, 28 August 1998, fl. cult. 28 June 2013, fl., *G. Martinelli* 15093 (RB); Cacimba de Dentro, Próximo a caixa d'água da cidade, na descida das rochas do sítio Bela Vista, 27 October 1998, sterile, *E. A. Rocha* 499 (JPB, UFP, UESC); Cacimba de Dentro, Sítio Bela Vista, ca. 800 m, 28 July 1998, sterile, *G. S. Baracho & J. A. Siqueira-Filho* 808 (UFP); Gurinhém, PB 54, entrada para São José dos Ramos, Sítio Pedra d'água, 07°07'26"S, 35°25'28"W, 27 October 1998, fl., *G. S. Baracho et al.* 746/828 (UFP); without precise location, em regiões secas, 30 May 1959, *J. C. de Moraes* 2167 (K, US); without precise

location, em regiões secas, 30 May 1959, fl., *J. C. de Moraes* 2168 (NYBG, US). **Pernambuco:** Caruaru, Beira da BR-104, 27 April 2014, fl. cult. 19 May 2018, fl., *D. Cavalcanti et al.* 899 (UFP); Caruaru, Beira da BR-104, 27 April 2014, fl. cult. 23 May 2018, fl., *D. Cavalcanti et al.* 900 (RB); Caruaru, IPA, 638 m, 08°13'54"S, 35°55'13"W, 25 May 2002, sterile, *K. A. Silva, A. M. S. Reis & E. L. Araújo* 64 (IPA); Caruaru, IPA, 638 m, 08°13'54"S, 35°55'13"W, 25 May 2002, fl., *K. A. Silva & A. M. S. Reis* 33 (PEUFR); Caruaru, Serra Água Doce, 800 m, 08°21'15"S, 35°58'44"W, 17 June 2012, fl., *M. Sobral-Leite et al.* 1275b (UFP); Garanhuns, 1986, sterile, *R. Bedi* 323 (IPA); Gravatá, Estrada para Mandacaru, 19 June 1985, fl., *A. Chiappeta* 572 (UFP); Gravatá, Fazenda São José, Complexo Eco-Turístico de Karawá Tã, 22 February 2007, sterile, *M. Oliveira & J. T. Medeiros-Costa* 2674 (UFP); Gravatá, Maracajá, Fazenda Minha Deusa, no caminho para o povoado de Mandacaru, 548 m, 09 August 2002, sterile, *J. A. Siqueira-Filho* 1252 (UFP); Vitória, 15 May 1967, fl., *I. Pontual* 67-526 (PEUFR). **Sergipe:** Nossa Senhora da Glória, Assentamento Nossa Senhora Aparecida, 20 June 2013, fl., *A. P. Prata et al.* 3631 (ASE); Poço Redondo, Serra da Guia, 30 May 2010, fl., *W. J. Machado et al.* 424 (ASE); Poço Redondo, Serra da Guia, 750 m, 09°58'51", 37°52'07"W, 31 October 2014, fl. cult. 24 March 2017, fl., *J. M. P. Cordeiro et al.* 540 (UFP); Riachão do Dantas, 08 April 1986, fl., *G. Viana* 1410 (ASE); Riachão do Dantas, Faz. Solobre, 07 March 1986, fl., *G. Viana* 1697 (ASE); Riachão do Dantas, 22 June 1984, fl., *G. Viana* 978 (ASE); without precise location, sterile, *M.B. Foster* 2449 (US), without precise location, sterile, *M. B. Foster* 2498 (US), without precise location, fl., *M. B. Foster* 3465 (US).

6. *Cryptanthus beuckeri* E. Morren, *Belgique Hort.* 30: 241 (1880). [Fig. 2B, 4K-M, 9].

Type:—BRAZIL. Unknown origin, Morren Icon (lectotype, designated by Ramírez M. (1998: 223): K photo!).

Etymology:—It is honor to M. S. De Beucker that took the Brazil plant to Edouard Morren (Morren 1880).

Distribution and Habitat:—*Cryptanthus beuckeri* is only known from the Bahia (municipality of Belmonte, Camacan, Ilhéus, Itapebi, Jaguaribe, Jussari, Mascote, Porto Seguro, Santa Cruz Cabrália, Una and Wenceslau Guimarães) and Espírito Santo (Aracruz, Conceição da Barra, Jaguaré, Linhares, Rio Bananal and São Mateus) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 17 to 478 m elevation. It occurs in the following vegetation types: lowland tropical moist forest, submontane tropical moist forest

and restinga forest. It is terricolous and forms small groups spread in the area and it grows on dense litter layer of clayey or sandy soils.

Phenology:—Flowering in nature in January, March, April, May, June, July, August, September, October, November and December and in cultivation in September. Fruiting in nature in October.

Conservation status:—*C. beuckeri* is known to twenty-eight locations, four of which are located in conservation units: Reserva Biológica do Mico-leão, Parque Estadual de Itaúnas, Reserva Florestal da Companhia Vale do Rio Doce and RPPN Serra do Teimoso. The extent of occurrence (EOO) is 55,907.822 km² and the area of occupancy (AOO) is 104 km². The species is located in the Atlantic Forest that is severely fragmented and possibly the species can be suffering a decline in the area of occupancy. Thus, this species is classified as Endangered (EN) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. beuckeri* was the first plant with petiole described in *Cryptanthus*. It is differentiated from *C. lyman-smithii* Leme, *C. teretifolius* Leme and *C. walkerianus* Leme & L.Kollmann by the canaliculate petioles with revolute margins (vs. with straight margins).

Specimens examined:—BRAZIL. **Bahia:** Belmonte, próx. Rio Preto, ca. 4 Km do mar, 20-30 m, September 2016, *Joãozinho s.n.*, fl. cult. September 2016, fl., *E. M. C. Leme 9135* (RB); Camacan, Fazenda Jerusalém, entrada à direita no Km 15 da estrada Camacan/Faz. Ventania (BR 101), sede da Faz. no final do ramal à esquerda, 25 August 1998, fl., *L. A. Mattos Silva et al. 3062* (CEPEC, RB, NYBG); Camacan, undated, *A. P. Fontana s.n.*, fl. cult., fl., *E. M. C. Leme 7341* (RB); Ilhéus, CEPEC Plantação de cacau, 02 July 1971, fl., *R. S. Pinheiro 1411* (CEPEC); Ilhéus, Cidade de Ilhéus, Mata da Esperança, ca. de 2 Km NNE do Banco da Vitória, 14°46'38"S, 39°05'28"W, 08 June 1995, fl., *S. C. de Santa'Ana et al. 569* (CEPEC); Ilhéus, Estrada Ilhéus-Serra Grande, entre os Kms 17-19, 22 October 1983, fr., *G. Martinelli 9703* (CEPEC, RB, US); Itapebí, Faz. Lombardia BR.101. ao lado L., 12 August 1971, fl., *T. S. S. 1788* (CEPEC); Itapebí, Cabeceira do Rio São José, Pedra do Estevão, 478 m, 15°49'48.3"S, 39°34'39.5"W, 21 November 2006, fl. cult. September 2008, fl., *A. P. Fontana et al. 2512* (RB); Jaguaribe, Região Metropolitana de Salvad, 11 December 1998, fl., *A. L. Cotias et al. 10* (ALCB); Jussari, Fazenda Serra do Teimoso, Reserva Serra do Teimoso, Lowerforest, Northern portion of reserve, 16 March 2003, sterile, *W. W. Thomas et al. 13397* (CEPEC, US); Jussari, Rod. Jussari/Palmira, entrada ca. 7,5 km de Jussari, Faz. Teimoso, RPPN Serra do Teimoso, 15°09'29"S, 39°31'43"W, 09 April 1998, sterile, *A. M. Amorim et*

al. 2371 (CEPEC, NYBG); Jussari, Serra do Teimoso, 7.5 km N then W of Jussari on Road to Palmira, then 2 km S to Fazenda Teimoso, "Reserva da Fazenda Teimoso", southern end., ca. 300 m, 15°09.3'S, 39°31.4'W, 01 February 1999, sterile, *W. W. Thomas, J. Kallunki & J. Jardim* 11909 (CEPEC); Mascote, Forest on S side of Rio Pardo, 4.2 km E of BR-101 at S side of São João do Paraíso (Km 615), 190-200 m, 15°37'02"S, 39°24'28"W, 18 January 2005, sterile, *W.W. Thomas et al.* 14358 (CEPEC); [Porto Seguro], Arraial da Ajuda, June 1997, *F. de Azevedo s.n.*, fl. cult., fl., *E. M. C. Leme* 3890 (RB); Santa Cruz Cabralia, ca. 13,7 km da Ponta de Santo Antônio, rodovia para Belmonte, 15°10'22"S, 38°58'16"W, 19 June 2005, fl., *J. G. Jardim et al.* 4633 (CEPEC, UEC); Una, Estrada Olivença/Vila Brasil, 33 km a SW de Olivença, Maruim, fazenda 2 de Julho, 13 May 1981, fl., *A. M. de Carvalho et al.* 680 (CEPEC, RB, NYBG, US); Una, Reserva Biológica do Mico-leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus/Una, 15°09'S, 39°05'W, 13-14 July 1993, fl., *J. G. Jardim et al.* 206 (CEPEC, MBM, NYBG, US); Una, Reserva Biológica do Mico-Leão (IBAMA), entrada no Km 46 da Rod. BA-001, Ilhéus/Una, 15°09'S, 39°05'S, undated, sterile, *I. Ramírez, S. Sant'Ana & A. M. de Carvalho* 476 (CEPEC); Una, Reserva Biológica do Mico-leão (IBDF), Km 8 da Rodovia Una/ Ilhéus (BA-001), 20 November 1987, fl., *E. B. dos Santos & M. C. Alves* 154 (CEPEC); Una, Reserva Biológica de Una, trilha da roda da água, 15°10'08"S, 39°03'43"W, 01 June 2014, sterile, *D. Cavalcanti et al.* 726 (UFP, RB); Wenceslau Guimarães, Fazenda Santo Antônio, a ca. 5 Km NW da cidade, 279 m, 13°41'53"S, 39°30'25"W, 05 August 2007, fl., *D. Cardoso* 2112 (CEPEC); [without precise location], Rod. Lagoa Encantada, 23 Jul 1971, fl., *R. S. Pinheiro* 1411 (CEPEC); [without precise location], Rod. Lagoa Encantada, 23 Jul 1971, fl., *R. S. Pinheiro* 1482 (CEPEC). **Espírito Santo:** Aracruz, Comboios, 30 July 1992, fl., *O. J. Pereira, J. M. L. Gomes & S. V. Pereira* 3671 (VIES); Conceição da Barra, APA da Conceição da Barra - Quadrado, 17 m, 18°35'49"S, 39°46'44"W, 04 January 2012, fl., *A. M. Assis, R. Cipriano & H. Coutinho* 2916 (VIES); Conceição da Barra, APA de Conceição da Barra. Área do quadrado, 18°41'39"S, 39°47'38"W", 18 January 2018, fl., *D. A. Duarte et al.* 77 (SAMES); Conceição da Barra, Comunidade Lajinha, Fazenda Rancho Topical II, 05 August 2007, fl., *C. Farney* 4746 (SAMES, SP); Conceição da Barra, Parque Estadual de Itaúnas, 18 November 1999, fl., *C. N. de Fraga & Caxeli* 545 (MBML); Conceição da Barra, Parque Estadual de Itaúnas, fazenda Jequitiaia, 18.3981°S, 39.6944°W, 17 January 2012, fl., *L. Marcarini, A. G. Oliveira & M. Ribeiro* 52 (VIES, SAMES); Conceição da Barra, Parque Estadual de Itaúnas, Atrás da fazenda "Jequitaia", 25 August 2009, fl., *M. M. Monteiro et al.* 52 (SAMES, VIES); Conceição da Barra, Área 214 da Aracruz Celulose S. A., 25 March 1992, fl., *O. J. Pereira et*

al. 3098 (VIES); Conceição da Barra, Área 214 da Aracruz Celulose S. A., 05 November 1992, sterile, *O. J. Pereira et al.* 4158 (VIES); Conceição da Barra, Área 214 da Aracruz Celulose S. A., 27 March 1992, fl., *O. J. Pereira* 3236 (VIES); Conceição da Barra, Área 214 da Aracruz Celulose S. A., 09 October 1992, fl., *O. J. Pereira, J. M. L. Gomes & J. M. Simoes* 3846 (VIES); Conceição da Barra, Área 315 da Aracruz Celulose S. A., 10 June 1992, fl., *O. J. Pereira, J. M. L. Gomes & S. V. Pereira* 3487 (VIES); Jaguaré, Giral, 16 December 2009, fl. cult. 01 September 2009, fl., *L. Kollmann & R. Lopes* 11776 (MBML); Linhares, Reserva Florestal da Cia. Vale do Rio Dôce, quadra à direita da administração, 27 September 1978, fl., *A. M. de Carvalho* 118 (CEPEC); Rio Bananal, Prop. Jonas Grece, 300-450 m, 25 April 2007, fl. cult. 06 September 2007, fl., *R. R. Vervloet* 3398 (MBML); Rio Bananal, Alto Bananal, propr. Jonas Graci, 300-600 m, 25 April 2007, fl., *V. Demuner et al.* 3812 (MBML); Rio Bananal, Alto Bananal, propr. Jonas Graci, 300-600 m, 19°14'56"S, 40°24'59"W, fl. cult. 25 April 2007, fl., *V. Demuner et al.* 3803 (MBML); Rio Bananal, Alto Bananal, propr. Jonas Graci, 300-600 m, 25 April 2007, fl., *V. Demuner et al.* 3813 (MBML); São Mateus, 01 August 2007, fl., *A. G. Oliveira et al.* 77 (SAMES, VIES); São Mateus, Bairro Liberdade, 05 June 2012, fl., *E. M. Aoyama, F. Ribeiro & L. Zontele* 82 (SAMES, VIES); São Mateus, Bairro Liberdade, 17 August 2008, fl., *M. M. Monteiro, A. G. Oliveira & T. C. Souza* 38 (SAMES, VIES); São Mateus, Liberdade, 22 November 2005, fl., *A. G. Oliveira et al.* 398 (SAMES); São Mateus, Área da Petrobrás Inhambú, 18°53'41"S, 39°52'40"W, 28 July 2017, fl., *I. F. Ribeiro et al.* 13 (SAMES).

7. *Cryptanthus bibarrensis* Leme, *Cryptanthus Soc. J.* 17(3): 86 (2002a). [Fig. 2B].

Type:—BRAZIL. Bahia: Itapetinga, Duas Barras, Fazenda Santa Cruz, ca. 300 m elev., *R. F. Reis Júnior s.n.*, fl. cult. December 2001, fl., *E. Leme* 5016 (Holotype: HB digital image! [HB 89875])

Etymology:—It refers to the locality called “Duas Barras” where the specimen type was collected (Leme 2002a).

Distribution and Habitat:—*Cryptanthus bibarrensis* is only known from the Bahia State (municipality of Itapetinga). It occurs in the phytogeographic domain of the Atlantic Forest, at 300 m elevation. It is terricolous and forms small groups spread in the area (Leme 2002a). According to Leme (2002a), it occurs in sympathy with *Cryptanthus reisii* Leme. However, the type locality was visited and the species was not found.

Phenology:—Flowering in cultivation in December.

Conservation status:—*C. bibarrensensis* is known only from the type locality (one location) in a private area. However, the type locality was visited and the species was not found but it may have been due to the restricted distribution of the species. The forest fragment is small and the municipality's vegetation is very fragmented due to pasture activity. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. bibarrensensis* is similar to *C. bahianus* L.B.Sm., *C. sergipensis* I.Ramírez and *C. warren-loosei* Leme due to the leaf blades linear triangular or narrowly triangular but *C. bibarrensensis* differs from them by the ovary with 14 mm long (vs. 4.7–10.5 mm long). The information about ovary length of *C. bibarrensensis* was taken from Leme (2002a) for comparison with the close species.

Specimens examined:—BRAZIL. Bahia: Itapetinga, Duas Barras, Fazenda Santa Cruz, ca. 300 m elev., *R. F. Reis Júnior s.n.*, fl. cult. December 2001, fl., *E. Leme 5016* (HB).

8. *Cryptanthus boanovensensis* Leme, *J. Bromeliad Soc.* 65(2): 93 (2015). [Figs. 2B, 5A, 10].

Type:—BRAZIL. Bahia: Boa Nova, 700 m, June 2013, *P. C. Lima s.n.*, fl. cult., fl., *E. Leme 8769* (holotype: RB digital image! [RB 640189]).

Etymology:—It refers to the municipality Boa Nova where the species was found (Leme 2015).

Distribution and Habitat:—*Cryptanthus boanovensensis* is only known from the Bahia State (municipality of Boa Nova). It occurs in the phytogeographic domain of the Atlantic Forest in transition area between Atlantic Forest and *Caatinga*, at 700 to 800 m elevation. It is terricolous and grows on areas exposed to the sun at the edge of the dry forest and in closed forest with trees about 3 meters high. The vegetation type is called Mata de Cipó (Leme 2015).

Phenology:—Flowering in nature in May and in cultivation in May and June.

Conservation status:—*C. boanovensensis* is known only from the type locality (one location) in a private area. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. boanovensensis* is phylogenetically related to *C. warren-loosei* Leme and *C. crassifolius* Leme that together are included in the warren-loosei clade (Ferreira *et al.* Artigo 1). *C. boanovensensis* differs from *C. warren-loosei* by the flowers 41–52 mm long (vs. 30–37 mm long), petals connate for 7–13 mm long (vs. 3–5 mm long), callosities appearing 9–12 mm distant from the base (vs. 3–5.3 mm distant from the base), filaments 25–28 mm

long (vs. 15.2–19.8 mm long) and anther apices rounded (vs. acute). *C. boanovens* can be confused with *C. crassifolius* by the leaf blade color but *C. boanovens* differs from *C. crassifolius* by the adaxial surface of the leaf blades glabrous except for the base densely lepidote (vs. entirely densely lepidote in the older leaves), floral bracts $17.4\text{--}28 \times 6.7\text{--}19$ mm (vs. $11\text{--}15.5 \times 3.5\text{--}5$ mm), flowers 41–52 mm long (vs. 30.5–39.5 mm long), petals 24.5–36 mm long (vs. 22.5–28.2 mm long), connate for 7–13 mm long (vs. 4–5 mm long), callosities appearing 9–12 mm distant from the base (vs. 5.5–7 mm distant from the base) and filaments 25–28 mm long (vs. 16–20 mm long). *C. boanovens* is not included in the study of Maciel (2020) of the “Flora do Brasil 2020”.

Specimens examined:—BRAZIL. **Bahia:** Boa Nova, 700 m, June 2013, *P. C. Lima s.n.*, fl. cult., fl., *E. Leme 8769* (RB); Boa Nova, Fazenda Cotermaia, 781 m, $14^{\circ}22'27''\text{S}$, $40^{\circ}11'14''\text{W}$, 20 March 2018, fl. cult. 05 April 2018, fl., *D. Cavalcanti & L. Daneu 838* (CEPEC); Boa Nova, Fazenda Cotermaia, 781 m, $14^{\circ}22'27''\text{S}$, $40^{\circ}11'14''\text{W}$, 20 March 2018, fl. cult. 06 June 2018, fl., *D. Cavalcanti & L. Daneu 911* (UFP); Boa Nova, property of Gino Barros, 3.3 km E of Boa Nova on road to Dario Meira, 750–800 m, $14^{\circ}23.084' \text{S}$, $40^{\circ}11.261' \text{W}$, 18 May 2001, fl., *W.W. Thomas & S. Sant'Ana 12502* (NYBG, RB).

9. *Cryptanthus brevibracteatus* D.M.C. Ferreira & Louzada, *Phytotaxa* 523(1): 107 (2021a). [Figs. 2C, 11].

Type:—BRAZIL. Bahia: Boa Nova, Fazenda Cotermaia, 781 m, $14^{\circ}22'26.6''\text{S}$, $40^{\circ}11'14''\text{W}$, 18 October 2020, fl. cult. 29 October 2020, fl., *L. Daneu 744* (holotype: UFP!, isotype: CEPEC!, RB!).

Etymology:—It refers to the small length of floral bracts in relation to other species of the genus (Ferreira *et al.* 2021a).

Distribution and Habitat:—*C. brevibracteatus* is only known from the Bahia State (municipality of Boa Nova). It occurs in the phytogeographic domain of the Atlantic Forest in a transition area between Atlantic Forest and *Caatinga*, at 781 m elevation (Ferreira *et al.* 2021). It is terricolous and grows in forest areas called “Mata de Cipó” with trees becoming about 3 m high (Ferreira *et al.* 2021a).

Phenology:—Flowering in nature in October.

Conservation status:—Recently, *C. brevibracteatus* was classified as Critically Endangered (CR) based on the criterion B2 ab(ii) by Ferreira *et al.* (2021a) due to low number of locations

where the species occurs (only two localities) and due to a possible decline of the area of occupancy.

Taxonomic affinities:—*C. brevibracteatus* is morphologically related to the group of species with leaves sessile, contracted at the base above the leaf sheaths or not contracted at the base, adaxial surface of the leaf blades densely lepidote, glabrous with base and/or apices densely lepidote, sparsely lepidote or glabrous, leaf blades linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic, without longitudinal colored lines along the margins in the living plant with short stem (<8 cm long) and petals white. Among these species, *C. brevibracteatus* is distinguished by the floral bracts $9.2\text{--}10 \times 3.2$ mm (vs. $11\text{--}28 \times 4.7\text{--}22.1$ mm).

Specimens examined:—BRAZIL. **Bahia:** Boa Nova, Fazenda Cotermãia (owner Alipe Maia), entrance 1.2 km E of Boa Nova on Road to Dario Meira, $14^{\circ}22.389'S$, $40^{\circ}11.309'W$, 15 October 2001, fl., *W. W. Thomas et al.* 12642 (CEPEC); Boa Nova, 3.3 km east of Boa Nova on Road to Dario Meira, $14^{\circ}22.983'S$, $40^{\circ}11.177'W$, 15 October 2000, fl., *W. W. Thomas, J. Jardim & S. Sant'Ana* 12272 (CEPEC, NYBG); Boa Nova, Fazenda Cotermãia, 781 m, $14^{\circ}22'26.6''S$, $40^{\circ}11'14''W$, 18 October 2020, fl. cult. 29 October 2020, fl., *L. Daneu* 744 (UFP, CEPEC, RB).

10. *Cryptanthus cinereus* D.M.C.Ferreira & Louzada, *Syst. Bot.* 45(3): 460 (2020). [Figs. 2C, 12].

Type:—BRAZIL. Alagoas: Ibateguara, Sítio Duas Barras, 570 m, $09^{\circ}02'07.5''S$, $35^{\circ}52'31.3''W$, 08 May 2019, fl. and fr., *D. Cavalcanti, E. M. de Almeida, A. Melo, F. G. Silva, W. T. C. C. Santos & V. B. V. Souza* 921 (holotype: UFP!, isotypes: MAC!, RB!, UFRN!, SP!, NY!).

Etymology: — It refers to the densely lepidote indument with a cinereous appearance on the adaxial surfaces of the leaf blades and primary bracts (Ferreira & Louzada 2020).

Distribution and Habitat:—*Cryptanthus cinereus* is only known from the Alagoas State (municipality of Ibateguara). It occurs in the phytogeographic domain of the Atlantic Forest, at 570 m elevation (Ferreira & Louzada 2020). It is rupicolous and grows in areas exposed to the sun and in shaded areas on rocky outcrop (Ferreira & Louzada 2020).

Phenology:—Flowering and fruiting in nature in May.

Conservation status:—*C. cinereus* is known only from the type locality (one location) in a private area. Perhaps the species also occurs in municipality of São Luís do Quitunde, however, the herbarium specimen (*R.P. Lyra-Lemos et al.* 8241-MAC) could not be accurately identified (Ferreira & Louzada 2020). The rocky outcrop where the species occurs is surrounded by pasture areas (Ferreira & Louzada 2020). This species is classified as Critically Endangered (CR) based on the criterion B2 ab(iii).

Taxonomic affinities:—*C. cinereus* is phylogenetically related to *C. alagoanus* Leme & J.A.Siqueira, *C. pickelii* L.B.Sm. and *C. pirambuensis* D.M.C. Ferreira & Louzada that are included in the pickelii clade. *C. cinereus* is differentiated these species mainly by the adaxial surface of the leaf blades entirely densely lepidote in the older leaves (*vs.* glabrous with base and/or apices densely lepidote, or glabrous in the older and younger leaves) and leaf blades narrowly triangular, wider at the base (*vs.* linear-oblongate, oblongate, lanceolate or narrowly elliptic, contracted at the base). *C. cinereus* can be distinguished from species from northeastern that present adaxial surface of the leaf blades entirely densely lepidote in the older leaves by the leaf blades narrowly triangular, wider at the base (*vs.* leaf blades oblongate, narrowly elliptic or elliptic, contracted at base)

Specimens examined:—BRAZIL. **Alagoas:** Ibateguara, Sítio Duas Barras, 570 m, 09°02'07.5"S, 35°52'31.3"W, 08 May 2019, fl. and fr., *D. Cavalcanti et al.* 921 (UFP, MAC, RB, UFRN, SP, NY).

11. *Cryptanthus colnagoi* Rauh & Leme, *J. Bromeliad Soc.* 39: 258 (1989). [Figs. 2C, 5B].

Type:—BRAZIL. Bahia: Potiraguá, 1000 m, *E. Colnago s.n.*, fl., B.G.H. 69 073 (Holotype: HEID digital image! [HEID69073; 700020-sheet 1; HEID69073; 602145-sheet 2]).

Etymology:—It is honor to Euclido Colnago who discovered the species (Rauh *et al.* 1989).

Distribution and Habitat:—*Cryptanthus colnagoi* is only known from the Bahia State (municipality of Potiraguá). The municipality of Potiraguá is included in the phytogeographic domain of the Atlantic Forest. It is terricolous and occurs at 1000 m elevation (Rauh *et al.* 1989).

Phenology:—Unknown.

Conservation status:—*C. colnagoi* is known only from the type locality and another specimen of the Bahia State but without precise locality. There is no precise information about where the species was found (Rauh *et al.* 1989). Since the publication of the species

(thirty-one years ago), no other samples have been collected. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. colnagoi* can be distinguished from other northeastern species that present leaf blades linear, linear-triangular, narrowly triangular or triangular by the leaf blades with revolute margin (*vs.* with straight margin).

Specimens examined:—BRAZIL. **Bahia:** Potiraguá, 1000 m, *E. Colnago s.n.*, fl., B.G.H. 69 073 (HEID); without precise location, 07 July 1981, *L. C. Gurken 152*, fl. cult., fl., *Burle-Marx* (RB).

12. *Cryptanthus crassifolius* Leme, *J. Bromeliad Soc.* 58(1): 17 (2008). [Figs. 2C, 13].

Type:—BRAZIL. Bahia: Ituaçu, Vale do Rio Mato Grosso, 18 March 2002, *M. Moreira s.n.*, fl. cult., fl., *E. Leme 6059* (Holotype: HB photo! [HB 093257]).

Etymology:—It refers to the leaves with succulent texture.

Distribution and Habitat:—*Cryptanthus crassifolius* is only known from the Bahia State (municipality of Ituaçu). It occurs in the phytogeographic domain of the Caatinga, at 525 m elevation. It is terricolous or rupicolous (shallow soil) and occurs in areas exposed to the sun and in partially shaded areas on rock outcrops or around the rock outcrops along of the Mato Grosso river valley .

Phenology:—Flowering in nature in March.

Conservation status:—*C. crassifolius* is known only from the type locality (one location). The population has less than ten individuals and it is located in a touristic area where it can be illegally collected for use as an ornamental plant. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. crassifolius* is phylogenetically close to *C. boanovensisi* Leme and *C. warren-loosei* Leme that together form the warren-loosei clade (Ferreira *et al.* Artigo 1). *C. crassifolius* is easily distinguished of these species by the adaxial surface of the leaf blades entirely densely lepidote in the older leaves (*vs.* glabrous except on the base densely lepidote). For the northeastern, *C. crassifolius* differs from species that have adaxial surface of the leaf blades entirely densely lepidote in the older leaves by the plants with leaf blades 1.1–1.5 cm wide (*vs.* > 2 cm wide).

Specimens examined:—BRAZIL. **Bahia:** Ituaçu, Vale do Rio Mato Grosso, 18 March 2002, *M. Moreira s.n.*, fl. cult., fl., *E. Leme 6059* (HB); Ituaçu, acesso pela cachoeira, entre as pedras do Vale do Rio Mato Grosso, 525 m, 13°48'15"S, 41°17'35"W, 22 March 2018, fl., *D. Cavalcanti & L. Daneu 848* (UFP).

13. *Cryptanthus cruzalmensis* Leme & E.H.Souza, *Phytotaxa* 430(3): 159 (2020). [Figs. 2C, 14].

Type:—BRAZIL. Bahia: Cruz das Almas, Mata do Cazuzinha, near Cruz das Almas downtown, 135 m elevation, 12°39'59"S, 39°06'19.4" W, 19 February 2019, *E. Leme & E. Hilo de Souza 9568* (holotype: RB).

Etymology:—It refers to municipality Cruz das Almas where the species was collected (Leme *et al.* 2020).

Distribution and Habitat:—*Cryptanthus cruzalmensis* is only known from the Bahia State (municipality of Cruz das Almas). It occurs in the phytogeographic domain of the Atlantic Forest, at 135 m elevation (Leme *et al.* 2020). It is terricolous and grows on the shaded forest floor (Leme *et al.* 2020). The population have ca. 250 individuals that occur more or less sparsely distributed in the area (Leme *et al.* 2020).

Phenology:—Flowering in nature in August and December.

Conservation status:—Recently, *C. cruzalmensis* was classified as Critically Endangered (CR) based on the criterion B2 ab(ii, iii) by Leme *et al.* (2020) due to low number of locations that the species occurs (only one locality) and uncontrolled access to the area that is located in a public park and which causes a threat to the species.

Taxonomic affinities:— The information about reproductive characters of *C. cruzalmensis* was taken from Leme *et al.* (2020) for comparison with the close species. *C. cruzalmensis* can be distinguished from species from northeastern that present adaxial surface of the leaf blades entirely densely lepidote in the older leaves by the plants with leaf blades >2 cm wide, leaf blades oblanceolate, narrowly elliptic or elliptic, contracted at base, sepals 12–14 mm long and filaments adnate to the petals for 20 mm. The individuals of *C. cruzalmensis* that have adaxial surface of the leaf blades glabrous with base and/or apices densely lepidote can be confused with *C. ubairensis*. They can be differentiated from *C. ubairensis* by the sepal lobes 5–6 × 5 mm (vs. 4 × 2–2.5 mm) and ovary 7 mm long (vs. 5 mm long). The information

about reproductive characteres of *C. ubairensis* was taken from Ramírez M. (1998) for comparison with *C. cruzalmensis*.

Specimens examined:—BRAZIL. **Bahia:** Cruz das Almas, Mata do Cazuzinha, near Cruz das Almas downtown, 135 m elevation, 12°39'59"S, 39°06'19.4" W, 19 February 2019, *E. Leme & E. Hilo de Souza* 9568 (RB); Cruz das Almas, Mata dentro de la ciudade de Cruz das Almas, 13 August 1994, fl., *I. Ramírez & H. S. Brito* 490 (CEPEC, MO, NYBG); Cruz das Almas, Mata da Cazuzinha, 12°40'39" S, 39°06'23" W, 27 April 2012, *S.S. Simões et al.* 35 (HURB); Cruz das Almas, Mata da Cazuzinha, 12°40'39" S, 39°06'23" W, 30 August 2012, fl., *S.S. Simões et al.* 113 (HURB, HUEFS); Cruz das Almas, Mata da Cazuzinha, 12°39'58.2" S, 39°06'20" W, December 2018, fl., *E.H. Souza* 726 (HURB).

14. *Cryptanthus diamantinensis* Leme, *Harvard Pap. Bot.* 4(1): 137 (1999). [Fig. 2D, 5C].

Type:—BRAZIL. Bahia: Palmeiras, Caeté-Açú, Chapada Diamantina, March 1997, *J. C. Garcia & R. de Oliveira*, fl. cult. April 1997, fl., *E. Leme* 3812 (Holotype: HB image! [HB 81972]).

Etymology:—It refers to Chapada Diamantina where the species was found (Leme 1999).

Distribution and Habitat:—*Cryptanthus diamantinensis* is only known from the Bahia State (municipality of Palmeiras). It occurs in the phytogeographic domain of the Caatinga. It is rupicolous and grows on reasonably flat rocky surfaces in the Chapada Diamantina (Leme 1999).

Phenology:—Flowering in cultivation in April.

Conservation status:—*C. diamantinensis* is known only from the type locality (one location). Since its discovery (21 years ago), no other samples have been collected. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:— The information about reproductive characteres of *C. diamantinensis* was taken from Leme (1999) for comparison with the close species. *C. diamantinensis* is morphologically related to the group of species with leaves sessile, contracted at the base above the leaf sheaths or not contracted at the base leaf blades linear, linear triangular, narrowly triangular or triangular, straight margin, adaxial surface of the leaf blades glabrous with base and/or apices densely lepidote, or glabrous in the older and younger leaves, leaf blades without longitudinal colored lines along the margins in the living plant,

short stem < 8 cm and petals white that includes the species *C. bahianus* L.B.Sm., *C. boanovensensis* Leme, *C. seidelianus* W. Weber, *C. reisii* Leme, *C. sergipensis* I. Ramírez and *C. warren-loosei* Leme. Among these species, *C. diamantinensis* is distinguished by the floral bracts 9 mm long (vs. 10–31 mm long) and apices anthers apiculate (vs. emarginate, rounded or acute).

Specimens examined:—BRAZIL. **Bahia:** Palmeiras, Caeté-Açú, Chapada Diamantina, March 1997, *J. C. Garcia & R. de Oliveira*, fl. cult. April 1997, fl., *E. Leme 3812* (HB); Palmeiras, Caeti-Açu, Chapada Diamantina, March 1997, *R. de Oliveira s.n.*, fl. cult., fl., *E.M.C. Leme 3813* (RB).

15. *Cryptanthus diana*e Leme, *Cryptanthus Soc. J.* 5(2): 10. 1990a. [Figs. 2D, 15].

Type:—BRAZIL. Goiás: Ceres, *A. Seidel 1072*, fl. cult. August 1989, *E.M.C. Leme 1172* (Holotype: HB photo! [HB 73717])

Etymology:—It is honor to Diana Seidel that is daughter of Alvim Seidel who collected the species (Leme 1990a).

Distribution and Habitat:—*Cryptanthus diana*e is known from the Alagoas (Boca da Mata, Chã Preta, Coruripe, Flexeiras, Ibateguara, Joaquim Gomes, Quebrangulo, Maceió, Messias, Murici, Penedo, Piaçabuçu, Satuba, São Miguel dos Campos, São Sebastião and União dos Palmares) and Pernambuco (municipality of Lagoa dos Gatos, Quipapá, Jaqueira, São Benedito do Sul, São Lourenço da Mata, São Vicente Ferrer and Tapera) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 47 to 737 m elevation in the following vegetation types: lowland semideciduous seasonal forest and submontane tropical moist forest. It is terricolous or rupicolous (shallow soil) and grows on dense litter layer of clayey soils.

Phenology:—Flowering in nature in February, April, May, June, July, August, September, October and November and in cultivation in February, August and September.

Conservation status:—*C. diana*e is known to 24 locations, five of which are located in conservation units: Parque Estadual da Pedra Talhada, Estação Ecológica de Murici, Reserva Ecológica do Tapacurá, RPPN Frei Caneca, APA do Catolé and Usina Serra Grande. The extent of occurrence (EOO) is 20,107.997 km² and the the area of occupancy (AOO) is 112 km². The species is located in the Atlantic Forest that is severely fragmented and possibly the species can be suffering a decline in the extent of occurrence and area of occupancy. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(i, ii, iii).

Taxonomic Notes:—The species occurs in the state of Pernambuco and Alagoas, however, the holotype erroneously indicates that the species occurs in the Goiás State.

Taxonomic affinities:—*C. diana* is phylogenetically close to *C. reptans* Leme & J.A.Siqueira and *C. zonatus* (Vis.) Vis. that together form the *zonatus* clade (Ferreira *et al.* Artigo 1). Ferreira & Louzada (2020) include *C. reptans*, *C. diana* and *C. zonatus* in the *C. zonatus* (Vis.) Vis. complex due to their morphological overlap. This relationship is confirmed in the study of Ferreira *et al.* (Artigo 1). The authors recommend population genetic studies to resolve this complex. Some individuals of *C. diana* have adaxial surface of the leaf blades entirely densely lepidote in the older leaves and they can be confused with *C. pseudopetiolatus* Philcox but *C. diana* differs from *C. pseudopetiolatus* by the petals 33–42.5 mm long (vs. 24.5–29.5 mm long), styles 26.2–36 mm long (vs. ca. 24.5 mm long) and epigynous tube 1–1.2 mm long (vs. 2.3–4 mm long). Individuals long caulescent of *C. diana* can be confused with *C. vexatus* but *C. diana* differs from *C. vexatus* by the sepals connate for 10–11 mm (vs. 4–5 mm long), petals 33–45 mm long (vs. 25 mm long) and filaments 22–36 mm long (vs. 13 mm long). The information about reproductive characteres of *C. vexatus* was taken from Leme (1995) for comparison with *C. diana*.

Specimens examined:—BRAZIL. **Alagoas:** Boca da Mata, Fazenda Daniel, Mata da Bitonha, próximo à Serra da Naceia, 208 m, 09°36'24.2"S, 36°12'07.7"W, 01 November 2002, fl., J. A. Siqueira-Filho 1309 (MAC, UFP); Chã Preta, Serra Lisa, 06 May 2009, fl., C. Mota & N. Ramos 3572 (MAC); Coruripe, Al-425, 29 July 1981, fl., R. P. de Lyra & G. L. Esteves 329 (MAC); Coruripe, Fazenda Águas de Pituba II, 26 July 2008, fl., M. N. Rodrigues & F. Pinto s.n. (MAC 35056); Coruripe, Usina Coruripe, Mata do Rio das Pedras, 25 September 1999, fl., A. M. Amorim, R. Lyra-Lemos & I. A. Bayma 3117 (MAC); Coruripe, Capiatã, 04 February 2011, fl., Chagas-Mota 10141 (MAC); Divisa dos Municípios de Flecheiras e Maceió, Serra da Cachoeira, 09°23'38.2"S, 35°43'40"W, 30 October 2002, fl., J.A. Siqueira-Filho 1299 (UFP); Ibateguara, Coimbra, Cerrado da Burra, 09 September 2002, fl., M. Oliveira & A. A. Grillo 1097 (UFRN, UFP); Ibateguara, Coimbra, Grota da Burra, 29 March 2011, fl., Chagas-Mota 10577 (MAC); Ibateguara, Usina Serra Grande, Engenho Coimbra, Grota da Burra, 450 m, 08°59'25"S, 35°50'35.9"W, 01 August 2003, fl., J.A. Siqueira-Filho 1385 (UFP); Joaquim Gomes, 245 m, 09°01'27"S, 35°29'28"W, 04 July 2016, fl., A. A. S. Mascarenhas, T. V. A. Santos & D. Carvalho 79 (MAC); Quebrangulo, Parque Estadual da Pedra Talhada, 23 September 1987, fl., R. P. Lyra-Lemos & I. Moreira 1453 (IPA); Quebrangulo, REBIO Pedra Talhada, 04 September 2012, fl., B. S. Amorim *et al.* 1621 (JPB); Quebrangulo, Parque Estadual da Pedra Talhada, próximo ao lajedo tres Lagoas, 23

July 1987, fl., *M. N. R. Staviski et al.* 1096 (MAC); Quebrangulo, Reserva Biológica Pedra Talhada, 05 October 2010, fl., *Chagas-Mota* 8842 (MAC); Quebrangulo, Reserva Biológica Pedra Talhada, Lajedo do Junco, 9°14'30"S, 36°25'12"W, 06 October 2013, fl., *R. P. Lyra-Lemos, J. S. Correia & A. Santos* 13828 (MAC); Maceió, Parque Municipal, 23 May 2008, fl., *R. P. Lyra-Lemos & L. Conserva* 11344 (MAC); Maceió, Serra da Saudinha, Fazenda Cela, 14 June 2008, fl., *Chagas-Mota* 638 (MAC); Maceió, Serra da Saudinha, 06 May 2006, fl., *P. A. F. Rios s.n.* (MAC 29108); Messias, Eng. Oriente, Serra da Cachoeira, 11 June 1980, fl., *Andrade-Lima, F. Gallindo & Correia-Lima* 45 (IPA); Murici, Estação Ecológica de Murici, Fazenda Bananeiras, 21 April 2012, fl., *M. C. S. Mota, E. C. O. Chagas & J. M. Silva* 11537 (MAC); Murici, Poço D'Anta, ca. 16-19 km NNW of Murici by road. Mata de Murici, 550-600 m, 09°13.530'S, 35°52.776'W, 15 May 2001, fl., *W.W. Thomas et al.* 12451 (RB, NYBG); Murici, Fazenda Itamaracá, Mata da Pedreira, 136 m, 09°21'25.1"S, 35°51'07.6"W, 29 October 2002, fl., *J.A. Siqueira-Filho* 1285 (UFP); Murici, ESEC Murici, Mata das Bananeiras, 09°12'52"S, 35°52'22"W, 02 April 2013, fl., *B.S. Amorim, J.L. Costa-Lima & E. Pessoa* 1794 (UFP); Murici, Estação Ecológica de Murici, Fazenda Experimental de floração e cruzamento de Serra do Ouro, UFAL, 468 m, 09°14'25.3'S, 35°50'15.1"W, 18 March 2005, sterile, *J. A. Siqueira-Filho* 1481 (UFP); Murici, Mata Atlântica em encosta, caminho para a "Pedra da Moça", 24 April 1993, fl., *R. P. Lyra-Lemos* 2719 (MAC); Murici, Estação Ecológica de Murici, 21 October 2011, fl., *Chagas-Mota & J. W. Alves-Silva* 11225 (MAC); Murici, Estação Ecológica de Murici, Fazenda Bananeiras, 14 September 2012, fl., *M. C. S. Mota & E. C. O. Chagas* 11758 (MAC); Penedo, Usina Paísa, Fazenda Santa Amélia, 30 October, fl., *J.A. Siqueira-Filho, E.M.C. Leme & J.B. Oliveira* 1433 (UFP); Piaçabuçu, acesso ao pontal do Peba, September 1983, fl., *R. Rocha* 551 (MAC); Satuba, APA do Catolé, Propriedade da CEAL, 47 m, 09°33'38.9"S, 35°47'44.7"W, 31 October 2002, fl., *J.A. Siqueira-Filho* 1301 (UFP); Satuba, APA do Catolé e Fernão Velho, 10 February 1999, fl., *M. N. R. Staviski* 1509 (MAC); São Miguel dos Campos, Km 127 da BR-101, Faz. Pau-Brasil, 15 July 1980, sterile, *M. N. R. Staviski* 3 (MAC); São Miguel dos Campos, Km 127 da BR-101, Faz. Pau-Brasil, 15 July 1980, sterile, *M. N. R. Staviski* 2 (MAC); São Sebastião, Fazenda Indiana, 04 October 2009, fl. and fr., *Chagas-Mota & V. G. Ramalho* 6017 (MAC); União dos Palmares, sopé ocidental da Serra do Frio, 12 June 1980, fl., *G. L. Esteves et al.* 420 (MAC); [without precise location], Cachoeira do Mirim, 28 September 2002, fl., *A. Frassy & J. Simplicio s.n.* (ALCB 80351, MAC 17637). **Pernambuco:** Lagoa dos Gatos, Serra do Urubú, 680 m, 08°43'59"S, 35°50'43"W, 03 March 2016, sterile, *R. A. Pontes* 1130 (UFRN); Quipapá, 16 June 1972, fl., *Andrade-Lima* 72-8270 (IPA); Jaqueira Serra do Urubu, RPPN

Frei Caneca, Mata do Quengo, 28 April 2014, fl. cult. 21 August 2017, fl., *D. Cavalcanti et al.* 679 (UFP); Jaqueira, Serra do Urubu, RPPN Frei Caneca, Mata do Quengo, 737 m, 08°42'44"S, 35°50'31"W, 20 September 2017, fl., *D. Cavalcanti et al.* 801 (UFP); Jaqueira, Serra do Urubu, RPPN Frei Caneca, Mata do Quengo, 737 m, 08°42'44"S, 35°50'31"W, 28 April 2014, fl. cult. 12 September 2017, *D. Cavalcanti et al.* 912 (UFP, RB); Jaqueira, Serra do Urubu, RPPN Frei Caneca, Mata das Moças, 610 m, 08°43'33"S, 35°50'32"W, 21 September 2017, fl., *D. Cavalcanti et al.* 799 (UFP, RB); Jaqueira, Serra do Urubu, fl. cult. 23 February 2018, fl., *D. Cavalcanti & M. L. Bazante* 898 (UFP); Jaqueira, Usina Colônia, Mata da Serra do Quengo, 750 m, 08°42'37"S, 35°50'01"W, 08 July 2000, fl., *J.A. Siqueira-Filho* 1088 (UFP); Jaqueira, Usina Catende, Engenho flor do bosque, 08°44'04"S, 35°46'15"W, 18 April 2004, fl., *J.A. Siqueira-Filho* 1430 (UFP); São Benedito do Sul, Mata do Periperi (terras pertencentes a falida Usina Água Branca), 250 m, 28 September 1997, fr., *J. A. Siqueira-Filho & M. J. A. Campelo* 741 (UFP); São Lourenço da Mata, Reserva Ecológica do Tapacurá, Mata do Camocim, 08°04'00"S, 35°14'00"W, 15 May 1997, fl., *J. A. Siqueira-Filho* 607 (UFP); São Lourenço da Mata, Reserva Ecológica do Tapacurá, Mata do Camocim, 21 February 1977, *I. Pontual* 77-1537 (PEUFR); São Vicente Ferrer, Mata do Estado, 12 November 2014, fl., *D. Cavalcanti, R. Farias & R. Louzada* 771 (UFP); Tapera, Mata do Toró, 23 September 1969, fl., *H. Alves* 16 (UFP).

16. *Cryptanthus* sp. [Figs. 2D, 16].

Distribution and habitat:—*Cryptanthus* sp. is only known from the Bahia State (municipality of Lençóis, Jacobina, Miguel Calmon, Mucugê and Pindobaçu). It occurs in the phytogeographic domain of the Caatinga, at 590 to 760 m elevation. It is rupicolous and grows on litter in areas exposed to the sun and in shaded areas in the Chapada Diamantina.

Phenology:—Flowering in nature is in December and in cultivation is in March.

Conservation status:—*Cryptanthus* sp. is known to four locations, one of which is located in conservation units: Parque Nacional da Chapada Diamantina. The extent of occurrence (EOO) is 8,092.690 km² and the the area of occupancy (AOO) is 16 km². The species is known for few localities where only one is included in one protected area. And it can be declining the quality of habitat since the species occurs in an area that may be collected for use as ornamental. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(iv).

Taxonomic affinities:—*Cryptanthus sp.* is morphologically related to *C. arelli* H. Luther by the leaf blades color. Both occur in the Chapada Diamantina in Bahia State. However, *Cryptanthus sp.* can be distinguished from *C. arelli* by the apical glomerule of the inflorescence with ca. 14 flowers (vs. 8–10 flowers) and floral bracts white (vs. cream or pale green). The information about morphological characters of *C. arelli* was taken from Luther (1999) for comparison with *C. sp.*

Specimens examined:—BRAZIL. **Bahia:** Lençóis, Cachoeira da Cravada, 12°22'S, 41°23'W, 15 December 2005, fl., *A. A. Conceição & A. Caetano 1622* (HUEFS); Miguel Calmon, Piemonte da Diamantina, trilha para a Grota de Dona Antônia, 11°20'S, 40°31'W, 03 August 2006, sterile, *G. Carvalho et al. 120* (ALCB, HUNEB); Mucugê, Canyon da Fumacinha, 760 m, 13°17'10"S, 41°15'37"W, 16 December 2019, fl. cult. 03 March 2020, fl., *E. M. Almeida 3432* (UFP); Pindobaçu, Serra da Fumaça, 750 m, 10°41'44"S, 40°22'48"W, 08 April 2014, sterile, *A.P. Fontana 8914* (MBML).

17. *Cryptanthus felixii* J.A.Siqueira & Leme, *Fragm. Atlantic Forest N. E. Brazil*: 285 (2007). [Figs. 2D, 17].

Type:—Brazil, Pernambuco: Bonito, Fazenda Muito Tudo, 789 m, 8°30'37.6"S, 35°43'14.3"W, 6 December 2003, fl., *J.A. Siqueira-Filho & L. P. Felix 1422* (Holotype: UFP! [UFP 39386]; Isotype: HB image! [HB 093236]).

Etymology:—It is honor to botanist Dr. Leonardo Pessoa Felix from Paraíba Federal University in Areia (Leme & Siqueira-Filho 2007).

Distribution and Habitat:—*Cryptanthus felixii* is known from the Alagoas (Chã Preta and Ibateguara) and Pernambuco (municipality of Bonito) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 789 m elevation. It is terricolous or rupicolous (shallow soil) and occurs in closed forest next to the river in Brejos de Altitude.

Phenology:—Flowering in nature in December and in cultivation in February.

Conservation status:—*C. felixii* is known to three locations, one of which is in conservation unit: Usina Serra Grande. The species is located in the Atlantic Forest that is severely fragmented and possibly the species can be suffering a decline in the extent of occurrence and area of occupancy. Thus, this species is classified as Critically Endangered (CR) based on the criterion B2 ab(i, ii).

Taxonomic affinities:— The information about reproductive characteres of *C. felixii* was taken from Leme & Siqueira-Filho (2007) for comparison with the close species. *C. felixii* is morphologically related to the group of species with adaxial surface of the leaf blades densely lepidote, glabrous with base and/or apices densely lepidote, sparsely lepidote or glabrous, leaf blades linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic, without longitudinal colored lines along the margins in the living plant with long stem (≥ 8 cm long) and petals white. Among these species, *C. felixii* is distinguished by the ovary 15–20 mm long (vs. 2.5–10.5 mm long).

Specimens examined:—BRAZIL. **Alagoas:** [Chã Preta], Serra Lisa, August 2002, *A. Frassy s.n.*, fl. cult. February 2004, fl., *E. Leme 5540* (HB); Ibatiguara, Usina Serra Grande, Engenho Coimbra, 17 December 2002, fl., *J.A.Siqueira-Filho s.n.*, *E. Leme 5671* (HB). **Pernambuco:** Bonito, Fazenda Muito Tudo, 789 m, 8°30'37.6"S, 35°43'14.3"W, 6 December 2003, fl., *J.A. Siqueira-Filho & L. P. Felix 1422* (UFP).

18. *Cryptanthus ilhanus* Leme, *Phytotaxa* 108(1): 16 (2013). [Fig. 2D].

Type:—BRAZIL. Bahia: Guaratinga, São João do Sul, Pedra Pontuda, 415 m, 16° 36' 32.63" S 39° 55' 39.96" W, May 2009, *A. Ilha s.n.*, fl. cult. *E. Leme 7842* (holotype: RB digital image! [RB 303384]).

Etymology:—It is honor to André Ilha from Instituto Estadual do Ambiente (Leme & Kollmann 2013).

Distribution and Habitat:—*Cryptanthus ilhanus* is only known from the Bahia State (municipality of Guaratinga). It occurs in the phytogeographic domain of the Atlantic Forest, at 369 to 415 m elevation. It is terricolous and grows on shallow soils partially shaded by small trees and shrubs near the foothill of an inselberg (Leme & Kollmann 2013).

Phenology:—Flowering in nature in April and in cultivation in May.

Conservation status:—*C. ilhanus* is known to two locations and no population is included in conservation unit. The type locality was visited but the species was not found possibly due to the restricted and grouped distribution of the species. In addition, the species was collected by André Ilha alpinist and may have difficult access. The inselberg of the type locality is surrounded by pasture areas and the cattle can climb part of the inselberg. Thus, this species is classified as Critically Endangered (CR) based on the criterion B2 ab(iii).

Taxonomic affinities:—The information about leaf blade color of *C. ilhanus* was taken from Leme & Kollmann (2013) for comparison with the close species. *C. ilhanus* differs from all species of the northeastern by its distinct leaf blade color with two longitudinal lines reddish to bronze colored along the margins with the median longitudinal zone green to yellowish-green in the living plant (vs. leaf blades without longitudinal colored lines along the margins in the living plant).

Specimens examined:—BRAZIL. **Bahia:** Guaratinga, Córrego Jacutinga, 369 m, 16°38'27"S, 39°47'54"W, 23 April 2009, fl., *A. P. Fontana et al.* 5913 (MBML); Guaratinga, São João do Sul, Pedra Pontuda, 415 m, 16° 36' 32.63" S 39° 55' 39.96" W, *A. Ilha s.n.*, fl. cult. May 2009, fl., *E. Leme* 7842 (RB).

19. *Cryptanthus lacerdae* Antoine, *Wiener Ill. Gart.-Zeitung* 7: 254 (1882). [Figs. 3A, 5-D].

Type:—BRAZIL. Without more precise locality, *Vienna Hortus s.n.* (Holotype: W, lost according to Ramírez M. (1998: 223)); Without precise locality, from cultivation: *M. B. & R. Foster* 1176 (Neotype, designated by Ramírez M. (1998: 223): GH digital image! [Barcode 00139555]).

Etymology:—It is honor to Dr. João Baptista de Lacerda from National Museum of Brazil (Ramírez-Morillo 1996).

Distribution and Habitat:—*C. lacerdae* is only known from the Bahia State. However, there is no more information about where the species was found. Most herbarium specimens have no precise location.

Phenology:—Unknown.

Conservation status:—Almost all specimens of *C. lacerdae* are from cultivated plants without a precise location. Ramírez-Morillo (1996) indicates that the species has never been collected in the field and it is probably extinct. However, one specimen was collected for the Bahia State, but there is no more information about where the species was found. Thus, the species is classified as Data Deficient (DD).

Taxonomic affinities:—*C. lacerdae* can be recognized by the adaxial surface of the leaf blades with three longitudinal lines of lepidote trichomes. However, some individuals may not have this characteristic. Thus, *C. lacerdae* is morphologically related to the group of species with petals white with apices green or greenish. Among these species, *C. lacerdae* is distinguished by the leaf blades that never exceed 7.5 cm long (vs. leaf blades that exceed 7.5

cm long in the adult leaf blades). The information about color of the petals of *C. lacerdae* was taken from Ramírez-Morillo (1996) for comparison with the close species.

Specimens examined:—BRAZIL. **Bahia:** [without precise location], 1981, *L. K. C. Araújo s.n.*, *E.M.C. Leme 200* (RB). **Without precise location:** October 1951, *M. B. & R. Foster 1176* (GH); fl. cult. March 1950, fl., *N. B. Foster 1176* (US); fl. cult. 1952, fl., *N. B. Foster s.n.* (US 2169555).

20. *Cryptanthus lyman-smithii* Leme, *Harvard Pap. Bot.* 4(1): 135 (1999). [Fig. 3A].

Type:—BRAZIL. Bahia: Jaguaripe, Road Aratuípe to Camassandi, 24 July 1998, fl. cult. September 1998, fl., *E. Leme, S. Linhares & R. Alves 4342* (Holotype: HB digital image! [HB 84096]; Isotype: HB digital image! [HB 89578]).

Etymology:—It is honor to Lyman B. Smith that described many *Cryptanthus* species (Leme 1999).

Distribution and Habitat:—*Cryptanthus lyman-smithii* is only known to the Bahia State (municipality of Jaguaripe). It occurs in the phytogeographic domain of the Atlantic Forest (Leme 1999). It is terricolous and grows on dense litter layer, the population occurs sparsely spread (Leme 1999).

Phenology:—Flowering in cultivation in September.

Conservation status:—*C. lyman-smithii* is known only from the type locality (one location) in the Atlantic Forest in the municipality of Jaguaripe that is severely fragmented. Since its discovery (21 years ago), no other samples have been collected. Possibly the species can be suffering a decline in the area of occupancy. Thus, this species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic Notes:—Leme (1999) indicates that the isotype is in CEPEC herbarium, however, the isotype is in HB herbarium.

Taxonomic affinities:—*C. lyman-smithii* is differentiated from other species that present petioles (*C. beuckeri* E. Morren, *C. teretifolius* Leme and *C. walkerianus* Leme & L.Kollmann) by the petals white except for slightly greenish apex (vs. petals white). The information about color of the petals of *C. lyman-smithii* was taken from Leme (1999) for comparison with the close species.

Specimens examined:—BRAZIL. **Bahia:** Jaguaripe, Road Aratuípe to Camassandi, 24 July 1998, fl. cult. September 1998, fl., *E. Leme, S. Linhares & R. Alves 4342* (HB).

21. *Cryptanthus osiris* W.Weber, *Feddes Repert.* 93 (5): 337 (1982). [Figs. 3A, 5E].

Type:—BRAZIL. Brasilia sine loco, 1974, fl. cult. in Hortus Weberi 18 July 1979, fl., *Amanda et Michael Bleher* 125 (Holotype: HAL! [HAL075359])

Etymology:—Unknown.

Distribution and Habitat:— There is no indication of the state where the species occurs in Weber (1982). However, the holotype indicates that the species occurs in Bahia State near the coast.

Phenology:—Flowering in cultivation in July.

Conservation status:—*C. osiris* is known only from the type locality (one location). Since its discovery (thirty-eight years ago), no other samples have been collected. The species is located in the Atlantic Forest that is severely fragmented. However, there is no precise information about the place of collection of the species. Thus, this species is classified as Data Deficient (DD).

Taxonomic affinities:—*C. osiris* is morphologically related to the group of species with leaves sessile, contracted at the base above the leaf sheaths or not contracted at the base, adaxial surface of the leaf blades densely lepidote, glabrous with base and/or apices densely lepidote, sparsely lepidote or glabrous, leaf blades linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic, without longitudinal colored lines along the margins in the living plant with short stem (<8 cm long), petals white and floral bracts 11–28 × 4.7–22.1 mm. Among these species, *C. osiris* is distinguished by the sepals connate for 2 mm long (vs. 4–16 mm). *C. osiris* can be confused with *C. pseudopetiolatus* due to the leaf blades shape but *C. osiris* differs from *C. pseudopetiolatus* by the sepals connate for 2 mm long (vs. 7–7.3 mm long). For Ramírez-Morillo (1996), the holotype of *C. osiris* is a young plant of *C. pseudopetiolatus* Philcox.

Specimens examined:—BRAZIL. Brasilia sine loco, 1974, fl. cult. in Hortus Weberi 18 July 1979, fl., *Amanda et Michael Bleher* 125 (HAL).

22. *Cryptanthus pickelii* L.B.Sm., *Smithsonian Misc. Collect.* 126(1): 25 (1955). [Figs. 3A, 18].

Type:— BRAZIL. Pernambuco: São Lourenço da Mata, collected in forest, Toró, Escola de São Bento, near Tapera, 12 March 1925, fl., *B.J. Pickel* 909 (Holotype: IPA, US image! [Barcode 0026819; US2198828]).

Etymology:—It is honor to Bento José Pickel who collected the species.

Distribution and Habitat:—*Cryptanthus pickelii* is known to the Paraíba (municipality of João Pessoa, Mamanguape and Santa Rita) and Pernambuco (Camaragibe, Goiana, Gravatá, Ipouca, Paulista, Rio Formoso, São Lourenço da Mata and Tamandaré) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 14 to 681 m elevation. It is terricolous and grows on clay soil in semideciduous seasonal forest and Brejos de Altitude.

Phenology:—Flowering in nature in January, March, April, May, July, September and October, and in cultivation in January, February, March, June and December. Fruiting in nature in October.

Conservation status:—*C. pickelii* is known to 14 locations, four of which are located in conservation units: Estação Ecológica de Caetés, RPPN Serra do Contente, Reserva Biológica de Tapacurá and Reserva Biológica de Saltinho. The extent of occurrence (EOO) is 10,877.087 km² and the area of occupancy (AOO) is 48 km². The species is located in the Atlantic Forest that is severely fragmented and it can be suffering a decline in the extent of occurrence and area of occupancy. Thus, this species is classified as Endangered (EN) based on the criterion B2 ab(i, ii).

Taxonomic affinities:—*C. pickelii* is phylogenetically related to *C. alagoanus* Leme & J.A.Siqueira, *C. cinereus* D.M.C. Ferreira & Louzada and *C. pirambuensis* D.M.C. Ferreira & Louzada that together are included in the *pickelii* clade. Ferreira & Louzada (2020) include *C. alagoanus* and *C. pickelii* in *Cryptanthus pickelii* L. B. Sm. complex due to their morphological overlap. In the phylogenetic study of Ferreira *et al.* (Artigo 1), the authors confirm the complex and recommend population genetic studies to resolve this complex.

Specimens examined:—BRAZIL. **Paraíba:** João Pessoa: Jardim Botânico, 47 m, 29 September 2004, sterile, *P.C. Gadelha-Neto et al.* 1285 (JPB); Mamanguape, Estação Ecológica do Pau Brasil, 06°36'16"S, 35°07'45"W, 06 July 2008, fl., *S. Satyro* 94 (JPB); Rio Tinto [Mamanguape], mata da Reserva Ecológica do Pau Brasil, 28 April 2005, fl., *R. A. Pontes & P. C. Gadelha-Neto* 205 (RB); Rio Tinto [Mamanguape], mata da Reserva Ecológica do Pau Brasil, 28 April 2005, fl., *R. A. Pontes & P. C. Gadelha-Neto* 206 (JPB); Mamanguape, Estação Ecológica do Pau Brasil, 82 m, 06°36'20"S, 35°08'04"W, 08 October 2017, fr., *D. Cavalcanti & F. M. Guedes* 827 (UFP); Mamanguape, Estação Ecológica do Pau Brasil, Pitanga da Estrada, 82 m, 06°36'20"S, 35°08'04"W, 08 October 2017, fl. cult. 01 March 2018, *D. Cavalcanti & F. M. Guedes* 905 (UFP, RB); Santa Rita, Mata da Usina São João, October 2011, fl., *R. A. Pontes & G. S. Baracho* 50 (JPB); Santa Rita, Mata da Usina São João, 17 September 2002, fl., *R. A. Pontes & G. S. Baracho* 53 (JPB). **Pernambuco:**

Camaragibe, Aldeia, Mata do Condomínio Torquato Castro, n°11.971, 7°56'38"S, 35°02'09"W, 17 July 2017, fl. cult. 04 December 2017, fl., *D. Cavalcanti & V. Aya* 782 (RB); Camaragibe, Aldeia, Mata do Condomínio Torquato Castro, n°11.971, 7°56'38"S, 35°02'09"W, 17 July 2017, fl. cult. 22 December 2017, fl., *D. Cavalcanti & V. Aya* 908 (UFP); Camaragibe, Aldeia, Mata do Condomínio Torquato Castro, n°11.971, 7°56'38"S, 35°02'09"W, 17 July 2017, fl. cult. 28 June 2018, fl., *D. Cavalcanti & V. Aya* 909 (JPB); Goiana, RPPN Fazenda Tabatinga, 07°36'22"S, 34°49'14"W, 30 May 2011, fl. cult. January-February 2014, *D. Cavalcanti et al.* 536 (UFP); Gravatá, RPPN Serra do Contente, 08°15'50"S, 35°33'07"W, 03 July 2014, fl. cult. 12 December 2014, fl., *D. Cavalcanti, R. Louzada & F. Silva* 730 (UFP); Ipojuca, Mata do Cupe, 08°26'28"S, 34°59'33"W, 13 October 2014, *D. Cavalcanti et al.* 766 (UFP); Paulista, Estação Ecológica de Caetés, 61 m, 07°55'45"S, 34°55'47"W, 16 December 2014, fl. cul. 29 June 2017, fl., *D. Cavalcanti & J. Oliveira-Júnior* 773 (UFP); Paulista, Estação Ecológica de Caetés, 61 m, 07°55'45"S, 34°55'47"W, 16 December 2014, fl. cul. 28 December 2018, fl., *D. Cavalcanti & J. Oliveira-Júnior* 913 (UFP); Paulista, Cova da Onça, Sítio Pankararu, RPPN/IBAMA, 14 m, 07°56'S, 34°52'W, 20 June 1998, sterile, *G.S. Baracho & J.A. Siqueira-Filho* 739/805 (UFP); Rio Formoso Usina Trapiche, Mata de Jindaí, 35 m, 08°27'01.8"S, 34°59'15.8"W, 27 March 2004, fl., *J.A. Siqueira-Filho & E.M.C. Leme* 1428 (UFP); São Bento, Tapéra, Mata do Toró, 27 January 1955, fl., *J.C. de Moraes* 1237 (EAN); São Lourenço da Mata, Reserva Ecológica de Tapacurá, Mata do Camocim, 85 m, 08°04'00"S, 35°14'00"W, 15 May 1997, sterile, *J.A. Siqueira-Filho* 611 (UFP); São Lourenço da Mata, Toró, Escola de São Bento, near Tapera, 12 March 1925, fl., *B. J. Pickel* 999 (IPA); São Lourenço da Mata, Escola de São Bento, Mata do Córrego da Bexiga, May 1927, fl., *B. J. Pickel* 909 (IPA, US); Tamandaré, Reserva Biológica de Saltinho, bolha mamucaba, 08°43'91"S, 35°10'66"W, 02 September 1998, fl., *G. Martinelli et al.* 15133 (RB).

23. *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada, Artigo 2. [Figs. 3A, 19].

Type:—BRAZIL. Sergipe: Pirambu: Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 18 April 2018, fl., *D. Cavalcanti & E. Ferreira* 904 (UFP!).

Etymology:—It refers to the municipality where the species was found (Ferreira & Louzada Artigo 2).

Distribution and Habitat:—*Cryptanthus pirambuensis* is known from the Sergipe State (municipality of Pirambu). It occurs in the phytogeographic domain of the Atlantic Forest

from sea level to about 50 m elevation. It is terricolous and grows on clay soil in semideciduous seasonal forest and on sandy soils in closed forests formations of Restinga.

Phenology:—Flowering in cultivation in January, April and July.

Conservation status:—*Cryptanthus pirambuensis* is known to two locations, one of which is in conservation unit: Reserva Biológica de Santa Isabel. The second population occurs in a forest remnant with evidences of wood cutting. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*Cryptanthus pirambuensis* can be confused with *C. pseudopetiolatus* Philcox due to the leaf blades color and the number of flowers in lateral glomerule but *C. pirambuensis* differs from *C. pseudopetiolatus* by the floral bracts 27.5–34 mm long (vs. 19–23 mm long), flowers 44–61 mm long (vs. 29.5–37 mm long), sepals 20–22.5 mm long (vs. 15.5–17.5 mm long), sepals lobes narrowly elliptic or elliptic (vs. ovate or lanceolate), petals connate for 12–22 mm (vs. 3.2–6 mm long), callosities of the petals appearing 12.5–22 mm distant from the base (vs. 4–5 mm distant from the base), stigma lobes 6–7.2 mm in the perfect flowers (vs. 3.2 mm long in the perfect flowers) and ovary with 15–17 ovules per locule in the perfect flowers (vs. 8–9 ovules per locule in the perfect flowers). *C. pirambuensis* is compared to *C. alagoanus* Leme & J.A. Siqueira but *C. pirambuensis* differs from *C. alagoanus* by the number of flowers in the apical glomerule of the inflorescence with 17–24 flowers (vs. ca. 8 flowers) (Ferreira & Louzada Artigo 2).

Specimens examined:—BRAZIL. **Sergipe:** Pirambu, Margem esquerda da estrada no bosque, 46 m, 10°36'52.40"S, 36°42'25.90"W, 19 October 2012, sterile, *J.A. Siqueira-Filho* 2866 (HURB); Pirambu, Mata de Sambaíba, 40 m, 10°39'22.20"S, 36°51'48.50"W, 02 July 2010, fl. cult. 19 January 2013, *J. A. Siqueira-Filho et al.* 2896 (HURB); Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 28 June 2018, *D. Cavalcanti & E. Ferreira* 829 (UFP); Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 11 April 2018, *D. Cavalcanti & E. Ferreira* 903 (ASE); Pirambu, Mata de Sambaíba, 41 m, 10°39'19"S, 36°51'53"W, 09 November 2017, fl. cult. 18 April 2018, *D. Cavalcanti & E. Ferreira* 904 (UFP); Pirambu, Reserva Biológica de Sta Isabel, September 1994, sterile, *M. Landim* 732 (ASE); Pirambu, Reserva Biológica de Santa Isabel, 0–50 m, 10°41'17"S, 36°47'75"W, 06 May 1999, fl., *G. Martinelli & T. Barbará* 15349 (CEPEC, RB).

24. *Cryptanthus pseudopetiolatus* Philcox, *Kew Bull.* 47(2): 265 (1992). [Figs. 3B, 20].

Type:—BRAZIL. Bahia: 29 km from Una and 19 km from Nova Colonial, West along Road to Rio Branco, by the Fazenda Iguaçu, Dendhevea, 24 January 1977, fl., *R. M. Harley et al.* 18221 (holotype: CEPEC! [CEPEC 21258]; isotype: K digital image! [K000294461]).

Etymology:—It refers to leaf blades pseudopetiolate.

Distribution and Habitat:—*Cryptanthus pseudopetiolatus* is only known from the Bahia State (municipality of Caravelas, Eunápolis, Igrapiúna, Ilhéus, Itacaré, Itagibá, Itamarajú, Porto Seguro, Prado, Una, Uruçuca, Varzedo and Valença). It occurs in the phytogeographic domain of the Atlantic Forest, at 100 to 125 m elevation in the vegetation type submontane tropical moist forest. It is terricolous and grows on dense litter layer of clayey soil.

Phenology:—Flowering in nature in January, April, May, June, July, August, October, November and December and in cultivation in June and July. Fruiting in August, September, October and December.

Conservation status:—*C. pseudopetiolatus* is known to about 28 locations, two of which occur in conservation units: Parque Estadual do Conduru and Reserva Biológica do Mico-leão. The extent of occurrence (EOO) is 23,915.287 km² and the area of occupancy (AOO) is 112 km². The species is located in the Atlantic Forest that is severely fragmented and can be suffering a decline in the extent of occurrence and area of occupancy. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(i, ii).

Taxonomic affinities:—*C. pseudopetiolatus* is also morphologically similar to *C. pirambuensis* D.M.C. Ferreira & Louzada due to the number of flowers in the lateral glomerule of the inflorescence but *C. pseudopetiolatus* differs from *C. pirambuensis* by the floral bracts 19–23 mm long (vs. 27.5–34 mm long), flowers 29.5–37 mm long (vs. 44–61 mm long), sepals 15.5–17.5 mm long (vs. 20–22.5 mm long), sepals lobes ovate or lanceolate (vs. narrowly elliptic or elliptic), petals connate for 3.2–6 mm long (vs. 12–22 mm), callosities of the petals appearing 4–5 mm distant from the base (vs. 12.5–22 mm distant from the base), stigma lobes 3.2 mm long in the perfect flowers (vs. 6–7.2 mm in the perfect flowers) and ovary with 8–9 ovules per locule in the perfect (vs. 15–17 ovules per locule in the perfect flowers). Some individuals of *C. pseudopetiolatus* have adaxial surface of the leaf blades entirely densely lepidote in the older leaves and they can be confused with *C. diana* but *C. pseudopetiolatus* can be differentiated from *C. diana* by the petals 24.5–29.5 mm long (vs. 33–42.5 mm long), styles ca. 24.5 mm long (vs. 26.2–36 mm long) and epigynous tube 2.3–4 mm long (vs. 1–1.2 mm long).

Specimens examined:—BRAZIL. **Bahia:** Caravelas, 17°43'S, 39°56'W, March 2007, fl., *A. L. Cotias et al. s.n.* (ALCB); Eunápolis, Itabela, 02 1970, fl., *T.S. dos Santos* 872 (CEPEC); Igrapiúna, BA 001 RPPN da Michellin, Trilha do Guigó, 13°49'15"S, 39°12'14"W, 29 December 2018, fl., *E.H. Souza* 180 (HURB); Ilhéus, estrada Olivença-Vila Brasil, 27 July 1979, fl., *G. Martinelli & A.M. de Carvalho* 6113 (RB); Ilhéus, estrada Olivença-Vila Brasil (Maruim), 27 July 1979, fl., *G. Martinelli & A.M. de Carvalho* 7621 (RB); Ilhéus, estrada Olivença-Maruí, entre os Kms 7-10, 19 May 1985, fl. cult. 25 June 1985, fl., *G. Martinelli & F. Zuloaga* 11107 (RB); Ilhéus, Cidade de Ilhéus, 3 km north of Rodoviária, Mata reservoir, 14°46'55"S, 39°04'09"W, 15 September 1994, fl., *W.W. Thomas et al.* 10488 (CEPEC, NYBG); Ilhéus, Along ra from Ilhéus to Serra Grande (ca. 19 km N of Ilhéus), just N os Tulha, 14°41'S, 39°09'W, 08 May 1992, fl., *W.W. Thomas et al.* 9212 (CEPEC, NYBG, US); Ilhéus, 22 Km na estrada Ilhéus-Serra Grande, 14°35'03"S, 39°03'28"W, 11 August 1994, fr., *I. Ramírez, S. Sant'Ana & A. M. de Carvalho* 468 (CEPEC, HUEFS, NYBG); Ilhéus, Road from Olivença to Maruí, 6.1 km W of Olivença. Forest on N side of Road, 14°59'S, 39°03'W, 01 May 1992, fl., *W.W. Thomas et al.* 9055 (CEPEC, NYBG); Itacaré, Estrada Ilhéus-Itacaré, Ramal de estrada à esquerda sentido Ilhéus-Itacaré, Trilha após 1,5 km no ramal, 14°19'59.3"S, 39°01'49"W, 05 April 2008, fl., *C.P. Bruniera & M. Groppo* 95 (RB); Itacaré, Marambaia, 1 km N and 2.5 km W of junction Marambaia rd and rd from BR 101 to Itacaré (BA 654), 6 km W of Itacaré, 14°20'S, 39°05'W, 16 May 1992, fl., *W.W. Thomas et al.* 9392 (CEPEC, NYBG, US); Itacaré, 6.7 km south of junction with BA 654 at "Loteamento Marambaia" on road to Serra Grande, the junction 6 km west of Itacaré, 14°15'S, 39°16'W, 02 May 1993, fl., *W. Thomas, A. Amorim & J. Jardim* 9776 (CEPEC); Itacaré, 10 km W of jet. Road from Ilhéus to Itacaré (BA 001) on road from Itacaré to BR 101, then 1.6 km S on fazenda road to Reserva Fazenda Capitao, 125 m, 14°20.70'S, 39°05.31'W, 04 August 2002, fr., *W.W. Thomas et al.* 13037 (NYBG); Itacaré, Rodovia Itacaré/Taboquinhas entrada a 6 Km de Itacaré, Loteamento Marambaia, 16 July 1995, fl., *J.G. Jardim et al.* 649 (NYBG); Itagibá, Mata da Botinha, 14°10'53"S, 39°42'27"W, 28 October 2008, fl., *C.E. Ramos et al.* 543 (ALCB); Itamarajú, Faz. Pau-Brasil. Entrada no Km 5 da Rod. Itamarajú/Eunápolis, 03 November 1983, fl., *A.M. de Carvalho, R. Callejas & L.A. Mattos-Silva* 2046 (RB, NYBG); Porto Seguro, Trancoso; Estância do Icatú, 16°35'82"S, 39°06'43"W, 15 May 1999, fr., *G. Martinelli, T. Barbará & J. Mourão* 15443 (RB); Porto Seguro, Estrada de Arraial D'Ajuda para Trancoso, 16°35'50.1"S, 39°09'5.6"W, 10 July 2016, fl., *E.H. Souza et al.* 167 (HURB); Prado, 27 August 1998, fl. and fr., *T. Fontoura* 424 (UESC); Prado, Parque Nacional do Descobrimento, trilha aberta para os estudos do plano de

manejo do PARNA, Km 22 da estrada principal que atravessa o Parque, 90 m, 17°11'0"S, 39°20'0"W, 12 November 2009, fl., *L. Dane et al.* 225 (CEPEC); Una, Reserva Biológica do Mico-leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus/Una, coletas efetuadas na mata próxima a entrada da sede, 15°09'S, 39°05'W, 31 Aug 1995, fl. and fr., *A. Amorim* 1722 (CEPEC, NYBG); Una, Reserva Biológica do Mico-leão (IBAMA), entrada no km 46 da Rod. BA-001 Ilhéus/Una, "Picada Paralela ao Rio", 15°09'S, 39°05'W, 28 July 1994, fl., *J. G. Jardim et al.* 540 (CEPEC); Una, Reserva Biológica do Mico-Leão (IBAMA), entrada no Km 46 da Rod. BA-001, Ilhéus/Una, 15°09'S, 39°05'W, 12 August 1994, fl., *I. Ramírez, S. Sant'Ana, J. Jardim & R. Silva* 473 (CEPEC); Una, Reserva Biológica do Mico-Leão (IBAMA), entrada no Km 46 da Rod. BA-001, Ilhéus/Una, 15°09'S, 39°05'W, 13-14 July 1993, fl., *J.G. Jardim et al.* 151 (CEPEC); Una, Reserva Biológica do Mico-leão (IBAMA), Entrada no km 48 da Rod. BA-001 Ilheus/Una, 15°09'S, 39°05"W, 18 June 1997, fl., *A.M. Amorim et al.* 2058 (CEPEC, NYBG); Una, Reserva Biológica de Una, 15°06'20"S, 39°05'56"W, 24 October 2006, fl., *T. Fontoura, V. & R.* 512 (UESC); Una, Reserva Biológica de Una, 28 July 2006, fl., *T. Fontoura & M. Garcia* 494 (UESC); Una, Reserva Biológica de Una na direção da Fazenda, 25 October 1998, fl., *T. Fontoura & A. Matim* 429 (UESC); Una, Fazenda São Rafael (antiga Fazenda Dendhevea), 10 December 1998, sterile, *L.A. Mattos-Silva, J.B. Jorda Jr. & B. dos Santos* 3893 (UESC); Una, 29 km from Una and 19 km Nova Colonial west along road to Rio Branco, By the Fazenda Iguaçu, Dendhevea, 15°15'S, 39°18'W, 24 January 1977, fl., *R. M. Harley* 18221 (CEPEC, K); Una, Estrada Una-Olivença, km 4, 12 August 1994, fl., *I. Ramírez & H. S. Brito* 484 (CEPEC, NYBG); Una, estrada Una-Olivença, Km 4, 16 October 1983, fr., *G. Martinelli & T. Soderstrom* 9691 (CEPEC, RB, MBM, US); Una, carretera Una-Olivença, km 4, 10-20 m, 15°28'S, 39°20'W, 12 August 1994, fl., *I.M. Ramírez et al.* 477 (NYBG, US); Una, estrada Una-Olivença, Km 11, 15 December 1982, fr., *G. Martinelli & A.M. de Carvalho* 8943 (RB); Una, estrada Olivença-Una, Km 35, 19 May 1985, fl. cult. 22 June 1985, fl., *G. Martinelli & F. Zuloaga* 11113 (RB); Uruçuca, ca. 7.3 km na estrada Serra Grande/Itacaré, 100-120 m, 14°25'25"S, 39°33'07"W, 11 August 1994, fl., *I. Ramírez, S. Sant'Ana & A. M. de Carvalho* 471 (CEPEC); Uruçuca, Ca. De 6 Km ao S do Distrito de Serra Grande em direção ao povoado do Retiro, 28 March 1994, fl., *J.G. Jardim et al.* 435 (CEPEC); Uruçuca, Distrito de Serra Grande 7.3 Km da estrada Serra Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S, 39°01'W, 01-12 July 1991, fl., *A.M. de Carvalho et al.* 3357 (CEPEC, NYBG); Uruçuca, Antiga estrada que liga Ubaitaba à Maraú, Fazenda Água Boa, 14°10'40"S, 39°01'W, 11 June 2006, fl., *A.M. Amorim et al.* 6048 (CEPEC); Uruçuca, Distrito de Serra Grande, 7.3 Km na estrada Serra

Grande/Itacaré, Fazenda Lagoa do Conjunto Fazenda Santa Cruz, 14°25'S, 39°01'W, 25 July 1994, fl., *S.C. de Sant'Ana et al.* 549 (CEPEC, NY); Uruçuca, Parque Estadual do Conduru, 28 May 2006, fl., *T. Fontoura & J. Reis* 489 (UESC); Uruçuca, Serra Grande, Rodovia BA-001-Itacaré-Ilhéus, 14°25'40.8"S, 39°03'14.2"W, 18 June 2019, fl., *E.H. Souza et al.* 162 (HURB); Valença, Estrada para Guaibim, Fazenda Macarina, 13°18'01"S, 39°00'04"W, 17 June 2000, fl., *F. França & E. Melo* 3410 (HUEFS); Varzedo, Recôncavo Sul, Fazenda do Sr. Getulio, Rio Cai Camarão, 12°96'08"S, 39°44'63"W, 07 December 2015, fl., *M. L. Guedes & M. Casaes* 24273 (ALCB).

25. *Cryptanthus reisii* Leme, *Cryptanthus Soc. J.* 17(3): 87 (2002a). [Figs. 3B, 21].

Type:—BRAZIL. Bahia: Itapetinga, Duas Barras, Fazenda Santa Cruz, ca. 300 m, *R. F. Reis Júnior s. n.*, fl. cult. July 2001, fl., *E. Leme* 5015 (Holotype: HB image! [HB90733]).

Etymology:—It is honor to Raymundo Fernandes Reis who collected the species (Leme 2002a).

Distribution and Habitat:—*Cryptanthus reisii* is only known from the Bahia State (municipality of Itapetinga, Itororó and Maracás). It occurs in the phytogeographic domain of the Atlantic Forest, at 300 to 861 m elevation. It occurs in the vegetation type deciduous seasonal forest. It is terricolous and grows on shaded forest.

Phenology:—Flowering in nature in November and in cultivation in April, May and June.

Conservation status:—*C. reisii* is known only from three locations and no locations is included in conservation units. The forest fragment of type locality is small and the area is severely fragmented. The municipality has many pasture areas. Thus, the species is classified as Endangered (CR) based on the criterion on the criterion B2 ab(ii).

Taxonomic affinities:—*C. reisii* can be confused with *C. sergipensis* I.Ramírez due to the leaf blades shape but *C. reisii* differs from *C. sergipensis* by the apical glomerule of the inflorescence with 15–29 flowers (vs. ca. 82 flowers), sepals connate for 8.5–11.2 mm long (vs. 5–7 mm long), lobes 2.5–3.5 mm wide (vs. 4.3–6.5 mm wide), petals 3–4 mm wide (vs. 5–7 mm wide), styles 30 mm long (vs. 22.5–22.7 mm long) and ovary with 6 ovules per locule in the perfect flowers (vs. 9–10 ovules per locule in the perfect flowers). *C. reisii* is morphologically similar to *C. boanovenssis* Leme due to the length of the connation of the petals, length of the filaments and anther apices shape but *C. reisii* differs from *C.*

boanovens by the plants with leaf blades that exceed 1.2 cm wide in the adult leaf blades (vs. plants with leaf blades leaves that never exceed 1.2 cm wide), apical glomerule of the inflorescence with 15–29 flowers (vs. apical glomerule of the inflorescence with ca. 4 flowers), ovary with 6 ovules per locule in the perfect flowers (vs. 7–9 ovules per locule in the perfect flowers). *C. reisii* is also morphologically similar to *C. ruthiae* due to the number of flowers in the apical glomerule of the inflorescence but *C. reisii* differs from *C. ruthiae* by the styles 26 mm long (vs. 30 mm long).

Specimens examined:—BRAZIL. **Bahia:** Itapetinga, Duas Barras, Fazenda Santa Cruz, ca. 300 m, *R. F. Reis Júnior s. n.*, fl. cult. July 2001, fl., *E. Leme 5015* (HB); Itapetinga, Fazenda Santa Cruz, proprietário Vardão, Sentido Crescêncio, Duas Barras, passando pela ponte de concreto (ponte rodoviária Santinho Ferraço) do rio 2 barras, depois do terceiro mata burro a direita, Antiga propriedade de Salvador, 308 m, 15°07'49"S, 40°14'39"W, 19 March 2018, fl. cult. 27 April 2018, fl., *D. Cavalcanti & L. Daneu 836* (UFP); Itapetinga, Fazenda Santa Cruz, proprietário Vardão, Sentido Crescêncio, Duas Barras, passando pela ponte de concreto (ponte rodoviária Santinho Ferraço) do rio 2 barras, depois do terceiro mata burro a direita, Antiga propriedade de Salvador, 308 m, 15°07'49"S, 40°14'39"W, 19 March 2018, fl. cult. 19 May 2018, fl., *D. Cavalcanti & L. Daneu 837* (UFP); Itapetinga, Fazenda Santa Cruz, proprietário Vardão, Sentido Crescêncio, Duas Barras, passando pela ponte de concreto (ponte rodoviária Santinho Ferraço) do rio 2 barras, depois do terceiro mata burro a direita, Antiga propriedade de Salvador, 308 m, 15°07'49"S, 40°14'39"W, 19 March 2018, fl. cult. 06 June 2018, fl., *D. Cavalcanti & L. Daneu 914* (UFP); Itororó, ca. 5,0 km E da sede municipal, 15°05'46"S, 40°02'21"W, 02 November 2000, fl., *J. G. Jardim, S. C. de Sant'Ana & F. Juchum 3125* (CEPEC); Maracás, 17,9 Km antes do trevo de Maracás, ramal à direita da BA 026, 861 m, 13°28'45"S; 40°16'55"W, 03 November 2007, fl., *F. M. Ferreira et al. 1731* (CEPEC).

26. *Cryptanthus reptans* Leme & J.A.Siqueira, *Fragm. Atlantic Forest N. E. Brazil*: 287 (2007). [Figs. 3B, 22].

Type:—BRAZIL. Pernambuco: Água Preta, Fazenda Camarão, Mata da Cinza, 91 m, 8°45'39"S, 35°28'38.3"W, 16 March 2005, sterile, *E. Leme, J. A. Siqueira-Filho & M. S. Leite 6591* (Holotype: HB photo! [HB90750]; Isotype: UFP! [UFP43912])

Etymology:—There is no information in Leme & Siqueira-Filho (2007) but it must be due to the crawling habit.

Distribution and Habitat:—*Cryptanthus reptans* is only known from the Alagoas (municipality of Penedo) and Pernambuco States (municipality of Água Preta). It occurs in the phytogeographic domain of the Atlantic Forest, at 91 to 183 m elevation. It is terricolous and grows on clay soil at the shaded edge of the semideciduous seasonal forest.

Phenology:—Flowering in nature in January, March and October and in cultivation in June.

Conservation status:—*C. reptans* is known only from two locations and no locations is included in conservation units. The species is located in the Atlantic Forest that is severely fragmented and can be suffering a decline in the area of occupancy. Thus, this species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. reptans* is phylogenetically close to *C. diana* Leme and *C. zonatus* (Vis.) Vis. that together form the *zonatus* clade (Ferreira *et al.* Artigo 1). Ferreira & Louzada (2020) include them in the *C. zonatus* (Vis.) Vis. complex. This relationship is confirmed in the study of Ferreira *et al.* (Artigo 1). The authors recommend population genetic studies to resolve this complex. Individuals long caulescent of *C. reptans* can be confused with *C. vexatus* Leme but *C. reptans* differs from *C. vexatus* by the sepals connate for 8.2–9 mm long (vs. 4–5 mm long), petals 29.2–34.5 mm long (vs. 25 mm long) and filaments 24–28 mm long (vs. 13 mm long). The information about reproductive characters of *C. vexatus* was taken from Leme (1995) for comparison with *C. reptans*.

Specimens examined:—BRAZIL. **Alagoas:** Penedo, Usina Paísa, Fazenda Mundes, 30 October 2004, fl., E.M.C. Leme & J.A. Siqueira-Filho 6502 (RB). **Pernambuco:** Água Preta, Fazenda Camarão, Mata da Cinza, 91 m, 8°45'39"S, 35°28'38.3"W, 16 March 2005, sterile, E. Leme, J. A. Siqueira-Filho & M. S. Leite 6591 (HB, UFP); Água Preta, Fazenda Camarão, Mata Cinza, 08°45'34.7"S, 35°28'39.1"W, 183 m, 24 January 2019, fl., D. Cavalcanti, R.B. Louzada & K. Ferreira 910 (UFP); Água Preta, Fazenda Camarão, Mata Cinza, 08°45'34.7"S, 35°28'39.1"W, 183 m, 24 January 2019, fl. cult. 19 June 2019, fl., D. Cavalcanti, R.B. Louzada & K. Ferreira 946 (UFP, RB); Água Preta, Fazenda Camarão, Mata Cinza, 08°45'34.9"S, 35°28'39.4"W, 05 January 2012, fl., J. A. Siqueira-Filho & C. F. Marques 2687 (RB, HURB).

27. *Cryptanthus robsonianus* Leme, *J. Bromeliad Soc.* 64(3): 150 (2014). [Figs. 3B, 23].

Type:—BRAZIL. Espírito Santo: Jaguaré, Palmitinho, Mussununga Córrego do Mosquito, near Fazenda Alegre, 15 m elevation, 19° 00' 55" S, 39° 51' 16" W, 20 June 2014, E. Leme, R. Lopes & V. Leme 8895 (holotype: RB digital image! [RB 640187]; isotype: HB photo!)

Etymology:—It is honor to biologist and conservationist Robson Lopes (Leme 2014).

Distribution and Habitat:—*Cryptanthus robsonianus* is only known from the Bahia (municipality of Maraú) and Espírito Santo (Jaguaré) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 15 m elevation in the following vegetation types: *Mussununga* that comprises herbaceous and shrub formations or occurring as thinned forests (Leme 2014) and Restinga Forest. It is terricolous and grows on dense litter layer of sandy soils.

Phenology:—Flowering in nature in May and June and in cultivation in January and February. Fruiting in nature in May.

Conservation status:—*C. robsonianus* is known only from two locations and no locations is included in conservation units. The species occurs in the Atlantic Forest that is severely fragmented. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. robsonianus* is phylogenetically related to *C. teretifolius* Leme and *C. walkerianus* Leme & L. Kollmann that are included in the walkerianus clade (Ferreira *et al.* Artigo 1). These species are similar due to the apical glomerule of the inflorescence having many flowers. However, *C. robsonianus* is differentiated from *C. teretifolius* and *C. walkerianus* by the leaves sessile, contracted at base above the leaf sheaths (*vs.* leaves petiolate). In addition, *C. robsonianus* is morphologically similar to *C. viridovinosus* Leme and *C. santateresinhensis* Leme due to the short stem (<8 cm) and petals white with apices greenish but *C. robsonianus* differs from *C. santateresinhensis* by the floral bracts white on the base and vinaceous or greenish on the apex (*vs.* castaneous or castaneous-hyaline), sepals 17–21.2 mm long (*vs.* 12–15 mm long), lobes 14–17 mm long (*vs.* 5–6 mm long), lanceolate (*vs.* ovate or oblong-elliptic) and petals connate for 6.5–9.3 mm (*vs.* 16–17 mm long). The information about reproductive characteres of *C. viridovinosus* and about morphological characters of *C. santateresinhensis* were taken from the Leme *et al.* (2010) and Leme *et al.* (2020), respectively, for comparison with *C. robsonianus*. *C. robsonianus* can also be confused with *C. argyrophyllus* due to the some individuals have the adaxial surface of the leaf blades entirely densely lepidote and petals white with apices greenish but *C. robsonianus* differs from *C. argyrophyllus* by the floral bracts 17.5–28.2 mm long (*vs.* 15 mm long), sepals connate for 6–7.5 mm (*vs.* 10 mm), lobes 11–14 mm long (*vs.* 8–9 mm long), petals 2–4.5 mm wide and epigynous tube present 2.5–3 mm long (*vs.* absent). The information about morphological characteres of *C. argyrophyllus* was taken from the Leme (2001) for

comparison with *C. robsonianus*. *C. robsonianus* also is morphologically related to *C. zonatus* (Vis.) Vis. due to the adaxial surface of the leaf blades with crossbars of lepidote trichomes but *C. robsonianus* differs from *C. zonatus* by the petals white with apices greenish (vs. petals white). *C. robsonianus* is a morphologically variable species, in the Northeastern the leaf blades are narrowly elliptic while in the Southeastern the leaf blades are oblanceolate. *C. robsonianus* is not included in the study of Maciel (2020) of the “Flora do Brasil 2020”.

Specimens examined:—BRAZIL. **Bahia:** Maraú, Caminho para a Lagoa do Cassange, cerca de 8 km do Povoado Saquaira, 13°59'02"S, 38°56'53"W, 26 May 2014, fl. and fr., *D. Cavalcanti, J. R. Maciel & B. S. Amorim 703* (UFP); Maraú, Caminho para a Lagoa do Cassange, cerca de 8 km do Povoado Saquaira, 13°59'02"S, 38°56'53"W, 26 May 2014, fl. and fr., *D. Cavalcanti, J. R. Maciel & B. S. Amorim 704* (UFP); Maraú, Caminho para a Lagoa do Cassange, cerca de 8 km do Povoado Saquaira, 13°59'02"S, 38°56'53"W, 26 May 2014, fl. cult. 11 January 2014, fl., *D. Cavalcanti, J. R. Maciel & B. S. Amorim 919* (UFP); Maraú, Caminho para a Lagoa do Cassange, cerca de 8 km do Povoado Saquaira, 13°59'02"S, 38°56'53"W, 26 May 2014, fl. cult. 07 February 2018, fl., *D. Cavalcanti, J. R. Maciel & B. S. Amorim 920* (UFP); Maraú, ca. 20 km de Maraú para o porto Campinhos, 22 May 1991, fl., *A. M. de Carvalho 3270* (CEPEC, NYBG). **Espírito Santo:** Jaguaré, Palmitinho, Mussununga Córrego do Mosquito, near Fazenda Alegre, 15 m, 19°00'55" S, 39°51'16" W, 20 June 2014, fl., *E. Leme, R. Lopes & V. Leme 8895* (RB, HB).

28. *Cryptanthus ruthiae* Philcox, *Kew Bull.* 47(2): 268 (1992). [Figs. 3B, 24].

Type:—BRAZIL. Bahia: 5 km SE of Maraú at junction with new road N to Ponta do Mutá, 2 February 1977, fl., *Harley et al. 18507* (holotype: CEPEC! [CEPEC 21257]; isotype: K image! [K000294462]).

Etymology:—It is honor to Ruth Storr who collected bromeliads in Bahia State (Philcox 1992).

Distribution and Habitat:—*Cryptanthus ruthiae* is known from the Bahia State (municipality of Cairu, Itacaré, Ituberá, Jaguaripe and Maraú). It occurs in the phytogeographic domain of the Atlantic Forest from sea level to 133 m elevation. It is terricolous and grows on sandy soils in closed forests of Restinga and forest hygrophilous.

Phenology:—Flowering in nature in January, February, June, August, October, November and December and in cultivation in June.

Conservation status:—*C. ruthiae* is known to 10 locations, two of which are located in conservation units: Área de Proteção Ambiental (APA) Tinharé/Boipeba and APA Baía de Camamu. The extent of occurrence (EOO) is 1,284.161 km² and the the area of occupancy (AOO) is 36 km². The species is located in the Atlantic Forest that is severely fragmented. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. ruthiae* is compared to *C. pickelii* L.B. Smith by Philcox (1992). In fact, *C. ruthiae* is morphologically similar to *C. pickelii* due to the shape and color of the leaf blades but differs by the apical glomerule of the inflorescence with *ca.* 32 flowers (*vs.* 5–11 flowers). Ramírez-Morillo (1996) considers *C. ruthiae* as a synonym for *C. pseudopetiolatus* Philcox. These species are very similar. However, we differentiate *C. ruthiae* from *C. pseudopetiolatus* by the sepals lobes 3.5–7.5 mm long (*vs.* 9–10 mm long), petals connate for 11.5–12.2 mm long (*vs.* 4.8–6 mm long), anther apices rounded (*vs.* emarginate) and ovary with 0–2 ovules per locule in the perfect flowers (*vs.* with 8–9 ovules per locule in the perfect flowers). *C. ruthiae* is also morphologically similar to *C. reisii* due to the number of flowers in the apical glomerule of the inflorescence but *C. ruthiae* differs from *C. reisii* by the styles 30 mm long (*vs.* 26 mm long).

Specimens examined:—BRAZIL. **Bahia:** Cairu, Ilha de Boipeba, Arquipélago do Município de Cairu, APA Tinharé/Boipeba, 50 m, 13°37'10"S, 38°55'80"W, 03 January 2007, fl., *A.M. Amorim, R.A.X. Borges & L.C. Magnavita 6809a** (CEPEC); Cairu, Ilha de Boipeba, Arquipélago do Município de Cairu, APA Tinharé/Boipeba, 13°37'10"S, 38°55'80"W, 18 August 2008, fl., *A.M. Amorim et al. 7671* (CEPEC); Itacaré, Mata próxima ao Campinho, 133 m, 14°23'06"S, 39°02'01"W, 05 November 2017, fl., *A. Melo et al. 1730* (UFP); Ituberá, Pratigi, 13°42'15"S, 39°01'02"W, 05 October 2011, fl., *E.N. de Matos, T. Araújo & G. Vidal 644* (HUEFS); Ituberá, Ligação entre a Rod. BA 001 e a praia Pratigi, 15 February 1999, fl., *G. Hatschbach 68972* (MBM); Jaguaripe, Recôncavo sul, 13°06'S, 38°53'W, 11 December 1199, fl., *A. L. Cotias et al. s.n.* (ALCB 042966); Jaguaripe, Pinaco (Faz. Reunidas Vale do Jiquiriçá), 13°14'0"S, 38°58'35"W, 12 June 2012, fl., *E.N. Matos 3513* (RB, HUEFS); Maraú, Rod. Maraú/Campinhos, *ca.* 8.6 km do povoado Saquaira, Estrada que leva à praia próximo a Lagoa do Casange, 13°59'46"S, 38°56'56"W, 15 August 1999, fl., *J. G. Jardim et al. 2248* (RB, NYBG); Maraú, Maraú a Ubaitaba, 09 October 1968, fl., *J. Almeida & T.S. Santos 110* (RB, US); Maraú, Km 14 da estrada Maraú-Ubaitaba, 18 May 1985, fl. cult. 24 June 1985, fl., *G. Martinelli & F. Zuloaga 11077* (RB); Maraú, 5 km SE of Maraú at the Junction with the

new road North to Ponta do Mutá, 14°08'S, 39°00'W, 02 February 1977, fl., *R.M. Harley 18507* (CEPEC, K).

29. *Cryptanthus santateresinhensis* Leme, *Phytotaxa* 430(3): 163 (2020). [Fig. 3C].

Type:—BRAZIL. Bahia: Santa Teresinha, close to the border with Castro Alves, Serra da Jibóia, ca. 600 m elevation, 12°51' S, 39°28' W, May 1998, *S. Linhares s.n.*, cult. *E. Leme 4222* (holotype RB).

Etymology:—It refers to the municipality of Santa Teresinha where the species was collected (Leme *et al.* 2020).

Distribution and Habitat:—*Cryptanthus santateresinhensis* is known from the Bahia State (municipality of Santa Teresinha) (Leme *et al.* 2020). It is distributed in the phytogeographic domain of the Atlantic Forest, at 600 m elevation (Leme *et al.* 2020). It is terricolous and grows on dry closed forests on hill named Serra da Jibóia (Leme *et al.* 2020).

Phenology:—Unknown.

Conservation status:—The conservation status of *C. santateresinhensis* was recently evaluated by Leme *et al.* (2020). It is classified as Critically Endangered (CR) based on the criterion A1cd and B1ab(iii) due to the fact species that the species occurs type locality only (Leme *et al.* 2020).

Taxonomic affinities:— The information about reproductive characteres of *C. viridovinosus* and about morphological characters of *C. santateresinhensis* were taken from the Leme *et al.* (2010) and Leme *et al.* (2020), respectively, for comparison between them. *C. santateresinhensis* is morphologically related to *C. viridovinosus* Leme due to the short stem (<8 cm), leaf blades lanceolate or narrowly elliptic and petals white with apices green or greenish but *C. santateresinhensis* differs from *C. viridovinosus* by the flowers 44 mm long (vs. 40 mm long), sepals 15 mm long (vs. 12–13 mm long), connate for 10 mm long (vs. 6–7 mm long), lobes ovate (vs. oblong-elliptic) and petals 35 mm long (vs. 30–33 mm long).

30. *Cryptanthus seidelianus* W.Weber, *Feddes Repert.* 97 (3/4): 119. 1986. [Figs. 3C].

Type:—BRAZIL. Bahia: Milagres, 550 msm, July 1983, fl., *A. Seidel 963* (Holotype: HAL digital image! [HAL075357]).

Etymology:—It is honor to A. Seidel who collected the species.

Distribution and Habitat:—*Cryptanthus seidelianus* is known to the Bahia State (municipality of Milagres). This municipality is included in the Caatinga phytogeographic domain. It grows on area exposed to the sun (Ramírez-Morillo 1996).

Phenology:—Flowering in nature in July.

Conservation status:—*C. seidelianus* is known only from the type locality (one location) in the Caatinga. Since its discovery (31 years ago), no other samples have been collected. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. seidelianus* is very similar to *Cryptanthus bahianus* L.B.Sm. And *C. seidelianus* may be synonymous from *C. bahianus*. Vegetatively all characters overlap between them. The information about reproductive characteres of *C. seidelianus* was taken from Weber (1986) for comparison with the close species. The differences between *C. seidelianus* and *C. bahianus* are in the sepals lobes lanceolate (vs. elliptic), petals apices acuminate (vs. obtuse), anthers 2 mm long (vs. 2.5–4.6 mm long), stigma 4 mm (vs. 0.8–3 mm) and ovary 6 mm wide (vs. 2–5.5 mm wide). Ramírez-Morillo (1996) compares *C. seidelianus* to *C. warren-loosei* due to the similar geographic distribution. We distinguish *C. seidelianus* from *C. warren-loosei* by the leaf blades green (vs. brown or reddish), floral bract $10\text{--}13 \times 7$ mm (vs. $17.3\text{--}18.5 \times 3.6\text{--}4.7$ mm), sepals 13 mm long (vs. $15.3\text{--}18.2$ mm long), anthers 2 mm long (vs. $2.4\text{--}3$ mm long), stigma 4 mm (vs. $0.3\text{--}3.5$ mm) and ovary 10×6 mm (vs. $6.5\text{--}9.5 \times 3\text{--}3.2$ mm).

Specimens examined:—BRAZIL. **Bahia:** Milagres, July 1983, fl., *A. Seidel* 963 (HAL).

31. *Cryptanthus sergipensis* I.Ramírez, *Harvard Pap. Bot.* 3(2): 219 (1998). [Figs. 3C, 5F, 25].

Type:—BRASIL. Sergipe: Santa Luzia do Itanhi, cerca de 50 m ao sul do Distrito de Crasto (passando pelo cemitério); mata de restinga em solo arenoso, $11^{\circ}23'43''\text{S}$, $37^{\circ}25'20''\text{W}$, 14 June 1994, fl., *J.G. Jardim, L.A. Mattos Silva, A.C. de Sant'Ana & E.B. dos Santos* 489 (Holotype: NY digital image! [NY 23392]; isotype: CEPEC! [CEPEC 61692])

Etymology:—It refers to the Sergipe state where the species was collected (Ramírez M. 1998).

Distribution and Habitat:—*Cryptanthus sergipensis* is known from the Bahia (municipality of Entre Rios, Indiaroba, Jandaíra and Mata de São João) and Sergipe (Areia Branca, Itabaiana and Santa Luzia do Itanhy) States. It occurs in the phytogeographic domain of the

Atlantic Forest, at 16 to 220 m elevation in the vegetation type restinga forest. It is terricolous and grows on dense litter layer of sandy soil. In the type area, the species population occurs in a restinga next to a mangrove, being the litter formed by leaves of mangrove plants.

Phenology:—Flowering in nature in April, May, June, July and October and in cultivation in June and July. Fruiting in nature in November.

Conservation status:—*C. sergipensis* is known to nine locations, one of which is located in conservation unit: Parque Nacional da Serra de Itabaiana. The extent of occurrence (EOO) is 5,120.715 km² and the area of occupancy (AOO) is 40 km². The species is located in the Atlantic Forest that is severely fragmented and a population is located in an area of development that is likely to be devastated. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. sergipensis* is morphologically similar to *C. bahianus* L.B.Sm. due to the leaf blades linear triangular or narrowly triangular but *C. sergipensis* differs from *C. bahianus* by the apical glomerule of the inflorescence with ca. 82 flowers (vs. 13–33 flowers) and ovary with 9–13 ovules per locule in the perfect flowers (vs. 22–29 ovules per locule in the perfect flowers).

Specimens examined:—BRAZIL. **Bahia:** Entre Rios, Fazenda Rio do Negro, 12°4'S, 38°0'W, 13 June 2011, fl., *A. V. Popovkin* 888 (HUEFS); Entre Rios, BA-099, ca. Km 83,5 Km, sentido Mata de São João-Conde, 40 m, 12°17'19"S, 37°53'24"W, 2012, fl. cult. 08 July 2012, fl., *C.N. Fraga* 3283 (RB); Entre Rios, Litoral Norte, Sauípe, Empreendimento da Odebrecht, 08 June 2000, fl., *M.L. Guedes* 7362 (ALCB); Indiaroba, 9 June 1996, fl., *G. Hatschbach* 65185 (MBM); Jandaíra, Próximo a entrada faz. Luzomar, 11°36'46"S, 37°27'30"W, 23 July 2011, fl., *E. Matos et al.* 166 (HUEFS); Jandaíra, Fazenda Rio Fundo, 11°35'42"S, 37°43'62"W, 11 May 2000, fl., *N. G. Jesus et al.* 939 (HUEFS, CEPEC, ALCB, HUNEB, RB, CEN, UESC); Mata de São João, Parque Sauípe (Odebrecht), 35 m, 12°23'50"S, 37°55'58"W, 14 April 2012, fl., *E. M. C. Leme & P. Lima* 8651 (RB). **Sergipe:** Areia Branca, Parna Serra de Itabaiana, Serra de Itabaiana, 29 June 2010, fl., *D. S. Melo et al.* 124 (ASE, MAC); Areia Branca, Serra de Itabaiana, 220 m, 10°45'14"S, 37°20'35"W, 20 April 2008, sterile, *B. S. Amorim et al.* 304 (ASE, UFP, RB); Itabaiana, Serra de Itabaiana, 29 July 1976, fl., *M. Fonseca s.n.* (ASE 373); Santa Luzia do Itanhi, RPPN Mata do Crasto, 11°23'54"S, 37°25'14"W, 12 June 2012, fl., *L. A. Gomes et al.* 528 (ASE, JPB); Santa Luzia do Itanhi, RPPN Mata do Crasto, 11°20'59"S, 37°25'14"W, 04 Jul 2010, fl., *D. S. Melo et al.* 126 (ASE, JPB); Santa Luzia do Itanhi, Cerca de 2,5 m do distrito de Crasto, 6 October 1993,

fl., *S. C. Sant'Ana et al.* 388 (ASE, CEPEC); Santa Luzia do Itanhi, Cerca de 50 m ao sul do Distrito de Crasto (passando pelo cemitério), 11°23'43"S, 37°25'20"W, 14 June 1994, fl., *J. G. Jardim et al.* 489 (CEPEC, NYBG); Santa Luzia do Itanhi, Mata do Crasto, 16 m, 11°23'38"S, 37°25'16"W, 08 November 2017, fl. cult. 28 June 2018, fl., *D. Cavalcanti & N. Souza* 902 (UFP, RB); Santa Luzia do Itanhi, Mata do Crasto, 16 m, 11°23'38"S, 37°25'16"W, 08 November 2017, fr., *D. Cavalcanti & N. Souza* 828 (UFP).

32. *Cryptanthus teretifolius* Leme, *Cryptanthus Soc. J.* 17(1): 15 (2002b). [Figs. 3C, 26].

Type:—BRAZIL. Espírito Santo: próximo a Vitória, na zona costeira, leg. Roberto A. Kautsky 1032, fl. cult. July 2001, fl., *E. Leme* 3073 (Holotype HB photo! [HB 82553])

Etymology:—It refers to petioles terete (Leme 2002b).

Distribution and Habitat:—*Cryptanthus teretifolius* is only known from the Bahia (municipality of Ubaíra) and Espírito Santo (Vitória) States. It occurs in the phytogeographic domain of the Atlantic Forest of the low to 503 m elevation. It is terricolous and grows on sandy soil of closed forest in the coastal zone (Leme 2002) and on clay soil of the vegetation type submontane tropical moist forest.

Phenology:—Flowering in cultivation in April and July.

Conservation status:—*C. teretifolius* is known to two locations and none is included in conservation unit. The species is located in the Atlantic Forest that is severely fragmented. In the municipality of Ubaíra, the vegetation is very fragmented. The forest fragment where the species was found in Ubaíra has evidence of clear cutting of wood. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. teretifolius* is phylogenetically related to *C. robsonianus* Leme and *C. walkerianus* Leme & L. Kollmann that together are included in the walkerianus clade (Ferreira *et al.* Artigo 1). These species have many flowers in the apical glomerule of the inflorescence. *Cryptanthus teretifolius* is differentiated from *C. robsonianus* by the leaves petiolate (vs. leaves sessile, contracted at base above the leaf sheaths). *C. teretifolius* is morphologically similar to *C. walkerianus* Leme & L. Kollmann by the canaliculate petioles with straight margins and petals white but *C. teretifolius* differs from *C. walkerianus* by the floral bracts of the staminate flower 21–22 mm long (vs. 26–32 mm long) and filaments of the staminate flower 24–27 mm long (vs. 20 mm long).

Specimens examined:—BRAZIL. **Bahia:** Ubaíra, Fazenda Santa Euflorzina-proprietário Mário Muniz, Fica a cerca de 3 Km da entrada de Ubaíra sentido Mutuípe, entrada a esquerda, depois da estação de tratamento da Embasa, 503 m, 13°15'22", 39°37'57"W, 24 March 2018, fl. cult. 27 April 2018, fl., *D. Cavalcanti & L. Daneu* 852 (UFP). **Espírito Santo:** próximo a Vitória, na zona costeira, leg. *Roberto A. Kautsky* 1032, fl. cult. July 2001, fl., *E. Leme* 3073 (HB).

33. *Cryptanthus ubairensis* I.Ramírez, *Harvard Pap. Bot.* 3(2): 221 (1998). [Figs. 3C, 5G].

Type:—BRAZIL. Bahia: Ubaíra, ca. 3 Km E of Ubaíra on Road to Mutuípe, 28 April 1976, fl., *Sodestrom, Russel & Hage* 2175 (Holotype: US digital image! [US2781988-sheet1; US2781; Isotypes: CEPLAC, K digital image! [K000294463-sheet 1; K000294464-sheet 2], RB image! [RB189811], W digital image! [W 1981-0002361]).

Etymology:—It refers to the municipality of Ubaíra where the species was collected (Ramírez M. 1998).

Distribution and Habitat:—*Cryptanthus ubairensis* is only known from the Bahia State (municipality of Ubaíra and Amargosa). It occurs in the phytogeographic domain of the Atlantic Forest, at 340 m elevation in the vegetation type submontane tropical moist forest. It is terricolous and grows on sandy soil of an open woodland on a slope with diffuse light (Ramírez M. 1998).

Phenology:—Flowering in nature in April.

Conservation status:—*Cryptanthus ubairensis* occurs in two locations. In the municipality of Ubaíra, the vegetation is very fragmented due to cattle breeding. Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:— The information about reproductive characteres of *C. ubairensis* was taken from Ramírez M. (1998) for comparison with the close species. *C. ubairensis* is morphologically related to the group of species with adaxial surface of the leaf blades densely lepidote, glabrous with base and/or apices densely lepidote, sparsely lepidote or glabrous, leaf blades linear-oblongate, oblongate, lanceolate, obovate, ovate, narrowly elliptic or elliptic, without longitudinal colored lines along the margins in the living plant with long stem (≥ 8 cm long), petals white and ovary 2.5–10.5 mm long. Among these species, *C. ubairensis* is distinguished by sepal lobes 4×2 –2.5 mm (vs. 6.4 – 10×3 –6 mm) and ovary 5 mm long (vs. 7–11.2 mm long). *C. ubairensis* is differentiated from other species of the genus by the

leaves arranged in spiral along a long stem and leaf blades green or purplish green (Ramírez M. 1998). Some individuals of *C. ubairensis* are short caulescent (stem < 8 cm) and may be confused with *C. cruzalmensis*. They differ from *C. cruzalmensis* by the sepal lobes $4 \times 2\text{--}2.5$ mm (vs. $5\text{--}6 \times 5$ mm) and ovary 5 mm long (vs. 7 mm long). The information about reproductive characteres of *C. cruzalmensis* was taken from Leme *et al.* (2020) for comparison with *C. ubairensis*.

Specimens examined:—BRAZIL. **Bahia:** Amargosa, Serra do Timbó, Mata do Centro Sapucaia, $13^{\circ}10'00''\text{S}$, $39^{\circ}09'00''\text{W}$, 24 April 2007, fl., Paixão, J.L., Nascimento, M.S. & M. 1185 (HUEFS); Ubaira, ca. 3 Km E of Ubaira on Road to Mutuípe, 28 April 1976, fl., Sodestrom, Russel & Hage 2175 (US, CEPLAC, K, RB, W).

34. *Cryptanthus vexatus* Leme, *Cryptanthus Soc. J.* 10(4): 9. 1995. [Figs. 3D, 27A-B].

Type:—BRAZIL. Bahia: Road Una-São José, km 25, 25 April 1995, fl., E.M.C. Leme, P. Nahoum, A.M. de Carvalho & J.C. da Silva 3014 (Holotype: HB photo! [HB 77782]).

Etymology:—It refers to the environment where the species was found (Leme 1995).

Distribution and Habitat:—*Cryptanthus vexatus* is only known from Bahia State (municipality of Una). It occurs in the phytogeographic domain of the Atlantic Forest, at 126 m elevation in the vegetation type submontane tropical moist forest. It is terricolous and grows on dense litter layer of clayey soil in closed forest.

Phenology:—Flowering in nature in April.

Conservation status:—*C. vexatus* occurs only in the type locality (one location) in the Atlantic Forest. When the species was discovered the type locality was almost destroyed by fire and felling (Leme 1995). The type locality was visited in 2018 and is in a good state of preservation. However, the area is not included in a conservation unit and possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:— The information about reproductive characteres of *C. vexatus* was taken from Leme (1995) for comparison with the close species. *Cryptanthus vexatus* is morphologically similar to *Cryptanthus diana* Leme and *Cryptanthus reptans* Leme & J.A.Siqueira due to the long stem and leaf blades shape but *Cryptanthus vexatus* differs from them by the sepals connate for 4–5 mm long (vs. 8.2–11 mm long), petals 25 mm long (vs. 29.2–45 mm long) and filaments 13 mm long (vs. 22–36 mm long). *Cryptanthus vexatus* can be confused with *C. pseudopetirolatus* Philcox due to the leaf blades shape but *C. vexatus*

differs from *C. pseudopetiolatus* by the absence of an epigynous tube (vs. present with 2.5–4 mm long). *C. vexatus* is also morphologically similar to *C. cruzalmensis* Leme & E.H. Souza due to the leaf blades shape and both do not have epigynous tube but *C. vexatus* differs from *C. cruzalmensis* by the lateral glomerule of the inflorescence that has 2 flowers (vs. 5–7 flowers), sepals connate for 4–5 mm long (vs. 6–8 mm long), sepals lobes suboblong (vs. elliptic), petals 25 mm long (vs. 35–42 mm long) and filaments 13 mm long (vs. 33 mm long). The information about reproductive characteres of *C. cruzalmensis* was taken from Leme *et al.* (2020) for comparison with the *C. vexatus*.

Specimens examined:—BRAZIL. **Bahia:** Una, Road Una-São José, km 25, 25 April 1995, fl., E.M.C. Leme *et al.* 3014 (HB); Una, Km-25 da rodovia Una-São José, mata do lado esquerdo da rodovia, 126 m, 15°10'54"S, 39°11'51"W, 06 April 2018, sterile, D. Cavalcanti & L. Daneu 887 (UFP).

35. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada, Artigo 2. [Figs. 3D, 27C-K].

Type:—BRAZIL. Bahia: Itapetinga, Fazenda Santa Cruz, antiga propriedade de Salvador, atualmente de Vardão, 308 m, 15°07'48.9"S, 40°14'38.9"W, 19 March 2018, fl. cult. 17 July 2019, D. Cavalcanti & L. Daneu 834 (UFP).

Etymology:—It refers to the floral bracts color (Ferreira & Louzada Artigo 2).

Distribution and Habitat:—*Cryptanthus vinosibracteatus* is known from the Bahia State (municipality of Itapetinga). It occurs in the phytogeographic domain of the Atlantic Forest, at 308 m elevation in the vegetation type deciduous seasonal forest. It is terricolous and grows on dense litter layer.

Phenology:—Flowering in cultivation in July.

Conservation status:—*Cryptanthus vinosibracteatus* is known only from the type locality (one location) in a private area. Perhaps the species also occurs in municipality of Jequié, however, the herbarium specimen (*W.W. Thomas et al.* 12599-CEPEC) could not be accurately identified because it is sterile. Possibly the species can be suffering a decline in the area of occupancy. Thus, this species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—*Cryptanthus vinosibracteatus* is morphologically related to *C. arelii* H. Luther and *C. sp.* due to the leaf blades color but *C. vinosibracteatus* differs from them by

the floral bracts 25–26 mm long (vs. 12.2–22.5 mm long), white-greenish on the base and vinaceous on the apices (vs. white, cream or pale green). The information about morphological characters of *C. arelli* was taken from Luther (1999) for comparison with *C. vinosibracteatus*.

Specimens examined:—BRAZIL. **Bahia:** Itapetinga, Fazenda Santa Cruz, antiga propriedade de Salvador, atualmente de Vardão, 308 m, 15°07'48.9"S, 40°14'38.9"W, 19 March 2018, fl. cult. 17 July 2019, *D. Cavalcanti & L. Daneu 834* (UFP).

36. *Cryptanthus viridovinosus* Leme, *Rodriguésia* 61(1): 33 (2010). [Fig. 3D].

Type:—BRAZIL. Bahia: Alagoinhas, near Icatu, ca. 80 m elev., September 2000, fl., *S. Linhares & R. Alves 678* (holotype: HB photo! [HB093258]).

Etymology:—It refers to the leaves color that are wine on basal portion and apple green on the apical portion (Leme *et al.* 2010).

Distribution and Habitat:—*Cryptanthus viridovinosus* is only known from Bahia State (municipality of Alagoinhas). It occurs in the area of transition between Atlantic Forest and Caatinga, at 80 m elevation (Leme *et al.* 2010). It is terricolous and grows on sandy soils partially shaded by forest to shrubby semideciduous vegetation (Leme *et al.* 2010).

Phenology:—Flowering in nature in September.

Conservation status:—*C. viridovinosus* is known only from the type locality (one location). According to Leme *et al.* (2010), the habitat is affected by sand extraction (Leme *et al.* 2010). Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Critically Endangered (CR) based on the criterion B2 ab(ii).

Taxonomic affinities:—The information about reproductive characteres of *C. viridovinosus* and about morphological characters of *C. santateresinhensis* were taken from Leme *et al.* (2010) and Leme *et al.* (2020), respectively, for comparison between them. *C. viridovinosus* is morphologically similar to *C. santateresinhensis* due to the short stem (<8 cm), leaf blades lanceolate or narrowly elliptic and petals white with apices green or greenish but *C. viridovinosus* differs from *C. santateresinhensis* by the flowers 40 mm long (vs. 44 mm long), sepals 12–13 mm long (vs. 15 mm long), connate for 6–7 mm (vs. connate for 10 mm), lobes oblong-elliptic (vs. ovate), petals 30–33 mm long (vs. 35 mm long).

Specimens examined:—BRAZIL. **Bahia:** Alagoinhas, near Icatu, ca. 80 m elev., September 2000, fl., *S. Linhares & R. Alves 678* (HB).

37. *Cryptanthus walkerianus* Leme & L.Kollmann, *Phytotaxa* 177(2): 83 (2014). [Figs. 3D, 5H-J, 28].

Type:—BRAZIL. Bahia: Camamu, at the border with Igrapiuna, Pinaré, old Fazenda Bonsucesso, Reserva Florestal Novo Milênio, owner Ian Walker, 141 m elevation, 13°54'33" S, 39° 10'11" W, 06 June 2013, *E. M. C. Leme, L.Kollmann & P.Lima. 8749* (holotype: RB digital image! [RB 306140]; isotype: HB).

Etymology:—It is honor to Ian Walker that is an English geneticist owner of the reserve where the specimen type was found (Leme *et al.* 2014).

Distribution and Habitat:—*Cryptanthus walkerianus* is only known from Bahia State (municipality of Camamu, Ituberá, Nilo Peçanha and Valença). It occurs in the phytogeographic domain of the Atlantic Forest, at 104 to 168 m elevation in the vegetation type submontane tropical moist forest. It is terricolous and grows on dense litter layer of clayey soil.

Phenology:—Flowering in nature in February, April, June, July and August and in cultivation in April and May.

Conservation status:—*C. walkerianus* is known to four locations, one of which is located in conservation unit: Reserva Florestal Novo Milênio. The extent of occurrence (EOO) is 185.807 km² and the area of occupancy (AOO) is 16 km². The species is located in the Atlantic Forest that is severely fragmented and possibly the species can be suffering a decline in the area of occupancy. Thus, this species is classified as Endangered (EN) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. walkerianus* is phylogenetically related to *C. teretifolius* Leme and *C. robsonianus* Leme that together are included in the walkerianus clade (Ferreira *et al.* Artigo 1). *C. walkerianus* and *C. teretifolius* are similar due to the canaliculate petioles with straight margins and petals white but *C. walkerianus* differs from *C. teretifolius* by the floral bracts of the staminate flower 26–32 mm long (vs. 21–22 mm long) and filaments of the staminate flower 20 mm long (vs. 24–27 mm long). *C. walkerianus* is also morphologically similar to *C. robsonianus* due to the apical glomerule of the inflorescence to have many flowers but *C. walkerianus* differs from *C. robsonianus* by the leaves petiolate (vs. leaves sessile, contracted at base above the leaf sheaths).

Specimens examined:—BRAZIL. **Bahia:** Camamu, at the border with Igrapiuna, Pinaré, old Fazenda Bonsucesso, Reserva Florestal Novo Milênio, owner Ian Walker, 141 m elevation, 13°54'33"S, 09°10'11" W, 06 June 2013, fl., *E. M. C. Leme, L.Kollmann & P.Lima. 8749*

(RB, HB); Camamu, Reserva Floresta Novo Milênio, 168 m, 13°54'42"S, 39°10'18"W, 27 March 2018, fl. cult. 27 April 2018, fl., *D. Cavalcanti & L. Daneu* 884 (UFP); Camamu, Reserva Floresta Novo Milênio, 168 m, 13°54'42"S, 39°10'18"W, 27 March 2018, fl. cult. 08 May 2018, fl., *D. Cavalcanti & L. Daneu* 915 (UFP); Camamu: Pinaré, Terr. Ian Walker, 06 June 2013, fl., *L. Kollmann, E. Leme & P. Lima* 12762 (MBML); Ituberá/Graipiúna, fragmento pacangê, 14 July 2007, fl., *R. Valadão & M.L. Guedes* 747 (ALCB); Nilo Peçanha, entrada ca. 4 Km da comunidade Quilombola de Jatimane na entrada para Ituberpa, fazenda Outeiro do Chapéu, 104 m, 13°40'06"S, 39°04'50"W, 15 June 2012, fl., *L.P. Queiroz & F.H.F. Nascimento* 15472 (HUEFS); Valença: Estrada Valença-Guaibim, km 8 a E de Valença, 27 July 1981, fl., *A.M. de Carvalho & J. Gatti* 825 (CEPEC, RB); Valença: Ramal à esquerda da Rodovia que liga Valença à Guaibim, km 9, 12 August 1960, fl., *L.A. Mattos Silva, A.M.V. de Carvalho & J.L. Hage* 1046 (CEPEC); Valença, Km 10 da Rod Valença/Guaibi, 22 February 1975, fl., *T. S. Santos* 2901 (US).

38. *Cryptanthus warren-loosei* Leme, *Cryptanthus Soc. J.* 8(2–3): 17 (1993). [Figs. 3D, 29].

Type:—BRAZIL. Bahia: Itaberaba-Lençóis, BR 242, 11 January 1983, fl. cult. December 1992, fl., *E. M. C. Leme, J. Kent & R. L. Frasier* 481 (Holotype: HB image! [HB 73937], isotype: RB image! [RB 324438])

Etymology:—It is honor to Warren Loose that is a member of the Cryptanthus Society (Leme 1993).

Distribution and Habitat:—*Cryptanthus warren-loosei* is only known from Bahia State (municipality of Conceição de Feira, Itaberaba, Lençóis, Morro do Chapéu and Ruy Barbosa). It occurs in the phytogeographic domain of the Caatinga, at 40 to 1067 m elevation. It is terricolous and grows on closed forest formations in the Chapada Diamantina.

Phenology:—Flowering in nature in April, May, November and December and in cultivation in December.

Conservation status:—*C. warren-loosei* is known to eight locations, however none of these locations are included in a conservation unit. The extent of occurrence (EOO) is 10,501.345 km² and the the area of occupancy (AOO) is 32 km². Possibly the species can be suffering a decline in the area of occupancy. Thus, the species is classified as Endangered (EN) based on the criterion B2 ab(ii).

Taxonomic affinities:—*C. warren-loosei* is phylogenetically related to *C. boanovensisi* Leme and *C. crassifolius* Leme that together are included in the warren-loosei clade (Ferreira *et al.* Artigo 1). *C. warren-loosei* differs from *C. boanovensisi* by the flowers 30–37 mm long (vs. 41–52 mm long), petals connate for 3–5 mm long (vs. 7–13 mm long), callosities appearing 3–5.3 mm distant from the base (vs. 9–12 mm distant from the base), filaments 15.2–19.8 mm long (vs. 25–28 mm long) and anther apices acute (vs. rounded). *C. warren-loosei* differs from *C. crassifolius* by the abaxial surface of the leaf blades glabrous except on the base densely lepidote (vs. entirely densely lepidote in the older leaves). In addition, *C. warren-loosei* is morphologically similar to *C. bahianus* due to leaf blades linear triangular or narrowly triangular but *C. warren-loosei* differs from *C. bahianus* by the ovary with 22–29 ovules per locule in the perfect flowers (vs. 3–4 ovules per locule in the perfect flowers).

Specimens examined:—BRAZIL. **Bahia:** Conceição de Feira, Margem da Represa de Bananeiras, 12°31'50"S, 39°03'33"W, 18 November 1981, fl., *A. M. de Carvalho et al.* 566 (CEPEC, HUEFS, RB); Itaberaba-Lençóis, BR 242, 11 January 1983, fl. cult. December 1992, fl., *E. M. C. Leme, J. Kent & R. L. Frasier* 481 (HB, RB); Morro do Chapéu, Estrada para o buraco do Possidônio, 2016, fl. cult. 27 April 2018, fl., *D. Cavalcanti & R. B. Louzada* 901 (UFP); Morro do Chapéu, Estrada para o buraco do Possidônio, 2016, fl. cult. 23 May 2018, fl., *D. Cavalcanti & R. B. Louzada* 895 (UFP); Morro do Chapéu, Seguindo em direção a Irecê, pegar a estrada de chão para carrasco atrás do Posto Sidel, depois de 2,1 km pegar primeira bifurcação a esquerda, seguir ca. 1,5 km, antes do sítio Novo Horizonte, 11°30'03"S, 41°06'14"W, 08 April 2008, fl., *C. A. Bastos & C. Van den Berg* 198 (HUEFS); Morro do Chapéu, Fazenda Guariba, 1067 m, 11°20'23"S, 41°04'37"W, 29 April 2011, fl., *E. Melo et al.* 9625 (HUEFS); Ruy Barbosa, Trilha para o Pátio das Orquídeas, 509 m, 12°18'07"S, 40°29'16"W, 13 November 2004, fl., *L. P. Queiroz et al.* 9793 (HUEFS); Ruy Barbosa, Paraguaçu, margem do Rio Água Branca, 12°04'01"S, 40°33'48"W, 19 May 2001, fl., *L. J. Alves et al.* 293 (ALCB, CEPEC); Morro Belo, Cachoeira/Bahia-Vale dos Rios Paraguaçu e Jacupe, 40/120 m, 12°32'S, 39°05'W, December 1980, fl., *Grupo Pedra do Cavalo* 982 (CEPEC).

39. *Cryptanthus zonatus* (Vis.) Vis., *Pl. Nuove Bromel.*: 9. 1854. [Figs. 3D, 30].

Basionym:—*Pholidophyllum zonatum* Vis., *Ind. Sem. Hort. Patav.*: 4. 1847.

Type:—BRAZIL. Pernambuco: Prov. Caruaru, fl. cult., 25 Jun 1972, *E. Waras s.n.* (neotype, designated by Ramírez M. (1998: 223): HB image! [HB58090]).

Cryptanthus zonatus var. *fuscus* (Vis.), Fam. Bromel.: 76. 1856.

Cryptanthus zonatus var. *viridis* Beer, Fam. Bromel.: 76. 1856.

Cryptanthus fosterianus L.B.Sm., Bromeliad Soc. Bull 2: 63. 1952.

Type: Brazil, Pernambuco: Terrestrial, Serra Negra, near Paraíba boundary, altitude 350 meters, October 13, 1948, *M. B. Foster 2431* (Holotype: US! [US 2057909-sheet 1; US 2057910-sheet 2])

Cryptanthus burle-marxii Leme, *Cryptanthus Soc. J.* 5(1): 12. 1990b.

Type: Brazil, state of Pernambuco, Gravata, August 1989, *Roberto Burle Marx s.n.*, fl. cult. *E.M.C. Leme* (Holotype: HB image! [HB 73716]; Isotype: RB).

Etymology:—It refers to the crossbars of lepidote trichomes on the leaf blade (Ramírez-Morillo 1996).

Distribution and Habitat:—*Cryptanthus zonatus* is known from the Alagoas (Marechal Deodoro, Paripueira and São Luis do Quintude), Paraíba (Mataraca), Pernambuco (Cabo de Santo Agostinho, Gravatá, Igarassu, Ipojuca, Jaqueira, Paulista, Quipapá, Recife and Timbaúba) and Rio Grande do Norte (municipality of Baía Formosa, Ceará-Mirim, Maxaraguape, Natal and Nísia Floresta) States. It occurs in the phytogeographic domain of the Atlantic Forest, at 14.5 to 681 m elevation. It is terricolous and grows on sandy soil of closed forest of Restinga and on clay soil on semideciduous seasonal forest and Brejos de Altitude.

Phenology:—Flowering in nature in February, March, April, May, July, August, September, October, November and December and in cultivation in January, February, March, May, June, August, September and October.

Fruiting in nature are in April and September.

Conservation status:—*C. zonatus* is known to 22 locations, eight of which are located in conservation units: APA Bonfim-Guaráiras, Estação Ecológica de Caetés, Parque da Cidade Dom Nivaldo Monte, Parque Estadual das Dunas de Natal, RPPN Mata Estrela, RPPN Nossa Senhora do Oiteiro de Maracáipe, RPPN Placas (O Sabiá) and RPPN Serra do Contento. The conservation status of *C. zonatus* was recently evaluated by Ferreira *et al.* (2021). The extent of occurrence (EOO) is 32,036.834 km² and the area of occupancy (AOO) is 116 km² (Ferreira *et al.* 2021). Ferreira *et al.* (2021) indicate that the species is classified as Endangered (EN) based on the criterion B2ab(iii), (iv) due to the occurrence area being

severely fragmented, decline of the quality of its habitat and reduction in the number of locations where it occurs.

Taxonomic affinities:—*C. zonatus* is phylogenetically close to *C. diana* Leme and *C. reptans* Leme & J.A.Siqueira that together form the *zonatus* clade (Ferreira *et al.* Artigo 1). *C. zonatus* is readily distinguished from other species from the region by the leaf blades with crossbars of lepidote trichomes. However, there are individuals with leaf blades glabrous and green. Thus, *C. zonatus* can be confused with *C. diana* and *C. reptans*. These three species are included in the *C. zonatus* (Vis.) Vis. complex by Ferreira & Louzada (2020) due to overlapping of morphological characters between them. In the phylogenetic study (Ferreira *et al.* Artigo 1), *C. zonatus* emerges as non-monophyletic. The authors recommend population genetic studies to resolve this complex. Another name (*Cryptanthus burle-marxii* Leme) also was included in the *C. zonatus* (Vis.) Vis. complex but it was recently synonymized in *C. zonatus* by Ferreira *et al.* (2021b). We recommend population genetic studies to resolve the *C. zonatus* (Vis.) Vis. complex.

Specimens examined:—BRAZIL. **Alagoas:** Marechal Deodoro, CESMAC, 09°71'03"S, 35°89'50"W, 15 July 2009, fl., N. R. Santos, M. V. Caju & L. M. Leão 40 (MAC); Marechal Deodoro, Dunas do Cavalo Russo, 18 September 2010, fl., Chagas-Mota 8607 (MAC); Paripueira, RPPN Placas (O Sabiá), 50 m, 09°26'17"S, 35°36'07"W, 01 October 2017, fl. cult. 22 August 2018, D. Cavalcanti & R. B. Louzada 907 (UFP); São Luis do Quintude, Serra da Cachoeira, Fazenda Lagoa Vermelha, 150 m, 09°19'43"S, 35°40'16"W, 07 March 2016, sterile, R. A. Pontes 1141 (UFRN); São Luis do Quintude, Serra da Cachoeira, Fazenda Lagoa Vermelha, 180 m, 09°19'48"S, 35°40'12"W, 07 March 2016, sterile, R. A. Pontes 1142 (UFRN). **Bahia (cultivated):** Salvador, Região Metropolitana de Salvador, Cultivada, 05 September 2006, fl., A. L. Cotias *s.n.* (ALCB 74917); Santa Terezinha, Recôncavo Sul, Cultivada, 12°46'S, 39°31'W, 07 August 2002, fl., R. de O. Alves *s.n.* (ALCB 57938). **Paraíba:** Mataraca, empresa mineradora Millenium Chemical do Brasil, December 2004, fl., R.A. Pontes & P.C. Gadelha Neto 224 (RB); Mataraca, Millennium Inorganic Chemicals Mineração LTDA, 30 m, 06°30'59"S, 34°58'24"W, 25 August 2010, sterile, R. A. Pontes, J. R. Lima & C. S. Silva 545 (JPB); Mataraca, empresa mineradora Layonel, December 2004, fl., R. A. Pontes & Gadelha Neto 325 (JPB); Mataraca, empresa mineradora Layonel, December 2004, fl., R. A. Pontes & Gadelha Neto 326 (JPB); Mataraca, Millennium Inorganic Chemicals Mineração LTDA, 06°29'37,02"S, 34°58'43,08"W, 04 October 2007, sterile, P. C. Gadelha Neto, I. B. Lima, R. S. Lima & C. S. Silva 1850 (JPB); Mataraca, Mineradora Cristal,

06°31'04"S, 34°58'04"W, 16 September 2015, sterile, *D. Cavalcanti, T. Coutinho & I. Fernandes* 779 (UFP); Mataraca, Mineradora Cristal, 06°31'04"S, 34°58'04"W, 16 September 2015, fl. cult. 12 March 2017, fl., *D. Cavalcanti, T. Coutinho & I. Fernandes* 917 (UFP); Mataraca, empresa mineradora Layonel, December 2004, fl., *R. A. Pontes & Gadelha Neto* 201 (JPB). **Pernambuco:** Cabo de Santo Agostinho, Pontezinha, fábrica da pólvora, 26 May 1994, fl., *K. Pôrto s.n.* (UFP 10131); Gravatá, Jussará, 666 m, 08°17'51"S, 35°34'59"W, 25 March 2017, fl. cult. 23 May 2018, fl., *F. Gomes-Silva et al.* 292 (UFP); Gravatá, RPPN Serra do Contente, Trilha para o Mirante, 681 m, 08°15'50"S, 35°33'07"W, 14 August 2017, *D. Cavalcanti et al.* 784 (UFP); Gravatá, RPPN Serra do Contente, Trilha para o Mirante, 681 m, 08°15'50"S, 35°33'07"W, 03 July 2014, *D. Cavalcanti & R. B. Louzada* 728 (UFP); Igarassu, Usina São José, Mata de Piedade, 07°50'18"S, 34°59'57"W, 2017, fl. cult. 21 June 2018, fl., *D. Cavalcanti & R. B. Louzada* 894 (UFP); Igarassu, Usina São José, Mata de Piedade, 07°50'18"S, 34°59'57"W, fl. cult. 14 March 2014, fl., *D. Cavalcanti & R. B. Louzada* 897 (UFP); Igarassu, Usina São José, Mata de Piedade, 07°50'18"S, 34°59'57"W, 17 August 2011, fl., *B. S. Amorim et al.* 992 (UFP); Igarassu, matas do Engenho Piedade, 27 August 1998, fl., *G. Martinelli et al.* 15101 (RB); Ipojuca, Engenho Canto, 08°31'42.1"S, 35°01'13.30"W, 12 March 2015, fl., *J.A. Siqueira-Filho & E.D.S. Almeida* 3320 (HURB); Ipojuca, Mata do Cupe, 08°26'28"S, 34°59'33"W, fl. cult. 25 October 2017, fl., *R. B. Louzada* 208 (UFP); Ipojuca, Mata do Cupe, 08°26'28"S, 34°59'33"W, 03 October 2014, fl., *D. Cavalcanti et al.* 764 (UFP); Ipojuca, Mata do Cupe, 08°26'28"S, 34°59'33"W, 03 October 2014, fl. cult. 30 June 2016, fl., *D. Cavalcanti et al.* 916 (IPA); Ipojuca, RPPN Nossa Senhora do Oiteiro de Maracaípe, Mata do Oiteiro, 14,5 m, 08°31'11,5"S, 35°01'12,2"W, 04 August 2007, fl., *M. Sobral Leite, J. B. Oliveira & T. L. Nadia* 407 (UFP, IPA); Ipojuca, Mata do Outeiro de Maracaípe, Área fora da RPPN, 08°31'48"S, 35°01'05"W, 13 October 2014, fl., *D. Cavalcanti & J. Oliveira-Júnior* 765 (UFP); Jaqueira, Usina Catende, Engenho flor do Bosque, 08°44'04"S, 35°46'15"W, 18 April 2004, fl., *J. A. Siqueira-Filho* 1429 (UFP, HURB); Quipapá, Engenho Brejinho, 15 September 1972, fl., *I. Pontual* 72-1230 (PEUFR); Recife, Dois Irmãos, prox. Chã do Visgueiro Grande, 02 November 1954, fl., *A. Lima* 54-1920 (IPA, US); Recife, Proveniente das matas de água mineral em Gravatá, 15 May 1995, fl., *L. P. Félix* 7144 (HST); Timbaúba, Engenho Xixá, 22 February 2016, fl., *M. L. Bazante et al.* 529 (UFP); [without precise location], Serra Negra near Paraíba boundary, 13 October 1948, fl. cult. 29 September 1952, fl., *M. B. Foster* 2431(US); [without precise location], 09 July 1981, fl., *G. Martinelli* 7623 (RB). **Rio Grande do Norte:** Baía Formosa, Reserva Particular do Patrimônio Natural (RPPN) Mata Estrela, trilha do Pagão, 60 m, 06°23'43"S,

35°00'50"W, 18 May 2015, fl., *J. L. Costa-Lima et al.* 2170 (UFRN); Baía Formosa, RPPN Mata Estrela, Dunas ao norte da estrada para Baía Formosa, 25 m, 06°37'79"S, 35°01'19"W, 07 September 2015, fl. and fr., *G. S. Garcia & L. M. G. Gonçalves* 20 (UFRN, RB); Baía Formosa, Mata Estrela, Trilha do pau ferro, 10 March 2013, fl., *R. E. C. Magalhães* 18 (UFRN); Baía Formosa, Mata Estrela, Trilha do Pagão, 14 April 2013, fl., *R. E. C. Magalhães* 200 (UFRN); Baía Formosa, Mata Estrela, 50 m, 06°22'40"S, 35°01'22"W, 09 March 2012, fl., *W. M. B. São-Mateus et al.* 101 (UFRN); Baía Formosa, RPPN Mata Estrela, trilha da gameleira, 06°22'40"S, 35°01'22"W, 29 August 2014, fl. cult. 22 February 2017, fl., *D. Cavalcanti & R. B. Louzada* 763 (UFP); Baía Formosa [Tibáu do Sul], Mata Estrela, 10 July 2004, fl. cult. 08 May 2006, fl., *N. T. Lima* 35928 (JPB); Baía Formosa, Mata Estrela, 100 m, 06°25'27"S, 34°59'19"W, August 1998, fl. cult. 20 May 2013, fl., *G. Martinelli* 15079 (RB); Baía Formosa, Mata Estrela, *G. Martinelli* 15081, fl. cult. 15 February 2008, fl., *N. Vasconcellos* 15 (RB); Ceará-Mirim, Área do empreendimento Dunas de Miriú, 33 m, 05°31'57"S, 35°15'41"W, 11 February 2016, sterile, *E. O. Moura & P. B. C. S. Moura* 527 (UFRN); Ceará-Mirim, Área do empreendimento Dunas de Miriú, 28 m, 05°31'52"S, 35°15'47"W, 11 February 2016, sterile, *E. O. Moura & P. B. C. S. Moura* 528 (UFRN); Maxaranguape, Mancha de floresta prox. BR 101, 35 m, 05°28'07"S, 35°19'43"W, 24 April 2016, fl., *G. S. Garcia & L. M. G. Gonçalves* 146 (UFRN); Maxaranguape, Mancha de floresta prox. BR 101, 35 m, 05°28'07"S, 35°19'43"W, 03 October 2017, fl. cult. 07 February 2018, fl., *D. Cavalcanti, F. M. Guedes & G. S. Garcia* 896 (UFP); Maxaranguape, Mancha de floresta prox. BR 101, 35 m, 05°28'07"S, 35°19'43"W, 03 October 2017, fl. cult. 23 February 2018, fl., *D. Cavalcanti, F. M. Guedes & G. S. Garcia* 918 (UFP); Natal, Parque da Cidade Dom Nivaldo Monte, trilha Pau Brasil, 68 m, 05°50'57"S, 35°13'46"W, 02 May 2015, sterile, *A. A. Roque, P. L. Costa & A. W. Vitorino* 1571 (UFRN); Natal, Parque da Cidade Dom Nivaldo Monte, 68 m, 05°50'57"S, 35°13'46"W, 30 April 2016, fl., *A. A. Roque* 1792 (UFRN); Natal, Parque da Cidade Dom Nivaldo Monte, depois do ponto de descanso, entrada a esquerda, 05°50'57"S, 35°13'46"W, 28 August 2017, fl. cult. 09 March 2017, fl., *D. Cavalcanti & R. B. Louzada* 758 (UFP); Natal, Parque Estadual das Dunas, Trilha do Visconde, subida do morro, 06 May 2006, fl., *R. T. Queiroz & A. M. Marinho* 792 (UFRN); Natal, Parque das Dunas, Trilha Perobinhas, 65 m, 05°51'39"S, 35°11'05"W, 16 August 2012, sterile, *A. S. M. Medeiros, E. Tomaz & R. E. C. Magalhães* 9 (UFRN); Natal, Parque das Dunas, trilha da Peroba, 20 April 2012, fl. and fr., *A. S. M. Medeiros, E. Tomaz & R. E. C. Magalhães* s.n. (UFRN 14841); Natal, Parque das Dunas, Trilha do Parque, 64 m, 05°48'35"S, 35°11'12"W, 06 May 2011, fl., *L. M. Versieux* 511 (UFRN); Natal, Trilha da

Geologia, 09 April 2012, sterile, *L. M. Versieux* 519 (UFRN); Natal, Pitimbu, Terreno da Ecocil, vizinho ao Parque da Cidade, Sunset Boulevard, 46 m, 05°51'34"S, 35°23'26"W, 14 December 2016, sterile, *L. M. Versieux et al.* 874 (UFRN); Natal, mata úmida litorânea duna de natal-RN, material em cultivo em Pacoti-CE, 14 January 1995, fl., *L. Félix s.n.* (EAC 21842); Natal, exótica de Natal-RN, material cultivado no Ceará, Pacoti, Sítio Olho d'Água dos Tangarás, sede, 27 May 1995, fl., *L. W. Lima-Verde s.n.* (EAC 22992); Nisea Floresta, APA Bonfim-Guarairas, prox. Lago Azul, 35 m, 05°59'35"S, 35°11'53"W, 13 April 2016, fl., *G. S. Garcia, J. C. Corrêa & L. M. G. Gonçalves* 135 (UFRN). [without precise location], cult. Montreal Bot. Gard., 11 May 1905, sterile, *J. Roehrs* 1719-55 (US).

Excluded taxon

Cryptanthus bivittatus (Hook.) Regel, *Gartenflora* 14: 2 (1865).

Basionym:—*Billbergia bivittata* Hook., Bot. Mag. 17: t. 5270. 1861.

Billbergia bivittata var *luddemannii* Baker, Handb. Bromel.: 16. 1889.

Notes:—There is no indication of the nomenclature type (Hooker 1861). The author indicates that the species is native of South America but he doesn't know in which country the species was found. There is also no occurrence information in Regel (1865). Posteriorly, Baker (1889) described a variety based on the drawing of Professor Morren's of a plant cultivated in Kew that was introduced by Linden from Porto Seguro, but there is no indication of the exsiccate. There is a material in Kew herbarium indicated as holotype (K 000322188) and it was identified as *Cryptanthus bivittatus* by Ramírez-Morillo, but, there is no information about the collection location and collector in the sample. Thus, because the place of occurrence is imprecise, we decided not to include this species in the study.

References

- APG (The Angiosperm Phylogenetic Group) IV (2016) An update of the angiosperm phylogenetic group classification for the orders and families of flowering plants: APG IV. *Botanical Journal of the Linnean Society* 181: 1-20.
- Bachman, S., Moat, J., Hill, A.W., de la Torre, J. & Scott, B. (2011) Supporting Red List threat assessments with GeoCAT: geospatial conservation assessment tool. *Zookeys* 150: 117–126.
- Baker, J.G. (1889) *Handbook of the Bromeliaceae*. Bell & Sons, London, 243 pp.

- Beer, J. G. (1856) *Die Familie der Bromeliaceen nach ihrem habituellen charakter bearbeitet mit besonderer berücksichtigung der Ananassa*. Wien, Tendler & Comp., 271 pp.
- Braun, P. & Brito, B.G. (2019) Xeromorfe Bromelien aus Brasilien (III): *Cryptanthus heimenii*, eine neue Art aus Sergipe. Xeromorphic Bromeliads from Brazil (III): *Cryptanthus heimenii*, a New Species from Sergipe. *Die Bromelie* 2: 54-6.
- Cruz, G.A.S., Zizka, G., Silvestro, D., Leme, E.M.C., Schulte, K. & Benko-Iseppon, A. M. (2017) Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). *Molecular Phylogenetics and Evolution* 107: 152–165.
- Ferreira, D.M.C. & Louzada, R.B. (Artigo 2) Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from Atlantic Forest of northeastern Brazil.
- Ferreira, D.M.C. & Louzada, R.B. (Capítulo de livro 1) *Cryptanthus*. In: *Flora de Alagoas*.
- Ferreira, D.M.C. & Louzada, R.B. (2015) *Cryptanthus*. In: Prata, A.P. do, Farias, M.C.V. & Ladim, M.F. (Eds.) *Flora de Sergipe*. 1. Ed. v. 2. Criação Editora, Aracaju, p. 1-300.
- Ferreira, D.M.C. & Louzada, R.B. (2020) A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus. *Systematic Botany* 45: 460–465.
- Ferreira, D. M. C.; Almeida, E. M de; Louzada, R. B. (2021a) Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from northeastern Brazil. *Phytotaxa* 523: 099–109.
- Ferreira, D. M. C., Palma-Silva, C., Néri, J., Medeiros, M. C. M. P. de, Pinangé, D. S., Benko-Iseppon, A. M. & Louzada, R. B. (2021b) Population genetic structure and species delimitation in the *Cryptanthus zonatus* complex (Bromeliaceae). *Botanical Journal of the Linnean Society* 196: 123-140.
- Ferreira, D.M.C., Vasconcelos, S., Nunes, G. L., Pires, E.S., Oliveira, G. & Louzada, R.B. (Artigo 1) Phylogenetic relationships of the genus *Cryptanthus* Otto & A. Dietr. (Bromelioideae, Bromeliaceae) using Next-Generation Sequencing data.
- Forzza, R.C., Costa, A.F., Maciel, J.R., Kessous, I.M., Monteiro, R.F., Faria, A.P.G., Tardivo, R.C., Büneker, H.M., Saraiva, D.P., Moreira, B.A., Jacques, S.S.A., Almeida, M.M., Santos-Silva, F., Louzada, R.B., Moura, R.L., Couto, D.R., Neves, B., Oliveira, F.M.C., Araújo, C.C., Gonçalves-Oliveira, R.C., Versieux, L.M., Romanini, R.P., Machado, T.M., Silva, R.S.A.d., Paixão Souza, B., Gomes-da-Silva, J., Uribbe, F.P., Guarçoni, E.A.E., Sousa, L.O.F., Pontes, R.A.S., Nogueira, M.G.C., Sousa, G.M., Koch, A.K., Picanço, W.L., Cardoso, P.H., Martins, S.E., Barbosa-Silva, R.G. & Wanderley, M.G.L. (2020) *Bromeliaceae in Flora do Brasil 2020*. Jardim Botânico do Rio de Janeiro, Rio de Janeiro. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB66> (accessed: 08 Nov 2021)
- Givnish, T.J., Millan, K.C., Berry, P.E. & Sytsma, K. J. (2007) Phylogeny, adaptative radiation, and historical biogeography of Bromeliaceae inferred from *ndhF* sequence data. *Aliso: A Journal of Systematic and Evolutionary Botany* 23: 3-26.

- Givnish, T.J., Barfuss, M.H.J., Ee, B.V., Riina, R., Schulte, K., Horres, R., Gonsiska, P.A., Jabaily, R.S., Crayn, D.M., Smith, J.A.C., Winter, K., Brown, G.K., Evans, T.M., Holst, B.K., Luther, H., Till, W., Zizka, G., Berry, P.E. & Sytsma, K.J. (2011) Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. *American Journal of Botany* 98: 872–895.
- Gouda, E.J., Butcher, D. & Gouda, K. (cont. updated) Encyclopaedia of Bromeliads, Version 4. University Utrecht Botanic Gardens, Utrecht. Available from: <http://bromeliad.nl/encyclopedia/> (accessed: 08 Nov 2021).
- Harris, J.G. & Harris, M.W. (2001) *Plant Identification Terminology: an illustrated glossary*. ed. 2. Spring Lake Publishing, Utah, 206 pp.
- Hooker, W. J., H., K., Oxon., D. C. L. (1861) *Billbergia bivittata* t. 5270.
- IUCN Standards and Petitions Subcommittee (2019) *Guidelines for using the IUCN red list categories and criteria*. Version 14. Standards and Petitions Subcommittee. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (accessed 23 Nov 2020).
- Leme, E.M.C. (1990a) A new *Cryptanthus* species from the state of Goias, Brazil. *The Cryptanthus Society Journal* 5: 10-12.
- Leme, E.M.C. (1990b) A new ornamental *Cryptanthus* from Pernambuco. *The Cryptanthus Society Journal* 5: 12-13.
- Leme, E. M. C. (1993) A new very prolific species from Bahia, Brazil. *The Cryptanthus Society Journal* 8: 17-19.
- Leme, E.M.C. (1995) Two new *Cryptanthus* species from Brazil. *The Cryptanthus Society Journal* 10: 9-11.
- Leme, E.M.C. (1999) New species of Brazilian Bromeliaceae: A tribute to Lyman B. Smith. *Harvard Papers in Botany* 4: 135-168.
- Leme, E.M.C. (2001) New *Cryptanthus* species from Espírito Santo, Brazil. *The Cryptanthus Society Journal* 16: 12-13.
- Leme, E.M.C. (2002a) Two New sympatric *Cryptanthus* species. *The Cryptanthus Society Journal* 17: 86-89.
- Leme, E.M.C. (2002b) *Cryptanthus teretifolius*, a new species from the coastal zone of Espírito Santo State. *The Cryptanthus Society Journal* 17: 15-16.
- Leme, E.M.C. (2014) A New Species of *Cryptanthus* from Espírito Santo, Brazil. *Journal of the Bromeliad Society* 64: 150-155.
- Leme, E.M.C. (2015) Two new bromelioid species from Brazil. *Journal of the Bromeliad Society* 65: 87-99.
- Leme, E.M.C. & Kollmann, L.J.C. (2013) Miscellaneous new species of Brazilian Bromeliaceae. *Phytotaxa* 108: 1-40.
- Leme, E.M.C. & Siqueira-Filho, J. A. (2001) Studies in Bromeliaceae of Northeastern Brazil. I. *Selbyana* 22: 146-154.

- Leme, E.M.C. & Siqueira-Filho, J.A. (2007) Taxonomia das bromélias dos fragmentos de mata atlântica de Pernambuco e Alagoas. In: Siqueira-Filho, J.A & Leme, E.M.C. (Eds.) *Fragmentos de mata atlântica do Nordeste – biodiversidade, conservação e suas bromélias*. Andrea Jakobsson Estúdio, Rio de Janeiro, pp. 190-381.
- Leme, E.M.C., Kollmann, L.J.C. & Fontana, A.P. (2008) Three New *Cryptanthus* Species from Espírito Santo and Bahia, Brazil. *Journal of the Bromeliad Society* 58: 12-19.
- Leme, E. M. C., Fraga, C.N. de, Kollmann, L.J.C., Brown, G.K., Till, W., Ribeiro, O.B.C., Machado, M.C., Monteiro, F.J.S. & Fontana, A.P. (2010) Miscellaneous new species in the Brazilian Bromeliaceae Miscellaneous new species in the Brazilian Bromeliaceae. *Rodriguésia* 61: 021-067.
- Leme, E.M.C., Till, W., Kollmann, L.J.C., Moura, R.L.de & Ribeiro, O.B.C. (2014) Miscellaneous New Species of Brazilian Bromeliaceae – III. *Phytotaxa* 177: 061–100.
- Leme, E.M.C., Heller, S., Zizka, G. & Halbritter, H. (2017) New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318: 001-008.
- Leme, E.M.C., Ribeiro, O.B.C., Souza, F.V.D., Souza, E.H. de, Kollmann, L.J.C. & Fontana, A.P. (2020) Miscellaneous new species in the “Cryptanthoid complex” (Bromeliaceae: Bromelioideae) from Eastern Brazil. *Phytotaxa* 430 : 157-202.
- Louzada, R.B., Schulte, K., Wanderley, M.G.L., Silvestro, D., Zizka, G., Barfuss, M.H.J. & Palma-Silva, C. (2014) Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (Bromelioideae, Bromeliaceae) and its implications on morphological character evolution. *Molecular Phylogenetics and Evolution* 77: 54-64.
- Luther, H. E. (1999) *Cryptanthus arelii*, an "Old" New species from Bahia, Brazil. *The Cryptanthus Society Journal* 14: 54-55.
- Maciel, J.R. (2020) *Cryptanthus* in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro, Rio de Janeiro. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB5991> (accessed: 10 Jun 2021)
- Mez, C. (1891) Bromeliaceae. In: Martius, C.F.P. von, Eichler, A.W. & Urban, I. (Eds.) *Flora Brasiliensis* 3 (3). F. Fleischer, Leipzig, pp. 173–286.
- Morren, E. (1880) Broméliacées nouvelles. *La Belgique Horticole, Annales de Botanique et D'Horticulture*: 238-252.
- Osbeck, P. (1757) Dagbok öfwer en ostindisk resa åren 1750, 1751, 1752: Med anmärkningar uti naturkunnigheten, främmande folkslags språk, seder, hushållning, m. m. Stockholm, pp. 1–376.
- Otto, F. & Dietrich, A. (1836) Eine neue gattung aus der familie der Bromeliaceae. *Allgemeine Gartenzeitung* 38: 297–299.
- Peixoto, A.L. & Maia, L.C. (2013) Manual de Procedimentos para Herbários. Editora Universitária UFPE, Recife, 104pp.
- Philcox, D. (1992) Notes on South American Bromeliaceae. *Kew Bulletin* 47: 261-276.

- Radford, A.E., Dickison, W.C., Massey, J.R. & Bell, C.R. (1974) *Vascular Plant Systematics*. Harper and Row, New York, 70pp.
- Ramírez, I.M. (1996) Systematic, phylogeny and chromosome number evolution in *Cryptanthus* (Bromeliaceae). PhD thesis, University of Missouri, St. Louis.
- Ramírez M., I.M. (1998) Five new species of *Cryptanthus* (Bromeliaceae) and some nomenclatural novelties. *Havard Papers in Botany* 3: 215-224.
- Rauh, W., Gross, E. & Leme, E.M.C. (1989) A new species of *Cryptanthus* from Brazil. *Journal of the Bromeliad Society* 39: 258-261.
- Regel, E. (1865) Originalabhandlungen. *Gartenflora*: 1-18.
- Schulte, K., Barfuss, M. H. J. & Zizka, G. (2009) Phylogeny of Bromelioideae (Bromeliaceae) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. *Molecular Phylogenetics and Evolution* 51: 327–339.
- Silvestro, D., Zizka, G. & Schulte, K. (2013) Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). *Evolution* 68: 163–175.
- Smith, L.B. (1937-8). *Cryptanthus glaziovii*. Glaziou's *Cryptanthus*. Native of eastern Brazil. *Addisonia*: 9-10.
- Smith, L.B. (1944) Bromeliaceas novas ou interessantes do Brasil. *Arquivos de Botânica do Estado de São Paulo* 1: 53.
- Smith, L.B. (1952) A new ornamental bromeliad. *The Bromeliad Society Bulletin* 2: 62-64.
- Smith, L.B. (1955) The Bromeliaceae of Brazil. *Smithsonian Miscellaneous Collections* 126: 1-290.
- Smith L.B. & Downs R.J. (1979) Bromeliaceae (Bromelioideae). *Flora Neotropica Monograph* 14: 1493–2142.
- Thomas, W.W. & Barbosa, RV. (2008) Natural vegetation types in the Atlantic Coastal Forest of Northeastern Brazil. In: Thomas, W.W. (Ed.) *Atlantic Coastal Forest of Northeastern Brazil*. The New York Botanical Garden Press, New York, pp. 6-20.
- Weber, W. (1892) Species novae Bromeliacearum III¹). *Feddes Repertorium* 93: 337-341.
- Weber, W. (1986) *Feddes Repertorium* 97(3/4): 119.



FIGURE 1. Distribution map of the genus *Cryptanthus* in South America showing the Northeastern region from Brazil in grey.

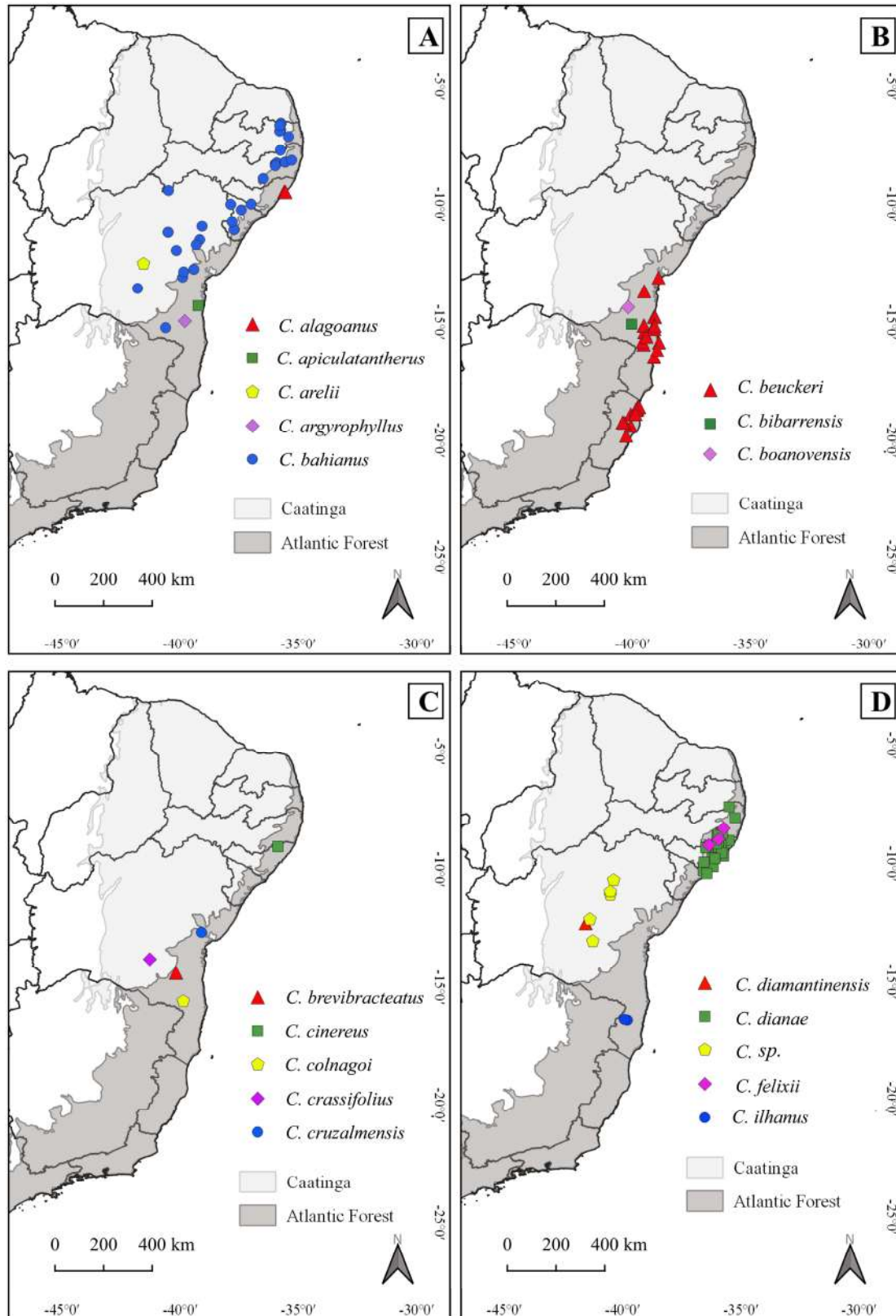


FIGURE 2. Geographical distribution of *Cryptanthus* species from Northeastern Brazil. **A.** *Cryptanthus alagoanus*, *C. apiculatantherus*, *C. arelii*, *C. argyrophyllus* and *C. bahianus*; **B.** *C. beuckeri*, *C. bibarrensensis* and *C. boanovensensis*; **C.** *C. brevibracteatus*, *C. cinereus*, *C. colnagoi*, *C. crassifolius* and *C. cruzalmensis*; **D.** *C. diamantinensis*, *C. diana*, *C. sp.*, *C. felixii* and *C. ilhanus*.

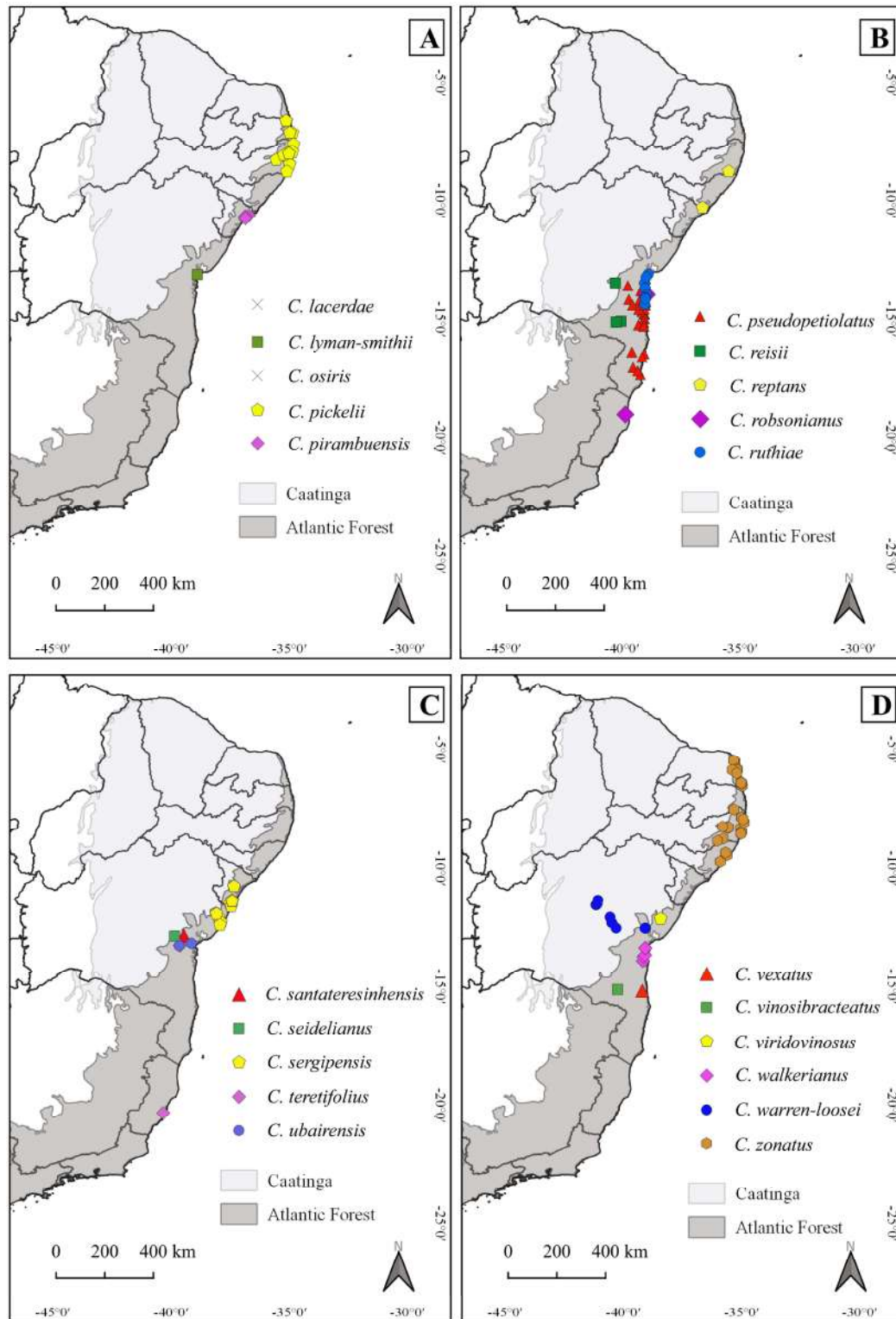


FIGURE 3. Geographical distribution of *Cryptanthus* species from Northeastern Brazil. **A.** *Cryptanthus lacerdae* (without precise locality), *C. lyman-smithii*, *C. osiris* (without precise locality), *C. pickelii* and *C. pirambuensis*; **B.** *C. pseudopetirolatus*, *C. reisii*, *C. reptans*, *C. robsonianus* and *C. ruthiae*; **C.** *C. santateresinhensis*, *C. seidelianus*, *C. sergipensis*, *C. teretifolius* and *C. ubairensis*; **D.** *C. vexatus*, *C. vinosibracteatus*, *C. viridovinosus*, *C. walkerianus*, *C. warren-loosei* and *C. zonatus*.

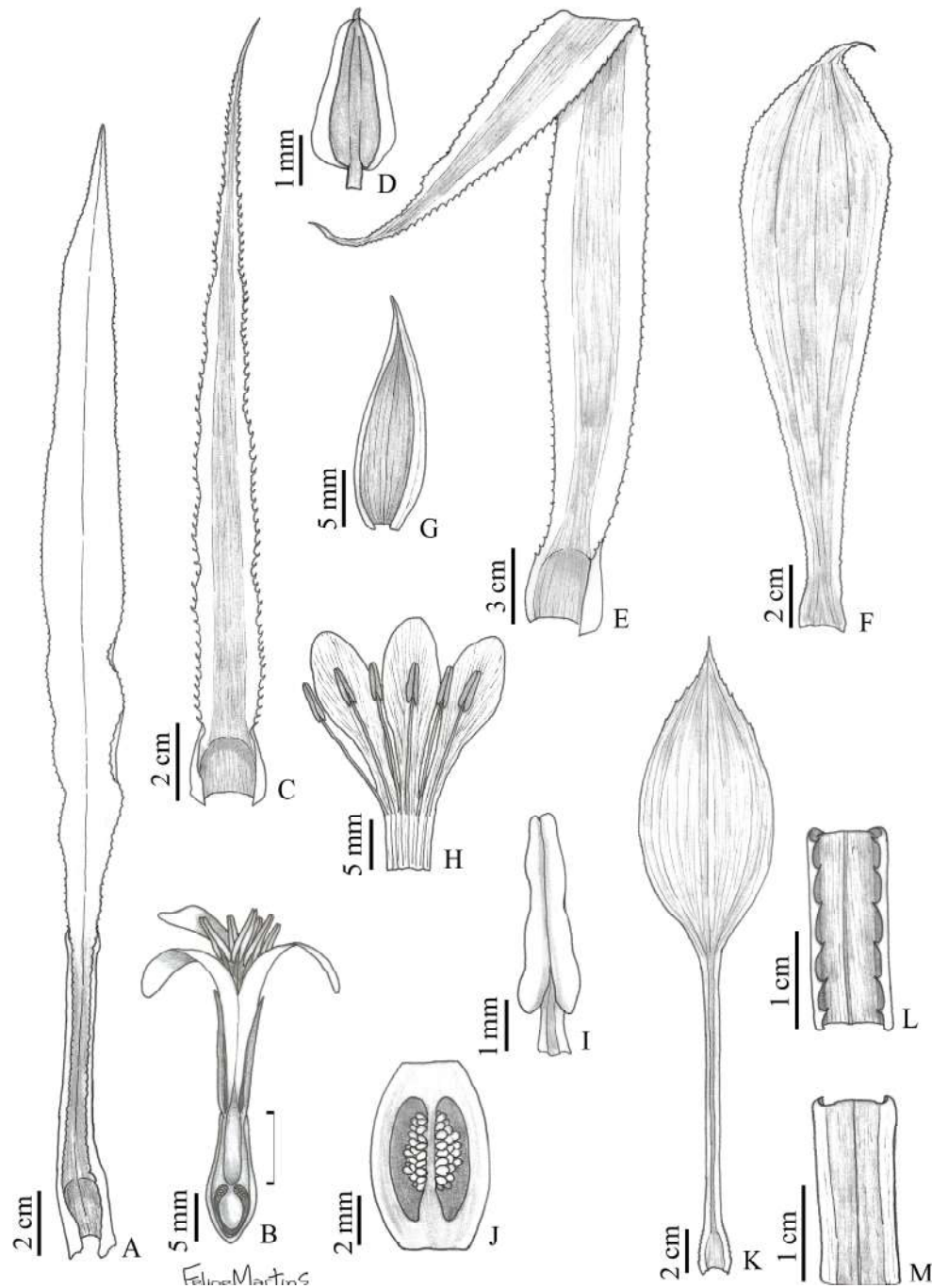


FIGURE 4. Species of *Cryptanthus*. A-B. *Cryptanthus alagoanus* (D. Cavalcanti et al. 906). A. Leaf blade linear-oblongate. B. Staminate flower evidencing the epigynous tube. C-D. *Cryptanthus apiculatantherus* (E. M. Almeida 3246). C. Leaf blade linear triangular. D. Anther apiculate. E. *Cryptanthus arelii* (R.L.Frasier, E.M.C. Leme & J. Kent s.n.) - Leaf blade lanceolate. F. *Cryptanthus argyrophyllus* (E. Leme 4872)- Leaf blade oblanceolate. G-J. *Cryptanthus bahianus*. G. Floral bract of the staminate flower. H. Petals obtuse and stamens. I. Anther emarginate. J. Ovary. K-M. *Cryptanthus beuckeri* (D. Cavalcanti et al. 726). K. Leaf with petiole. L. Portion of the adaxial surface of the canaliculate petiole with revolute margins. M. Portion of the abaxial surface of the canaliculate petiole with revolute margins.

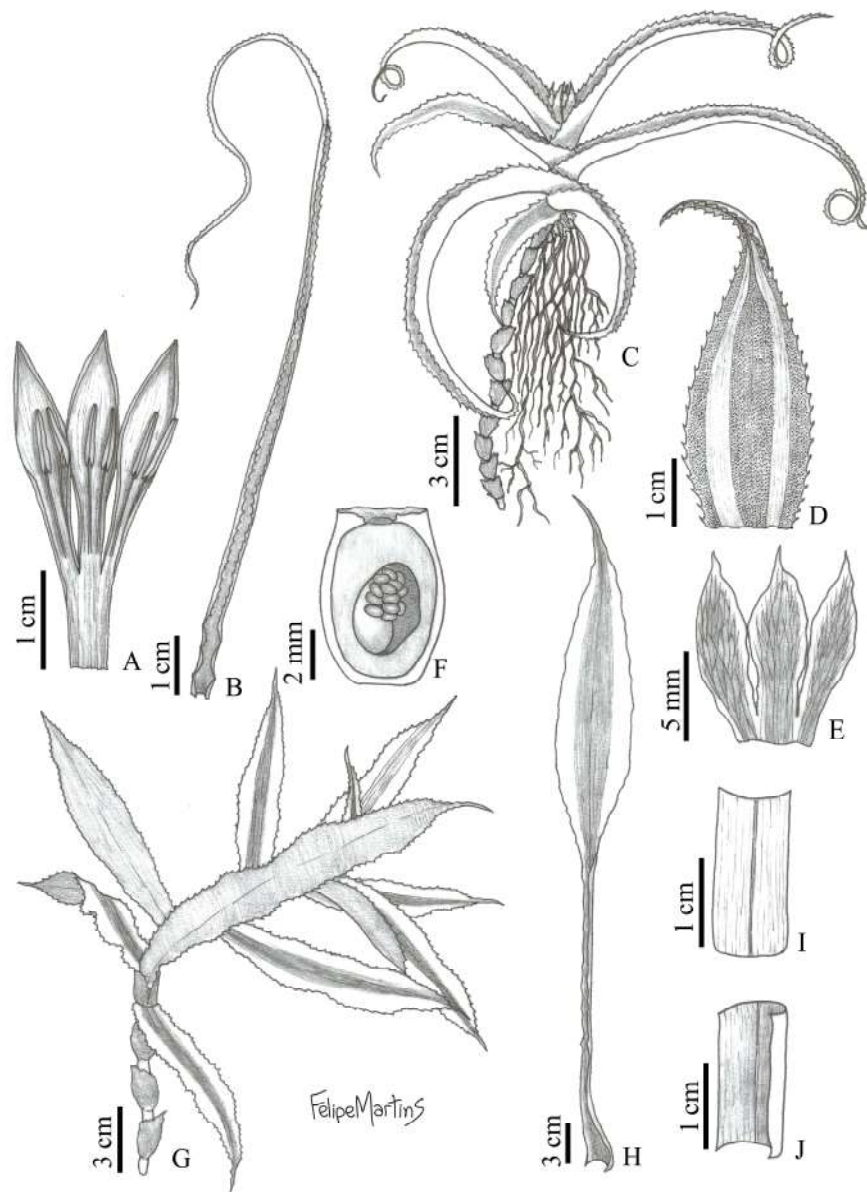


FIGURE 5. Species of *Cryptanthus*. A. *Cryptanthus boanovensensis* (D. Cavalcanti & L. Daneu 838) - Petals acute and stamens. B. *Cryptanthus colnagoi* (E. Colnago s.n.) - abaxial surface of the leaf blade with revolute margins. C. *Cryptanthus diamantinensis* (E. Leme 3812) - Plant short caulescent. D. *Cryptanthus lacerdae* (E.M.C. Leme 200) - adaxial surface of the leaf blade with three longitudinal lines of lepidote trichomes. E. *Cryptanthus osiris* (Amanda et Michael Bleher 125) - sepals connate for 2 mm long. F. *Cryptanthus sergipensis* (D. Cavalcanti & N. Souza 902) - ovary. G. *Cryptanthus ubairensis* (T. R. Soderstrom 2175) - Plants long caulescent. H-J. *Cryptanthus walkerianus* (D. Cavalcanti & L. Daneu 884). H. Leaf with petiole. I. Portion of the abaxial surface of the canaliculate petiole with revolute margins. J. Portion of the adaxial surface of the canaliculate petiole with revolute margins.

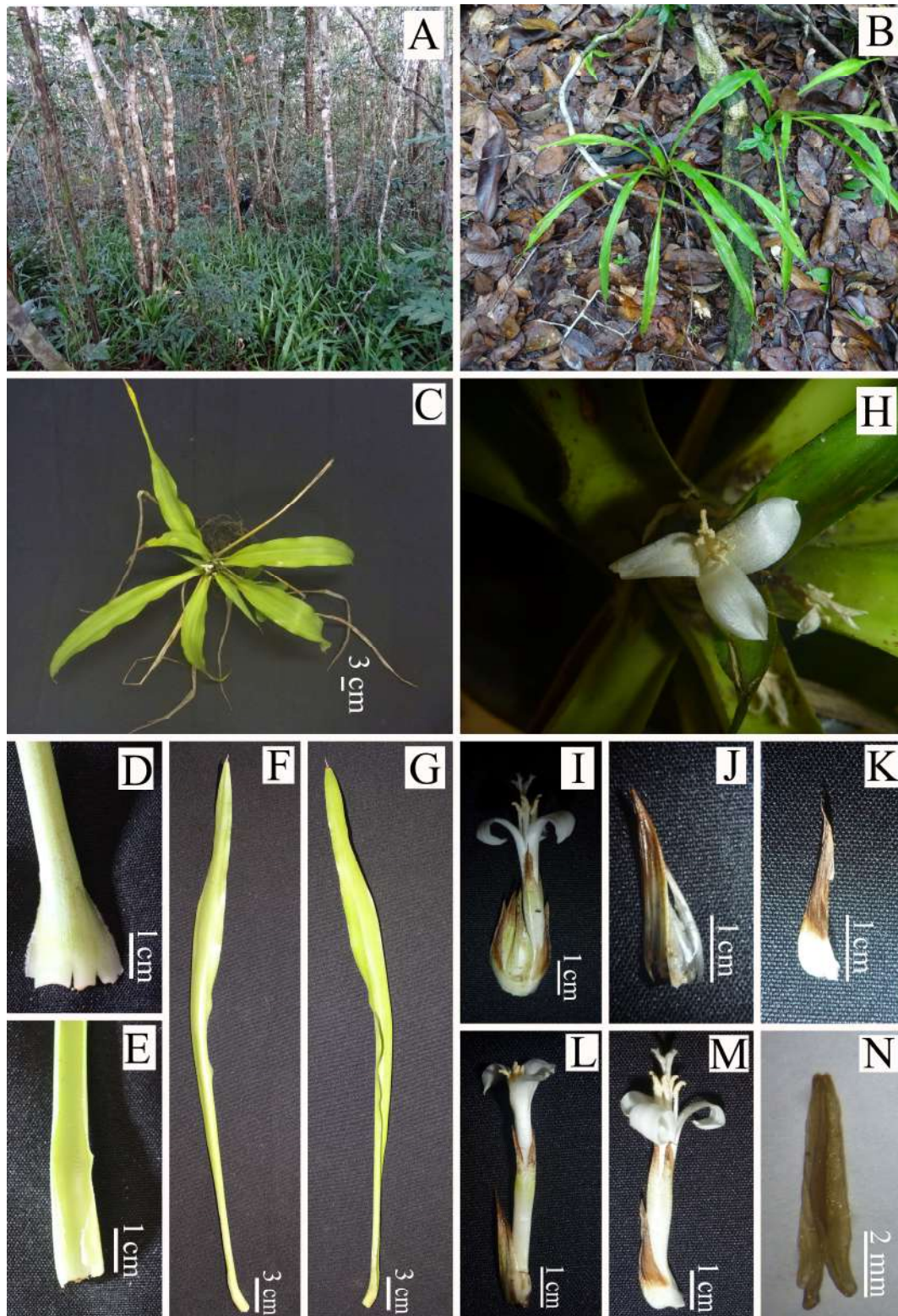


FIGURE 6. *Cryptanthus alagoanus* Leme & J.A.Siqueira. A. Habitat - Atlantic Forest (semideciduous seasonal forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Floral bract of staminate flower. K. Floral bract of perfect flower. L. Staminate flower. M. Perfect flower. N. Anther.

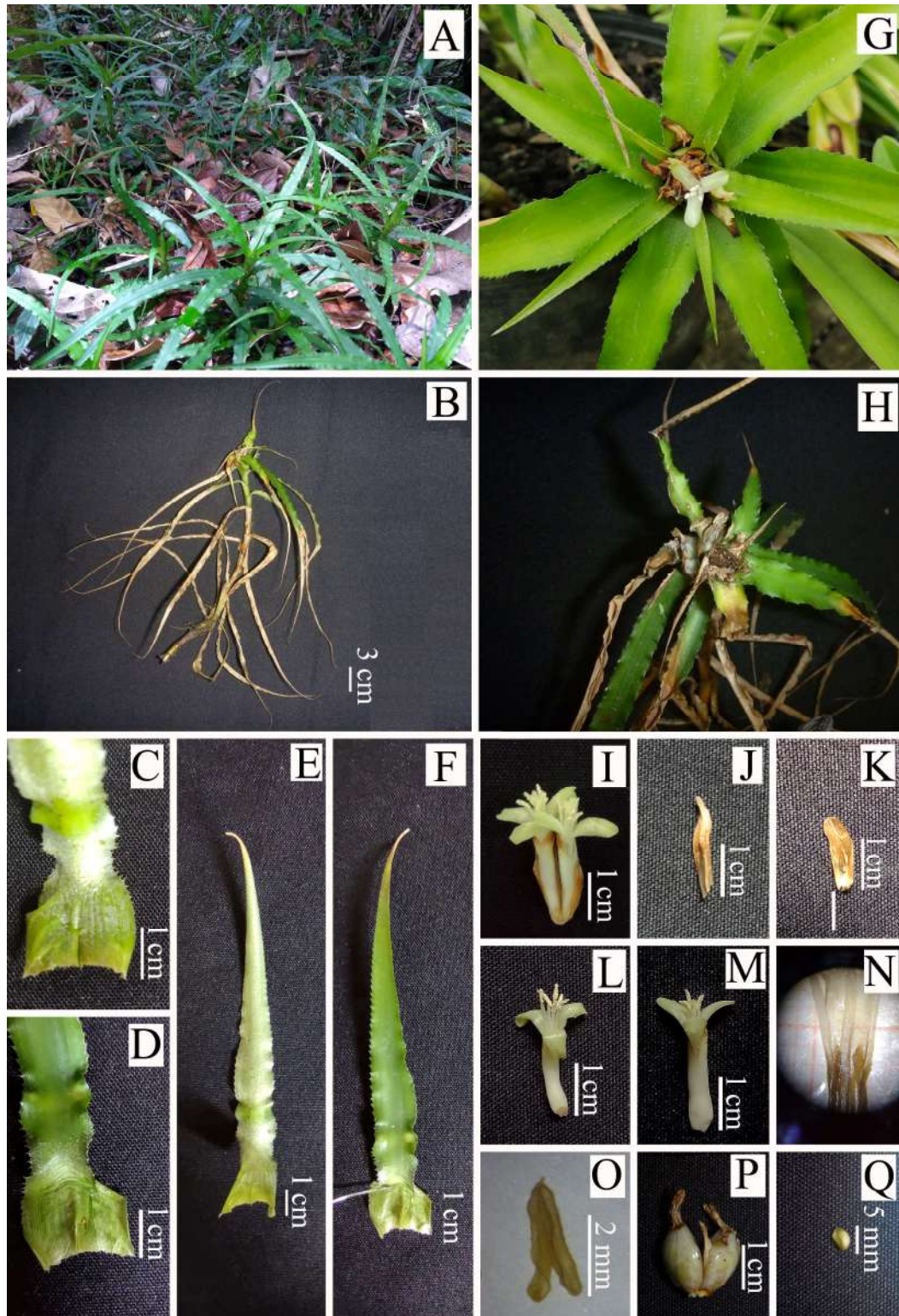


FIGURE 7. *Cryptanthus apiculatantherus* D.M.C. Ferreira, E.M. Almeida & Louzada. A. Population in nature (Photo: E. Mendonça). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G-H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Bract of perfect flower. L. Staminate flower. M. Perfect flower. N. Detail of two conspicuous callosities. O. Anther apiculate. P. Fruits. Q. Seed.

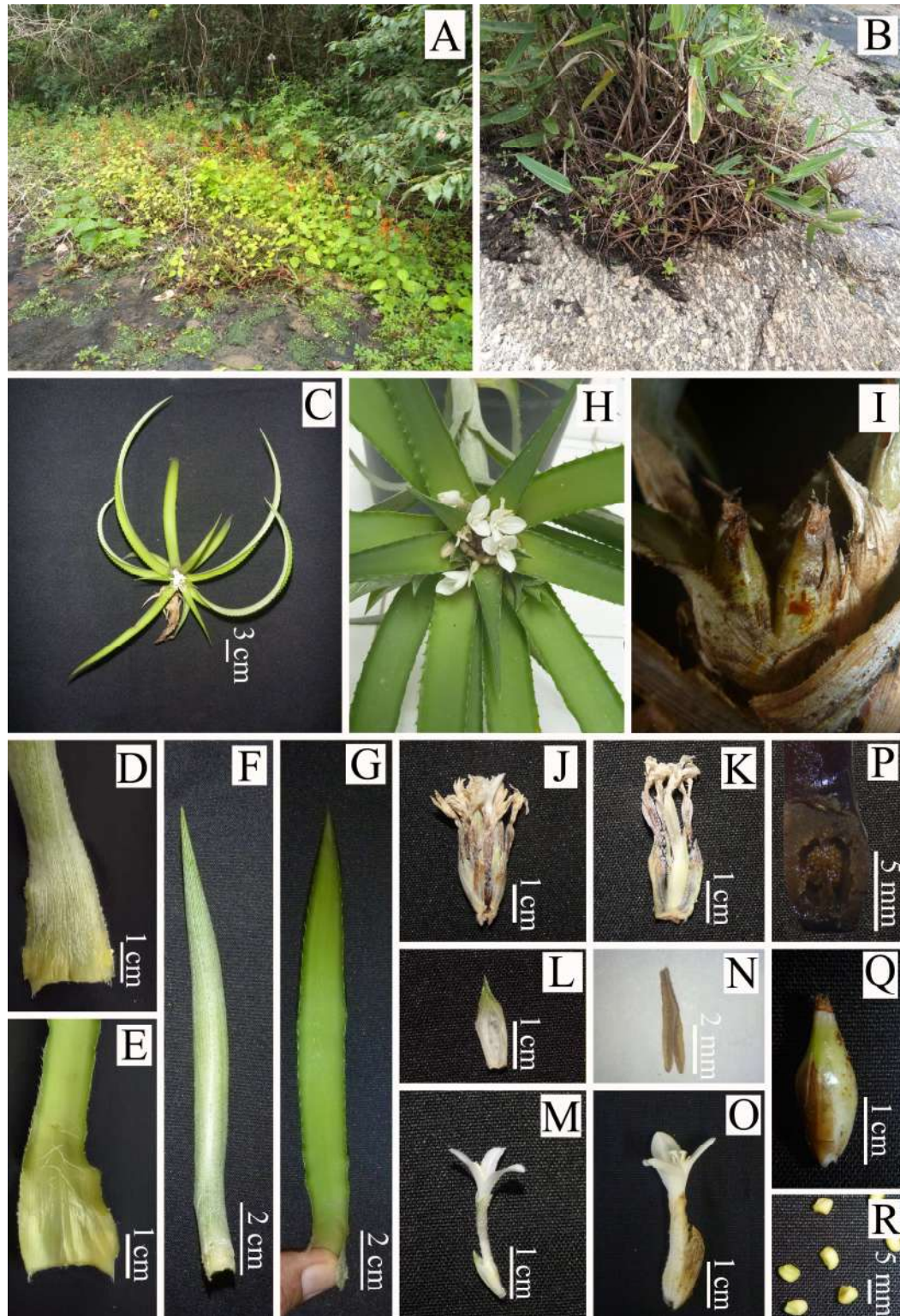


FIGURE 8. *Cryptanthus bahianus* L.B.Sm. A. Habitat - Brejo de altitude (Photo: E. Mendonça). B. Population in nature (Photo: E. Mendonça). C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical gloremule of the inflorescence. K. Lateral glomerule of the inflorescence. L. Floral bract of staminate flower. M. Staminate flower. N. Anther. O. Perfect flower. P. Ovary of perfect flower. Q. Fruit. R. Seeds.

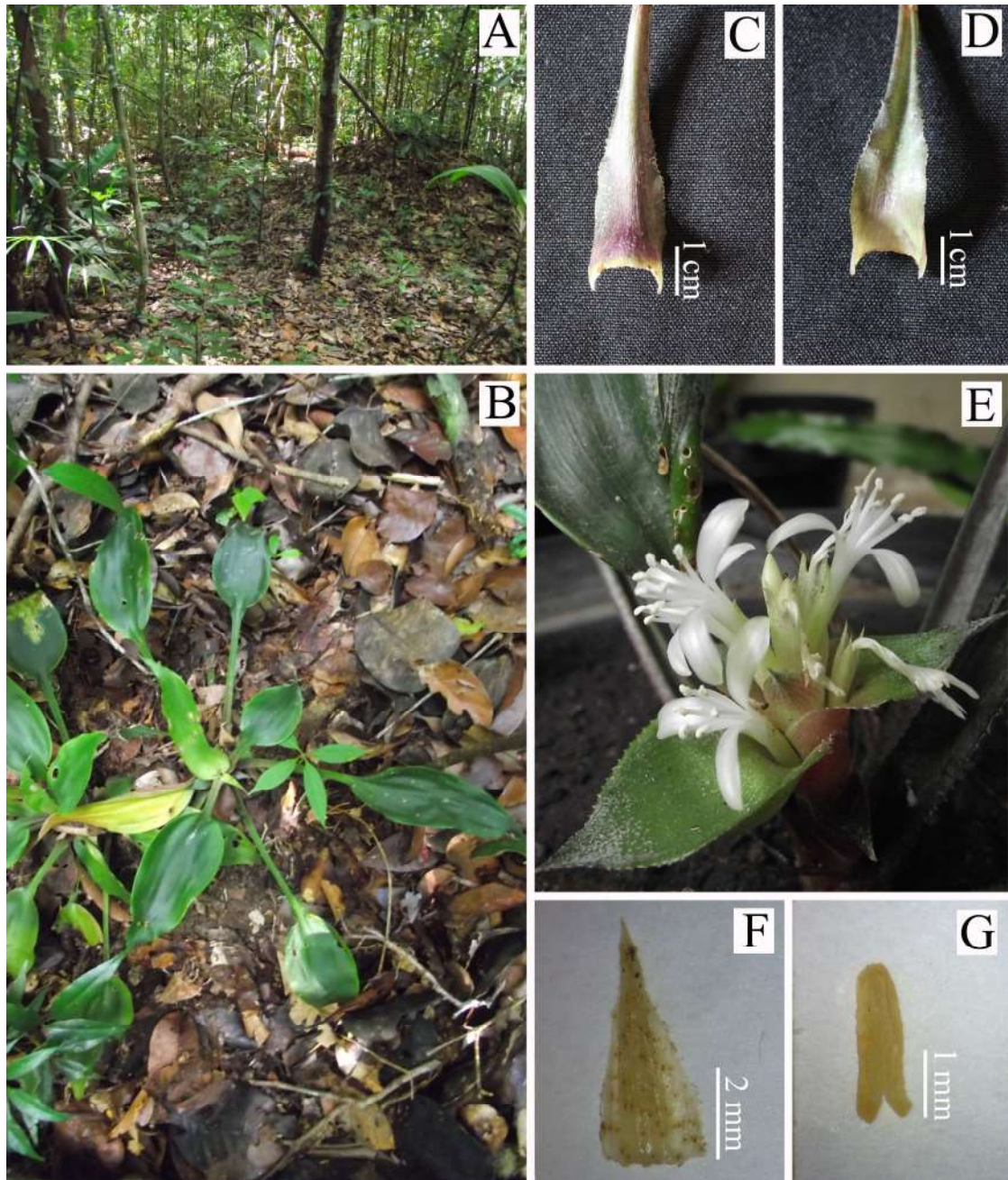


FIGURE 9. *Cryptanthus beuckeri* E. Morren. A. Habitat - Atlantic Forest (Lowland Tropical Moist Forest). B. individual in nature. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Inflorescence. F. Sepal lobe. G. Anther.



FIGURE 10. *Cryptanthus boanovenssis* Leme. A. Habitat - transition area between Atlantic Forest and Caatinga with vegetation type called as Mata de Cipó. B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Top view of the rosette showing the inflorescence. I. Lateral glomerule of the inflorescence. J. Staminate flower. K. Bract of perfect flower. L. Perfect flower. M. Sepal lobe. N. Anther.

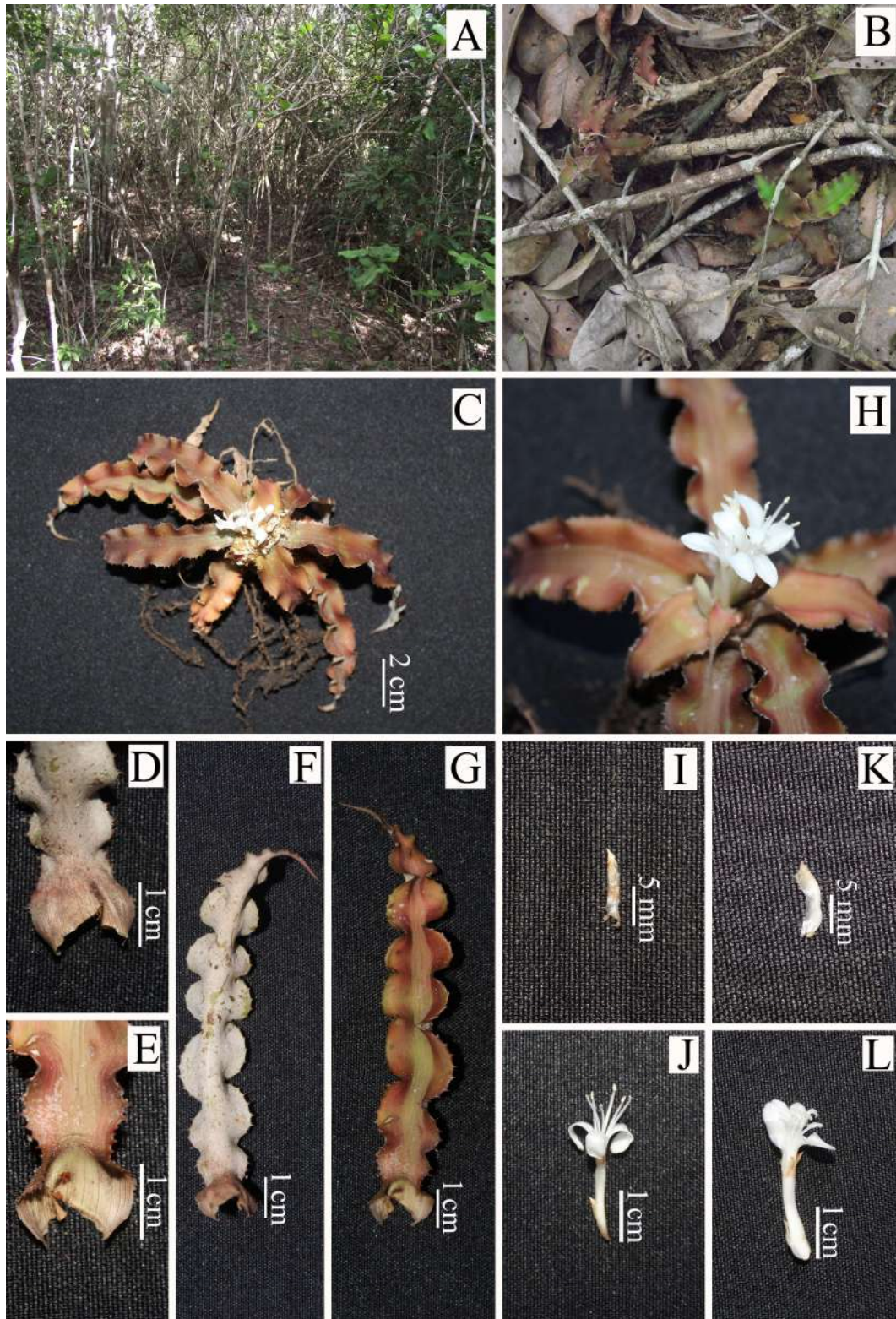


FIGURE 11. *Cryptanthus brevibracteatus* D.M.C. Ferreira & Louzada. A. Habitat - transition area between Atlantic Forest and Caatinga with vegetation type called as Mata de Cipó. B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Bract of staminate flower. J. Staminate flower. K. Bract of perfect flower. L. Perfect flower.

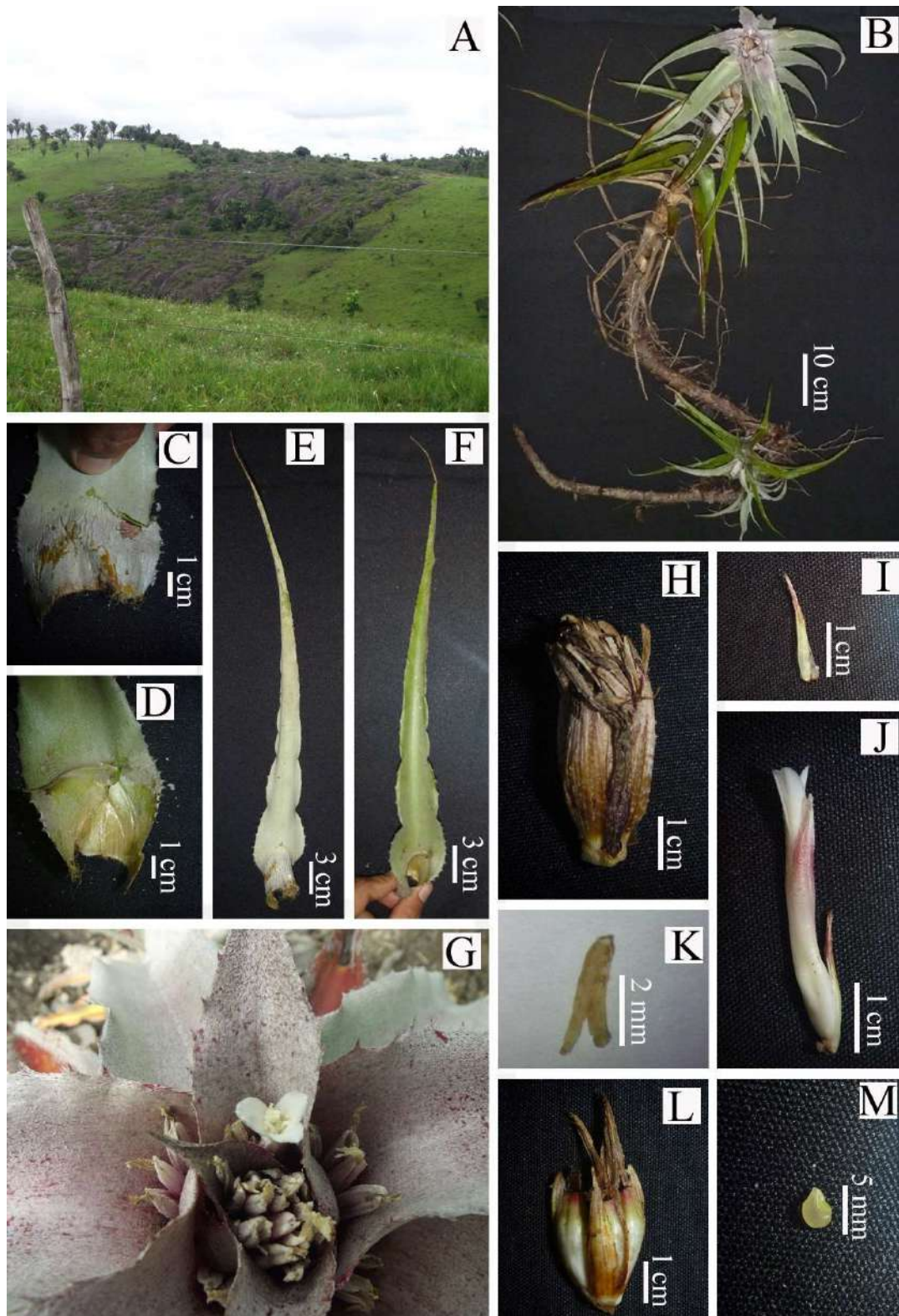


FIGURE 12. *Cryptanthus cinereus* D. M. C. Ferreira & Louzada. A. Habitat - Atlantic Forest (rocky outcrop). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence. H. Apical glomerule of the inflorescence. I. Bract of staminate flower. J. Staminate flower. K. Anther. L. Fruits. M. Seed.

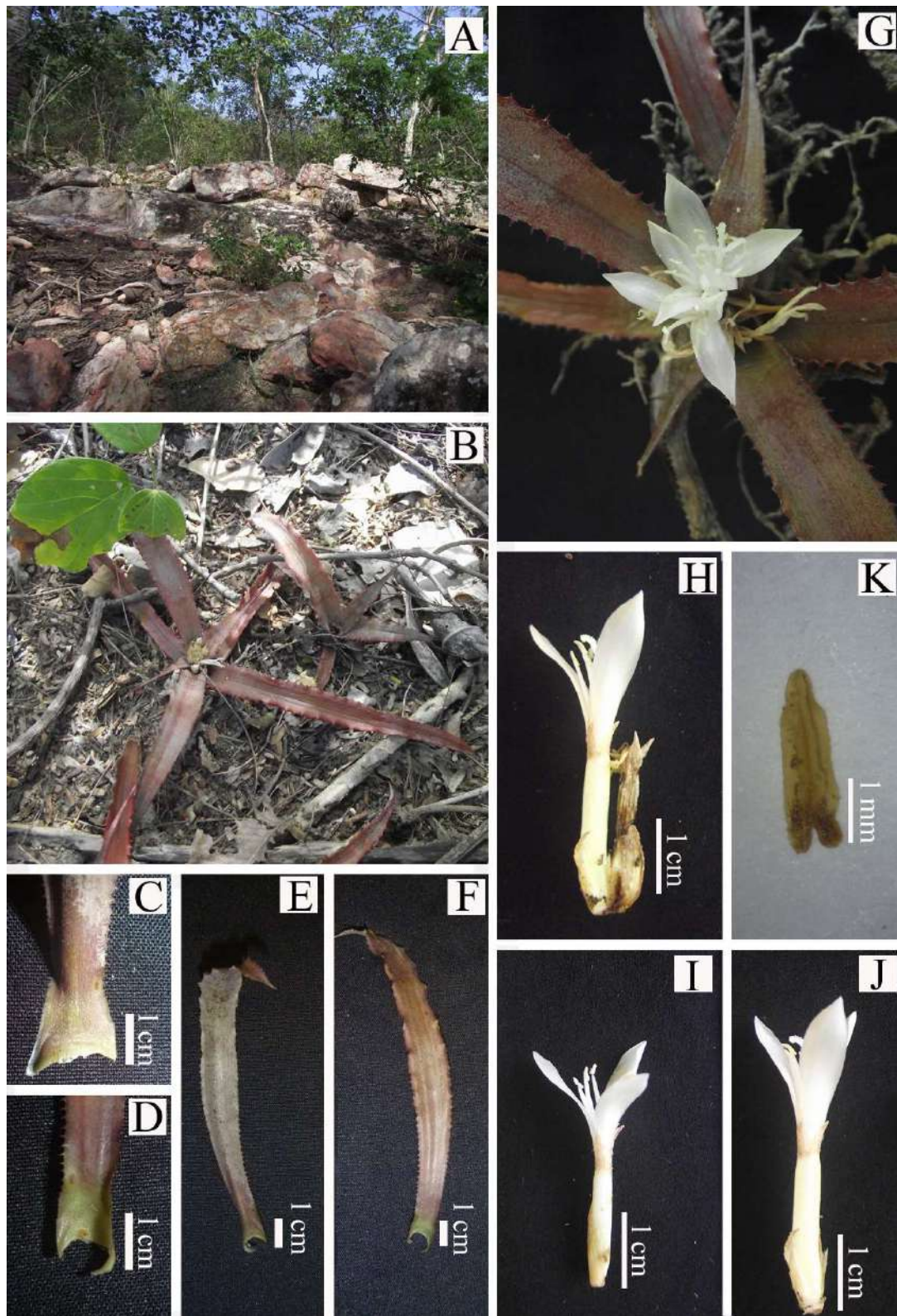


FIGURE 13. *Cryptanthus crassifolius* Leme. A. Habitat - Caatinga (rock outcrops along of the Mato Grosso river valley). B. Population in nature. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence. H. Lateral glomerule of the inflorescence. I. Staminate flower. J. Perfect flower. K. Anther.

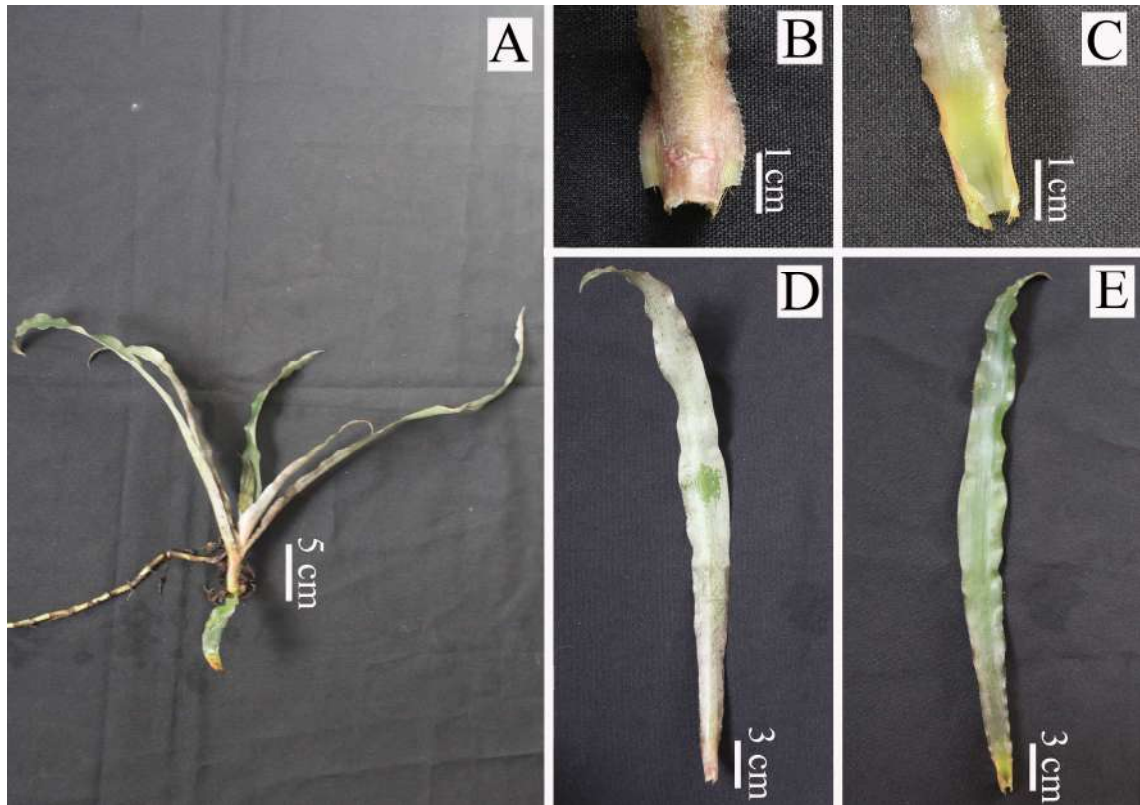


FIGURE 14. *Cryptanthus cruzalmensis* Leme & E.H.Souza. A. Individual. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf (abaxial surface). E. Leaf (adaxial surface).

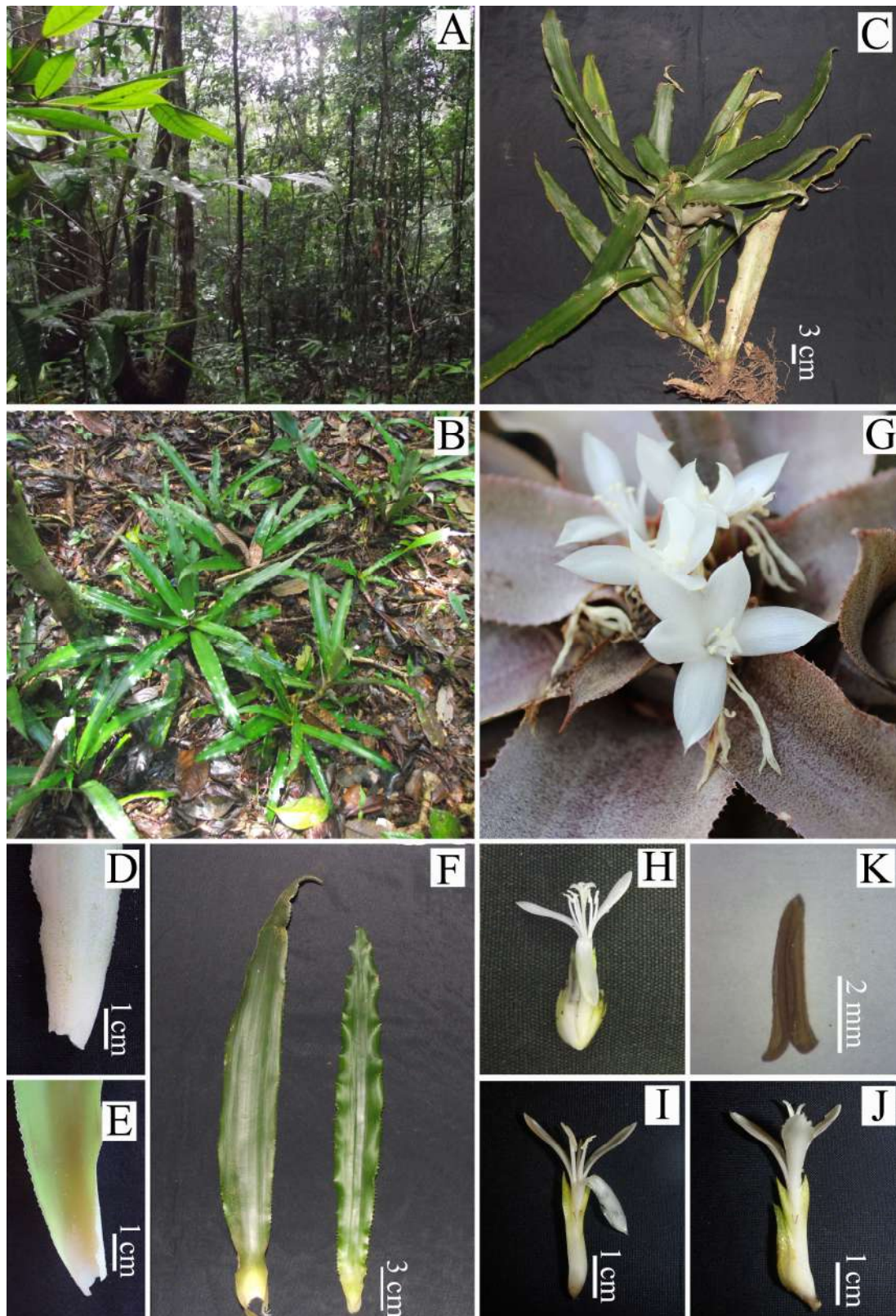


FIGURE 15. *Cryptanthus diana* Leme. A. Habitat - (Atlantic Forest) Submontane Tropical Moist Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf blades (adaxial surface). G. Inflorescence. H. Lateral glomerule of the inflorescence. I. Staminate flower. J. Perfect flower. K. Anther.

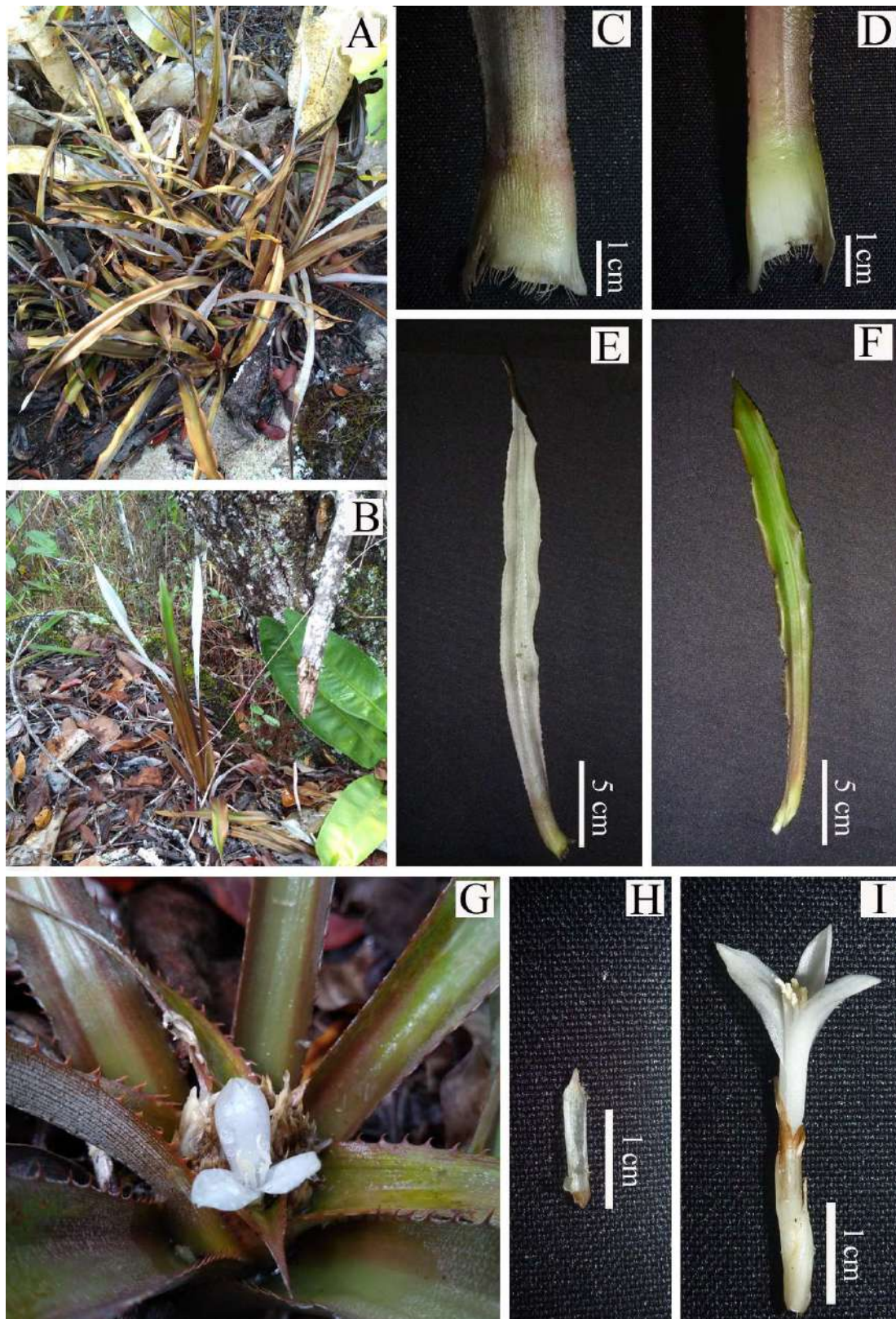


FIGURE 16. *Cryptanthus* sp. A. Population in nature (Photo: E. Mendonça). B. Individual in nature (Photo: E. Mendonça). C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence (Photo: E. Mendonça). H. Bract of staminate flower. I. Staminate flower.

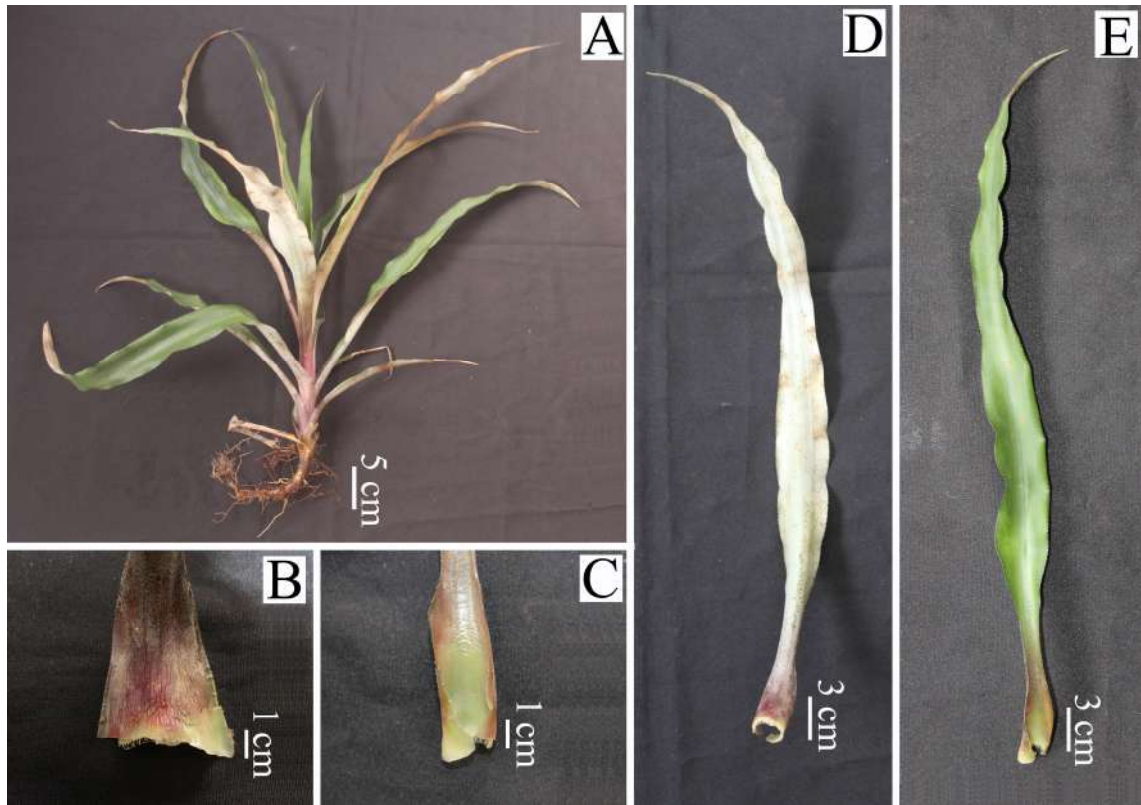


FIGURE 17. *Cryptanthus felixii* J.A.Siqueira & Leme. A. Individual. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf (abaxial surface). E. Leaf (adaxial surface).

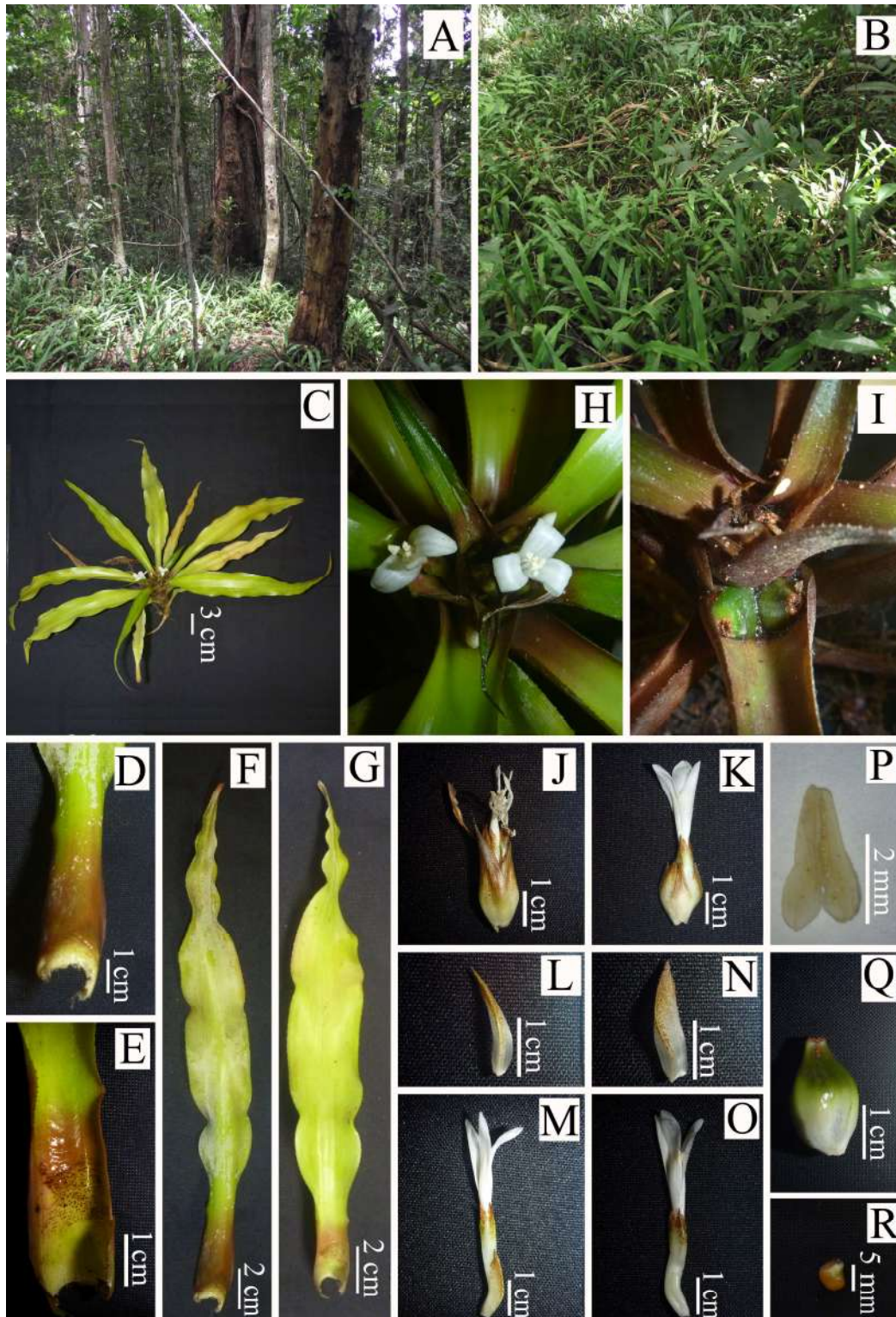


FIGURE 18. *Cryptanthus pickelii* L.B.Sm.. A. Habitat - Atlatic Forest (semideciduous seasonal forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical glomerule of the inflorescence. K. Lateral glomerule of the inflorescence. L. Bract of staminate flower. M. Staminate flower. N. Bract of perfect flower. O. Perfect flower. P. Anther. Q. Fruit. R. Seed.

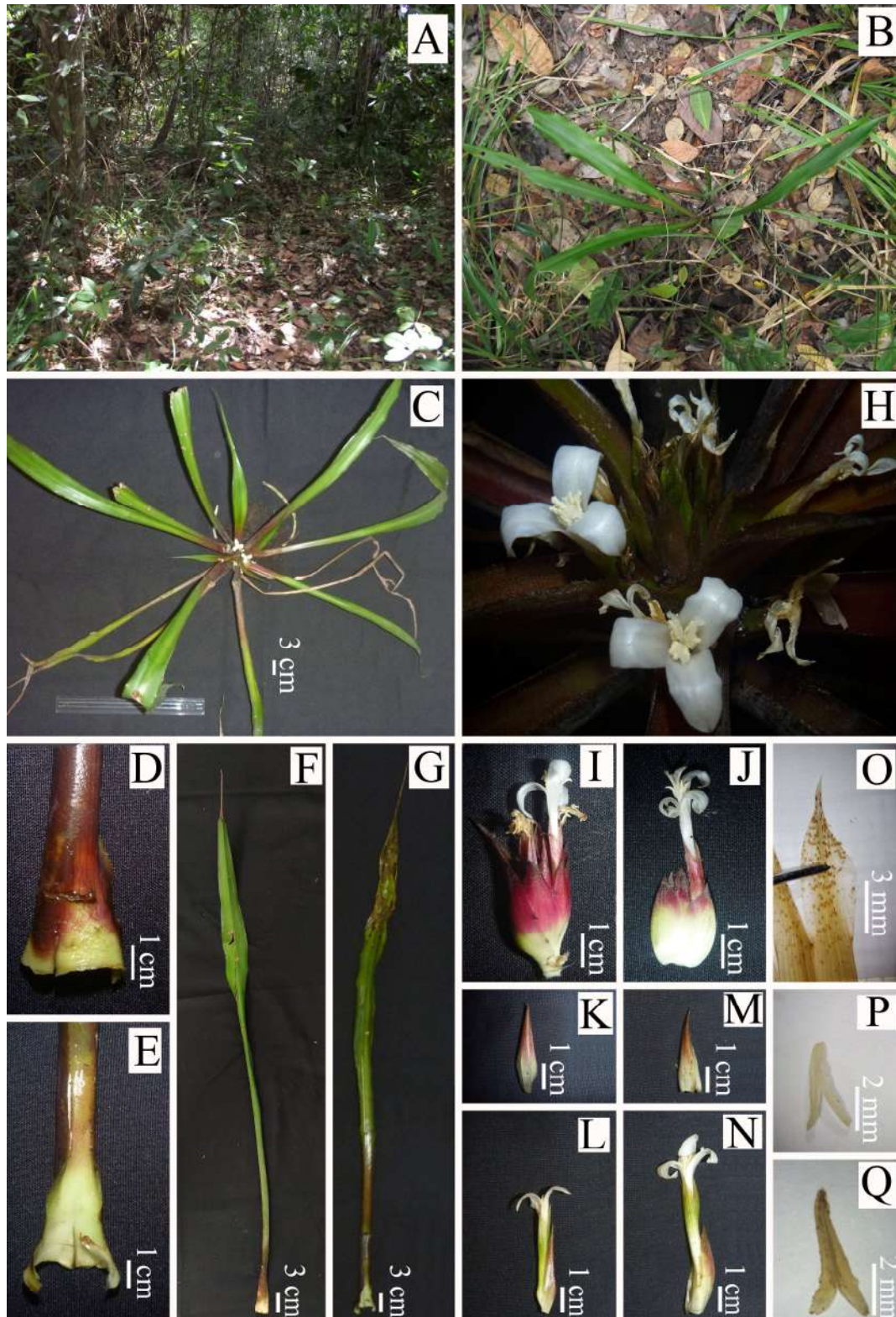


FIGURE 19. *Cryptanthus pirambuensis* D.M.C. Ferreira & Louzada. A. Habitat - Atlatic Forest (semideciduous seasonal forest). B. Individual in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Apical glomerule of the inflorescence. J. Lateral glomerule of the inflorescence. K. Bract of staminate flower. L. Staminate flower. M. Bract of perfect flower. N. Perfect flower. O. Sepal lobe. P-Q. Anther.

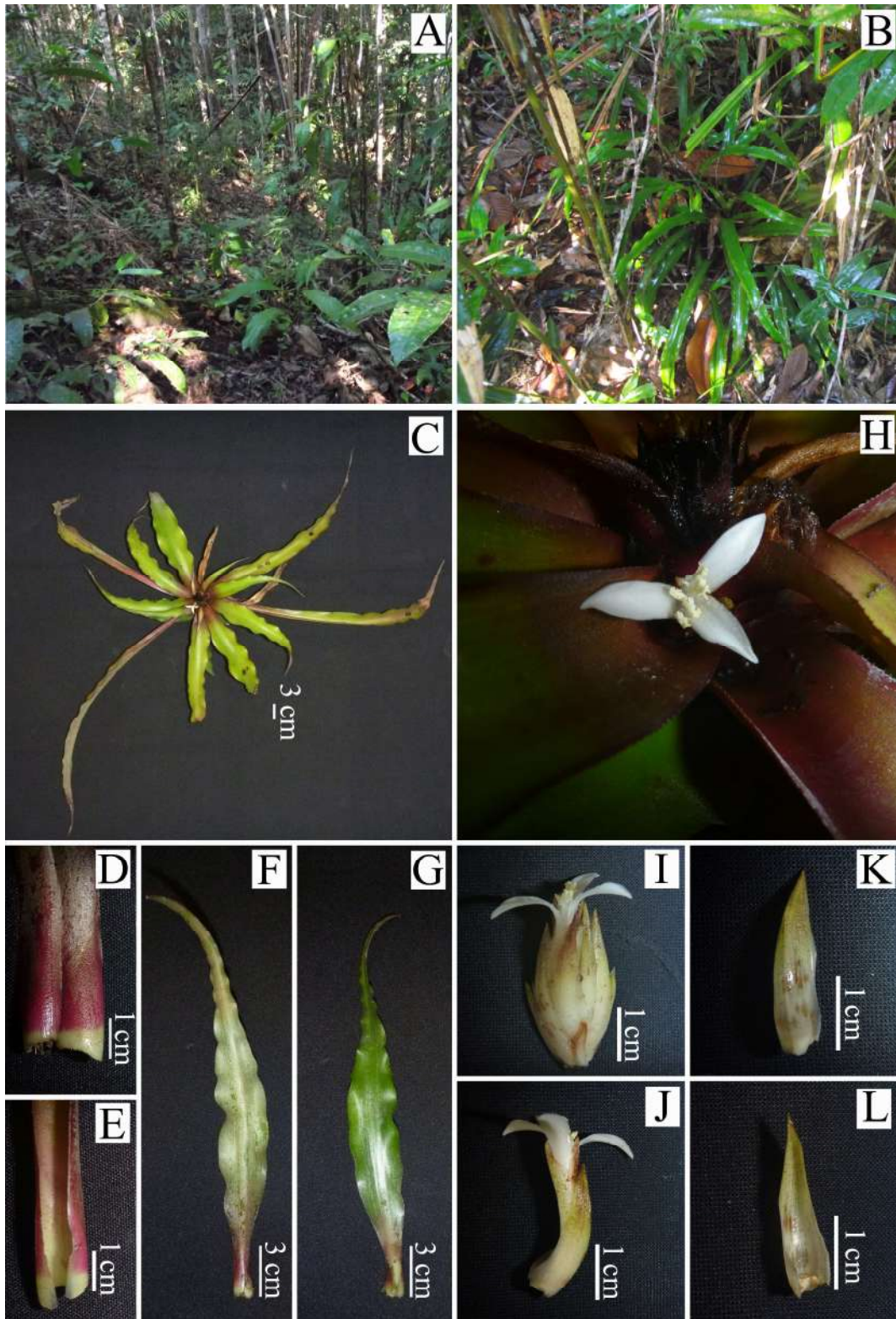


FIGURE 20. *Cryptanthus pseudopetiolaris* Philcox. A. Habitat - Atlantic Forest (Lowland Tropical Moist Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Staminate flower. K. Floral bract of staminate flower (abaxial surface). L. Floral bract of staminate flower (adaxial surface).

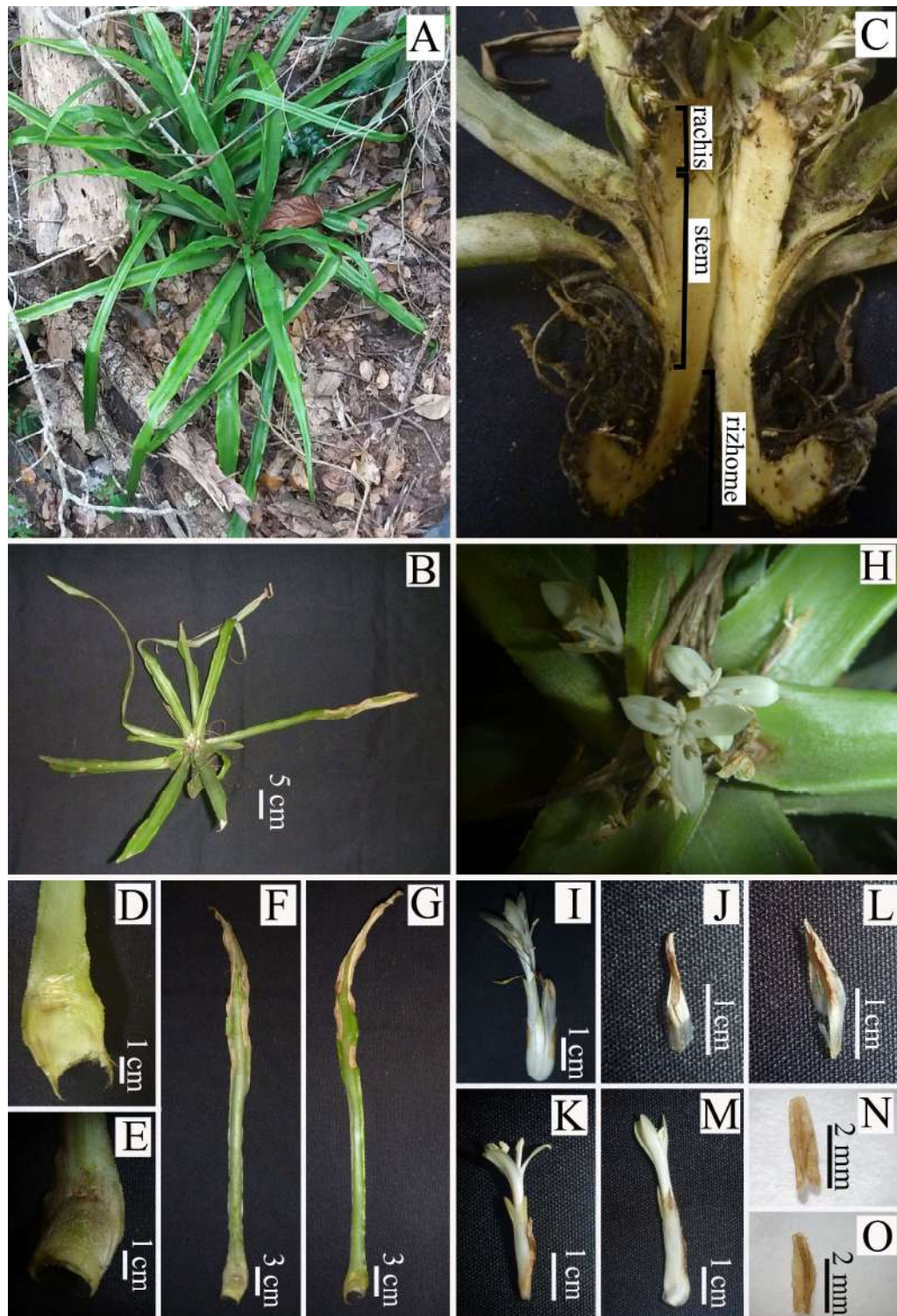


FIGURE 21. *Cryptanthus reisii* Leme. A. Population in nature (Photo: L. Daneu). B. Individual. C. Plant in longitudinal section showing the rachis, stem and rhizome. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Staminate flower. L. Bract of perfect flower. M. Perfect flower. N. Anther apex rounded. O. Anther apex emarginate.

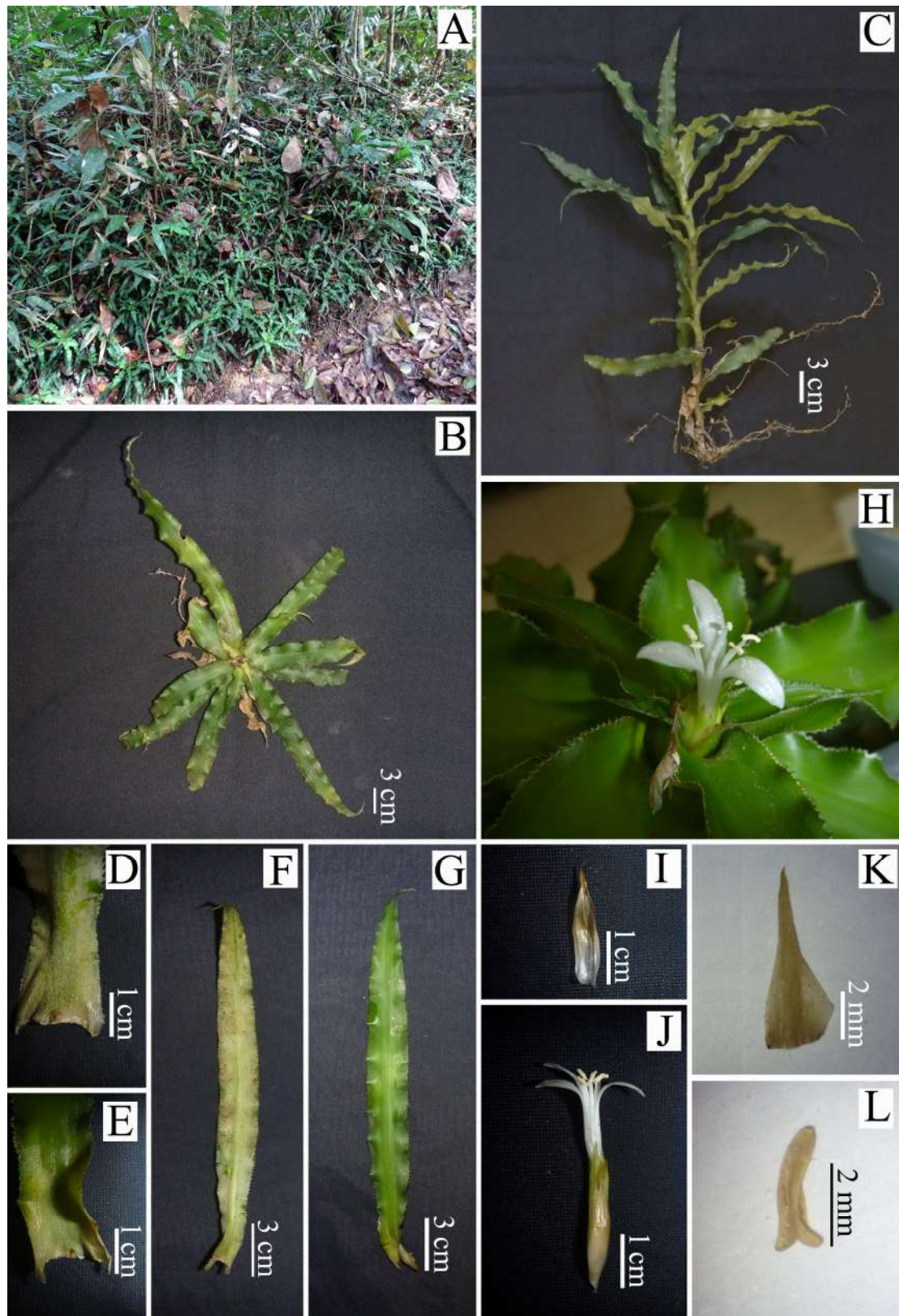


FIGURE 22. *Cryptanthus reptans* Leme & J.A.Siqueira. A. Population in nature. B. Individual. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Floral bract of staminate flower. J. Staminate flower. K. Sepal lobe. L. Anther.

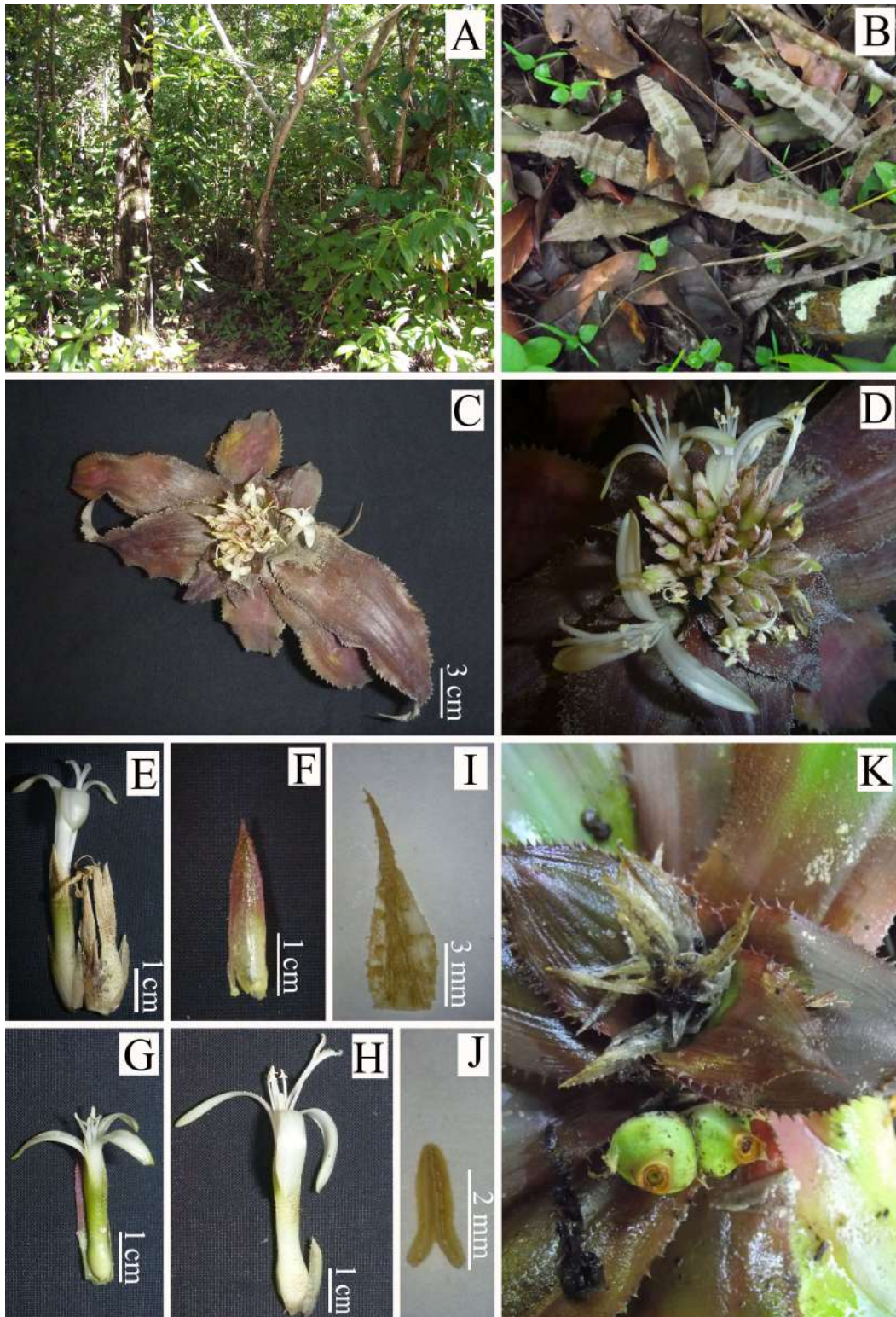


FIGURE 23. *Cryptanthus robsonianus* Leme. A. Habitat - Atlantic Forest (Restinga Forest). B. Individual in nature with adaxial surface of the leaf blades with crossbars of lepidote trichomes. C. Individual. D. Inflorescence. E. Lateral glomerule of the inflorescence. F. Bract of staminate flower. G. Staminate flower. H. Perfect flower. I. Sepal lobe. J. Anther. K. Fruits.

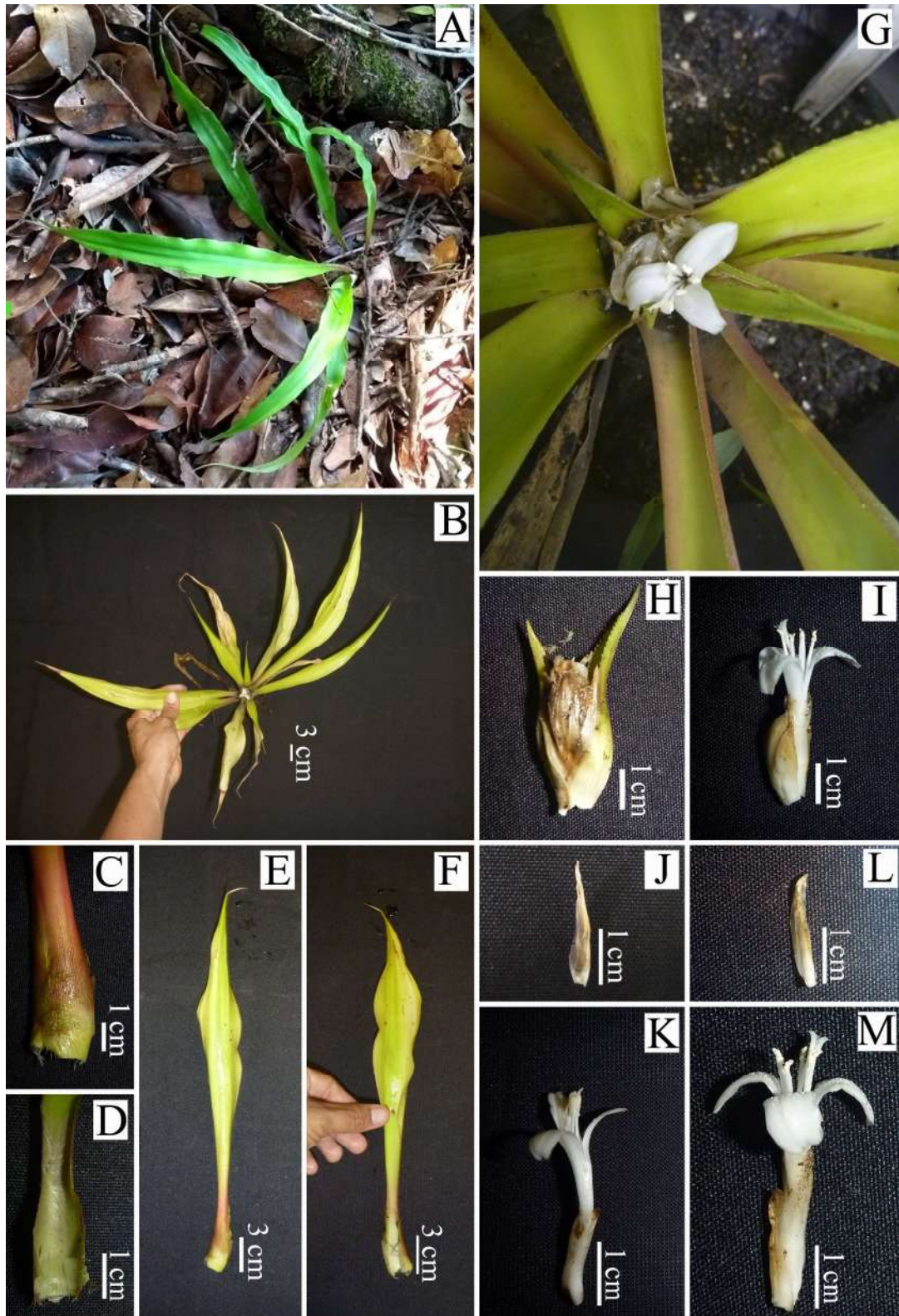


FIGURE 24. *Cryptanthus ruthiae* Philcox. A. Individual in nature (Photo: G. Alves). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Apical glomerule of the inflorescence. I. Lateral glomerule of the inflorescence. J. Bract of staminate flower. K. Staminate flower. L. Bract of perfect flower. M. Perfect flower.

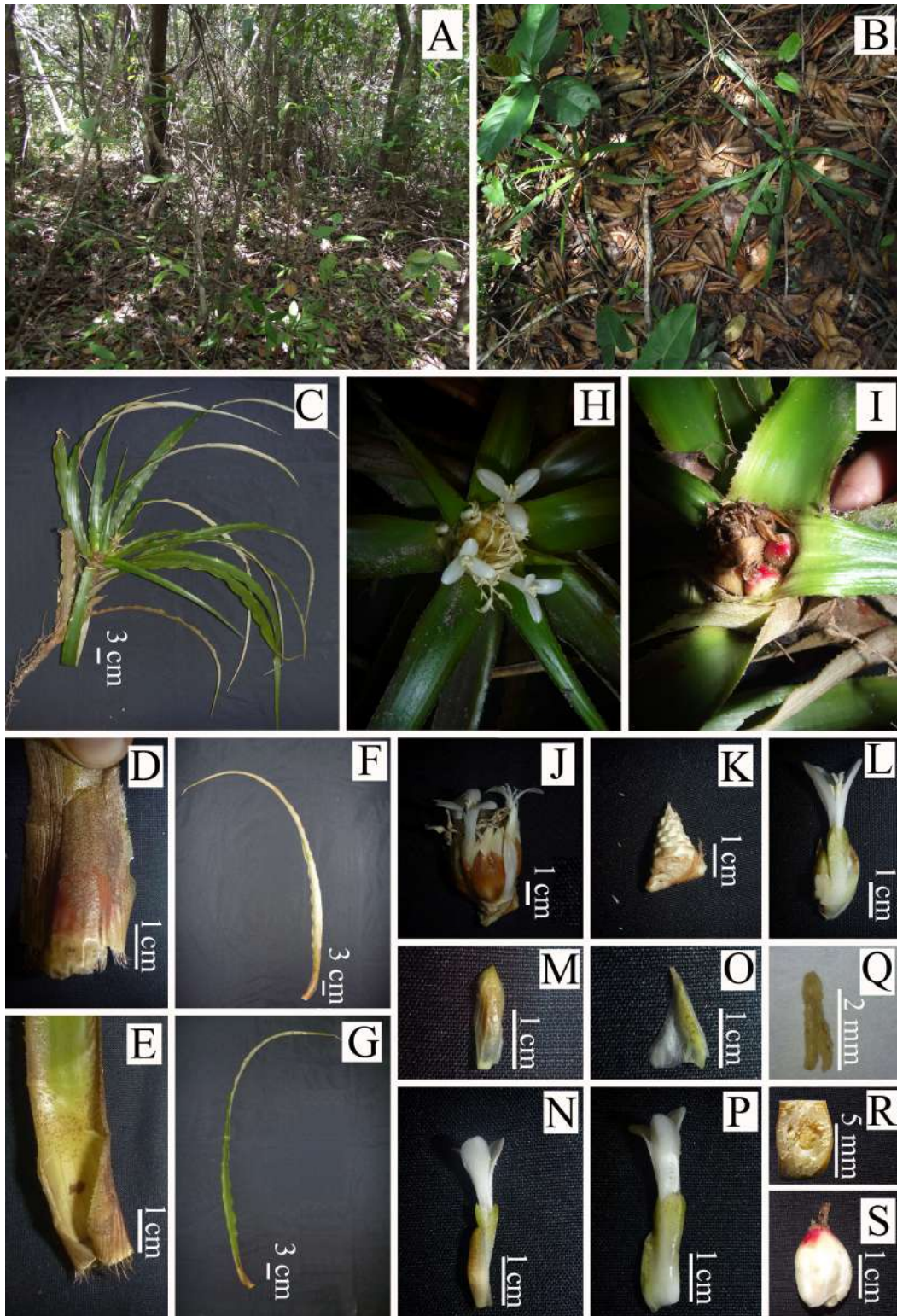


FIGURE 25. *Cryptanthus sergipensis* I.Ramírez. A. Habitat - Atlantic Forest (Restinga Forest). B. Population in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H-I. Inflorescence. J. Apical glomerule of the inflorescence. K. Portion of the rachis. L. Lateral glomerule of the inflorescence. M. Floral bract of staminate flower. N. Staminate flower. O. Floral bract of perfect flower. P. Perfect flower. Q. Anther. R. Ovary of perfect flower. S. Fruit.

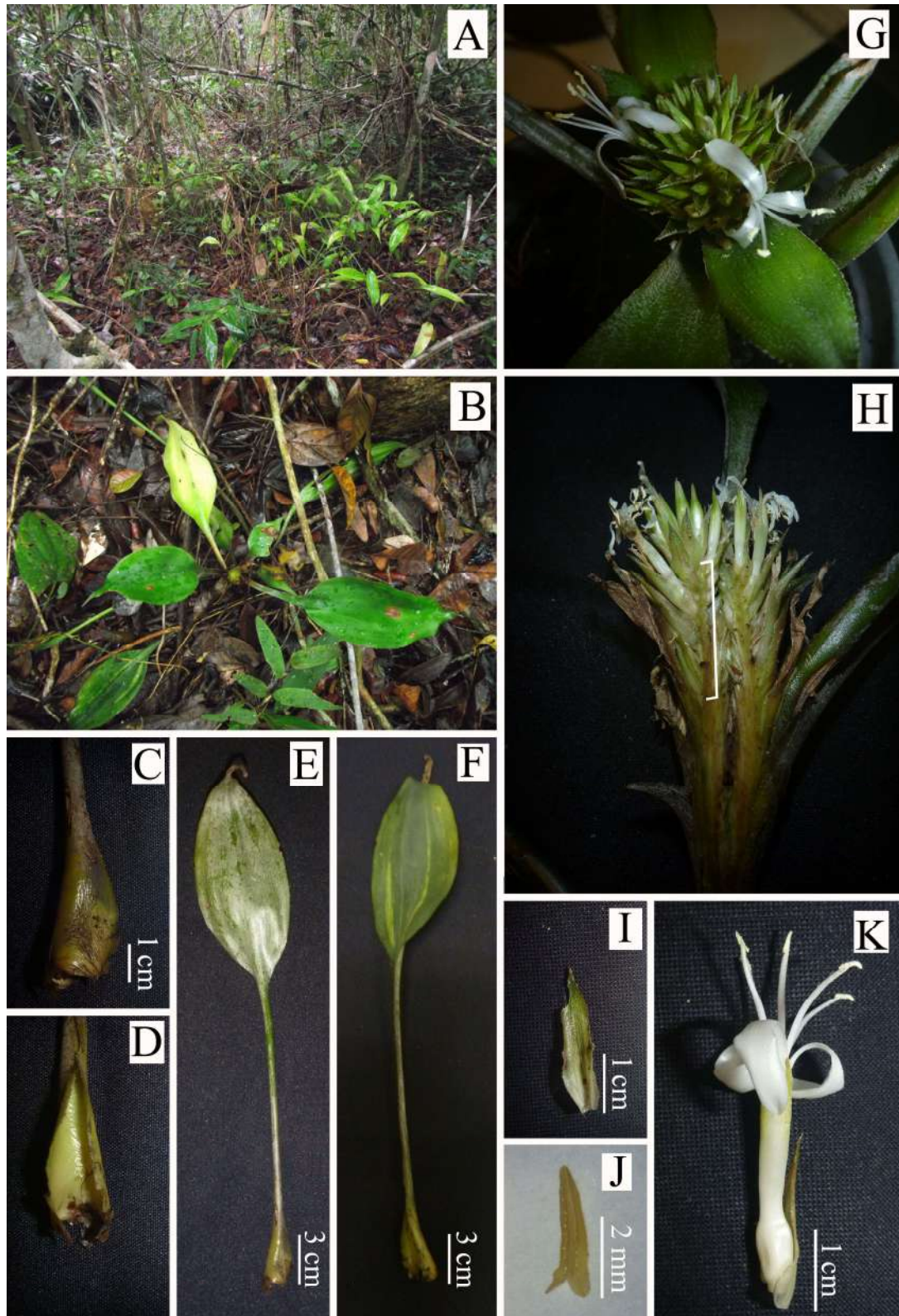


FIGURE 26. *Cryptanthus teretifolius* Leme. A. Habitat - Atlantic Forest (Submontane Tropical Moist Forest). B. Individual in nature. C. Leaf sheath (abaxial surface). D. Leaf sheath (abaxial surface). E. Leaf (adaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Inflorescence in longitudinal section showing the rachis. I. Floral bract of staminate flower. J. Anther. K. Staminate flower.

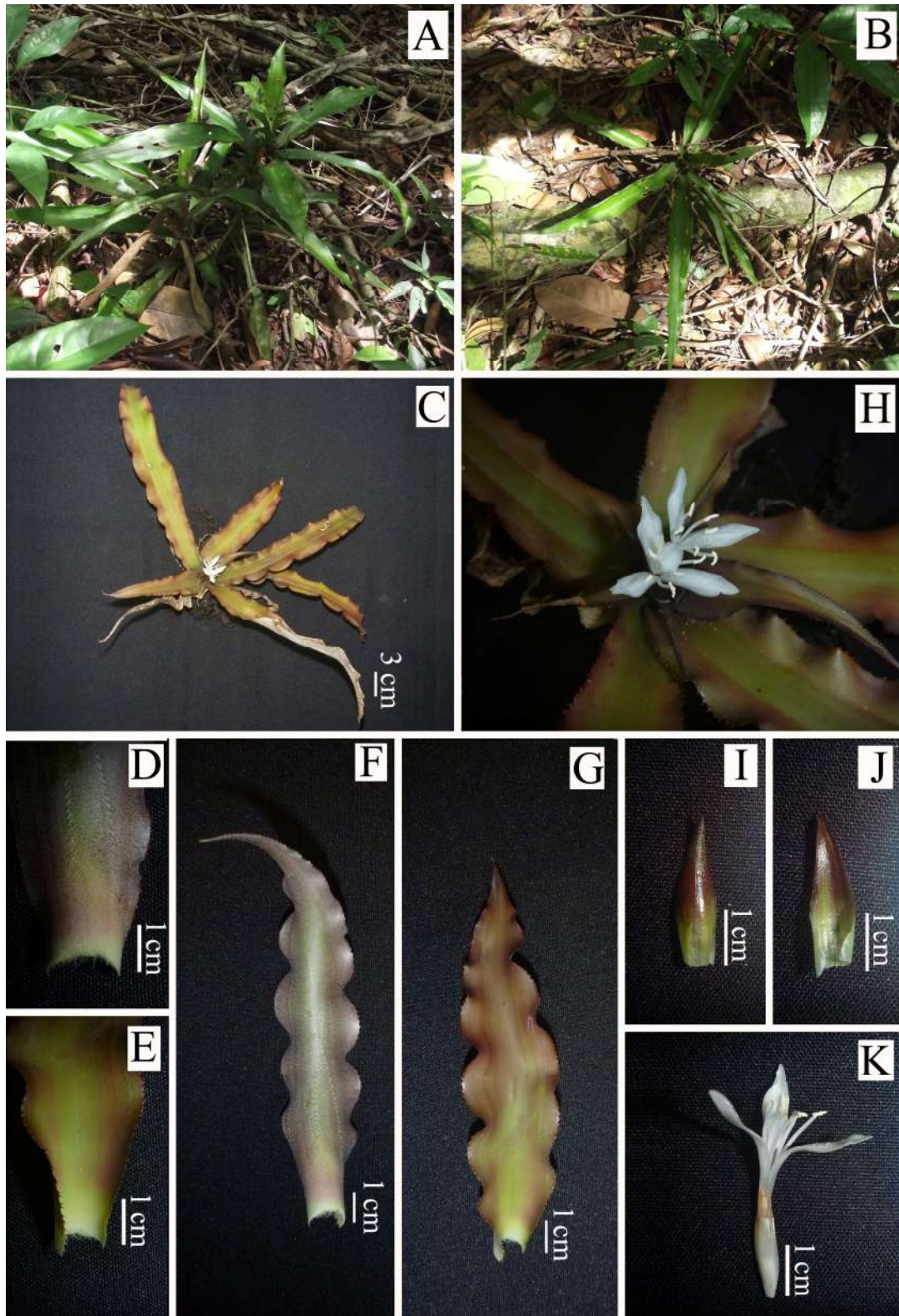


FIGURE 27. A-B. *Cryptanthus vexatus* Leme. A. Population in nature. B. Individual in nature. C-K. *Cryptanthus vinosibracteatus* D.M.C. Ferreira & Louzada. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Leaf (adaxial surface). H. Inflorescence. I. Floral bract of staminate flower (abaxial surface). J. Floral bract of staminate flower (adaxial surface). K. Staminate flower.

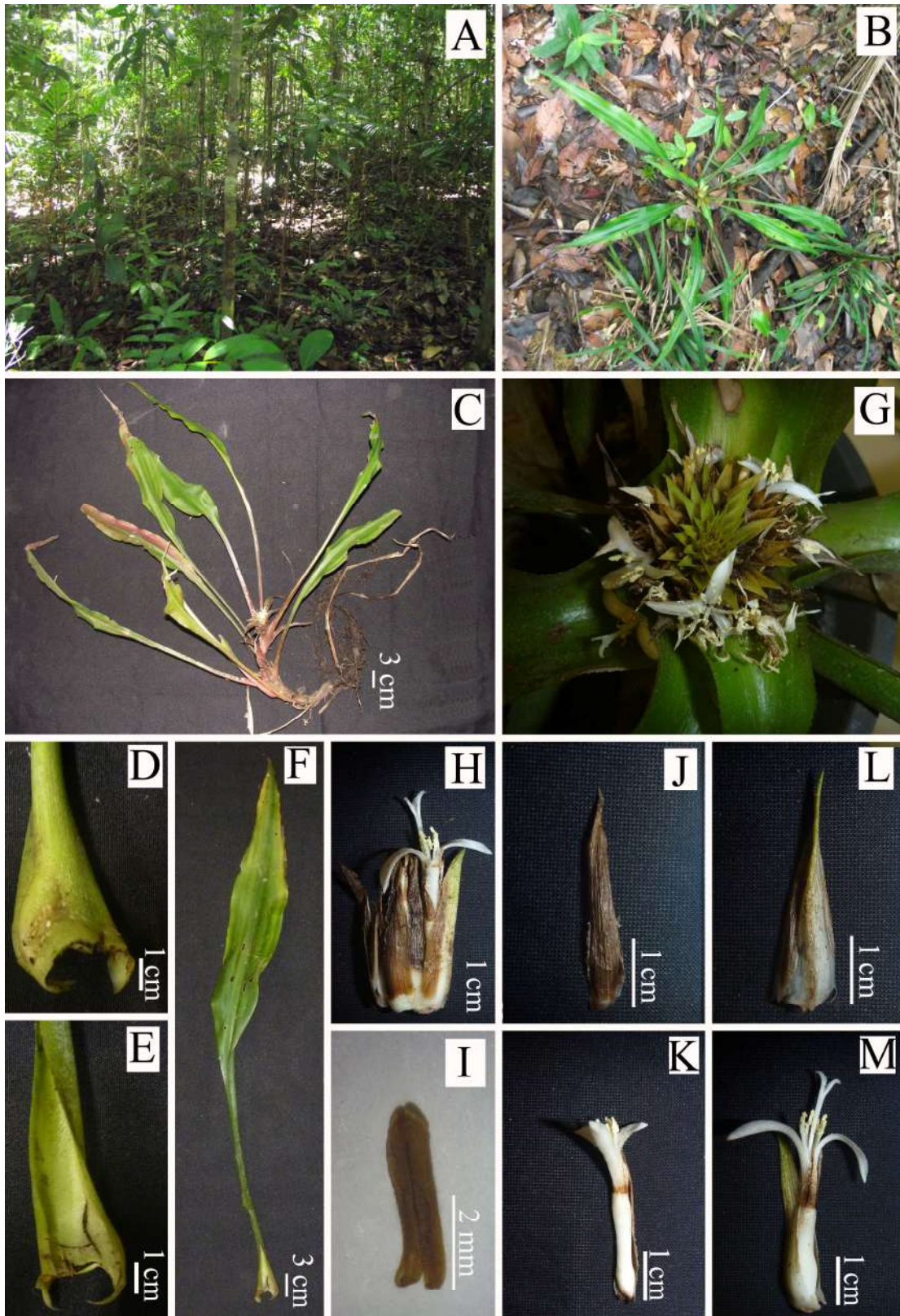


FIGURE 28. *Cryptanthus walkerianus* Leme & L.Kollmann. A. Habitat - Atlantic Forest (Submontane Tropical Moist Forest). B. Individuals in nature. C. Individual. D. Leaf sheath (abaxial surface). E. Leaf sheath (adaxial surface). F. Leaf (abaxial surface). G. Inflorescence. H. Lateral glomerule of the inflorescence. I. Anther. J. Floral bract of staminate flower. K. Staminate flower. L. Floral bract of perfect flower. M. Perfect flower.

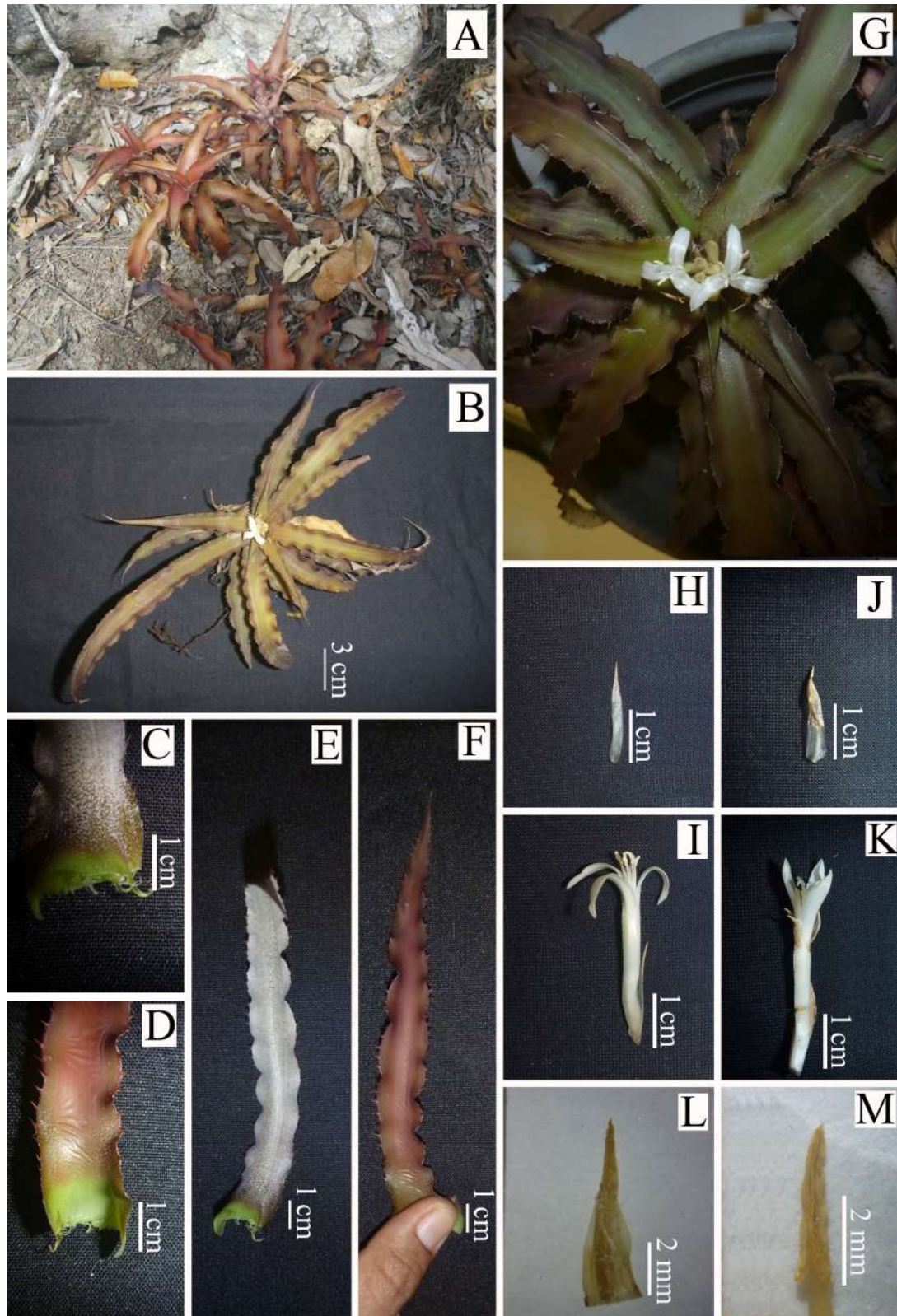


FIGURE 29. *Cryptanthus warren-loosei* Leme. A. Population in nature (Photo: R. Valentin). B. Individual. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Inflorescence. H. Floral bract of staminate flower. I. Staminate flower. K. Staminate flower. J. Floral bract of perfect flower. K. Perfect flower. L. Sepal lobe. M. Anther.

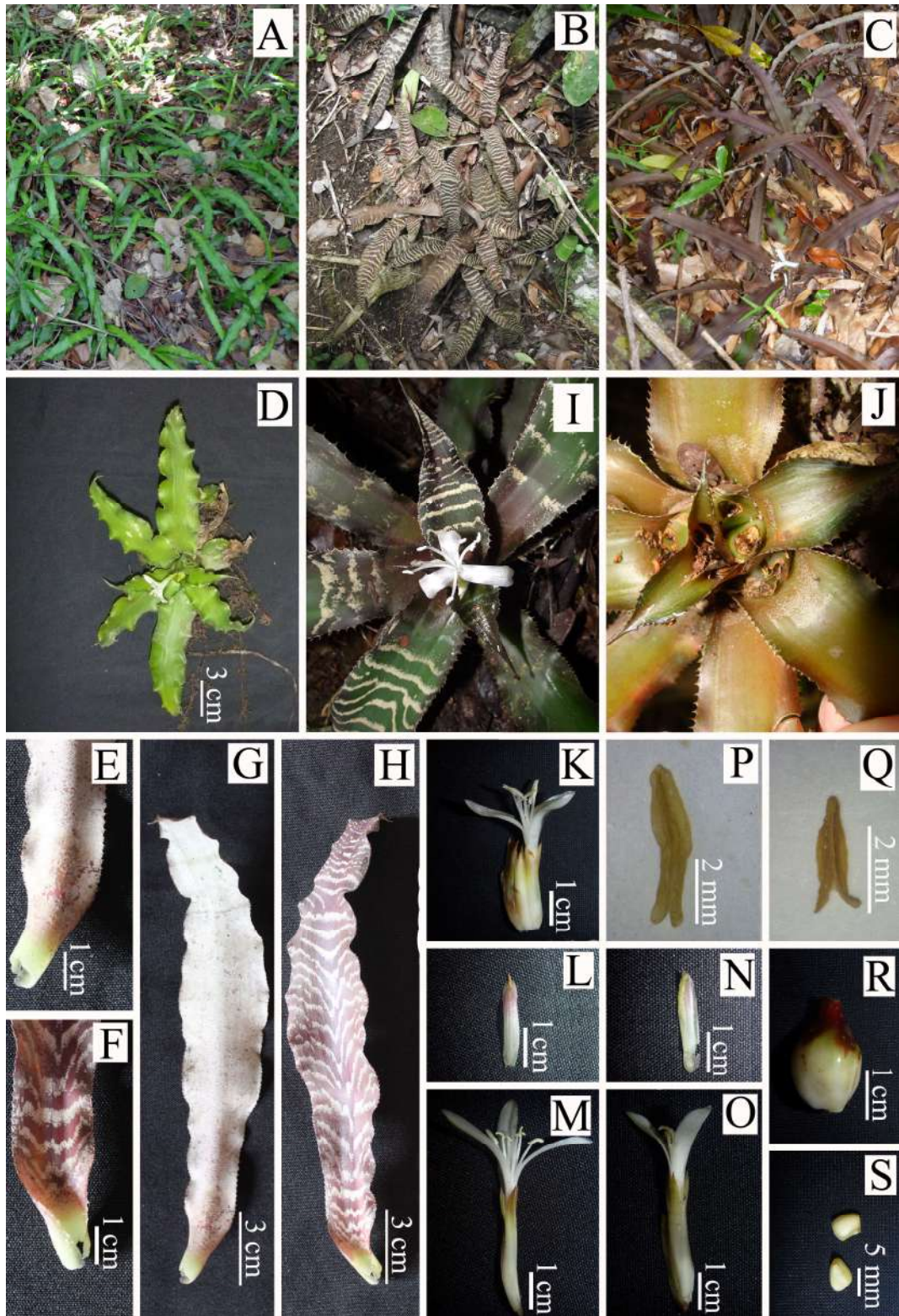


FIGURE 30. *Cryptanthus zonatus* (Vis.) Vis.. A-C. Population in nature. D. Individual. E. Leaf sheath (abaxial surface). F. Leaf sheath (adaxial surface). G. Leaf (abaxial surface). H. Leaf (adaxial surface of the leaf blades with crossbars of lepidote trichomes). I-J. Inflorescence. K. Lateral glomerule of the inflorescence. L. Floral bract of staminate flower. M. Staminate flower. N. Floral bract of perfect flower. O. Perfect flower. P-Q. Anther. R. Fruit. S. Seeds.

4.4 CAPÍTULO DE LIVRO 1- FLORA DE ALAGOAS: *CRYPTANTHUS*

CRYPTANTHUS

Débora Maria Cavalcanti Ferreira & Rafael Batista Louzada

Cryptanthus Otto & A. Dietr.

Ervas terrícolas ou rupícolas, propagação por rizomas, estolões ou brotos axilares. Caules eretos ou decumbentes, curtos ou longos. Bainhas foliares muito amplamente ovadas, ovadas ou largamente ovada, aculeadas; lâminas foliares linear-oblongas, oblanceoladas, lanceoladas, estreito-elípticas, linear-triangulares, estreitamente triangulares, deltóides, ovadas ou amplamente ovadas, mais largas na base, levemente estreitas na base (nas folhas mais desenvolvidas) ou estreitas na base (nas folhas mais desenvolvidas), verdes, verdes e róseas, verdes com base avermelhadas, róseas, avermelhadas, ou marrons, face abaxial densamente lepidota, face adaxial glabra, glabra com base e ápice densamente lepidoto, glabra com base densamente lepidota, glabra com ápice densamente lepidoto, ou com faixas transversais de tricomas lepidotos, margens levemente onduladas ou onduladas, aculeadas, ápices acuminados ou caudados. Inflorescência em espiga de glomérulos, com flores estaminadas e perfeitas; brácteas primárias foliáceas, similares as folhas, linear-triangulares, triangulares, lanceoladas, oblanceoladas, deltóides, estreitamente triangulares, ovadas ou estreito-elípticas, face abaxial densamente lepidota, face adaxial glabra, glabra com base esparsamente lepidota, densamente lepidota, ou com faixas transversais de tricomas lepidotos, margens onduladas ou levemente onduladas, aculeadas, ápices acuminados ou caudados; brácteas florais ovadas, ovadas-cimbiformes, lanceoladas-cimbiformes, oblongas-cimbiformes, elípticas-cimbiformes, ou estreitamente triangulares-carinadas, alvas na base e marrons no ápice, alvas na base e verdes no ápice, marrons, castanhas com bases esverdeadas-hialinas, verde-amarronzadas, verdes, róseas, ou verdes com bases róseas; sépalas parcialmente conadas, lobos ovados, elípticos, lanceolados, ou estreitamente elípticos-ovados, ápices mucronados ou acuminados-caudados; pétalas oblanceoladas ou estreitamente subespatuladas, ápices agudos ou arredondados tornando-se emarginado na antese, arredondados, mucrunulados, subagudos a obtusos, ou obtusos, parcialmente conadas, alvas, com 2 calosidades conspícuas ou inconspícuas; estames 6, 3 antesépalos, 3 antepétalos, alvos, anteras com deiscência longitudinal; estiletos e estigmas rudimentares nas flores estaminadas e desenvolvidos nas flores perfeitas; ovários com tubo epigínico, placentação axial. Frutos bagas, alvos, alvos com

ápices verdes, alvos com ápices vermelhos, ou alvos com ápices verde-avermelhados. Sementes assimétricas.

Cryptanthus é um gênero endêmico do Brasil onde ocorre nas regiões nordeste e sudeste, desde o Rio Grande do Norte até o Rio de Janeiro, em áreas de Floresta Atlântica e Caatinga (Leme et al. 2017). Estudos filogenéticos indicam que *Cryptanthus* é polifilético (Silvestro et al. 2013; Louzada et al. 2014; Cruz et al. 2017; Leme et al. 2017), e assim, o último estudo realizado por Leme et al. (2017) faz a re-circunscrição do gênero para torná-lo monofilético. Parte das espécies do gênero foi segregada e inserida em três diferentes gêneros: *Hoplocryptanthus* (Mez) Leme, S. Heller & Zizka, *Forzzaea* Leme, S. Heller & Zizka e *Rokautskyia* Leme, S. Heller & Zizka (Leme et al. 2017). Portanto, atualmente são reconhecidas ca. 60 espécies para *Cryptanthus* que apresentam como sinapomorfia a andromonoiccia (Leme et al. 2017; Leme et al. 2020; Ferreira & Louzada 2020). Seis espécies do gênero são registradas em Alagoas, onde estão distribuídas na Floresta Atlântica, com exceção de *Cryptanthus bahianus* L. B. Sm. que ocorre na Caatinga. *Cryptanthus zonatus* (Vis.) Vis. é a única espécie encontrada em Alagoas que está indicada como ameaçada de extinção pelo Livro Vermelho da Flora do Brasil (Forzza et al. 2013).

Chave para as espécies de **Cryptanthus** ocorrentes em Alagoas

1. Lâminas foliares mais largas na base 2
2. Caules 4,5–8,2 cm de compr.; bainhas foliares 0,9–2,3 x 1,5–2,3 cm, face adaxial das brácteas primárias glabra ***Cryptanthus bahianus* 2**
2. Caules 18,2–45 cm de compr.; bainhas foliares 2,8–3,5 x 4,4–6 cm, face adaxial das brácteas primárias densamente lepidota ***Cryptanthus cinereus* 3**
1. Lâminas foliares estreitas ou levemente estreitas na base 3
3. Ovário 15-20 mm de compr..... ***Cryptanthus felixii* 5**
3. Ovário 6-12 mm de compr..... 4
4. Lâminas foliares linear-triangulares, estreitamente triangulares ou deltóides
..... ***Cryptanthus bahianus* 2**

4. Lâminas foliares estreito-elípticas, lanceoladas, oblanceoladas, ovadas ou muito amplamente ovadas..... 5
5. Lâminas foliares predominantemente linear-oblanceoladas ou lanceoladas (algumas estreito-elípticas).....*Cryptanthus alagoanus* 1
5. Lâminas foliares predominantemente estreito-elípticas (algumas lanceoladas, oblanceoladas, ovadas ou muito amplamente ovadas) 6
6. Lâminas foliares com face adaxial densamente lepidota, glabra com base densamente lepidota, ou completamente glabras*Cryptanthus diana* 4
6. Lâminas foliares com face adaxial com faixas transversais de tricomas lepidotos, glabra com ápice densamente lepidoto, ou completamente glabras*Cryptanthus zonatus* 6

1. *Cryptanthus alagoanus* Leme & J. A. Siqueira, Selbyana 22(2): 151. 2001.

Fig. 1A.

Ervas terrícolas, propagação por estolões ou brotos axilares. Caules 4,5 cm de compr., eretos ou decumbentes. Bainhas foliares 2,7–5 x 1,9–3,1 cm, ovadas ou amplamente ovadas, acúleos 0,1–0,3 mm de compr., 0,1–1 mm distantes; lâminas foliares 50,2–53 x 1,5–4,7 cm, linear-oblanceolada, oblanceoladas (predominante) ou estreito-elípticas, estreitas na base, verdes, face adaxial glabra com base e ápice densamente lepidoto, margens levemente onduladas, acúleos 0,2–0,5 mm de compr. 0,2–3 mm distantes, ápices acuminados. Inflorescência com ca. 6 glomérulos laterais; raques 1,5 cm de compr; brácteas primárias ca. 6 em número, 2–42,3 x 1–4,4 cm, oblanceoladas, lanceoladas ou triangulares, face adaxial glabra com base esparsamente lepidota, margens onduladas, acúleos 0,2–0,3 mm compr. 0,2–2,3 mm distantes, ápices acuminados; brácteas florais 23–47,2 x 7,5–22,1 mm, ovadas, ovadas-cimbiformes ou lanceoladas-cimbiformes, alvas na base e marrons no ápice. Flores 43–58 mm compr; sépalas 20–23,3 mm compr, conadas por 8,3–10,3 mm, lobos 11–13,7 x 4–5 mm, lanceolados ou ovados, ápices mucronados; pétalas 31,3–40 x 4,2–6,3 mm, oblanceoladas, ápices agudos ou arredondados tornando-se emarginado na antese, conadas por 11,5–16,7 mm, com 2 calosidades inconspícuas ou conspícuas; filetes 22,5–30 mm compr., anteras 5,7–8,5 mm compr; estigmas 5–5,5 mm compr; ovários 7–12 mm x 4,7–6,3 mm; tubo epigínico 4,5–9,3 mm de compr.

Material examinado: Paripueira, RPPN Placas (O Sabiá), 01/X/2017, (fl. em cultivo em 18/VII/2018), *D. Cavalcanti et al.* 906, UFP. Paripueira, RPPN Sabiá, 29/VIII/2009, (fr.), *Chagas-Mota & V.G. Ramalho* 5258, MAC. Paripueira, RPPN Placas, 11/I/2010, (fl.), *R. P. Lyra-Lemos* 12861, MAC.

Cryptanthus alagoanus ocorre nos estados da Paraíba, Pernambuco, Alagoas e Sergipe, em áreas sombreadas de Floresta Atlântica. Para o estado de Alagoas, a espécie só é registrada para o município de Paripueira. *Cryptanthus alagoanus* é morfologicamente similar a *Cryptanthus zonatus* (Vis.) Vis. pelo formato das lâminas foliares, porém, diferencia-se pelas folhas serem predominantemente oblanceoladas.

2. *Cryptanthus bahianus* L. B. Sm., Arq. Bot. Estado São Paulo n. ser. 1: 106. 1944.

Fig. 1B.

Ervas terrícolas ou rupícolas, propagação por brotos axilares. Caules 4,5–8,2 cm de compr., eretos ou decumbentes. Bainhas foliares 0,9–2,3 x 1,5–2,3 cm, amplamente ovadas, acúleos 0,4–0,5 mm de compr., 0,2–1 mm distantes; lâminas foliares 1,4–24,1 x 0,8–1,5 cm, linear-triangulares, estreitamente triangulares ou deltóides, levemente estreitas na base ou mais largas na base, verdes ou marrons, face adaxial glabra, margens levemente onduladas, acúleos 0,5–1,5 mm de compr., 1,5–4 mm distantes, ápices acuminados; Inflorescências com 5 glomérulos laterais; raques 0,5–0,9 cm de compr.; brácteas primárias 6 em número, 1,1–20,8 x 0,5–1,2 cm, linear-triangulares, estreitamente triangulares ou triangulares, face adaxial glabra, margens levemente onduladas, acúleos 1–1,2 mm de compr., 2–5 mm distantes, ápices acuminados; brácteas florais 12,3–20,8 x 5–11,5 mm, oblongas-cimbiformes, elípticas-cimbiformes ou lanceoladas-cimbiformes, marrons ou verde-amarronzadas; flores 25,3–43 mm de compr.; sépalas 11,2–18 mm de compr., conadas por 5–12 mm, lobos 3–8,8 x 2,3–4,5 mm, elípticos, ápices mucronados; pétalas 19–31,3 x 4–7 mm, oblanceoladas, ápices obtusos, conadas por 6–8,7 mm, com 2 calosidades inconspícuas; filetes 14–21,6 mm de compr., anteras 3–3,5 mm compr.; estigmas 3 mm de compr.; ovários 6–10 x 4,5–5,5 mm; tubo epigínico 1–2 mm de compr. Frutos 19–20 x 8,2–9 mm, alvos com ápices verdes; sementes 3,8–4,2 x 2,5–3,2 mm.

Material examinado: Traipu, Serra-da-Mão, 18/V/2011, (fl.), *A. Costa* 510, MAC.

Material adicional examinado: Pernambuco, Caruaru, Beira da BR-104, 27/IV/2014, (fl. em cultivo em 19/V/2018), *D. Cavalcanti, A. Melo, J. R. Maciel & B. S. Amorim* 899, UFP.

Paraíba, Areia, Engenho Cipó, 13/VIII/2018, (fl.), *E. M. Almeida* 2857, UFP.

Cryptanthus bahianus ocorre nos estados da Paraíba, Pernambuco, Alagoas, Sergipe e Bahia, na Caatinga, tanto em áreas expostas ao sol quanto em áreas sombreadas. Em Alagoas, a espécie é registrada apenas para uma localidade. *Cryptanthus bahianus* pode apresentar lâminas foliares mais largas na base ou levemente estreitadas na base. É diferenciada de *Cryptanthus cinereus* que apresenta lâminas foliares mais largas na base, pela face adaxial das lâminas foliares que é glabra.

3. *Cryptanthus cinereus* D.M.C. Ferreira & Louzada, Systematic Botany 45(3): 460. 2020.

Fig. 1C.

Ervas rupícolas, propagação por rizomas ou brotos axilares. Caules 18,2–45 cm de compr., eretos ou decumbentes. Folhas 30–49 em número; bainhas foliares 2,8–3,5 x 4,4–6 cm, largamente ovadas ou amplamente ovadas, acúleos 0,5–2 mm de compr., 0,2–2 mm distantes; lâminas foliares 0,8–37,5 x 2,4–4,5 cm, largura da mais larga lâmina foliar 3,3–4,5 cm, estreitamente triangulares, mais largas na base, róseas ou marrons nas áreas expostas ao sol, verdes ou verdes e róseas nas áreas sombreadas, face abaxial densamente lepidota, face adaxial tornando-se glabra na base da roseta e densamente lepidota no ápice da roseta, margens onduladas, acúleos 0,5–2 mm de compr., 2–14 mm distantes, ápices caudados ou acuminados. Inflorescências com 7 glomérulos laterais; raques 3 cm de compr.; brácteas primárias 8–9 em número, 1,9–24,2 x 1,3–4,9 cm, estreitamente triangulares ou deltóides, face adaxial densamente lepidota, margens onduladas; acúleos 0,5–3 mm de compr., 1–9 mm distantes, ápices acuminados ou caudados; brácteas florais 21–34 x 5–13 mm, lanceoladas-cimbiformes, verdes, róseas ou verdes com bases róseas; flores 39–52 mm compr; sépalas 19–22,2 mm de compr., conadas por 1,6–5 mm, lobos 14,2–20,5 x 4–5 mm, lanceolados, ápices mucronados; pétalas 21,5–26 x 3,5–5 mm, oblanceoladas, ápices arredondados, conadas por 1–1,2 mm, com 2 calosidades conspícuas; filetes 17–18,2 mm de compr., anteras 2,2–5 mm compr.; estigmas 2–2,2 mm compr.; ovários 11,3–19 x 5,2–8,5 mm; tubo epigínico 5–8 mm de compr. Frutos 21–25 x 9–9,2 mm, alvos com ápices verde-avermelhados; sementes 3,8–4 x 2–3 mm.

Material examinado: Ibateguara, Sítio Duas Barras, 08/V/ 2019, (fl.fr.), *D. Cavalcanti et al.* 921, UFP, MAC, RB, UFRN, SP, NY.

Cryptanthus cinereus é endêmica do estado de Alagoas, onde ocorre em Floresta Atlântica sobre afloramentos rochosos, em áreas sombreadas ou expostas ao sol (Ferreira & Louzada 2020). De acordo com Ferreira & Louzada (2020) ocorre em uma única localidade, porém, outra localidade (São Luís do Quitunde- Fazenda Garabu) é de possível ocorrência mas o material está jovem e estéril (*R. P. Lyra-Lemos et al.* 8241, MAC) o que não permite uma correta identificação. Junto com *C. bahianus* apresenta lâminas foliares mais largas na base, porém, diferencia-se por apresentar caules 18,2–45 cm de compr., bainhas foliares 2,8–3,5 x 4,4–6 cm e face adaxial das brácteas primárias densamente lepidota. Assemelha-se a *C. felixii* pelos caules longos, porém, é diferenciada por apresentar lâminas foliares mais largas na base e brácteas primárias densamente lepidota.

4. *Cryptanthus diana* Leme, *Cryptanthus Soc. J.* 5(2): 10. 1990.

Fig. 1D.

Ervas terrícolas, propagação por brotos axilares. Caules 1–21,5 cm, eretos. Bainhas foliares 1–3,2 x 1,5–2,8 cm, largamente ovadas, acúleos 0,2–1 mm de compr., 0,1–1 mm distantes; lâminas foliares 1–49 x 0,4–4,5 cm, estreito-elípticas (predominante), lanceoladas, oblanceoladas, ovadas ou muito amplamente ovadas, estreitas na base, verdes, face adaxial densamente lepidota, glabra com base densamente lepidota, ou glabra, margens onduladas, acúleos 0,2–1,9 mm de compr., 0,5–5 mm distantes, ápices acuminados. Inflorescências com 7–8 glomérulos laterais; raques 1–3 cm de compr.; brácteas primárias 4–12 em número, 1–36,5 x 0,4–4,2 cm, lanceoladas, oblanceoladas ou ovadas, face adaxial glabra, margens onduladas, acúleos 0,3–0,6 mm de compr., 0,2–3 mm distantes, ápices acuminados; brácteas florais 22,5–26,2 x 7–9 mm, lanceoladas-cimbiformes, alvas na base e verdes no ápice; flores 37–51 mm de compr.; sépalas 19–21 mm compr., conadas por 10–10,7 mm, lobos 7,2–10 x 3,4–4,5 mm, ovados, ápices mucrunados; pétalas 33–39,2 x 4,5–6 mm, oblanceoladas, ápices mucrunulados ou arredondados, conadas por 5,5–8 mm, com 2 calosidades conspícuas, filetes 22–25 mm de compr., anteras 5–6,5 mm de compr.; estigmas 2,2–3,2 mm de compr.; ovários 7–11,2 x 4,7–5,8 mm; tubo epigínico 1–1,2 mm de compr. Frutos 13–23,5 x 6,5–8,2 mm, alvos; sementes 2,5–5,5 x 1,7–3,4 mm.

Material examinado: Boca da Mata, Fazenda Daniel, Mata da Bitonha, próximo à Serra da Naceia, 01/XI/2002, (fl.), *J. A. Siqueira-Filho* 1309, MAC. Chã Preta, Serra Lisa, 06/V/2009, (fl.), *Chagas Mota & N. Ramos* 3572, MAC. Coruripe, Al-425, 29/VII/1981, (fl.), *R. P. de Lyra & G. L. Esteves* 329, MAC. Coruripe, Fazenda Águas de Pituba II, 26/VII/2008, (fl.), *M. N. Rodrigues & F. Pinto* s/n, MAC 35056. Ibateguara, Coimbra, Cerrado da Burra, 09/IX/2002, (fl.), *M. Oliveira & A. A. Grillo* 1097, UFRN. Joaquim Gomes, 04/VII/2016, (fl.), *A. A. S. Mascarenhas; T. V. A. Santos & D. Carvalho* 79, MAC; Quebrangulo, Parque Estadual da Pedra Talhada, 23/IX/ 1987, (fl.), *R. P. Lyra-Lemos & I. Moreira* 1453, IPA. Maceió, Parque Municipal, 23/V/2008, (fl.), *R. P. Lyra-Lemos & L. Conserva* 11344, MAC. Maceió, Serra da Saudinha, Fazenda Cela, 14/VI/2008, (fl.), *Chagas-Mota* 638, MAC. Maceió, Serra da Saudinha, 06/V/2006, (fl.), *P. A. F. Rios* s/n, MAC 29108. Messias, Eng. Oriente, Serra da Cachoeira, 11/VI/1980, (fl.), *Andrade-Lima, F. Gallindo & Correia-Lima* 45, IPA. Murici, Estação Ecológica de Murici, Fazenda Bananeiras, 21/IV/2012, (fl.), *M. C. S. Mota; E. C. O. Chagas & J. M. Silva* 11537, MAC.

Material adicional examinado: Cachoeira do Mirim, 28/IX/2002 (est.), *A. Frassy & J. Simplicio* s/n, ALCB 80351, MAC 17637. Pernambuco, Jaqueira, Serra do Urubu, RPPN Frei Caneca, Mata do Quengo, 20/IX/2017, (fl.), *D. Cavalcanti et al.* 801, UFP. Pernambuco, São Vicente Ferrer, Mata do Estado, 12/XI/2014, (fl.), *D. Cavalcanti, R. Farias & R. Louzada* 771, UFP.

Cryptanthus diana ocorre nos estados de Pernambuco e Alagoas, e áreas sombreadas de Floresta Atlântica. Assemelha-se a *Cryptanthus zonatus* pelo formato das lâminas foliares estreito-elípticas ou oblanceoladas, porém, diferencia-se por apresentar face adaxial da lâmina foliar densamente lepidota. Porém, há indivíduos com face adaxial das lâminas foliares glabra, havendo sobreposição de caracteres entre *C. diana* e *C. zonatus*, tratando-se portanto de um complexo de espécies como já evidenciado por Ferreira & Louzada (2020).

5. *Cryptanthus felixii* J.A. Siqueira & Leme, *Fragm. Atlantic Forest N. E. Brazil*: 285. 2007.

Fig. 1E.

Ervas terrícolas, propagação por brotos axilares. Caules 25 cm de compr., eretos. Bainhas foliares 1,5–6 x 2,5–3,7 cm, amplamente ovadas, acúleos 0,2–0,8 mm de compr., 0,1–1 mm distante; lâminas foliares 1–40,1 x 1–4,7 cm, oblanceoladas, estreito-elípticas, ou deltóides, estreitas na base, verdes com base avermelhadas, face adaxial glabra ou glabra com base

densamente lepidota, margens onduladas, acúleos 0,4–1,2 mm de compr., 0,1–5 mm distantes, ápices acuminados. Inflorescências com 5 glomérulos laterais; raques 2,5 cm de compr.; brácteas primárias 7 em número, 0,7–31 x 0,2–1,8 cm, estreito-elípticas ou estreitamente triangulares, face adaxial glabra ou glabra com base densamente lepidota, **margens** onduladas, acúleos 0,5–1 mm de compr., 0,5–5 mm distantes, ápices acuminados; brácteas florais 22–26 x 12–13 mm, estreitamente triangulares-carinadas, castanhas com bases esverdeadas-hialinas; flores 55–64 mm de compr.; sépalas 20–23 mm compr., conadas por 9–11 mm, lobos 11–13 x 4 mm, estreitamente elípticos-ovados, ápices acuminados-caudados; pétalas 31–47 x 5–6 mm, estreitamente subespatuladas, ápices subagudos a obtusos, conadas por 9–17 mm, com 2 calosidades inconspícuas ou conspícuas; filetes 22–35 mm de compr., anteras 3–4 mm de compr.; estigmas 6 mm de compr.; ovários 15–20 x 5 mm; tubo epigínico 4–7 mm de compr. Frutos não conhecidos.

Material examinado: Serra Lisa, VIII/2002 (fl. em cultivo em II/2004), *A. Frassy s/n*, HB 90724.

Material adicional examinado: Pernambuco, Bonito, Fazenda Tudo Muito, 06/XII/2003, (fl.), *J. A. Siqueira-Filho & L. P. Félix 1422*, UFP.

Cryptanthus felixii ocorre nos estados de Pernambuco e Alagoas, em áreas sombreadas de Floresta Atlântica. Assemelha-se a *Cryptanthus* sp., por apresentar caules longos, porém diferencia-se pelas folhas estreitadas na base. Devido à falta de material reprodutivo para análise, a descrição dos caracteres reprodutivos foi extraída da obra original da espécie (Leme & Siqueira-Filho 2007).

6. *Cryptanthus zonatus* (Vis.) Vis., Pl. Nuove Bromel. 9: 1854. *Pholidophyllum zonatum* Vis., Ind. Sem. Hort. Patav. 4: 29. 1847.

“bromélia-cascavél”, “xinxozinho”

Fig. 1F.

Ervas terrícolas, propagação por estolões ou brotos axilares. Caules 1 cm de compr., eretos. Bainhas foliares 2,5 x 4,1 cm, amplamente ovadas, acúleos 0,2 mm de compr., 0,2–0,5 mm distantes; lâminas foliares 12,5–36 x 1,9–3 cm, estreito-elípticas (predominante) ou oblanceoladas, estreitas na base, verdes ou avermelhadas, face adaxial glabra, glabra com

ápice densamente lepidoto, ou com faixas transversais de tricomas lepidotos, margens onduladas, acúleos 0,3–1 mm de compr., 1–3 mm distantes, ápices acuminados. Inflorescências com 3 glomérulos laterais; raques 0,5 cm de compr.; brácteas primárias 4 em número, 1–25,5 x 0,4–3,9 cm, ovadas, estreito-elípticas, ou lanceoladas, face abaxial densamente lepidota, face adaxial glabra ou com faixas transversais de tricomas lepidotos, margens onduladas, acúleos 0,3–0,5 mm de compr., 0,2–2 mm distantes, ápices acuminados; brácteas florais 14–20,5 x 4,2–10 mm, ovadas-cimbiformes ou lanceoladas-cimbiformes, alvas base e marrons no ápice; flores 50,5–52,2 mm compr.; sépalas 14,4–16,7 mm de compr., conadas por 8–10 mm, lobos 5,8–7,7 x 2,5–5,7 mm, elípticos, ápices mucrunados; pétalas 34,3–42,2 x 3,2–5,3 mm, oblanceoladas, ápices mucrunulados, conadas por 13–14 mm, com 2 calosidades conspícuas; filetes 29–32,5 mm compr., anteras 3,6–5,5 mm compr.; estigmas 4–4,5 mm de compr.; ovários 8–10 x 4,5–6 mm; tubo epigínico 1,5–4 mm de compr. Frutos 21,5 x 13 mm, alvos com ápices vermelhos; sementes 4,3–5 x 3,2–4 mm.

Material examinado: Marechal Deodoro, CESMAC, 15/VII/2009, (fl.), *N. R. Santos*; *M. V. Caju & L. M. Leão 40*, MAC. Marechal Deodoro, Dunas do Cavalo Russo, 18/IX/2010, (fl.), *Chagas-Mota 8607*, MAC. Paripueira, RPPN Placas (O Sabiá), 01/X/2017, (fl. em cultivo em 22/VIII/2018), *D. Cavalcanti & R. B. Louzada 907*, UFP. Paripueira, RPPN Placas, 11/I/2010, (fl.), *R. P. Lyra-Lemos 12860*, MAC.

Material adicional examinado: Alagoas, São Luis do Quintude, Serra da Cachoeira, Fazenda Lagoa Vermelha, 07/III/2016, (est.), *R. A. Pontes 1141*, UFRN. Alagoas, São Luis do Quintude, Serra da Cachoeira, Fazenda Lagoa Vermelha, 07/III/2016, (est.), *R. A. Pontes 1142*, UFRN. Pernambuco, Gravatá, RPPN Serra do Contente, trilha para o mirante, 14/VIII/2017, (fr.), *D. Cavalcanti et al. 784*, UFP. Pernambuco, Igarassu, Usina São José, Mata de Piedade, 2017, (fl. em cultivo em 21/VI/2018), *D. Cavalcanti & R. B. Louzada 894*, UFP.

Cryptanthus zonatus ocorre nos estados do Rio Grande do Norte, Paraíba, Pernambuco e Alagoas, em áreas sombreadas de Floresta Atlântica incluindo áreas de Restinga, Floresta Estacional Semidecidual e Brejos de Altitude. Em Alagoas, a espécie ocorre sobre solo arenoso ou solo argiloso. *Cryptanthus zonatus* apresenta como espécie irmã, a espécie *Cryptanthus diana* Leme (Leme et al. 2017). Morfologicamente são parecidas pelo formato das folhas e flores e são tratadas como um complexo de espécies devido à sobreposição de caracteres morfológicos (Ferreira & Louzada 2020). Os indivíduos de *Cryptanthus zonatus* que apresentam face adaxial das lâminas foliares com tricomas lepidotos transversais são

facilmente reconhecidos dos indivíduos de *C. diana* apresentam que face adaxial das lâminas foliares densamente coberta por tricomas lepidotos. Porém, tanto *Cryptanthus zonatus* quanto *Cryptanthus diana* apresentam indivíduos verdes e glabros, havendo sobreposição entre eles (Ferreira & Louzada 2020). *Cryptanthus zonatus* é indicada como vulnerável pelo Livro Vermelho da Flora do Brasil (Forzza et al. 2013).

Referências bibliográficas

- CRUZ, G. A. S.; ZIZKA, G.; SILVESTRO, D.; LEME, E. M. C.; SCHULTE, K. & BENKOISEPPON, A. M. 2017. Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). **Molecular Phylogenetics and Evolution** **107**: 152-165.
- FERREIRA, D. M. C. & LOUZADA, R. B. 2020. A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus. **Systematic Botany** **45(3)**: 460–465
- FORZZA, R. C.; COSTA, A. F.; LEME, E. M. C.; VERSIEUX, L. M.; WANDERLEY, M. G. L.; LOUZADA, R. B.; MONTEIRO, R. F.; JUDICE, D. M.; FERNANDEZ, E. P.; BORGES, R. A. X.; PENEDO, T. S. A.; MONTEIRO, N. P. & MORAES, M. A. 2013. Bromeliaceae. In: Martinelli G, Moraes MA, orgs. **Livro Vermelho da Flora do Brasil**. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro: Andrea Jakobsson, 315-396.
- LEME, E. M. C. & SIQUEIRA-FILHO, J. A. 2007. Taxonomia das bromélias dos fragmentos de mata atlântica de Pernambuco e Alagoas. Pp. 190-381 em **Fragmentos de mata atlântica do Nordeste – biodiversidade, conservação e suas bromélias**, eds. J. A. Siqueira-Filho and E. M. C. Leme. Rio de Janeiro: Andrea Jakobsson Estúdio.
- LEME, E. M. C.; HELLER, S.; ZIZKA, G. & HALBRITTER, H. 2017. New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. **Phytotaxa** **318**: 001-088.
- LEME, E. M. C.; RIBEIRO, O. B. C.; SOUZA, F. V. D.; SOUZA, E. H. de; KOLLMANN, L. J. C. & FONTANA, A. P. 2020. Miscellaneous new species in the “Cryptanthoid

- complex” (Bromeliaceae: Bromelioideae) from Eastern Brazil. **Phytotaxa** **430** (3): 157–202.
- LOUZADA, R. B.; SCHULTE, K.; WANDERLEY, M. G. L.; SILVESTRO, D.; ZIZKA, G.; BARFUSS, M. H. J. & PALMA-SILVA, C. 2014. Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (Bromelioideae, Bromeliaceae) and its implications on morphological character evolution. **Molecular Phylogenetics and Evolution** **77**: 54-64.
- SILVESTRO, D., G. ZIZKA, AND K. SCHULTE. 2013. Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). **Evolution** **68**: 163–175.



Figura 1. *Cryptanthus* de Alagoas. A. *Cryptanthus alagoanus* Leme & J. A. Siqueira. B. *Cryptanthus bahianus* L. B. Sm. (Foto: J. R. Maciel). C. *Cryptanthus cinereus* D.M.C. Ferreira & Louzada. D. *Cryptanthus diana* Leme. E. *Cryptanthus felixii* J. A. Siqueira & Leme (Foto: R. Pontes). F. *Cryptanthus zonatus* (Vis.) Vis.

4.5 GUIA DE CAMPO 1 - THE GENUS *CRYPTANTHUS* OTTO & A. DIETR.
(BROMELIACEAE). ENDEMIC GENUS TO
BRAZIL

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

1

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹

1 Universidade Federal de Pernambuco; 2 Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org | guide's number provided by us | version 11 *Cryptanthus alagoanus*2 *Cryptanthus alagoanus*3 *Cryptanthus alagoanus*4 *Cryptanthus alagoanus*5 *Cryptanthus alagoanus*6 *Cryptanthus alagoanus*7 *Cryptanthus alagoanus*8 *Cryptanthus alagoanus*
Lateral glomerule9 *Cryptanthus alagoanus*10 *Cryptanthus alagoanus*
Staminate flower11 *Cryptanthus alagoanus*12 *Cryptanthus alagoanus*
Perfect flower13 *Cryptanthus apiculatantherus*
Photo: Erton Mendonça14 *Cryptanthus apiculatantherus*15 *Cryptanthus apiculatantherus*16 *Cryptanthus apiculatantherus*17 *Cryptanthus apiculatantherus*18 *Cryptanthus apiculatantherus*19 *Cryptanthus apiculatantherus*20 *Cryptanthus apiculatantherus*
Lateral glomerule

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

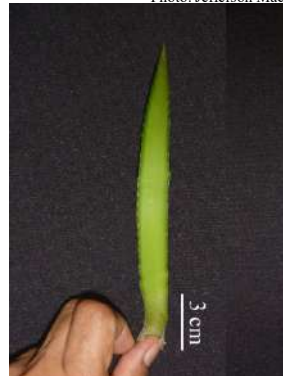
Endemic genus to Brazil

2

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹

1 Universidade Federal de Pernambuco; 2 Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org] [guide's number provided by us] version 121 *Cryptanthus apiculatantherus*22 *Cryptanthus apiculatantherus*
Staminate flower23 *Cryptanthus apiculatantherus*24 *Cryptanthus apiculatantherus*
Perfect flower25 *Cryptanthus apiculatantherus*26 *Cryptanthus apiculatantherus*27 *Cryptanthus bahianus*
Photo: Erton Mendonça28 *Cryptanthus bahianus*
Photo: Jefferson Maciel29 *Cryptanthus bahianus*30 *Cryptanthus bahianus*31 *Cryptanthus bahianus*32 *Cryptanthus bahianus*33 *Cryptanthus bahianus*34 *Cryptanthus bahianus*35 *Cryptanthus bahianus*
Apical glomerule36 *Cryptanthus bahianus*
Lateral glomerule37 *Cryptanthus bahianus*38 *Cryptanthus bahianus*
Staminate flower39 *Cryptanthus bahianus*
Perfect flower40 *Cryptanthus bahianus*
Photo: Erton Mendonça

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

3

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org | guide's number provided by us | version 141 *Cryptanthus bahianus*42 *Cryptanthus bahianus*43 *Cryptanthus beuckeri*44 *Cryptanthus beuckeri*45 *Cryptanthus beuckeri*46 *Cryptanthus beuckeri*47 *Cryptanthus boanovensensis*48 *Cryptanthus boanovensensis*49 *Cryptanthus boanovensensis*50 *Cryptanthus boanovensensis*51 *Cryptanthus boanovensensis*52 *Cryptanthus boanovensensis*53 *Cryptanthus boanovensensis*54 *Cryptanthus boanovensensis*
Lateral glomerule55 *Cryptanthus boanovensensis*
Staminate flower56 *Cryptanthus boanovensensis*57 *Cryptanthus boanovensensis*
Perfect flower58 *Cryptanthus brevibracteatus*59 *Cryptanthus brevibracteatus*60 *Cryptanthus brevibracteatus*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

4

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org | guide's number provided by us | version 161 *Cryptanthus brevibracteatus*62 *Cryptanthus brevibracteatus*63 *Cryptanthus brevibracteatus*64 *Cryptanthus brevibracteatus*65 *Cryptanthus brevibracteatus*66 *Cryptanthus brevibracteatus*
Staminate flower67 *Cryptanthus brevibracteatus*68 *Cryptanthus brevibracteatus*
Perfect flower69 *Cryptanthus capitellatus*70 *Cryptanthus capitellatus*71 *Cryptanthus capitellatus*72 *Cryptanthus capitellatus*73 *Cryptanthus capitellatus*74 *Cryptanthus capitellatus*75 *Cryptanthus cinereus*76 *Cryptanthus cinereus*77 *Cryptanthus cinereus*78 *Cryptanthus cinereus*79 *Cryptanthus cinereus*80 *Cryptanthus cinereus*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

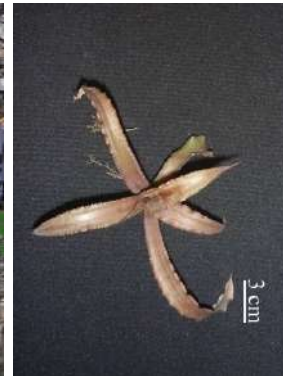
5

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹

1 Universidade Federal de Pernambuco; 2 Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author. fieldmuseum.org [guide's number provided by us] version 1

81 *Cryptanthus cinereus*82 *Cryptanthus cinereus*
Apical glomerule83 *Cryptanthus cinereus*84 *Cryptanthus cinereus*
Staminate flower85 *Cryptanthus cinereus*86 *Cryptanthus cinereus*87 *Cryptanthus cinereus*88 *Cryptanthus crassifolius*89 *Cryptanthus crassifolius*90 *Cryptanthus crassifolius*91 *Cryptanthus crassifolius*92 *Cryptanthus crassifolius*93 *Cryptanthus crassifolius*94 *Cryptanthus crassifolius*95 *Cryptanthus crassifolius*
Lateral glomerule96 *Cryptanthus crassifolius*
Staminate flower97 *Cryptanthus crassifolius*
Perfect flower98 *Cryptanthus cruzalmensis*99 *Cryptanthus cruzalmensis*100 *Cryptanthus cruzalmensis*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

6

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org | guide's number provided by us | version 1101 *Cryptanthus cruzalmensis*102 *Cryptanthus cruzalmensis*103 *Cryptanthus diana*104 *Cryptanthus diana*105 *Cryptanthus diana*106 *Cryptanthus diana*107 *Cryptanthus diana*108 *Cryptanthus diana*109 *Cryptanthus diana*110 *Cryptanthus diana*111 *Cryptanthus diana*112 *Cryptanthus diana*113 *Cryptanthus diana*
Lateral glomerule114 *Cryptanthus diana*
Staminate flower115 *Cryptanthus diana*
Perfect flower116 *Cryptanthus diana*117 *Cryptanthus dorothyae*118 *Cryptanthus dorothyae*119 *Cryptanthus dorothyae*120 *Cryptanthus dorothyae*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

7

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

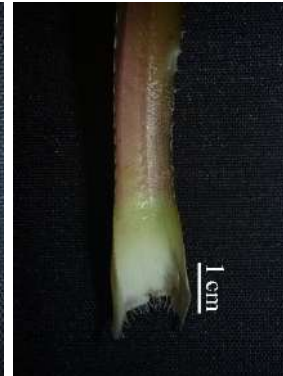
© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org] [guide's number provided by us] version 1121 *Cryptanthus dorothyae*122 *Cryptanthus dorothyae*123 *Cryptanthus dorothyae*124 *Cryptanthus dorothyae*
Apical glomerule125 *Cryptanthus dorothyae*
Lateral glomerule126 *Cryptanthus dorothyae*127 *Cryptanthus dorothyae*
Staminate flower128 *Cryptanthus dorothyae*129 *Cryptanthus dorothyae*
Perfect flower130 *Cryptanthus* sp.131 *Cryptanthus* sp.132 *Cryptanthus* sp.133 *Cryptanthus* sp.134 *Cryptanthus* sp.135 *Cryptanthus* sp.136 *Cryptanthus* sp.137 *Cryptanthus* sp.
Staminate flower138 *Cryptanthus* sp.139 *Cryptanthus felixii*140 *Cryptanthus felixii*

Photo: Ricardo Pontes

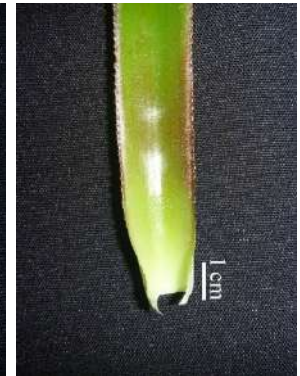
The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

8

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org] [guide's number provided by us] version 1141 *Cryptanthus felixii*142 *Cryptanthus felixii*143 *Cryptanthus felixii*144 *Cryptanthus felixii*145 *Cryptanthus felixii*146 *Cryptanthus giganteus*147 *Cryptanthus guanduensis*148 *Cryptanthus guanduensis*149 *Cryptanthus guanduensis*150 *Cryptanthus guanduensis*151 *Cryptanthus guanduensis*152 *Cryptanthus guanduensis*153 *Cryptanthus guanduensis*154 *Cryptanthus guanduensis*

Apical glomerule

155 *Cryptanthus guanduensis*

Lateral glomerule

156 *Cryptanthus guanduensis*157 *Cryptanthus guanduensis*
Staminate flower158 *Cryptanthus guanduensis*159 *Cryptanthus guanduensis*
Perfect flower160 *Cryptanthus pickelii*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

9

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author. fieldmuseum.org [guide's number provided by us] version 1

161 *Cryptanthus pickelii*162 *Cryptanthus pickelii*163 *Cryptanthus pickelii*164 *Cryptanthus pickelii*165 *Cryptanthus pickelii*166 *Cryptanthus pickelii*167 *Cryptanthus pickelii*
Apical glomerule168 *Cryptanthus pickelii*
Lateral glomerule169 *Cryptanthus pickelii*170 *Cryptanthus pirambuensis*
Staminate flower171 *Cryptanthus pirambuensis*172 *Cryptanthus pirambuensis*
Perfect flower173 *Cryptanthus pirambuensis*174 *Cryptanthus pirambuensis*175 *Cryptanthus pirambuensis*176 *Cryptanthus pirambuensis*177 *Cryptanthus pirambuensis*178 *Cryptanthus pirambuensis*
Apical glomerule179 *Cryptanthus pirambuensis*180 *Cryptanthus pirambuensis*
Staminate flower

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

10

Débora Maria Cavalcanti Ferreira¹² & Rafael Batista Louzada¹

¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org] [guide's number provided by us] version 1



181 *Cryptanthus pirambuensis*
Perfect flower



182 *Cryptanthus pseudopetiolatus*



183 *Cryptanthus pseudopetiolatus*



184 *Cryptanthus pseudopetiolatus*



185 *Cryptanthus pseudopetiolatus*



186 *Cryptanthus pseudopetiolatus*



187 *Cryptanthus pseudopetiolatus*



188 *Cryptanthus pseudopetiolatus*



189 *Cryptanthus pseudopetiolatus*
Lateral glomerule



190 *Cryptanthus pseudopetiolatus*



191 *Cryptanthus reisii*
Photo: Lukas Daneu



192 *Cryptanthus reisii*



193 *Cryptanthus reisii*



194 *Cryptanthus reisii*



195 *Cryptanthus reisii*



196 *Cryptanthus reisii*



197 *Cryptanthus reisii*



198 *Cryptanthus reisii*



199 *Cryptanthus reisii*
Staminate flower



200 *Cryptanthus reisii*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

11

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org [guide's number provided by us] version 1201 *Cryptanthus reisii*
Perfect flower202 *Cryptanthus reptans*203 *Cryptanthus reptans*204 *Cryptanthus reptans*205 *Cryptanthus reptans*206 *Cryptanthus reptans*207 *Cryptanthus reptans*208 *Cryptanthus reptans*209 *Cryptanthus reptans*210 *Cryptanthus reptans*211 *Cryptanthus reptans*
Staminate flower212 *Cryptanthus rigidifolius*213 *Cryptanthus rigidifolius*214 *Cryptanthus rigidifolius*215 *Cryptanthus rigidifolius*216 *Cryptanthus rigidifolius*217 *Cryptanthus robsonianus*218 *Cryptanthus robsonianus*219 *Cryptanthus robsonianus*220 *Cryptanthus robsonianus*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

12

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author. fieldmuseum.org [guide's number provided by us] version 1

221 *Cryptanthus robsonianus*
Lateral glomerule222 *Cryptanthus robsonianus*
Staminate flower223 *Cryptanthus robsonianus*
Perfect flower224 *Cryptanthus ruthiae*
Photo: Geyner Alves225 *Cryptanthus ruthiae*226 *Cryptanthus ruthiae*227 *Cryptanthus ruthiae*228 *Cryptanthus ruthiae*229 *Cryptanthus ruthiae*230 *Cryptanthus ruthiae*231 *Cryptanthus ruthiae*
Apical glomerule232 *Cryptanthus ruthiae*
Lateral glomerule233 *Cryptanthus ruthiae*234 *Cryptanthus ruthiae*
Staminate flower235 *Cryptanthus ruthiae*236 *Cryptanthus ruthiae*
Perfect flower237 *Cryptanthus sergipensis*238 *Cryptanthus sergipensis*239 *Cryptanthus sergipensis*240 *Cryptanthus sergipensis*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

13

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org [guide's number provided by us] version 1241 *Cryptanthus sergipensis*242 *Cryptanthus sergipensis*243 *Cryptanthus sergipensis*244 *Cryptanthus sergipensis*
Apical glomerule245 *Cryptanthus sergipensis*
Lateral glomerule246 *Cryptanthus sergipensis*247 *Cryptanthus sergipensis*
Staminate flower248 *Cryptanthus sergipensis*249 *Cryptanthus sergipensis*
Perfect flower250 *Cryptanthus sergipensis*251 *Cryptanthus teretifolius*252 *Cryptanthus teretifolius*253 *Cryptanthus teretifolius*254 *Cryptanthus teretifolius*255 *Cryptanthus teretifolius*256 *Cryptanthus teretifolius*257 *Cryptanthus teretifolius*258 *Cryptanthus teretifolius*259 *Cryptanthus teretifolius*
Staminate flower260 *Cryptanthus venecianus*
Photo: Álvaro Nepomuceno

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

14

Débora Maria Cavalcanti Ferreira¹² & Rafael Batista Louzada¹

1 Universidade Federal de Pernambuco; 2 Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcanti@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
fieldmuseum.org | guide's number provided by us | version 1261 *Cryptanthus venecianus*262 *Cryptanthus venecianus*263 *Cryptanthus venecianus*264 *Cryptanthus venecianus*265 *Cryptanthus venecianus*266 *Cryptanthus vexatus*267 *Cryptanthus vinosibracteatus*268 *Cryptanthus vinosibracteatus*269 *Cryptanthus vinosibracteatus*270 *Cryptanthus vinosibracteatus*271 *Cryptanthus vinosibracteatus*272 *Cryptanthus vinosibracteatus*273 *Cryptanthus vinosibracteatus*274 *Cryptanthus vinosibracteatus*275 *Cryptanthus viridipetalus*276 *Cryptanthus viridipetalus*277 *Cryptanthus viridipetalus*278 *Cryptanthus viridipetalus*279 *Cryptanthus viridipetalus*280 *Cryptanthus viridipetalus*

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

15

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹¹ Universidade Federal de Pernambuco; ² Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.

© Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author. fieldmuseum.org] [guide's number provided by us] version 1

281 *Cryptanthus walkerianus* 282 *Cryptanthus walkerianus* 283 *Cryptanthus walkerianus* 284 *Cryptanthus walkerianus* 285 *Cryptanthus walkerianus*286 *Cryptanthus walkerianus* 287 *Cryptanthus walkerianus* Lateral glomerule 288 *Cryptanthus walkerianus* 289 *Cryptanthus walkerianus* Staminate flower 290 *Cryptanthus walkerianus*291 *Cryptanthus walkerianus* Perfect flower 292 *Cryptanthus warren-loosei* Photo: Rayssa Valentin 293 *Cryptanthus warren-loosei* 294 *Cryptanthus warren-loosei* 295 *Cryptanthus warren-loosei*296 *Cryptanthus warren-loosei* 297 *Cryptanthus warren-loosei* 298 *Cryptanthus warren-loosei* 299 *Cryptanthus warren-loosei* 300 *Cryptanthus warren-loosei* Staminate flower

The genus *Cryptanthus* Otto & A. Dietr. (Bromeliaceae)

Endemic genus to Brazil

16

Débora Maria Cavalcanti Ferreira^{1,2} & Rafael Batista Louzada¹
 1 Universidade Federal de Pernambuco; 2 Programa de Pós-graduação em Biologia Vegetal

[fieldguides. Photos by the authors, except where indicated. Produced by Débora Maria Cavalcanti Ferreira. Format by The Field Museum.
 © Débora Maria Cavalcanti Ferreira [deboracavalcantif@hotmail.com] Research support from CNPq. This study is part of the doctoral thesis of the first author.
 fieldmuseum.org | guide's number provided by us | version 1



301 *Cryptanthus warren-loosei*



302 *Cryptanthus warren-loosei*
Perfect flower



303 *Cryptanthus zonatus*



304 *Cryptanthus zonatus*



305 *Cryptanthus zonatus*



306 *Cryptanthus zonatus*



307 *Cryptanthus zonatus*



308 *Cryptanthus zonatus*



309 *Cryptanthus zonatus*



310 *Cryptanthus zonatus*



311 *Cryptanthus zonatus*



312 *Cryptanthus zonatus*



313 *Cryptanthus zonatus*



314 *Cryptanthus zonatus*



315 *Cryptanthus zonatus*
Lateral glomerule



316 *Cryptanthus zonatus*



317 *Cryptanthus zonatus*
Staminate flower



318 *Cryptanthus zonatus*



319 *Cryptanthus zonatus*
Perfect flower



320 *Cryptanthus zonatus*

5 CONCLUSÃO

- A filogenia apresentada é a mais robusta até o momento e inclui dados de sequências plastidiais de 69 genes codificantes de proteína.
- A filogenia mostra que o gênero *Cryptanthus* é monofilético e os clados foram formados pela proximidade geográfica das espécies.
- A classificação infragenérica de *Cryptanthus* proposta por Ramírez-Morillo (1996) não é suportada pelos dados filogenéticos deste estudo
- A presença de pecíolos e coloração das pétalas alvas com ápice verde surgiram múltiplas vezes na história evolutiva do gênero.
- Estudos de genética de populações são recomendados para a delimitação dos complexo *C. pickelii* e *C. zonatus*.
- Os dez genes do cloroplasto mais informativos para o gênero *Cryptanthus* foram *rpl22*, *psbN*, *rps16*, *rpoA*, *ycf3*, *ndhF*, *psbI*, *matK*, *ycf2* e *ccsA*.
- A riqueza de espécies de *Cryptanthus* estava subestimada e cinco espécies novas foram descritas para o gênero.
- Para a região Nordeste, 39 espécies são reconhecidas e quase todas estão ameaçadas de extinção.
- Uma nova sinonimização é proposta onde *Cryptanthus heimenii* P.J.Braun & Gonç. Brito é sinonimizado em *Cryptanthus bahianus* L.B.Sm.
- Planos de conservação são necessários visto que grande parte das espécies são ameaçadas de extinção e são conhecidas apenas para a localidade do espécime tipo.

REFERÊNCIAS

- APG (The Angiosperm Phylogeny Group) IV. An update of the Angiosperm Phylogeny Group classification for the order and families of flowering plants: APG IV. **Botanical Journal of the Linnean Society**, London, v. 181, n. 1, p. 1-20, mar, 2016.
- BAKER, J. G. **Handbook of the Bromeliaceae**. Londres: George Bell & Sons, York Street, Covent Garden, 1889.
- BRAUN, P.; BRITO, B. G. Xeromorfe Bromelien aus Brasilien (III): *Cryptanthus heimenii*, eine neue Art aus Sergipe. Xeromorphic Bromeliads from Brazil (III): *Cryptanthus heimenii*, a New Species from Sergipe. **Die Bromelie**, v. 2, p. 54-61, 2019.
- BEER, J.G. **Die Familie der Bromeliaceen. Nach ihrem habituellen charakter bearbeitet mit besonderer berücksichtigung der Ananassa**. Viena: Tendler & Comp., 1857.
- CRAYN, D. M.; WINTER, K.; SMITH, A. C. Multiple origins of crassulacean acid metabolism and the epiphytic habitat in the Neotropical family Bromeliaceae. **Plant Biology**, v. 101, n. 10, p. 3703-3708, mar, 2004.
- CRUZ, G. A. S. Filogenia molecular, evolução e biogeografia do gênero *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). 2013. 93 f. Tese (Doutorado em Ciências Biológicas), Universidade Federal de Pernambuco, Recife, 2013.
- CRUZ, G. A. S. et al. Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). **Molecular Phylogenetics and Evolution**, v. 107, p. 152–165, out, 2017.
- CRUZ, G. A. S. et al. Genome size evolution and chromosome numbers of species of the cryptanthoid complex (Bromelioideae, Bromeliaceae) in a phylogenetic framework. **Botanical Journal of the Linnean Society**, v. 192, n. 4, pp. 887–899, dez, 2020.
- CHRISTENHUSZ, M. J. M.; FAY, M.F.; CHASE, M. W. Bromeliaceae. In: Christenhusz, M. J. M.; Fay, M.F.; Chase, M. W. **Plants of the world: an illustrated encyclopedia of vascular plants**. Chicago: The University of Chicago Press. Bromeliaceae, 2017, p. 194-196.

- FERREIRA, D. M. C. Delimitação de espécies e filogeografia do complexo *Cryptanthus zonatus* (Vis.) Vis. (Bromeliaceae). 2016. 84 f. Dissertação (Mestrado em Biologia Vegetal), Universidade Federal de Pernambuco, Recife, 2016.
- FERREIRA, D. M. C.; LOUZADA, R. B. *Cryptanthus*. In: Prata, A. P. do; Farias, M. C. V.; Ladim, M. F. **Flora de Sergipe**. 1. Ed. Aracaju: Criação Editora, 2015, v. 2, p. 1-300.
- FERREIRA, D. M. C.; LOUZADA, R. B. A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus. **Systematic Botany**, v. 45, n. 3, p. 460–465, ago, 2020.
- FERREIRA, D. M. C. ; ALMEIDA, E. M de ; LOUZADA, R. B. Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from northeastern Brazil. **Phytotaxa**, Auckland, v. 523, n. 1, p. 099–109, out, 2021.
- FERREIRA, D. M. C. et al. Cross-amplification of nuclear microsatellite markers in two species of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). **Brazilian Journal of Botany**, São Paulo, v. 40, n. 2, p. 475-480, jun, 2017.
- FERREIRA, D. M. C. et al. Population genetic structure and species delimitation in the *Cryptanthus zonatus* complex (Bromeliaceae). **Botanical Journal of the Linnean Society**, London, v. 196, n. 1, p. 123–140, mai, 2021.
- FORZZA, R. C. Revisão Taxonômica de *Encholirium* Mart. ex Schult. & Schult. f. (Pitcairnoideae - Bromeliaceae). **Boletim de Botânica**, São Paulo, v. 23, n.1, p. 1-49, 2005.
- FORZZA, R. C. Bromeliaceae. In: Martinelli, G.; Moraes, M. A. **Livro Vermelho da Flora do Brasil**. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro: Andrea Jakobsson, 2013, p. 315-396.
- FORZZA, R. C., COSTA, A. F., MACIEL, J. R., KESSOUS, I. M., MONTEIRO, R. F., FARIA, A. P. G., TARDIVO, R. C., BÜNEKER, H. M., SARAIVA, D. P., MOREIRA, B. A., JACQUES, S. S. A., ALMEIDA, M. M., SANTOS-SILVA, F., LOUZADA, R. B., MOURA, R. L., COUTO, D. R., NEVES, B., OLIVEIRA, F. M. C., ARAÚJO, C. C., GONÇALVES-OLIVEIRA, R. C., VERSIEUX, L. M., ROMANINI, R. P., MACHADO, T. M., SILVA, R. S. A. D., PAIXÃO SOUZA, B., GOMES-DA-SILVA, J., URIBBE, F.

- P., GUARÇONI, E. A. E., SOUSA, L. O. F., PONTES, R. A. S., NOGUEIRA, M. G. C., SOUSA, G. M., KOCH, A. K., PICANÇO, W. L., CARDOSO, P. H., MARTINS, S. E., BARBOSA-SILVA, R. G., WANDERLEY, M. G. L. 2020. Bromeliaceae in Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro. Disponível em: <<http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB66>>. Acesso em: 14 Jun. 2021, 10:47:00.
- GIVNISH, T. J. Ancient vicariance or recent long-distance dispersal? Inferences about phylogeny and South American-African disjunctions in Rapateaceae and Bromeliaceae based on *ndhF* sequence data. **International Journal of Plant Science**, Chicago, v. 165, p. S35-S54, dez, 2004.
- GIVNISH, T. J. et al. Phylogeny, adaptative radiation, and historical biogeography of Bromeliaceae inferred from *ndhF* sequence data. **Aliso: A Journal of Systematic and Evolutionary Botany**, Claremont v. 23, n. 1, p. 3-26, 2007.
- GIVNISH, T. J. et al. Phylogeny, adaptative radiation, and historical biogeography in Bromeliaceae: Insights from an eight-locus plastid phylogeny. **American Journal of Botany**, St. Louis, v. 98, n. 5, p. 872–895, mai, 2011.
- GIVNISH, T. J. Monocot plastid phylogenomics, timeline, net rates of species diversification, the power of multi-gene analyses, and a functional model for the origin of monocots. **American Journal of Botany**, St. Louis, v. 105, n. 11, p. 1888–1910, nov, 2018.
- GOUDA, E.J., BUTCHER, D. & GOUDA, K. Encyclopaedia of Bromeliads, Version 4. Disponível em: <<http://bromeliad.nl/encyclopedia>> Acesso em: 08 Nov. 2021, 10:00:00
- JABAILY, R. S.; SYTSMA, K. J. Phylogenetics of *Puya* (Bromeliaceae): placement, major lineages, and evolution of chilean species. **American Journal of Botany**, St. Louis, v. 97, n. 2, p. 337–356, fev, 2010.
- JUDD, W. S. et al. Relações filogenéticas das angiospermas. In: Judd, W. S. et al.; tradução Simões, A. O. **Sistemática vegetal: um enfoque filogenético**. 3. Ed. Porto Alegre: Artmed, 2009, p. 225-542.
- KRAPP, F. et al. A set of variable plastid SSR markers for the genus *Cryptanthus* (Bromeliaceae). **Research in Plant Biology**, Abu Dhabi, v. 3, n. 2, p. 18-21, mar, 2013.

- LEME, E. M. C. A ornamental *Cryptanthus* from Pernambuco. **The Cryptanthus Society Journal**, Spring, v. 5, n. 1, p. 12-13, 1990.
- LEME, E.M.C. Two new *Cryptanthus* species from Brazil. **The Cryptanthus Society Journal**, Spring, v. 10, n. 4, p. 9-11, nov, 1995.
- LEME, E. M. C. Two new *Cryptanthus* species from Brazil. **Cryptanthus Society Journal**, Spring, v. 11, n. 1, p. 6-8, fev, 1996.
- LEME, E. M. C. New species of Brazilian Bromeliaceae: A tribute to Lyman B. Smith. **Harvard Papers in Botany**, Cambridge, v. 4, n. 1, p. 135-168, 1999.
- LEME, E. M. C. New *Cryptanthus* species from Espírito Santo, Brazil. **Cryptanthus Society Journal**, v. 16, n. 1, p. 12-13, jan-mar, 2001.
- LEME, E. M. C. Two New sympatric *Cryptanthus* species. **Cryptanthus Society Journal**, v. 17, n. 3, p. 86-89, Jul-Set, 2002a.
- LEME, E. M. C. *Cryptanthus teretifolius*, a new species from the coastal zone of Espírito Santo State. **Cryptanthus Society Journal**, Spring, v. 17, n. 1, p. 15-16, jan-mar, 2002b.
- LEME, E. M. C.; KOLLMANN, L. J. C.; FONTANA, A. P. Three New *Cryptanthus* Species from Espírito Santo and Bahia, Brazil. **Journal of the Bromeliad Society**, Orlando, v. 58, n. 1, p. 12-19, jan-fev, 2008.
- LEME, E. M. C. Describing *Cryptanthus* ‘Bello # 2’. **Cryptanthus Society Journal**, Spring, v. 25, n. 3, jul-set, 2010.
- LEME, E. M. C. et al. Miscellaneous new species in the Brazilian Bromeliaceae. Miscellaneous new species in the Brazilian Bromeliaceae. **Rodriguésia**, Rio de Janeiro, v. 61, n. 1, p. 021-067, jan/mar, 2010.
- LEME, E. M. C. A New Species of *Cryptanthus* from Espírito Santo, Brazil. **Journal of the Bromeliad Society**, Orlando, v. 64, n. 3, p. 150-155, 2014.

- LEME, E. M. C. et al. Miscellaneous New Species of Brazilian Bromeliaceae – III. **Phytotaxa**, Auckland, v. 177, n. 2, p. 061–100, ago, 2014.
- LEME, E. M. C. Two new bromelioid species from Brazil. **Journal of the Bromeliad Society**, Orlando, v. 65, n. 2, p. 87-99, 2015.
- LEME, E. M. C. et al. New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. **Phytotaxa**, Auckland, v. 318, n. 1, p. 001-088, ago, 2017.
- LEME, E. M. C.; KOLLMANN, L. J. C. Miscellaneous new species of Brazilian Bromeliaceae. **Phytotaxa**, Auckland, v. 108, n. 1, p. 1-40, jun, 2013.
- LEME, E. M. C.; SIQUEIRA-FILHO, J. A. Studies in Bromeliaceae of Northeastern Brazil. I. **Selbyana**, Sararota, v. 22, n. 2, p. 146-154, 2001.
- LEME, E. M. C.; SIQUEIRA-FILHO, J. A. Taxonomia das bromélias dos fragmentos de mata atlântica de Pernambuco e Alagoas. In: Siqueira-Filho, J. A; Leme, E. M. C. **Fragmentos de mata atlântica do Nordeste – biodiversidade, conservação e suas bromélias**. Rio de Janeiro: Andrea Jakobsson Estúdio. 2007, p. 190-381.
- LEME, E. M. C. et al. Miscellaneous new species in the “Cryptanthoid complex” (Bromeliaceae: Bromelioideae) from Eastern Brazil. **Phytotaxa**, Auckland, v. 430, n. 3, p. 157-202, jan, 2020.
- LOUZADA, R. B. et al. Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (Bromelioideae, Bromeliaceae) and its implications on morphological character evolution. **Molecular Phylogenetics and Evolution**, v. 77, p. 54-64, mar, 2014.
- LOUZADA, R. B.; VERSIEUX, L. M. *Lapanthus* (Bromeliaceae, Bromelioideae): A New Genus from the Southern Espinhaço Range, Brazil. **Systematic Botany**, Laramie, v. 35, n. 3, p. 497-503, jul, 2010.

- LOUZADA, R. B.; WANDERLEY, M. das G. L. Revision of *Orthophytum* (Bromeliaceae): the species with sessile inflorescences. **Phytotaxa**, Auckland, v. 13, p. 1-26, dez, 2010.
- LOUZADA, R. B.; WANDERLEY, M. das G. L. Re-establishment of *Sincoraea* (Bromeliaceae). **Journal of the Bromeliad Society**, Orlando, v. 66, n. 1, p. 6-19, jan-mar, 2016.
- LUTHER, H. E. New *Cryptanthus* species from Espirito Santo, Brazil. **Cryptanthus Society Journal**, Spring, v.13, n. 2-4, p.12-13, 1999a.
- LUTHER, H. E. *Cryptanthus arelii*, an "Old" New species from Bahia, Brazil. **Cryptanthus Society Journal**, Spring, v. 14, n. 2, p. 54-55, summer, 1999b.
- MACHADO, T.M. et al. Systematics of *Vriesea* (Bromeliaceae): phylogenetic relationships based on nuclear gene and partial plastome sequences. **Botanical Journal of the Linnean Society**, London, v. 192, n. 4, abr, 2020.
- MAGALHÃES, R. E. C. Biossistemática do complexo *Cryptanthus zonatus* (Vis.) Beer. Dissertação (Mestrado em Sistemática e Evolução). 2013. 84 f. Universidade Federal do Rio Grande do Norte, Natal, 2013.
- MARTINELLI, G. et al. Bromeliaceae da Mata Atlântica Brasileira: Lista de espécies, distribuição e conservação. **Rodriguésia**, Rio de Janeiro, v. 59, n. 1, p. 209-258, 2008.
- MEZ, C. 1934-1935. Bromeliaceae. In: Engler, A. **Das Pflanzenreich**.V. 4, Stuttgart: J. Cramer, 1935, p. 161–667.
- MEZ, C. Bromeliaceae. In: von Martius, C. P. F.; Eichler, A. W.; Urban, I. **Flora brasiliensis**. V. 3. Leipzig: F. Fleischer, 1892, p. 172-634.
- MEZ, C. Bromeliaceae. In:Candolle, C.D. **Monographiae Phanerogamarum prodromi nunc continuatio, nunc revisio**. Parisiis: Sumptibus Masson & C., Parisiis. 1896, p. 1-900.
- MILET-PINHEIRO, P. et al. A Semivolatile Floral Scent Marks the Shift to a Novel Pollination System in Bromeliads. **Current Biology**, v. 31, p. 1-9, fev, 2021.

MORREN, E. Broméliacées nouvelles. **La Belgique Horticole, Annales de Botanique et D'Horticulture**, p. 238-252, 1880.

MMA (Ministério do Meio Ambiente). Portaria MMA Nº 443, DE 17 DE DEZEMBRO DE 2014, 2014. Disponível em: http://www.icmbio.gov.br/cepsul/images/stories/legislacao/Portaria/2014/p_mma_443_2014_lista_esp%C3%A9cies_amea%C3%A7adas_extin%C3%A7%C3%A3o.pdf Acesso em: 13 Jun. 2018, 13:55:30.

OLIVEIRA-JÚNIOR, J. B. O. Fenologia da floração e ecologia reprodutiva da Bromeliaceae ameaçada *Cryptanthus burle-marxii* Leme e simpatria com *Cryptanthus alagoanus* Leme & J.A. 2005. 73 f. Dissertação (Mestrado em Biologia Vegetal), Universidade Federal de Pernambuco, Recife, 2015.

OTTO, F.; DIETRICH, A. Eine neue gattung aus der familie der Bromeliaceae. **Allgemeine Gartenzeitung**, n. 38, p. 297-299, set, 1836.

PALMA-SILVA, C. et al. Advances in and perspectives on evolution in Bromeliaceae. **Botanical Journal of the Linnean Society**, London, v. 181, n. 3, p. 305–322, jun, 2016.

PAULE, P., SCHMICKL, R., FÉR, T., MATUSZAK-RENGER, S., HALBRITTER, H. & ZIZKA, G. Phylogenomic insights into the *Fascicularia-Ochagavia* group (Bromelioideae, Bromeliaceae). **Botanical Journal of the Linnean Society**, London, v. 192, n. 4, p. 642–655, abr, 2020.

RAMÍREZ-MORILLO, I. M. Systematics, Phylogeny, and Chromosome number evolution of *Cryptanthus* (Bromeliaceae). 1996. 282 f. Tese, University of Missouri-St. Louis, St. Louis, 1996.

RAMÍREZ-MORILLO, I. M. Five new species of *Cryptanthus* (Bromeliaceae) and some nomenclatural novelties. **Harvard Papers in Botany**, Cambridge, v. 3, n. 2, p. 215-224, 1998.

RAMÍREZ-MORILLO, I. M., BROWN, G. K. The Origin of the Low Chromosome Number in *Cryptanthus* (Bromeliaceae). **Systematic Botany**, v.26, n. 4, p. 722–726, out, 2001.

- RAVEN, P. H.; EVERT, R. F.; EICHHORN, S. E. O processo de evolução. In: Raven, P. H.; Evert, R. F.; Eichhorn, S. E. **Biologia Vegetal**. 6. Ed. Rio de Janeiro: Editora Guanabara Koogan S.A., 2001, p. 228-248.
- SCHULTE, K.; BARFUSS, M. H. J.; ZIZKA, G. Phylogeny of Bromelioideae (Bromeliaceae) inferred from nuclear and plastid DNA loci reveals the evolution of the tank habit within the subfamily. **Molecular Phylogenetics and Evolution**, v. 51, p. 327–339, fev, 2009.
- SILVESTRO, D.; ZIZKA, G.; SCHULTE, K. Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). **Evolution**, St. Louis, v. 68, n. 1, p. 163–175, jan, 2013.
- SIQUEIRA-FILHO, J. A.; MACHADO, I. C. Flowering phenology and pollination ecology of *Cryptanthus diana* Leme: a case of floral fragrance-collecting by Euglossinae bees in Bromeliaceae. **Selbyana**, Sarasota, v. 29, n. 2, p. 226-232, 2008.
- SMITH, L. B. The Bromeliaceae of Brazil. **Smithsonian Miscellaneous Collections**, Washington, v. 126, n. 1, p. 1-290, set, 1955.
- SMITH, L. B.; DOWNS, R. J. 1974. **Pitcairnioideae (Bromeliaceae), Flora Neotropica**. Monograph no. 14. New York: Hafner Press, 1974.
- SMITH, L. B.; DOWNS, R. J. 1977. **Tillandsioideae (Bromeliaceae), Flora Neotropica**. Monograph no.14, parte 2. New York: Hafner Press, 1977.
- SMITH, L. B.; DOWNS, R. J. **Bromelioideae (Bromeliaceae), Flora Neotropica**. Monograph no. 14, p.1979.
- STEENS, A. **Bromeliads, the connoisseur's guide**. Glebe: Florilegium, 2007.
- TERRY, R. G.; GREGORY, K. B.; OLMSTEAD, R. G. Examination of subfamilial phylogeny in Bromeliaceae using comparative sequencing of the plastid locus *ndhF*. **American Journal of Botany**, St. Louis, v. 84, n. 5, p. 664–670, mai, 1997.

- VERSIEUX, L. M. et al. Molecular phylogenetics of the Brazilian giant bromeliads (*Alcantarea*, Bromeliaceae): implications for morphological evolution and biogeography. **Molecular Phylogenetics and Evolution**, v. 64, p. 177-189, abr, 2012.
- VERSIEUX, L. M.; MAGALHÃES, R.; CALVENTE, A. Extension of the *Cryptanthus* range in Northeastern Brazil with new findings in the phenotypic variation including changes in the trichome's distribution, thus enhancing the understanding of the *Cryptanthus zonatus* complex (Bromeliaceae). **Phytotaxa**, Auckland, v. 109, n. 1, p. 54-60, jun, 2013.
- VERSIEUX, L. M.; WANDERLEY, M.G.L. **Bromélias-gigantes do Brasil**. 1. ed. Natal: Capim Macio & Offset, 2015.
- WANDERLEY, M. G. L. et al. Bromeliaceae. In: Wanderley, M. G. L.; Martins, S. E. **Flora Fanerogâmica do Estado de São Paulo**. V. 5. São Paulo: FAPESP, 2007, p. 39-161.
- ZIZKA, G.; TRUMPLER, K.; ZÖLLNER, O. Revision of the genus *Ochagavia* (Bromeliaceae, Bromelioideae). **Willdenowia**, v. 32, n. 2, p. 331-350, 2002.
- ZIZKA, A. et al. Biogeography and conservation status of the pineapple family (Bromeliaceae). **Diversity and Distribution**, v. 26, n. 2, p. 183–195, nov, 2020.

**APÊNDICE A - A NEW SPECIES OF *CRYPTANTHUS* (BROMELIACEAE,
BROMELIOIDEAE) IN THE BRAZILIAN ATLANTIC FOREST
NORTH OF THE SÃO FRANCISCO RIVER, AND ITS
CONTRIBUTION TO THE TAXONOMY OF THE GENUS**

A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus

Débora Maria Cavalcanti Ferreira¹ and Rafael Batista Louzada^{2,3}

¹Programa de Pós-Graduação em Biologia Vegetal, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil; deboracavalcantif@hotmail.com

²Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil; rafael.louzada@ufpe.br

³Author for correspondence (rafael.louzada@ufpe.br)

Communicating Editor: Martin F Wojciechowski

Abstract—*Cryptanthus cinereus* D.M.C. Ferreira & Louzada, a new rare species of Bromeliaceae restricted to northeastern Brazil, is described and illustrated. *Cryptanthus cinereus* is a rupicolous plant that occurs in the Atlantic Forest on the top of a rocky outcrop and is known only from a single record. This new species is morphologically similar to *Cryptanthus felixii*, but differs mainly by its narrowly triangular leaves that are wider at base, primary bracts with adaxial surfaces densely lepidote (vs. glabrous or glabrous with base densely lepidote), shorter flowers (39–52 mm), sepal lobes lanceolate, with shorter connate sepals (1.6–5 mm) and petals (1–1.2 mm). An identification key to *Cryptanthus cinereus* and other species that occur in the Atlantic Forest north of the São Francisco River is provided. In addition, two species complexes are characterized for the area.

Keywords—Bromeliad, Poales, rocky outcrop.

Cryptanthus Otto & A. Dietr. nom. cons. is a bromeliad genus of the subfamily Bromelioideae (Givnish et al. 2011). Phylogenetic studies suggest that the genus is not monophyletic (Silvestro et al. 2013; Louzada et al. 2014; Cruz et al. 2017; Leme et al. 2017). Thus, a recent study (Leme et al. 2017) proposed a new circumscription for *Cryptanthus* and segregated twenty-five homogamous species that were part of the genus into three genera: *Forzzaea* Leme, S. Heller & Zizka (three species), *Hoplocryptanthus* (Mez) Leme, S. Heller & Zizka (eight species), and *Rokautskyia* Leme, S. Heller & Zizka (fourteen species).

Currently, *Cryptanthus* includes 55 andromonoecious species (Leme et al. 2017) that are distributed in northeastern and southeastern Brazil (Leme et al. 2017). Most species of the genus are narrowly distributed (Cruz et al. 2017) and occur mainly in the Atlantic Forest (Leme et al. 2017). Additionally, some occur in Cerrado savanna and Caatinga (seasonally dry forests) (Leme et al. 2017).

In the northern part of the Atlantic Forest (north of the São Francisco River), there are seven species of the genus (Leme and Siqueira-Filho 2007): *C. alagoanus* Leme & J.A. Siqueira, *C. cinereus* D.M.C. Ferreira & Louzada, *C. diana* Leme, *C. felixii* J.A. Siqueira & Leme, *C. pickelii* L.B. Sm., *C. reptans* Leme & J.A. Siqueira and *C. zonatus* (Vis.) Vis. *Cryptanthus burle-marxii* Leme, formerly described for the region mentioned above, is now treated as a synonym of *C. zonatus* based on molecular and morphological evidence (Ferreira 2016).

We aim to contribute to the taxonomy of *Cryptanthus* in the Atlantic Forest north of the São Francisco River (AFNSFR) because little is known about the genus in this region. There is no identification key that encompasses all the species of this area, and it is difficult to identify the species of the genus in this area due to the overlap of morphological characters. In this paper we provide an identification key to the species of *Cryptanthus* in AFNSFR, characterize two species complexes, and describe a new species (*Cryptanthus cinereus*) from the area. *Cryptanthus cinereus* is rupicolous and occurs on the top of a rock outcrop in the Atlantic Forest of Alagoas State, in northeastern Brazil. The new species is compared with *Cryptanthus felixii* due to

similarities in the rhizome and stem, and because both occur in Atlantic Forest and in the same municipality.

MATERIALS AND METHODS

Samples of the new species were collected, georeferenced and photographed, and herbarium specimens were prepared according to Peixoto and Maia (2013). The morphological terminology follows Radford et al. (1974) and Harris and Harris (2001). For the description of the type of stigma, Leme et al. (2017) was used. The reproductive morphological characters of the morphologically similar taxon (*Cryptanthus felixii*) in the diagnosis and key were taken from the protologue in Leme and Siqueira-Filho (2007).

The species included in the identification key are distributed in the northern part of the Atlantic Forest, north of the São Francisco River, which covers portions of the Brazilian states of Rio Grande do Norte, Paraíba, Pernambuco, and Alagoas. The morphological characters used in the key and in the discussion were obtained from specimens collected in the field and deposited in the herbaria EAC, UFRN, JPB, UFP, HST, PEUFR, IPA, ASE, and ALCB (acronyms follow Thiers 2019). A stereomicroscope was used to examine the specimens. The measurements were taken using a ruler or millimeter paper. The stem length was taken from the base of the plant where there are roots to the first flowers in the glomerule, excluding the rhizome and the rachis.

TAXONOMIC TREATMENT

Cryptanthus cinereus D.M.C. Ferreira & Louzada, sp. nov.

TYPE: BRAZIL. Alagoas: Ibateguara, Sítio Duas Barras, 08 May 2019 (flower; fruit), D. Cavalcanti, E. M. de Almeida, A. Melo, F. G. Silva, W. T. C. Santos & V. B. V. Souza 921 (holotype: UFP!, isotypes: MAC!, RB!, UFRN!, SP!, NY!).

Cryptanthus cinereus differs from *C. felixii* J.A. Siqueira & Leme by its leaf blades narrowly triangular, wider at the base (vs. sublinear-lanceolate, distinctly narrowed toward the base), primary bracts with adaxial surfaces densely lepidote (vs. glabrous or glabrous with base densely lepidote), shorter flowers, 39–52 mm long (vs. 55–64 mm long), sepals connate 1.6–5 mm (vs. 9–11 mm), white at base and apex, and pink in the center (vs. greenish-hyaline toward at base and margins), sepal lobes lanceolate, 14.2–20.5 mm long (vs. narrowly elliptic-ovate, 11–13 mm long), petals 21.5–26 mm long, connate 1–1.2 mm (vs. 31–47 mm long, connate 9–17 mm), filaments 17–18.2 mm long (vs. 22–35 mm), and stigma 0.2–2.2 mm long (vs. 6 mm long).

Plants rupicolous, andromonoecious, propagation by rhizome and axillary shoot, rhizomes 5–99 cm long, 1.7–2.8 cm in

diameter. **Stems** 18.2–45 cm long, erect or decumbent. **Leaves** 30–49 in number; leaf sheaths $2.8\text{--}3.5 \times 4.4\text{--}6$ cm, very widely ovate or depressed ovate, brownish yellow and glabrate at the base, green or reddish pink and densely lepidote at the apex, prickles $0.5\text{--}2$ mm long, $0.2\text{--}2$ mm apart, generally antrorse; leaf blades $0.8\text{--}37.5 \times 2.4\text{--}4.5$ cm, narrowly triangular, pink or brown when exposed to the sun, green or pink and green in shaded areas, abaxial surface densely lepidote, adaxial surface glabrate on leaves at the base of the rosette and densely lepidote on younger leaves, cinereous, margins undulate, prickles $0.5\text{--}2$ mm long, $2\text{--}14$ mm apart, antrorse, apices acuminate or caudate. **Inflorescences** spikes of glomerules, with staminate and hermaphroditic flowers; spike with 7 lateral glomerules, each glomerule with 7 flowers, apical portion of the inflorescence with ca. 19 flowers; rachis 3 cm long; primary bracts $8\text{--}9$ in number, $1.9\text{--}24.2 \times 1.3\text{--}4.9$ cm, foliaceous, similar to the leaves, narrowly triangular or deltate, completely green, completely pink, or green with the base vinaceous, abaxial and adaxial surfaces densely lepidote, cinereous, margins undulate, prickles $0.5\text{--}3$ mm long, $1\text{--}9$ mm apart, antrorse, apices acuminate or caudate. **Staminate flowers:** floral bracts $21\text{--}27 \times 5\text{--}6$ mm, lanceolate-cymbiform, greenish white and glabrate at the base, pink and densely lepidote at the apex; flowers $39\text{--}48$ mm long; sepals $19\text{--}22.2$ mm long, connate $4.2\text{--}5$ mm, white at the base and apex, pink in the middle, lobes $14.2\text{--}16.2 \times 4\text{--}5$ mm, lanceolate, mucronate; petals $21.5\text{--}25.5 \times 4\text{--}5$ mm, oblanceolate, rounded, connate for 1 mm, white, with 2 conspicuous callosities bearing inconspicuous capitate trichomes, callosities appearing 3 mm distant from the base; stamens 6, in two whorls of three, filaments $17\text{--}17.4$ mm long, white, first whorl of three antepetalous (lower), second whorl of three antesealous (higher), adnate $1\text{--}3$ mm to the petal blades, anthers $3\text{--}5$ mm long, subbasifixed, dehiscence longitudinal; styles $0.5\text{--}1$ mm, atrophied, stigma $0.2\text{--}0.6$ mm, atrophied; ovary trigonous, $11.3\text{--}16 \times 5.2\text{--}8.5$ mm, epigynous tube $5\text{--}8$ mm long, ovules $10\text{--}14$ per locule, placentation axial. **Hermaphroditic flowers:** floral bracts $31.2\text{--}34 \times 9\text{--}13$ mm, lanceolate-cymbiform, white and glabrate at the base, pink and densely lepidote at the apex; flowers $51\text{--}52$ mm long, diurnal; sepals $21.5\text{--}22.2$ mm long, connate $1.6\text{--}2.4$ mm, white at the base and apex, pink in the center, lobes $20\text{--}20.5 \times 5$ mm, lanceolate, mucronate; petals $25.5\text{--}26 \times 3.5\text{--}4.2$ mm, oblanceolate, rounded, connate $1\text{--}1.2$ mm, white, with 2 conspicuous callosities bearing inconspicuous capitate trichomes, callosities appearing 3 mm distant from the base; stamens 6, in two whorls of three, filaments $18\text{--}18.2$ mm long, white, first whorl of three antepetalous (lower), second whorl of three antesealous (higher), adnate $1\text{--}1.2$ mm to the petal blades, anthers $2.2\text{--}5$ mm, subbasifixed, dehiscence longitudinal; styles $22.3\text{--}25.5$ mm, stigma $2\text{--}2.2$ mm, conduplicate-patent; ovary $16\text{--}19 \times 8\text{--}8.2$ mm, trigonous, epigynous tube $5\text{--}8$ mm, ovules $18\text{--}25$ per locule, placentation axial. **Fruits** $21\text{--}25 \times 9\text{--}9.2$ mm, berry, trigonous, white with reddish green apex. **Seeds** $3.8\text{--}4 \times 2\text{--}3$ mm, asymmetrical, asymmetrical-reniform or asymmetrical-conical. Figures 1, 2, 3.

Distribution and Habitat—The species is rupicolous and occurs in areas exposed to the sun and in shaded areas at around 570 m elevation, on a rocky outcrop in the Atlantic Forest (Fig. 1). The rocky outcrop is small and surrounded by pasture. The vegetation on the rocky outcrop is composed of small islands of soil containing herbs and shrubs. The area is humid and exposed to intense solar radiation. There are many individuals of ferns and the family Melastomataceae in the area.



FIG. 1. Distribution map of *Cryptanthus cinereus* (black circle) north of the São Francisco River, Brazil. Detail of the single collection point of *Cryptanthus cinereus* in the municipality of Iateguara, Alagoas State (colored in grey).

Phenology—Flowers in May and fruits in May, June, and July.

Etymology—The specific epithet refers to the color with a cinereous appearance due the densely lepidote indument on the adaxial surfaces of the leaf blades and primary bracts.

Conservation—The species is probably threatened since it is known only from one locality, which is on private property. However, additional fieldwork is needed to look for new localities because there are other suitable rocky outcrops around the type locality, and there is another possible record of the species (a possible paratype) from the municipality of São Luís do Quitunde (Fazenda Garabu), which is about 80 km from the type locality. The specimen (R. P. Lyra-Lemos et al. 8241 [MAC]) has leaf blades wider at the base and densely lepidote trichomes on both surfaces. However, it is sterile, young (very small), and could not be accurately identified.

DISCUSSION

Cryptanthus cinereus is easily differentiated from all other species in the Atlantic Forest north of the São Francisco River (AFNSFR) by the leaf blades that are wider at the base (vs. distinctly narrow toward the base). Other characteristics that help distinguish this species are the densely lepidote trichomes on the adaxial surfaces of the leaf blades and primary bracts. All other species distributed in the AFNSFR have adaxial surfaces of both the leaf blades and primary bracts that are glabrous, glabrate, glabrous with densely lepidote trichomes at the base, glabrous with densely lepidote trichomes at both the base and apices, or with crossbars of trichomes. The only exception is *Cryptanthus diana*, where some individuals can have densely lepidote trichomes on both surfaces (adaxial and adaxial) of the leaf blades and primary bracts. However, *C. diana* can be separated from *C. cinereus* by the narrowly elliptic, lanceolate, or oblanceolate (vs. narrowly triangular) leaf blades.

In this study two species complexes were recognized. The first complex includes two names: *C. alagoanus* and *C. pickelii* (*C. pickelii* complex). In the protologue of *C. alagoanus* (Leme and Siqueira-Filho 2001), these species are differentiated by propagation type, position of the leaves, and presence or absence of a central succulent zone (Table 1). Propagation type has been used to separate *C. burle-marxii* from *C. zonatus* (Leme

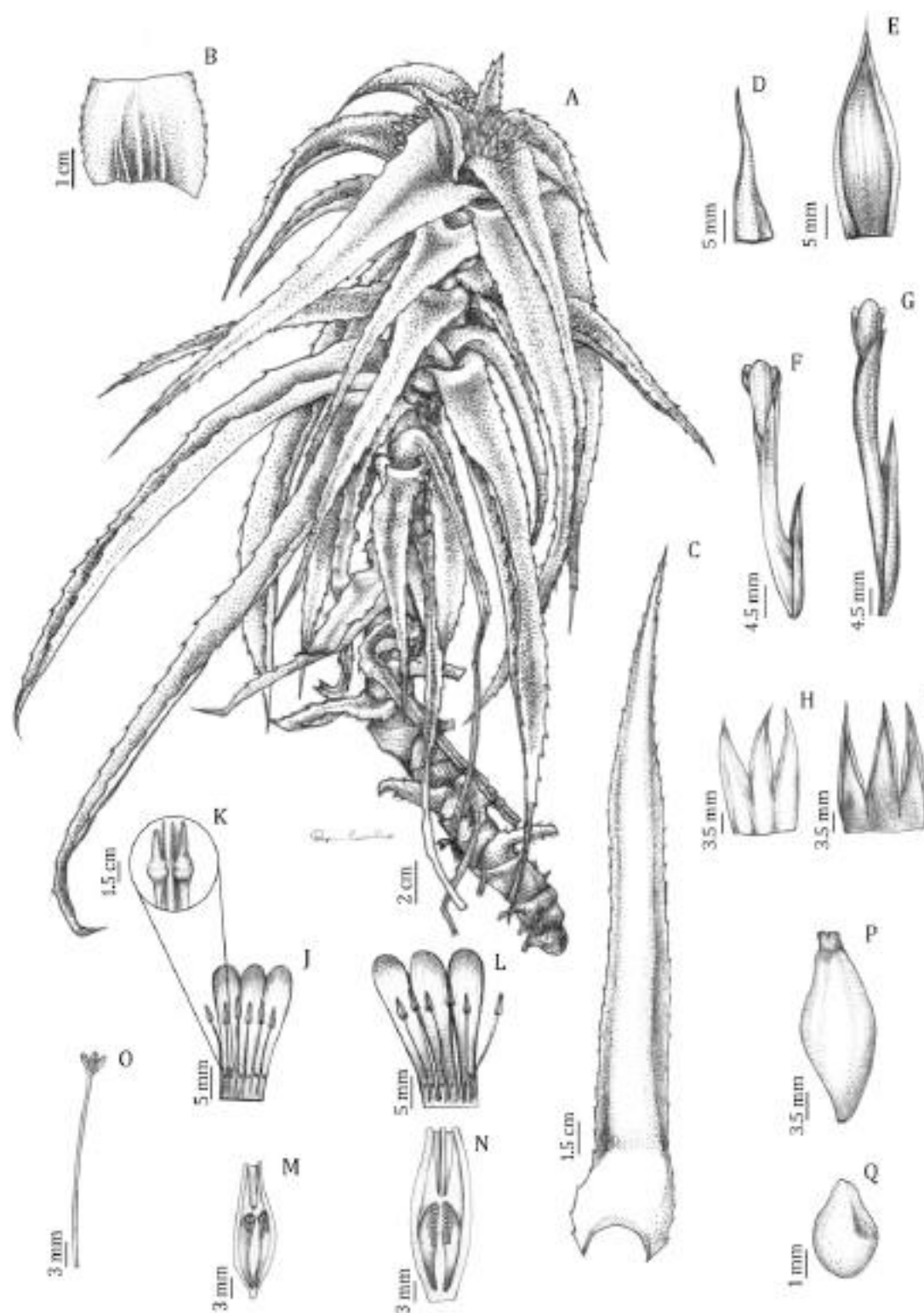


FIG. 2. *Cryptanthus cinereus*. A. Habit. B. Leaf sheath (adaxial surface). C. Leaf (adaxial surface). D. Floral bract of staminate flower (abaxial surface). E. Floral bract of hermaphroditic flower (adaxial surface). F. Staminate flower. G. Hermaphroditic flower. H. Sepals of staminate flower (abaxial surface). I. Sepals of hermaphroditic flower (adaxial surface). J. Petals and stamens of staminate flower. K. Detail of two conspicuous callosities. L. Petals and stamens of hermaphroditic flower. M. Ovary and epigynous tube of staminate flower. N. Ovary and epigynous tube of hermaphroditic flower. O. Style and stigma. P. Fruit. Q. Seed.

1990b); however, Ferreira (2016) indicate that *C. burle-marxii* is a synonym of *C. zonatus*. The study shows that populations of *C. burle-marxii* and *C. zonatus* are clustered together in STRUCTURE analysis, and that there are overlapping diagnostic features (Ferreira 2016). Therefore, propagation type is

not a consistent character because it may vary within the same species. Other characteristics in the protologue (Leme and Siqueira-Filho 2001) used to differentiate *C. alagoanus* from *C. pickelii* are length and width of the leaf blade and sepal lobes. However, Leme and Siqueira-Filho (2007) show that these

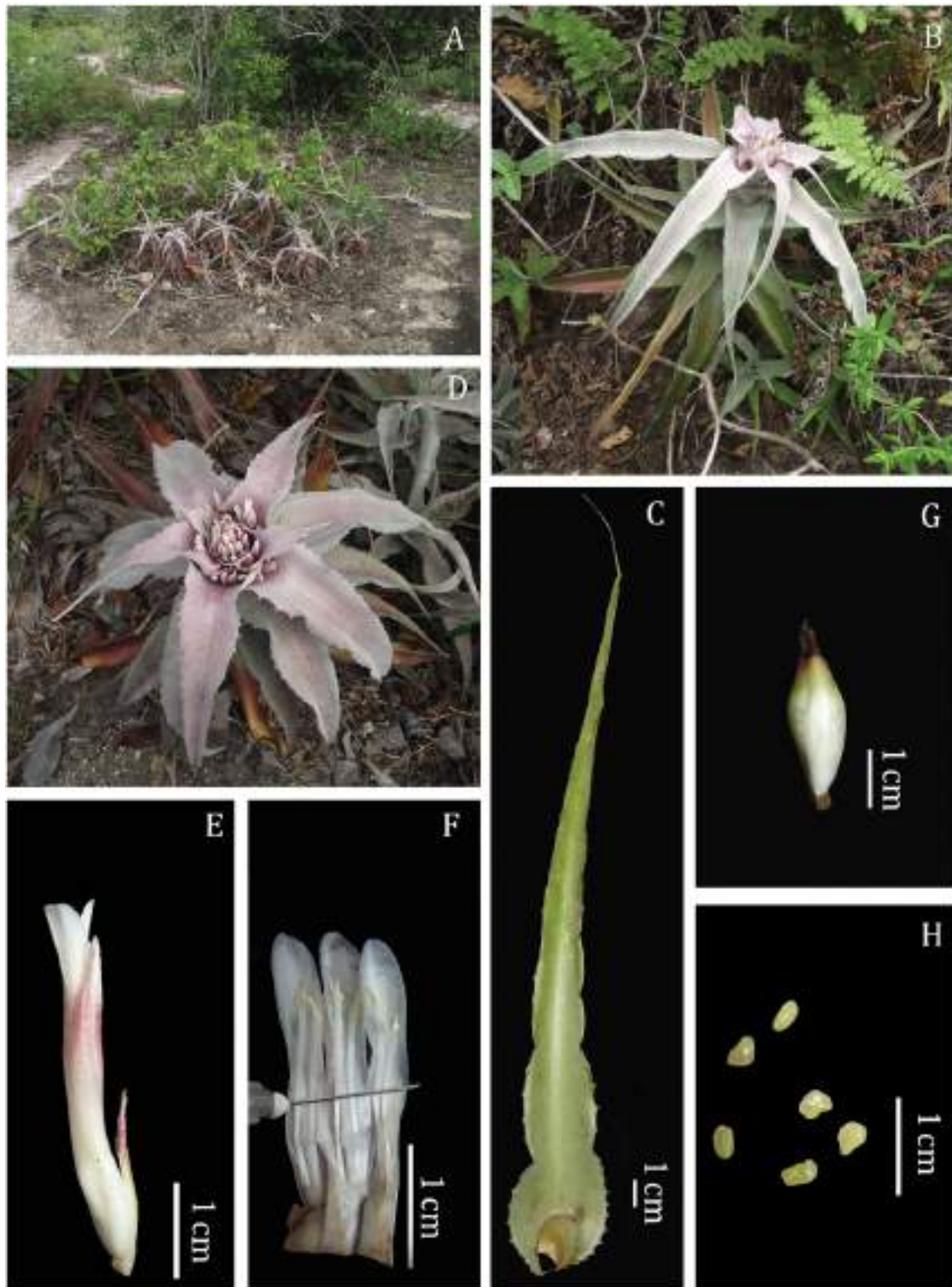


FIG. 3. *Cryptanthus cinereus*. A. Population in nature. B. Habit. C. Leaf. D. Top view of the rosette showing the inflorescence. E. Staminate flower. F. Detail of staminate flower showing petals, stamens and epigynous tube. G. Fruit. H. Seeds.

characters overlap between the species (Table 1). Leme and Siqueira-Filho (2007) also differentiate these species by length of the anthers and length of the epigynous tube. However, when analyzing the population (Estação Ecológica de Caetés, Pernambuco State) that is indicated in material examined as *C. pickelii* by Leme and Siqueira-Filho

(2007), we observed that the anther length (1.8–5.3 mm long) overlaps with *C. alagoanus* values and the epigynous tube (4–9 mm long) has higher values than indicated for *C. alagoanus* (Table 1).

The *Cryptanthus zonatus* complex, which includes *C. burle-marxii*, *C. diana*, *C. reptans*, and *C. zonatus*, is the second species

TABLE 1. *Cryptanthus pickelii* L. B. Sm. complex, differences between *Cryptanthus. alagoanus* Leme & J. A. Siqueira and *Cryptanthus pickelii* L. B. Sm.

Data source	Morphological characters	<i>C. alagoanus</i> Leme & J. A. Siqueira	<i>C. pickelii</i> L. B. Sm.
Protologue of <i>Cryptanthus alagoanus</i> (Leme and Siqueira-Filho 2001)	Propagation	Slender stolons	Basal shoots
	Leaves	Subspreading-arcuate at anthesis	Suberect
	Leaves	Without any central succulent zone	With a central succulent zone
	Leaf blade	3.2–4.2 cm wide	2.5 cm wide
Leme and Siqueira-Filho 2007	Sepal lobes	9 × 5 mm	7 × 3.5 mm
	Propagation	Slender stolons that sprout from the base of the plant	Suberect, elongate, rather stout shoots that arise near the base of inflorescence
	Leaves	Subspreading-arcuate at anthesis	Suberect at anthesis
	Leaf blade	3.2–5 cm wide	2–4 cm wide
	Sepal lobes	9–10 × 5 mm	7.5–10 × 3.5–4
	Antthers	3–4 mm	2 mm
	Epigynous tube	2.5–3 mm	1 mm

complex recognized in this study. In the protologue of *Cryptanthus burle-marxii* (Leme 1990b), *C. burle-marxii* and *C. zonatus* are differentiated by size (stature), type of vegetative propagation, distance between the crossbars of trichomes on the leaves, length of sepals, and connation of petals. However, *C. burle-marxii* is synonymized under *C. zonatus* by Ferreira (2016). The study shows that two genetic clusters (in a STRUCTURE analysis using ten nuclear microsatellite marker loci) were formed by geography (northern and southern) instead of by morphologic and taxonomic delimitations (Ferreira 2016). Thus, the study (Ferreira 2016) considers both the same species.

For another species in this complex, in its protologue (Leme 1990a) *Cryptanthus diana* is compared with *C. acaulis* (Lindley) Beer, but the morphologically similar species *C. zonatus* is not mentioned. In the last taxonomic revision of the genus, Ramírez-Morillo (1996) differentiates *C. diana* from *C. zonatus* by the indumenta on the adaxial surface of the foliar blades: in *C. diana*, the plants are uniformly covered by trichomes and do not have transverse silver lines or crossbars formed by peltate trichomes; in *C. zonatus*, specimens have a surface with transverse silver lines or crossbars (Table 2). Ramírez-Morillo (1996) does not mention that both species may have glabrous individuals as indicated by Leme and Siqueira-Filho (2007) for *C. diana* and by Versieux et al. (2013) and Ferreira (2016) for *C. zonatus*. Thus, it is easy to separate species when individuals have trichomes, but when individuals are glabrous there is overlap between the species.

In the study of Leme and Siqueira-Filho (2007) there are overlaps in almost all the characters used to differentiate these species (Table 2), except the callosities of petals, which are inconspicuous in *C. diana* and well-developed in *C. zonatus*. However, when analyzing the morphology of one population (Serra do Urubu- Pernambuco State) that is indicated as *C. diana* by Leme and Siqueira-Filho (2007), we also found well-developed callosities.

Another species that is part of this complex is *Cryptanthus reptans*, which is only known from one record. This species seems distinct from the others and is indicated by Leme and Siqueira-Filho (2007) as very different from the other species of AFNSFR. An important characteristic of the species is the longer stems (up to 19.5 cm long); however, we observed one population of *C. diana* (Serra do Urubu, Pernambuco State population) with some individuals that have stems about 21.5 cm long, which overlaps with *C. reptans*. In the protologue of *C. diana* (Leme 1990a), this species is indicated as stemless. When analyzing the population of *C. reptans* we also found short caulescent individuals with stems 3.4 cm long and, thus, overlapping with *C. diana* and *C. zonatus*. In general, *C. reptans* has several leaves but there are individuals with the same number of leaves as *C. diana* and *C. zonatus*. Besides this, in general, the flowers of *C. reptans* are smaller, but there are flowers of the same size as those of *C. diana* and *C. zonatus*. Genetic studies are being carried out to solve both complexes.

ARTIFICIAL KEY TO *CRYPTANTHUS* IN THE ATLANTIC FOREST NORTH OF THE SÃO FRANCISCO RIVER

1. Leaf blades narrowly triangular, wider at the base. Sepals short-connate 1.6–5 mm. Petals short-connate 1–1.2 mm, with 2 conspicuous callosities appearing 3 mm distant from the base *Cryptanthus cinereus* D.M.C. Ferreira & Louzada
1. Leaf blades lanceolate, oblanceolate, narrowly elliptic, linear triangular, ovate, very widely ovate or sublinear-lanceolate, distinctly narrow toward the base. Sepals long-connate 6–12 mm. Petals long-connate 4–22 mm, with 2 conspicuous or inconspicuous callosities appearing 4.5–22 mm distant from the base 2
2. Stems > 25 cm long. Ovary 15–20 mm long *C. felixii* J.A. Siqueira & Leme
2. Stems < 21.5 cm long. Ovary 6–12 mm long 3
3. Leaf blades predominantly oblanceolate *C. pickelii* L. B. Sm. complex (including *C. alagoanus* Leme & J.A. Siqueira)
3. Leaf blades predominantly narrowly elliptic *C. zonatus* (Vis.) Vis. complex (including *C. burle-marxii* Leme, *C. diana* Leme, and *C. reptans* Leme & J.A. Siqueira)

ACKNOWLEDGMENTS

This study is part of DMCF's Ph.D. dissertation conducted at the Programa de Pós-Graduação em Biologia Vegetal at the Universidade Federal de Pernambuco and supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico). RBL thanks CNPq for the

financial support (grants no. 310871/2014-0 and 449686/2014-0). The authors especially thank Dr. Leonardo Pessoa Felix who donated to RBL the sample of the living specimen collected by J. M. P. Cordeiro, L. P. Felix, E. M. Almeida and J. P. Araújo. The authors also thank Joel M. P. Cordeiro for the information about the occurrence locality, Erton M. Almeida for the help with fieldwork, and Andy Siekkinen for reviewing the English.

TABLE 2. *Cryptanthus zonatus* (Vis.) Vis. complex, differences between *Cryptanthus diana* Leme and *Cryptanthus zonatus* (Vis.) Vis. (* = in the taxonomic comments; ** = in the description).

Studies	Morphological characters	<i>C. diana</i> Leme	<i>C. zonatus</i> (Vis.) Vis.
Ramírez-Morillo 1996	Adaxial surface of foliar blades	Plant without transverse, wavy, silver lines on adaxial surface of foliar blades, usually green or uniformly covered by trichomes; plants from Pernambuco and other states	Plants with transverse silver lines across adaxial surface of the foliar blades, lines wavy, formed by peltate trichomes; plants from Pernambuco
Leme and Siqueira-Filho 2007	Adaxial leaf surface	No crossbars	With grayish-white crossbars
	Leaf blades generally*	4 cm wide	5 cm wide
	Leaf blades**	3–4 cm wide	3–5 cm wide
	Floral bracts	Equaling 1/2 to 3/5 sepal length	Slightly exceeding the ovary
	Connation of petals	10–14 mm	9–11 mm
	Callosities of petals	Inconspicuous	Well-developed
	Petal apex	Broadly acute to subrounded	Acuminate to acute

AUTHOR CONTRIBUTIONS

DMCF and RBL designed the study. DMCF wrote the manuscript, and produced the taxonomic treatment of the new species and the artificial key under the supervision of RBL. Both authors revised the manuscript.

LITERATURE CITED

- Cruz, G. A. S., G. Zizka, D. Silvestro, E. M. C. Leme, K. Schulte, and A. M. Benko-Iseppon. 2017. Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). *Molecular Phylogenetics and Evolution* 107: 152–165.
- Ferreira, D. M. C. 2016. *Delimitação de Espécies e Filogeografia do Complexo Cryptanthus zonatus (Vis.) Vis. (Bromeliaceae)*. M.S. thesis. Recife: Universidade Federal de Pernambuco.
- Givnish, J. T., M. H. J. Barfuss, B. van Ee, R. Riina, K. Schulte, R. Horres, P. A. Gonsiska, R. S. Jabaily, D. M. Crayn, J. A. C. Smith, K. Winter, G. K. Brown, T. M. Evans, B. K. Holst, H. Luther, W. Till, G. Zizka, P. E. Berry, and K. J. Sytsma. 2011. Phylogeny, adaptive radiation, and historical biogeography in bromeliaceae: Insights from an eight-locus plastid phylogeny. *American Journal of Botany* 98: 872–895.
- Harris, J. G. and M. W. Harris. 2001. *Plant Identification Terminology: An Illustrated Glossary*, ed. 2. Spring Lake, Utah: Spring Lake Publishing.
- Leme, E. M. C. 1990a. A new *Cryptanthus* species from the state of Goiás, Brazil. *Cryptanthus Society Journal* 5: 10–12.
- Leme, E. M. C. 1990b. A new ornamental *Cryptanthus* from Pernambuco. *Cryptanthus Society Journal* 5: 12–13.
- Leme, E. M. C. and J. A. Siqueira-Filho. 2001. Studies in Bromeliaceae of Northeastern Brazil. I. *Selbyana* 22: 146–154.
- Leme, E. M. C. and J. A. Siqueira-Filho. 2007. Bromeliad taxonomy in Atlantic Forest fragments of Pernambuco and Alagoas. Pp. 190–381 in *Fragments of the Atlantic Forest of Northeast Brazil. Biodiversity, Conservation and the Bromeliads*, eds. J. A. Siqueira-Filho and E. M. C. Leme. Rio de Janeiro: Andrea Jakobsson Estúdio.
- Leme, E. M. C., S. Heller, G. Zizka, and H. Halbritter. 2017. New circumscription of *Cryptanthus* and new *Cryptanthoid* genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318: 001–088.
- Louzada, R. B., K. Schulte, M. G. L. Wanderley, D. Silvestro, G. Zizka, M. H. J. Barfuss, and C. Palma-Silva. 2014. Molecular phylogeny of the Brazilian endemic genus *Orthophytum* (Bromelioideae, Bromeliaceae) and its implications on morphological character evolution. *Molecular Phylogenetics and Evolution* 77: 54–64.
- Peixoto, A. L. and L. C. Maia. 2013. *Manual de Procedimentos para Herbários*. Recife: Editora Universitária UFPE.
- Radford, A. E., W. C. Dickson, J. R. Massey, and C. R. Bell. 1974. *Vascular Plant Systematics*. New York: Harper and Row.
- Ramírez-Morillo, I. M. 1996. *Systematics, Phylogeny, and Chromosome Number Evolution of Cryptanthus (Bromeliaceae)*. Ph.D. dissertation. St. Louis: University of Missouri St. Louis.
- Silvestro, D., G. Zizka, and K. Schulte. 2013. Disentangling the effects of key innovations on the diversification of Bromelioideae (Bromeliaceae). *Evolution* 68: 163–175.
- Thiers, B. 2019. [continuously updated]. Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/science/ih/> (last accessed June 2019).
- Versieux, L. M., R. Magalhães, and A. Calvente. 2013. Extension of the *Cryptanthus* range in Northeastern Brazil with new findings in the phenotypic variation including changes in the trichome's distribution, thus enhancing the understanding of the *Cryptanthus zonatus* complex (Bromeliaceae). *Phytotaxa* 109: 54–60.

APÊNDICE B - Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from northeastern Brazil



Two new species of *Cryptanthus* (Bromelioideae, Bromeliaceae) from northeastern Brazil

DÉBORA MARIA CAVALCANTI FERREIRA^{1,3}, ERTON MENDONÇA DE ALMEIDA^{1,4} & RAFAEL BATISTA LOUZADA^{2,5}

¹ Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil

² Departamento de Botânica, Universidade Federal de Pernambuco, 50670-901, Recife, Pernambuco, Brazil

³ ✉ deboracavalcantif@hotmail.com; <https://orcid.org/0000-0003-2728-8561>

⁴ ✉ notre0@hotmail.com; <https://orcid.org/0000-0001-8033-5334>

⁵ ✉ rafael.louzada@ufpe.br; <https://orcid.org/0000-0002-0040-7690>

Abstract

Two new species of *Cryptanthus* from Bahia State, in northeastern Brazil, are described and illustrated. *Cryptanthus apiculatantherus* occurs in Atlantic Forest and *Cryptanthus brevibracteatus* was discovered in a transition area between Atlantic Forest and Caatinga. *Cryptanthus apiculatantherus* and *C. bibrarensis* have similar stem lengths and leaf blade shapes, but differ mainly by the stem diameter, width of the leaf sheaths, sepal and petal color, anther apex shape, and length and width of the ovary. *Cryptanthus brevibracteatus* and *C. warren-loosei* have a similar leaf blade color and are geographically close to each other, but differ by the number of flowers in the apical cluster of flowers of the inflorescence, length and width of the floral bracts, length of the sepals, connation of the sepals and length of the sepal lobes. Data about the geographic distribution, habitat, phenology, conservation status, taxonomic comments, a distribution map and photographs of the new species are provided. In addition, there are tables included that compare the new species to morphologically similar species.

Keywords: Bahia, Bromeliad, endemic, Poales

Introduction

Cryptanthus Otto & A. Dietr. (1836: 297) nom. cons. is a genus of Bromeliaceae in Bromelioideae (Givnish *et al.* 2011). Based on a recent circumscription, the genus is monophyletic (Leme *et al.* 2017) and comprises 60 species (Gouda *et al.* cont. updated) that occur in northeastern and southeastern Brazil (Leme *et al.* 2020, Ferreira & Louzada 2020). The species can be found in wet and dry forests in Atlantic Forest and Caatinga, respectively, from sea level to about 800 meters elevation (Leme & Siqueira-Filho 2007, Leme *et al.* 2020).

In general, *Cryptanthus* species are narrowly distributed (Cruz *et al.* 2017, Ferreira & Louzada 2020) and several species are known from a single location, such as *C. cinereus* Ferreira & Louzada (2020: 460), *C. crassifolius* Leme *et al.* (2008: 17), *C. rigidifolius* Leme & Kollmann (2013: 19) and *C. viridipetalus* Leme & Kollmann (2013: 24). However, only six species of the genus are listed as threatened in the *Livro Vermelho da Flora do Brasil* (Red List of the Brazilian Flora - Forzza *et al.* 2013).

Bahia is the Brazilian state with the highest number of *Cryptanthus* species (24 species; Flora do Brasil 2020). In this state, these species mainly occur in the Atlantic Forest; only *C. arelii* Luther (1999: 54), *C. bahianus* Smith (1944: 106), *C. crassifolius*, *C. diamantinensis* Leme (1999: 137), *C. viridovinosus* Leme *et al.* (2010: 33) and *C. warren-loosei* Leme (1993: 97) occur in the Caatinga (Flora do Brasil 2020).

In the present work, two new species of *Cryptanthus* from Bahia State, *Cryptanthus apiculatantherus* and *Cryptanthus brevibracteatus*, are described and illustrated. *Cryptanthus apiculatantherus* is compared to *C. bibrarensis* Leme (2002: 86) due to similarities in stem length and leaf blade shape, and *C. brevibracteatus* is compared to *C. warren-loosei* due to similarities in leaf blade color and because they are geographically close to each other. Data about the geographic distribution, habitat, phenology and conservation status, as well as taxonomic comments, a distribution

map and images are provided for the new species. We also include tables that compare the morphology of the new species to similar species.

Material & methods

Fieldwork was carried out in 2019 and 2020 at the sites with records in Bahia State to collect samples of the new species. The collections were georeferenced and photographed. The specimens were deposited in the UFP herbarium and duplicates were sent to CEPEC and RB. In addition, specimens of morphologically similar species from the following herbaria were analyzed: ALCB, ASE, CEPEC, MBML, VIES, IPA, JPB, MAC, UFP, UESC and PEUFR (acronyms follow *Index Herbariorum*: <http://sweetgum.nybg.org/ih/>).

Morphological terminology follows Radford *et al.* (1974) and Harris & Harris (2001); stem length and the type of stigma follow Ferreira & Louzada (2020) and Leme *et al.* (2017), respectively. The morphological characters of the specimens were analyzed using a ruler and a stereomicroscope and millimeter paper.

Information about some morphologically similar taxa, *C. bibarrensensis*, *C. diamantinensis* and *C. venecianus*, was taken from the protologues in Leme (2002), Leme (1999) and Leme *et al.* (2010), respectively.

The conservation status was evaluated according to the IUCN (2019). The extent of occurrence (EOO) and area of occupancy (AOO) were not analyzed due to the low number of locations of occurrence.

Taxonomic treatment

Cryptanthus apiculatantherus D.M.C. Ferreira, E.M. Almeida & Louzada, *sp. nov.* (Figures 1–3).

Type:—BRAZIL. Bahia: Itacaré, Serra dos Vinháticos, 124 m elev., 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, E. M. Almeida 2757 (holotype: UFP!)

Diagnosis:—*Cryptanthus apiculatantherus* differs from *C. bibarrensensis* by its stem that is 3.5–8 mm in diameter (vs. 15–30 mm), leaf sheaths 2–2.9 cm wide (vs. *ca.* 3.5 cm) with a glabrous adaxial surface, except for the base that is sparsely lepidote (vs. glabrous), flowers 15–29.5 mm long (vs. *ca.* 45 mm long), sepals basally white with brown lobes (vs. wholly greenish white), petals 11.4–22 × 2–4.5 mm (vs. 31 × 6 mm) and white, except for the greenish apices (vs. wholly white), filaments 10.5–19.5 mm long (vs. 22–23 mm), the antesealous ones basally adnate to the petals for 2.8–7.5 mm (vs. *ca.* 10 mm), anther apices apiculate (vs. obtuse), and ovary 3.2–8 × 2.8–6 mm (vs. *ca.* 14 × 6 mm).

Description:—**Plants** terrecolous, andromonoecious, propagating by axillary shoots, rhizomes of 2.2–5 cm long and 0.3–0.65 cm in diameter. Stems 8–20.7 cm long, *ca.* 0.35–0.8 cm in diameter, erect or decumbent. **Leaves** 10–19 in number; *sheath* 1.9–2.7 × 2–2.9 cm, very widely ovate, green, abaxial surface densely lepidote, adaxial surface glabrous except for the sparsely lepidote base; prickles 0.1–1 mm long, 0.1–1.5 mm apart, generally antrorse; *blade* 2.3–24.8 × 1.1–2.1 cm, linear triangular or narrowly triangular, green or greenish-brown, abaxial surface densely lepidote, adaxial surface glabrous except for the sparsely lepidote base, apices acuminate, margins undulate; prickles 0.1–1 mm long, 1–4.3 mm apart, antrorse. **Inflorescence** compound, spike-like with sessile clusters of flowers; 6–10 lateral clusters of flowers; each cluster with *ca.* 2 flowers, apical cluster with *ca.* 22 flowers; *rachis* (main axis) 1–2.7 cm long; primary bracts 0.7–26.8 × 0.2–1.7 cm, foliaceous, linear triangular or narrowly triangular (at the apex of the inflorescence), green, abaxial surface densely lepidote, adaxial surface glabrous except for the sparsely lepidote base, apex acuminate, margins undulate; prickles 0.1–1 mm long, 1–4 mm apart, antrorse. **Staminate flowers:** **floral bracts** 8.5–19.2 × 3.2–6 mm, ovate to lanceolate, cymbiform, brown, glabrous except for the sparsely lepidote apex, apex mucronate or emarginate; **flowers** 15–24 mm long (including the extended petals); **sepals** 8.4–11.5 mm long, connate for 3.5–6.5 mm, base white; **lobes** brown, 3–6 × 2.2–3.5 mm, very widely ovate to orbicular, mucronate; **petals** 11.4–19.5 × 2.1–3.7 mm, oblanceolate, rounded or emarginate, connate for 3.5–6.5 mm, white with greenish apex, with 2 callosities start on 3.5–6 mm from the base, covered with inconspicuous glandulose trichomes; **stamens:** *filament* 10.5–16 mm long, the antepetalous ones basally adnate to the petals for 2.8–5 mm, the antesealous ones basally adnate to the petals for 5–6.3 mm; *anther* 2.3–3.5 mm long, subbasifixed, base cordate, apex apiculate; **pistil:** *ovary* botuliform, 3.2–4.2 × 2.8–4 mm, placentation axial, ovules 0–3 per locule, epigynous tube 0.5–1 mm long, *style* reduced, 0.2–1.2 mm long, , *stigma* reduced, 0.5–3.5 mm long. **Perfect flowers:** **floral bracts** 15–18.7 × 3.8–8 mm, elliptic-falcate or ovate, cymbiform, abaxial surface glabrous or glabrous except the sparsely lepidote apex, adaxial

surface glabrous except the sparsely lepidote apex, apex mucronate or emarginate; **flowers** 28–29.5 mm long (including the extended petals); **sepals** 11.5–14 mm long, connate for 5.5–9 mm, base white; *lobes* brown, 4.2–5.3 × 2.5–4.2 mm, very widely ovate to orbicular, mucronate, obtuse or emarginate; **petals** 20.5–22 × 2–4.5 mm, oblanceolate, emarginate or rounded, connate for 6.2–7.3 mm, white except for the greenish apices, with 2 callosities start on 7 mm from the base, covered with inconspicuous glandulose trichomes; **stamens**: *filament* 17–19.5 mm long, the antepetalous ones basally adnate to the petals for ca. 5 mm, the antesepalous ones basally adnate to the petals for 6.5–7.5 mm; *anther* 3–5 mm long, subbasifixed, base cordate, apex apiculate; **pistil**: *ovary* trigonous, 5–8 × 4–6 mm, placentation axial, ovules 7–9 per locule, epigynous tube 1–2 mm long, *style* 16–21 mm long, *stigma* 2.2–3.5 mm long, conduplicate-patent. **Fruits** ca. 13 × 8.2 mm, trigonous, white. **Seeds** 3.8–4.5 × 2.5 mm, reniform, conical or pyriform.

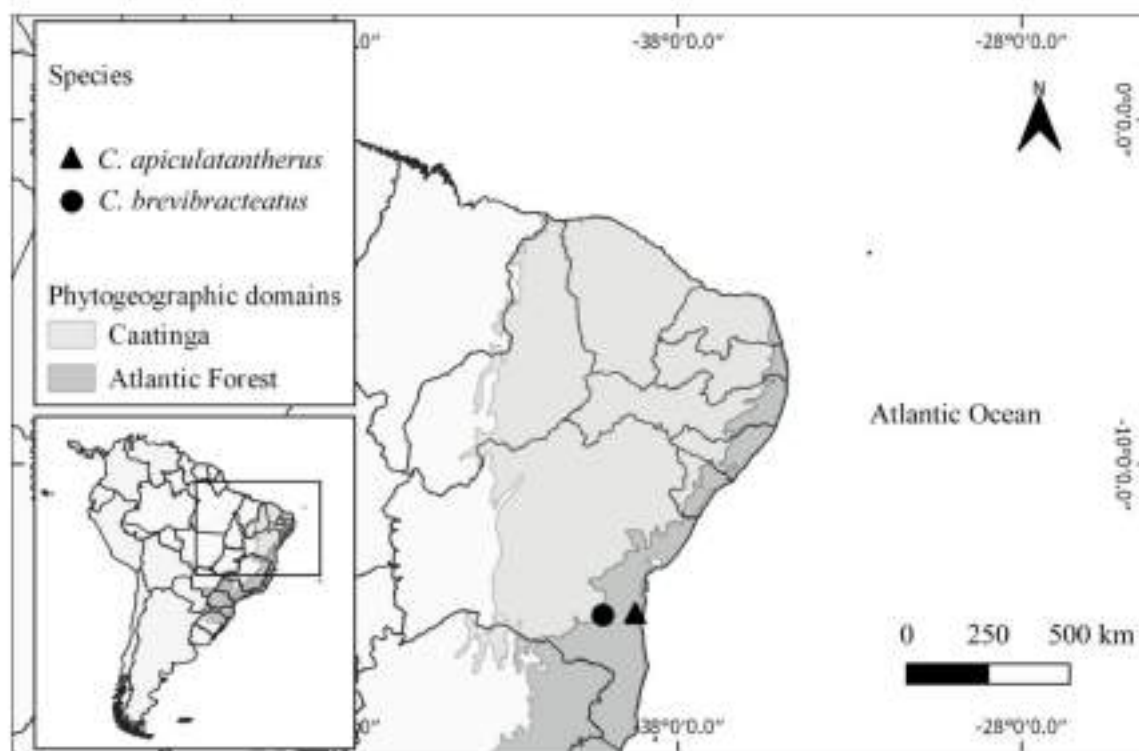


FIGURE 1. Distribution map of *Cryptanthus apiculatantherus* and *Cryptanthus brevibracteatus* in Bahia State, northeastern Brazil.

Etymology:—The specific epithet refers to the apiculate apices of the anthers.

Distribution and habitat:—*Cryptanthus apiculatantherus* is a terricolous plant and only known from a single locality from Atlantic Forest in the municipality of Itacaré, Bahia State, Brazil, at 124 m elevation (Fig. 1). It occurs in closed hygrophilous forest with trees of about 5 m tall and some areas with partial exposure to sun (Fig. 3A and 3B). The area is humid and is located on the edge of a rocky outcrop called Serra dos Vinháticos.

Phenology:—The specimens in cultivation were blooming in January and March and fruits were found in January in specimens in nature.

Conservation status:—The species is known only from one locality in a private property. It can be classified as Critically Endangered (CR) based on the criterion B2 ab(ii), since the species is only known from one location and possible decline of the area of occupancy.

Additional specimens examined (Paratypes):—BRAZIL. Bahia: Itacaré, Serra dos Vinháticos, 124 m, 14°18'45.1"S, 39°14'45.7"W, 24 January 2019, fl. cult. 27 August 2019, *E. M. Almeida* 3246 (UFP!); *ibidem*, 24 January 2019, fl. cult. 28 January 2021, *E. M. Almeida* 3318 (UFP!).

Notes on taxonomic affinities:—*Cryptanthus apiculatantherus* is morphologically similar to *C. bahianus*, *C. bibarrensis* and *C. warren-loosei*, due to the leaf blade shape, but it differs in petal color, and apiculate anther apex (see Table 1). Besides this, *C. bahianus* and *C. warren-loosei* occur in Brazilian dry forest called Caatinga, while *C. apiculatantherus* occurs in wet Atlantic Forest. *Cryptanthus apiculatantherus* is also morphologically similar with *C. venecianus* and *C. viridipetalus*, mainly due to the long caulescent habit and petal color. However, *C. apiculatantherus* differs from *C. venecianus* by flower length and apiculate anther apex (see Table 1), and can be also distinguished from *C. viridipetalus* by the apiculate anther apex.

TABLE 1. Comparison of characters of *Cryptanthus apiculatantherus* and morphologically similar species.

Species/ Characters	<i>C. apiculatantherus</i>	<i>C. bahianus</i>	<i>C. bibarrensis</i>	<i>C. venecianus</i>	<i>C. viridipetalus</i>	<i>C. warren-loosei</i>
Length of flowers (mm)	15–29.5	23.5–43	ca. 45	35	28.2–31	30–37
Petal apex color	Greenish	White	White	Green	Green	White
Sepal color	White at the base and brown at the lobes	White at the base, white-pink in the middle and brown at the lobes, or white at the base and green at the lobes	Greenish white	Hyaline near the base	White at the base and brown at lobes	White at the base and brown at lobes
Anther apices	Apiculate	Emarginate	Obtuse	Obtuse	Mucronulate	Acute
Length of ovary (mm)	3.2–8	5.7–10	14	6	7–9	6.5–9.5

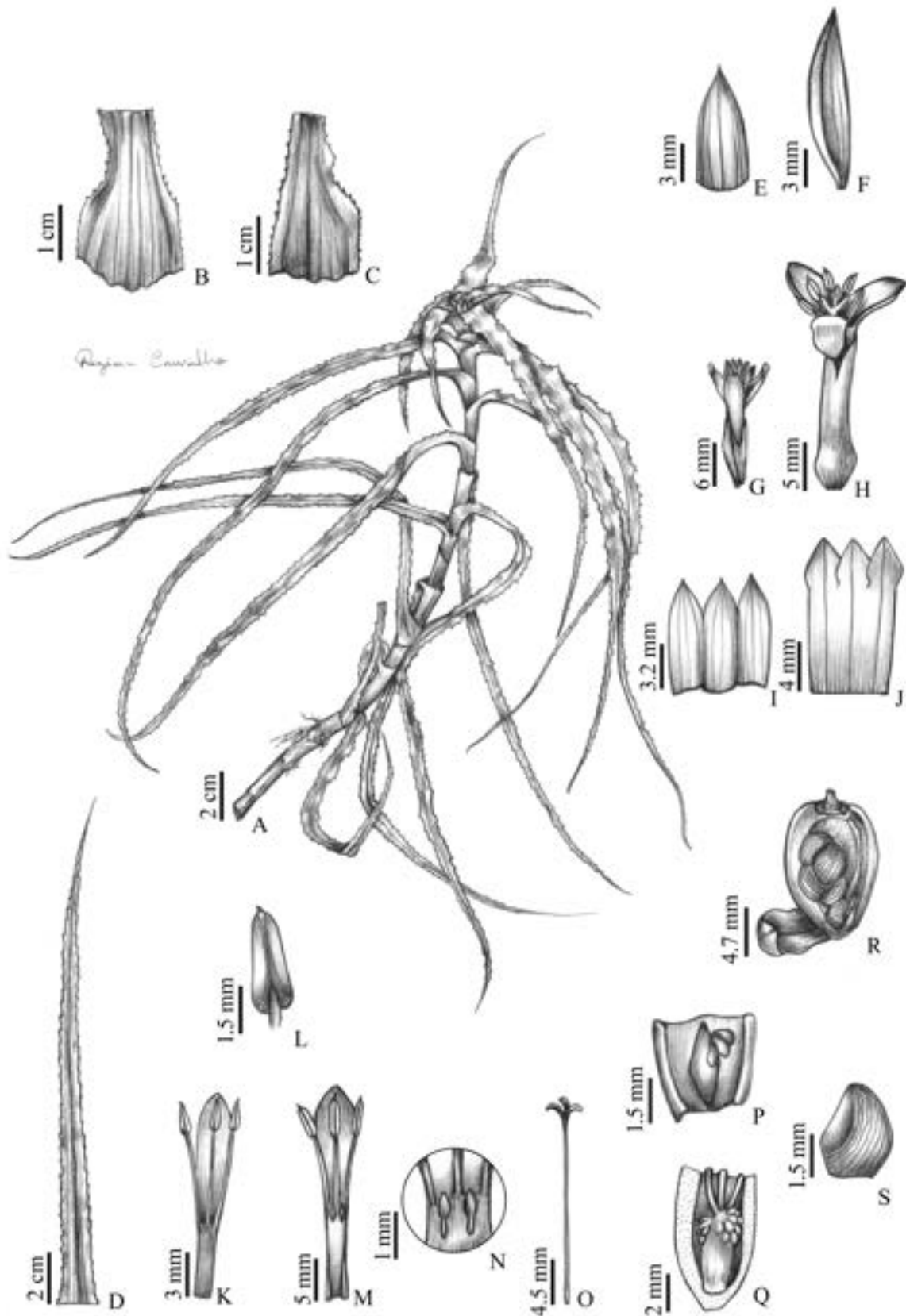


FIGURE 2. *Cryptanthus apiculatantherus*. A. Habit. B. Leaf sheath (abaxial surface). C. Leaf sheath (adaxial surface). D. Leaf blade (adaxial surface). E. Floral bract of staminate flower (abaxial surface). F. Floral bract of perfect flower (adaxial surface). G. Staminate flower. H. Perfect flower. I. Sepals of staminate flower (adaxial surface). J. Sepals of perfect flower (adaxial surface). K. Petal and stamens of staminate flower. L. Detail of anther. M. Petal and stamens of perfect flower. N. Detail of two conspicuous callosities. O. Style and stigma. P. Ovary of staminate flower. Q. Ovary and epigynous tube of perfect flower. R. Fruit. S. Seed. (A, B, C, D, F, R and S: *E. M. Almeida* 2757; E, G, I, K, L and P: *E. M. Almeida* 3246; H, J, M, N, O and Q: *E. M. Almeida* 3318). Drawing by Regina Carvalho.



FIGURE 3. *Cryptanthus apiculatantherus*. A. Population in nature, individuals partially exposed to sun. B. Population in nature, individuals not exposed to sun. C. Leaf sheath (abaxial surface). D. Leaf sheath (adaxial surface). E. Leaf (abaxial surface). F. Leaf (adaxial surface). G. Top view of the rosette showing the inflorescence and flowers. H. Bract of the staminate flower. I. Staminate flower. J. Anther. K. Side view of anther showing the apex. L. Bract of perfect flower. M. Perfect flower. N. Fruit with persistent sepals. O. Seeds. (C, D, E, F, H, I, L and M: E. M. Almeida 3318; J and K: E. M. Almeida 3246; N and O: E. M. Almeida 2757).

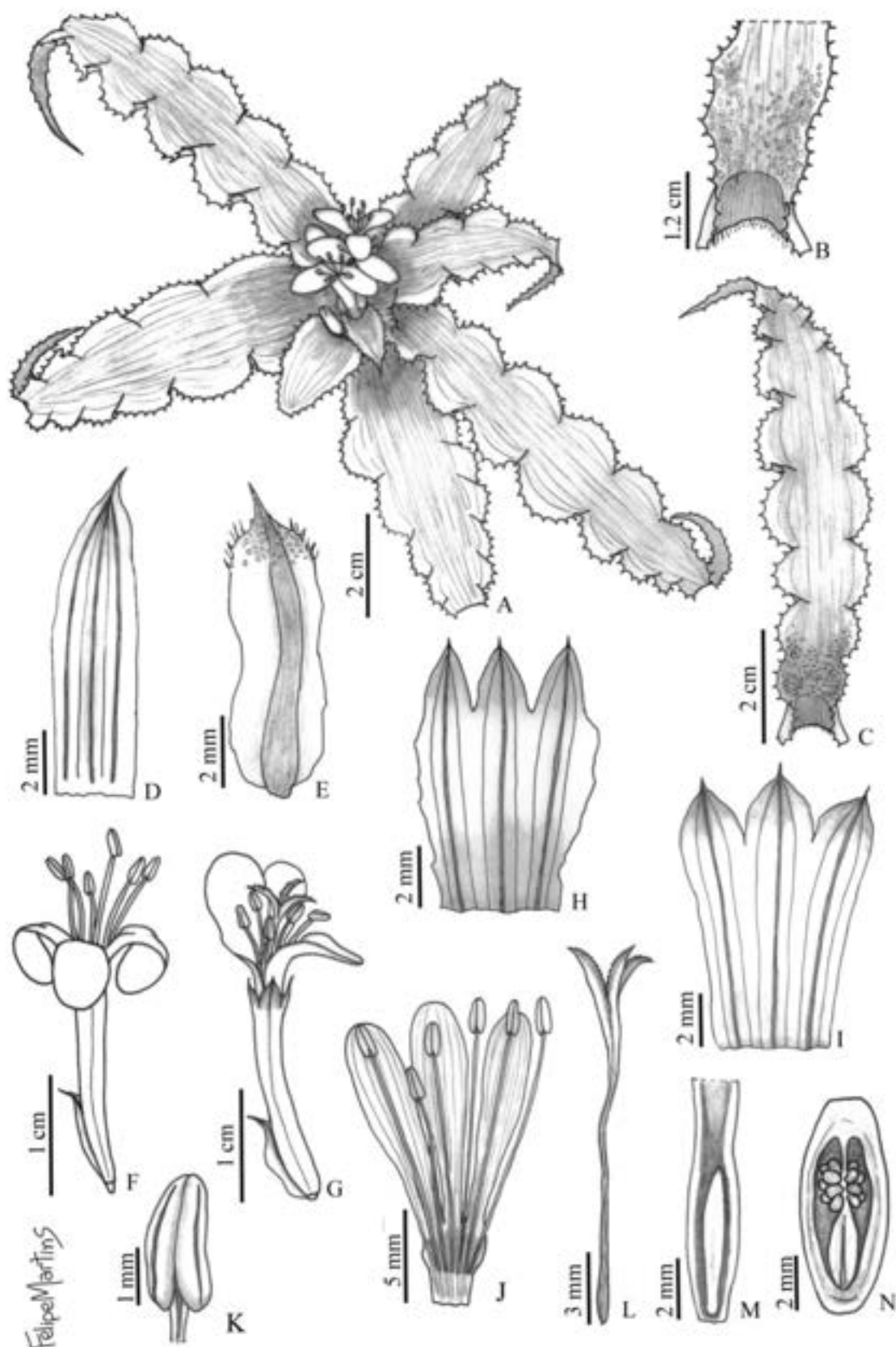


FIGURE 4. *Cryptanthus brevibracteatus*. A. Habit. B. Leaf sheath (adaxial surface). C. Leaf (adaxial surface). D. Floral bract of staminate flower (abaxial surface). E. Floral bract of perfect flower (abaxial surface). F. Staminate flower. G. Perfect flower. H. Sepals of staminate flower (abaxial surface). I. Sepals of perfect flower (abaxial surface). J. Petals and stamens of staminate flower. K. Anther. L. Style and stigma. M. Ovary and epigynous tube of staminate flower. N. Ovary of the perfect flower. (A–N: *L. Daneu* 744). Drawing by Felipe Martins.



FIGURE 5. *Cryptanthus brevibracteatus*. A. Habitat. B. Population in nature. C. Individual in nature. D. Top view of the rosette with flowers. E. Leaf sheath (abaxial surface). F. Leaf sheath (adaxial surface). G. Leaf (abaxial surface). H. Leaf (adaxial surface). I. Bract of staminate flower. J. Staminate flower. K. Bract of perfect flower. L. Perfect flower. (D–L: L. Daneu 744).

Cryptanthus brevibracteatus D.M.C. Ferreira & Louzada, sp. nov. (Figures 1, 4 and 5)

Type:—BRAZIL. Bahia: Boa Nova, Fazenda Cotermaia, 781 m elev., 14°22'26.6"S, 40°11'14"W, 18 October 2020, fl. in cult. 29 October 2020, L. Daneu 744 (holotype: UFP!, isotype: CEPEC!, RB!).

Diagnosis:—*Cryptanthus brevibracteatus* differs from *C. warren-loosei* in a fewer number of flowers in the apical cluster of the inflorescence (7 flowers vs. ca. 18 flowers), floral bracts 9.2–10 × 3.2 mm (vs. 17.3–18.5 × 3.6–4.7 mm), sepals 9.5–11.5 mm long (vs. 15.3–18.2 mm long), connate for 6.6–8 mm (vs. 8.5–10 mm) and sepal lobes 3.8–4.9 mm long (vs. 5.6–8 mm long), anther apices rounded (vs. acute).

Description:—**Plants** terri-colous, andromonoecious, propagating by axillary shoots, rhizomes of 1.5 cm long, and 0.25–0.45 cm in diameter. Stems 1.9–2 cm long, 0.4–0.6 cm in diameter, erect or decumbent. **Leaves** 5–7 in number; sheath 0.8–1.5 × 0.7–1.5 cm, very widely ovate, abaxial surface greenish-white, densely lepidote, adaxial surface greenish-white and glabrous at the base, brown and sparsely lepidote to at the apex; prickles 0.3–1 mm long, 0.5–1 mm apart, antrorse; blade 0.6–19.5 × 0.6–2.2 cm, narrowly elliptic, lanceolate or oblanceolate, brown, greenish-brown or reddish-brown, abaxial surface densely lepidote, adaxial surface glabrous except for the densely lepidote base, margins undulate, apex acuminate; prickles 0.5–0.7 mm long, 0.3–3 mm apart, antrorse. **Inflorescence** compound, spike-like with sessile clusters of flowers; 2–4 lateral clusters of flowers; each cluster with ca. 2 flowers, apical cluster with ca. 7 flowers; rachis (main axis) 2.5–4.5 cm long; primary bracts 0.3–22.1 × 0.2–2.2 cm, foliaceous, lanceolate, brown, greenish brown or reddish brown, abaxial surface densely lepidote, adaxial surface glabrous except for the densely lepidote base, margins undulate; prickles 0.2–0.8 mm long, 0.3–3.6 mm apart, antrorse, apices acuminate. **Staminate flowers:** floral bracts ca. 10 × 3.2 mm, narrowly triangular or narrowly elliptic-falcate, white at the base and brown at the apex, abaxial surface glabrous at the base and densely lepidote at the apex, adaxial surface glabrous, apex caudate-mucronate; flowers ca. 28 mm long (including the extended petals); sepals 9.5–11.5 mm long, connate for ca. 8 mm, base white; lobes brown, 2–4.9 × 1.7–2.2 mm, ovate, mucronate; petals 18.5–19.5 × 3.3–3.5 mm, oblanceolate, rounded, connate for ca. 5 mm, white, with 2 callosities start on 6–7 mm from the base, covered with inconspicuous glandulose trichomes; stamens: filament 17.3–18 mm long, the antepetalous ones basally adnate to the petals for ca. 7 mm, the antesepalous ones basally adnate to the petals for ca. 5 mm, anther 1.5–2.2 mm long, subbasifixed, base cordate, apex rounded; pistil: ovary trigonous, 6–8 × 2.5–4.2 mm, ovules absent, epigynous tube 2.2–4 mm long, style reduced, ca. 0.2 mm long; stigma reduced, ca. 0.2 mm long. **Perfect flowers:** floral bracts ca. 9.2 × 3.2 mm, irregular, oblong-falcate, glabrous at the base and sparsely lepidote at the apex on both surfaces, with fimbriate trichomes on the apex, apex mucronate; flowers ca. 31 mm long (including the extended petals), diurnal; sepals 10.8–11.5 mm long, connate for 6.6–7 mm, white at the base and brown at the apex; lobes 4.2 × 3–3.2 mm, ovate, glabrous at the base and sparsely lepidote to at the apex on both surfaces, mucronate; petals 14.2–27 × 4 mm, oblanceolate, rounded or obtuse, connate for ca. 7 mm, white, with 2 callosities start on ca. 7.5 mm from the base, bearing inconspicuous glandulose trichomes; stamens: filament ca. 12.5 mm long, white, the antepetalous ones basally adnate to the petals for ca. 4.5 mm, the antesepalous ones basally adnate to the petals for 6–7.5 mm; anther ca. 2.2 mm long, base cordate, apex rounded; pistil: ovary trigonous, ca. 8.2 × 3.2 mm, placentation axial, ovules 5–7 per locule, epigynous tube 2–2.2 mm long, style 9–20 mm long; stigma 2.2–3 mm long, conduplicate-patent.

Etymology:—The specific epithet '*brevibracteatus*' refers to the shorter floral bracts compared to the other species of the genus.

Distribution and habitat: *Cryptanthus brevibracteatus* is a terri-colous plant and is known only from two records from a transition area between Atlantic Forest and Caatinga, in the municipality of Boa Nova, Bahia State, Brazil, at 781 to 900 m elevation (Fig 1). It occurs in forest areas popularly known as "Mata de Cipó" with trees about 3 m tall (Fig. 5A). The site of occurrence of *C. brevibracteatus* is situated in a private property. The new species has a restricted and sparse occurrence in the area, of small groups. *Cryptanthus boanovens* Leme (2015: 93) is sympatric with this species.

Phenology:—Flowers in nature in October.

Conservation status:—The species is only known from two sites in a private property. *Cryptanthus brevibracteatus* is classified as Critically Endangered (CR) based on the criterion B2 ab(ii), due to the low number of locations where the species is found and possible decline in the area of occupancy.

Additional specimens examined (Paratypes):—BRAZIL. Bahia: Boa Nova, Fazenda Cotermaia (owner Alipe Maia), entrance 1.2 km E of Boa Nova on Road to Dario Meira, 790 m elev., 14°22.389'S, 40°11.309'W, 15 October 2001, W. W. thomas, A. M. Carvalho, M. R. Barbosa, s. sant'Ana & J. L. Paixão 12642 (CEPEC!); Boa Nova, 3.3 km east of Boa Nova on Road to Dario Meira, 850–900 m elev., 14°22.983'S, 40°11.177'W, 15 October 2000, W. W. t homas, J. Jardim & s. sant'Ana 12272 (CEPEC!, NY image!).

Notes on taxonomic affinities:—*Cryptanthus brevibracteatus* is morphologically similar to *C. crassifolius* due to the leaf blade shape, but can be differentiated by the glabrous adaxial surface of the leaf blades, except for the densely lepidote base (vs. leaves with densely lepidote adaxial surface), and 9.5–11.5 mm long sepals (vs. 13–16 mm, see Table 2). Compared to *C. diamantinensis*, *C. brevibracteatus* has a similar leaf blade size but differs from the former by the ovate sepals (vs. narrowly linear-lanceolate, see Table 2). *Cryptanthus brevibracteatus* is also similar to *C. warren-loosei* due to the leaf blade color, but differs from the latter mainly by the 9.2–10 mm long floral bracts (vs. 17.3–18.5 mm long) and rounded anther apex (vs. acute, see Table 2).

TABLE 2. Comparison of characters of *Cryptanthus brevibracteatus* and morphologically similar species.

Species/ Characters	<i>C. brevibracteatus</i>	<i>C. crassifolius</i>	<i>C. diamantinensis</i>	<i>C. warren-loosei</i>
Adaxial surface of leaf blades	Glabrous, except the densely lepidote base	Densely lepidote on older leaves	Sub-densely lepidote near the base and glabrous toward the apex	Glabrous, except the sparsely lepidote or densely lepidote base
Length of floral bracts (mm)	9.2–10	11–15.5	ca. 9	17.3–18.5
Shape of sepal lobes	Ovate	Ovate	Narrowly linear-lanceolate	Ovate or lanceolate
Length of sepals (mm)	9.5–11.5	13–16	10–11	15.3–18.2
Connation of sepals (mm)	6.6–8	8–10	6–7	8.5–10
Length of sepal lobes (mm)	3.8–4.9	4.8–6	--	5.6–8
Anther apices	Rounded	Rounded	Apiculate	Acute

Acknowledgments

This study is part of DMCF's Ph.D. dissertation that is supported by CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico). The research was conducted under the Programa de Pós-Graduação em Biologia Vegetal at the Universidade Federal de Pernambuco. This research was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES, Finance Code 001). RBL thanks CNPq for the financial support (grants no. 310871/2014-0 and 449686/2014-0). The authors thank the Jardim Botânico da Usina de Arte that donated to DMCF the sample of the living specimens and the Paula Mendes, who cultivated *Cryptanthus apiculatantherus*. The authors also thank Lukas Daneu for collecting *Cryptanthus brevibracteatus*, Dr. Benoit Loeuille for helping with the nomenclature, the scientific illustrators Regina Carvalho and Felipe Martins, and the reviewers and Eric Gouda (editor) which improved the manuscript a lot.

References

- Cruz, G.A.S., Zizka, G., Silvestro, D., Leme, E.M.C., Schulte, K. & Benko-Iseppon, A.M. (2017) Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). *Molecular Phylogenetics and Evolution* 107: 152–165.
<https://doi.org/10.1016/j.ympev.2016.10.019>
- Ferreira, D.M.C. & Louzada, R.B. (2020) A New Species of *Cryptanthus* (Bromeliaceae, Bromelioideae) in the Brazilian Atlantic Forest north of the São Francisco River, and its Contribution to the Taxonomy of the Genus. *systematic Botany* 45: 460–465.
<https://doi.org/10.1600/036364420X15935294613491>
- Flora do Brasil (2020) Bromeliaceae in Flora do Brasil 2020 em construção. Jardim Botânico do Rio de Janeiro, Rio de Janeiro, Brazil. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB5991> (accessed 23 November 2020)
- Forzza, R.C., Costa, A.F., Leme, E.M.C., Versieux, L.M., Wanderley, M.G.L., Louzada, R.B., Monteiro, R.F., Judice, D.M., Fernandez,

- E.P., Borges, R.A.X., Penedo, T.S.A., Monteiro, N.P. & Moraes, M.A. (2013) Bromeliaceae. In: Martinelli, G. & Moraes, M.A. (Eds.) *Livro Vermelho da Flora do Brasil*. Instituto de Pesquisas Jardim Botânico do Rio de Janeiro, Andrea Jakobsson, Rio de Janeiro, pp. 315–396.
- Givnish, T.J., Barfuss, M.H.J., Ee, B.V., Riina, R., Schulte, K., Horres, R., Gonsiska, P.A., Jabaily, R.S., Crayn, D.M., Smith, J.A.C., Winter, K., Brown, G.K., Evans, T.M., Holst, B.K., Luther, H., Till, W., Zizka, G., Berry, P.E. & Sytsma, K.J. (2011) Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. *American Journal of Botany* 98: 872–895.
<https://doi.org/10.3732/ajb.1000059>
- Gouda, E.J., Butcher, D. & Gouda, C.S. (cont. updated) *Encyclopaedia of Bromeliads*, Version 4. University Botanic Gardens, Utrecht. Available from: <http://bromeliad.nl/encyclopedia/?action=showLitRef&id=4574> (accessed 29 January 2021)
- Harris, J.G. & Harris, M.W. (2001) *Plant Identification terminology: an illustrated glossary*. ed. 2. Spring Lake Publishing, Utah. 206 pp.
- IUCN Standards and Petitions Subcommittee (2019) *Guidelines for using the IUCN red list categories and criteria*. Version 14. Prepared by the Standards and Petitions Subcommittee. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf> (accessed 23 November 2020)
- Leme, E.M.C. (1993) A new prolific species from Bahia, Brazil. *the Cryptanthus society Journal* 8: 17–19.
- Leme, E.M.C. (1999) New species of Brazilian Bromeliaceae: A tribute to Lyman B. Smith. *Harvard Papers in Botany* 4: 135–168.
- Leme, E.M.C. (2002) Two new sympatric *Cryptanthus* species. *Cryptanthus society Journal* 17: 86–90.
- Leme, E.M.C., Kollmann, L.J.C. & Paviotti, A. (2008) Three New *Cryptanthus* Species from Espírito Santo and Bahia, Brazil. *Journal of the Bromeliad society* 58: 12–19.
- Leme, E.M.C., de Fraga, C.N., Kollmann, L.J.C., Brown, G.K., Till, W., Ribeiro, O.B.C., Machado, M.C., Monteiro, F.J.S. & Fontana, A.P. (2010) Miscellaneous new species in the Brazilian Bromeliaceae. *Rodriguésia* 61: 21–67.
<https://doi.org/10.1590/2175-7860201061104>
- Leme, E.M.C. (2015) Two new bromelioid species from Brazil. *Journal of the Bromeliad society* 65: 87–99.
- Leme, E.M.C., Heller, S., Zizka, G. & Halbritter, H. (2017) New circumscription of *Cryptanthus* and new Cryptanthoid genera and subgenera (Bromeliaceae: Bromelioideae) based on neglected morphological traits and molecular phylogeny. *Phytotaxa* 318: 1–88.
<https://doi.org/10.11646/phytotaxa.318.1.1>
- Leme, E.M.C. & Kollmann, L.J.C. (2013) Miscellaneous new species of Brazilian Bromeliaceae. *Phytotaxa* 108: 1–40.
<https://doi.org/10.11646/phytotaxa.108.1.1>
- Leme, E.M.C., Ribeiro, O.B.C., Souza, F.V.D., Souza, E.H. de, Kollmann, L.J.C. & Fontana, A.P. (2020) Miscellaneous new species in the “Cryptanthoid complex” (Bromeliaceae: Bromelioideae) from Eastern Brazil. *Phytotaxa* 430: 157–202.
<https://doi.org/10.11646/phytotaxa.430.3.2>
- Leme, E.M.C. & Siqueira-Filho, J.A. (2007) Taxonomia das bromélias dos fragmentos de mata atlântica de Pernambuco e Alagoas. In: Siqueira-Filho, J.A. & Leme, E.M.C. (Eds.) *Fragmentos de mata atlântica do nordeste – biodiversidade, conservação e suas bromélias*. Andrea Jakobsson Estúdio. Rio de Janeiro, pp. 190–381.
- Luther, H.E. (1999) *Cryptanthus arelii*, an “Old” New species from Bahia, Brazil. *the Cryptanthus society Journal* 14: 54–55.
- Otto, F. & Dietrich, A. (1836) Eine neue Gattung aus der Familie der Bromeliaceae. *Allgemeine Gartenzeitung* 38: 297–299.
- Radford, A.E., Dickison, W.C., Massey, J.R. & Bell, C.R. (1974) *Vascular Plant systematics*. Harper and Row, New York. 70 pp.
- Smith, L.B. (1944) Bromeliaceas novas ou interessantes do Brasil. *Arquivos de Botânica do Estado de São Paulo* 1: 53.