

Research Article

Dyckia semperflorens sp. nov. (Bromeliaceae: Pitcairnioideae) from the cold region of Rio Grande do Sul, southern Brazil

Henrique Mallmann Büneker¹✉ and Jorge Ernesto de Araujo Mariath^{1,2}

¹Laboratório de Anatomia Vegetal (LAVeg), Instituto de Biociências, Departamento de Botânica, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, RS, Brazil

²Programa de Pós-graduação em Botânica, Instituto de Biociências, UFRGS, Porto Alegre, RS, Brazil

Correspondence: Henrique Mallmann Büneker (henriquemallmannbuneker@gmail.com)

Nordic Journal of Botany

2026: e05019

doi: [10.1002/njb.05019](https://doi.org/10.1002/njb.05019)

Subject Editor: Isa Lucia de Moraes

Editor-in-Chief: Torbjörn Tyler

Accepted 9 September 2025

Published 17 October 2025



Dyckia semperflorens (Bromeliaceae: Pitcairnioideae) is described as a new species from the temperate climate region of Rio Grande do Sul state, southern Brazil. The new species belongs to the *Dyckia encholirioides* complex and is closely related morphologically to *Dyckia monticola*, which is endemic to the Quiriri mountain range, a high-altitude region in the northeastern part of Santa Catarina state. *Dyckia semperflorens* is distinguished by having basal floral bracts of the main inflorescence axis exceeding the length of the flowers, flowers 2.3–2.5 cm long, anthers prior to dehiscence $4.5\text{--}5.0 \times 1.5\text{--}1.6$ mm, and stigmatic margins without trichomes. The new species is only known from a single population on a rocky escarpment on the banks of the Touros River and is assessed as ‘Data Deficient’ (DD) based on the IUCN criteria.

Keywords: bromeliad, *Dyckia encholirioides* complex, *Dyckia monticola*, monocot, taxonomy, xerophytes

Introduction

Dyckia Schult. & Schult. f. s. str. is one of the most species-rich genera within Pitcairnioideae (Bromeliaceae), currently comprising 188 recognized species (Gouda et al. 2023). These plants are characterized by succulent, spiny leaves and are strongly associated with xeric environments, primarily shallow soils and rocky outcrops (Büneker 2021, Büneker et al. 2021). The genus is distributed across Argentina, Bolivia, Paraguay, Uruguay, and Brazil, with Brazil hosting over two-thirds of the currently known species (Gouda et al. 2023). Most *Dyckia* species have highly restricted geographic distributions and many are endemic to small regions (Büneker et al. 2021). Several species are known from only a single population, such as *Dyckia retroflexa* S. Winkl. (Büneker 2021), *Dyckia pseudodelicata* Büneker & Mariath (Büneker and Mariath 2022), and *Dyckia nobilis* Büneker, K. Soares & L. C. Assis (Büneker et al. 2016), among many others.

Dyckia s. str. has been recovered as a monophyletic group in phylogenetic studies based on molecular data (Krapp et al. 2014, Pinagé et al. 2017). However, it



www.nordicbotany.org

emerges from a grade composed of species or species groups of *Encholirium* Mart. ex Schult. & Schult.f. The most widely accepted phylogenetic hypothesis places the clade including *Dyckia* s. str. and *Encholirium* (i.e. *Dyckia* s. str. + lineages of *Encholirium* = *Dyckia* s. lat.) as sister to *Deuterocohnia* Mez. These three xeric genera within Pitcairnioideae form a clade that is sister to the mesic genus *Fosterella* L.B.Sm. (Schütz et al. 2016, Büneker 2021). Gomes-da-Silva et al. (2019), in their total-evidence phylogenetic study, did not recover any of the xeric genera as monophyletic and proposed the merging of *Deuterocohnia* and *Encholirium* with *Dyckia* (i.e. *Dyckia* s. latissimo). However, this taxonomic proposal was not widely accepted among Bromeliaceae specialists (Leme et al. 2025) and was essentially adopted only in *Flora e Funga do Brasil* (Guarçoni et al. 2025). To clarify which classification is currently in use, Büneker (2021) proposed the terminology *Dyckia* s. str., *Dyckia* s. lat., and *Dyckia* s. lmo. to refer to these increasingly inclusive circumscriptions of the genus.

In southern Brazil (Paraná, Santa Catarina, and Rio Grande do Sul states), species of *Encholirium* and *Deuterocohnia* do not occur. However, a significant number of *Dyckia* s. str. species are present, many of which are endemic to this region (Büneker et al. 2021). Recent taxonomic efforts aimed at advancing the knowledge of *Dyckia* s. str. in this area have led to the discovery and cataloging of several new species, including *Dyckia strehliana* Büneker & R.Pontes, *Dyckia pontesii* Büneker, Witeck & K.Soaes, *Dyckia pampeana* Büneker, *Dyckia pseudodelicata*, and *Dyckia magnifica* Büneker & Mariath (Büneker et al. 2013, 2015, 2018a, 2018b, 2022, 2023). Additionally, these efforts have contributed to the taxonomic revision of the *Dyckia tuberosa* complex (Büneker et al. 2018a, 2018b, partially unpublished but largely incorporated into Büneker et al. 2021); the *Dyckia selloa* complex (Büneker 2021, Büneker and Mariath 2022, Büneker et al. 2023); the *Dyckia remotiflora* complex (Büneker et al., unpubl.), and, through this article, the initial results of the revision of the *Dyckia encholirioides* complex. This complex includes species predominantly distributed along the Atlantic coast and within the adjacent coastal mountain ranges of southern Brazil, occurring in the states of Rio Grande do Sul, Santa Catarina, Paraná, and São Paulo. The *D. encholirioides* complex includes *D. encholirioides* (Gaudich.) Mez, *Dyckia frigida* Hook.f., *Dyckia fosteriana* L.B.Sm., *Dyckia hatschbachii* L.B.Sm., *Dyckia irmgardiae* L.B.Sm., *Dyckia monticola* L.B.Sm. & Reitz, *Dyckia reitzii* L.B.Sm., and *Dyckia wilsonii* P.J.Braun & Gastaldi. As part of this ongoing revision, we propose a new species within the complex.

Material and methods

According to De Queiroz (2007), there is a distinction between species conceptualization and species delimitation criteria, and the lack of this distinction has generated controversy. Our species conception is partially influenced by the

ideas of Rapini (2004) and Fitzhugh (2009); it is a modified version of the taxonomic species conception, taking into account the conceptualist philosophical theory (Stamos 2003, Zachos 2016). Chiefly, we have employed morphological discontinuity as the primary criterion for species delimitation. The idealization of the limits and morphological variation of the treated species was based on quantitative and qualitative data gathered from the observation of the specimens analyzed.

Specimens of the new species from the natural population and cultivation were sampled and analyzed. The samples used in laboratory analysis were obtained from the living collection from Planeta Bromélia (managed by Jones Caldas da Silva). The *Dyckia* collections of the herbaria CTES, HAS, HBR, HDCE, HPBR, HUCCS, HURG, HVAT, ICN, LP, MBM, MPUC, MVFA, MVJB, MVM, PACA, PEL, R, RB, SI, SMDB, SP, SPF, and UPCB were reviewed, while digital collections of *Dyckia* of B, G, GH, K, NY, P, S, US, ULM, and WU were also consulted for the study of the *D. encholirioides* complex.

Quantitative and qualitative data were obtained from the herbarium specimen and three cultured individuals outside greenhouses in Porto Alegre, Rio Grande do Sul, Brazil. The measurements of the floral parts were obtained from the open flowers of the median region of the main axis of the inflorescence. The images and measurements of the anthers and stigma were obtained from the flowers in bud immediately next to the flowers already opening. The usual terminology for Bromeliaceae was used following the model of Smith and Downs (1974), with adaptations suggested by Scharf and Gouda (2008), Barfuss et al. (2016), Bernardello et al. (1991), Forzza (2001), and Siqueira et al. (2023).

Photos were captured of specimens in the field using a Nikon D5300 digital camera and a Nikon D90 digital camera equipped with a Nikon AF-S DX Nikkor 18–105 mm lens. Images of flower details were taken with a Leica M165 FC stereomicroscope and a Leica DFC 500 digital camera using LAS ver. 4.5 software, in the Laboratório de Anatomia Vegetal of UFRGS. The images were created by combining multiple focal planes obtained through the aforementioned microscopes using Zerene Stacker ver. 1.04 software.

Taxonomic treatment

***Dyckia semperflorens* Büneker & Mariath sp. nov.**
(Fig. 1–2)

Species morphologic proxima Dyckiae monticolae, differt bracteis floralibus basalibus axis principalis inflorescentiae longitudinem florum superantibus, apicalibus longitudinem sepalorum aequantibus vel superantibus (versus brevioribus quam sepala), floribus majoribus (2.3–2.5 versus 1.5–1.8 cm long.), antheris ante dehiscuntiam minoribus (4.5–5.0 × 1.5–1.6 versus 5.4–5.6 × 1.9–2.0 mm) et marginibus stigmaticis sine trichomatibus (versus trichomatibus uniseriatis praeditis).



Figure 1. *Dyckia semperflorens* sp. nov. (A–E: H.M. Büneker 620 et al.). (A) Habitat, (B) clumping habit, (C) flowering plant habit, (D) rosette, (E) detail of the inflorescence. Photos by Henrique Mallmann Büneker.



Figure 2. *Dyckia semperflorens* sp. nov. (A, C, E, G, I, K, M: H.M. Büneker 620 et al.) versus *D. monticola* (B, D, F, H, L, J, N: E.M.C. Leme 1664 & J.C. Silva). (A–B) Adaxial face of the leaf blade, (C–D) abaxial face of the leaf blade, (E–F) median portion detail of the main axis of the inflorescence, (G–H) flower buds, (I–J) adaxial face of the anther, (K–L) side view of anther, (M–N) apex of the ovary, style, and stigma. Photos by Henrique Mallmann Büneker. Scale bar: (A–D)=1 cm, (E–F)=2 cm, (G–H)=5 mm, (I) and (K)=2 mm, (L) and (J)=2 mm, (M)=1 mm, (N)=1 mm.

Type: Brazil, Rio Grande do Sul: Bom Jesus, escarpa rochosa às margens do Rio dos Touros, 8 Feb. 2017, H.M. Büneker 620, R.C. Pontes & J.C. Silva (holotype: ICN; isotypus: RB).

Etymology

The specific epithet was suggested by J.C. Silva and refers to the continuous flowering observed in cultivated specimens throughout all seasons of the year since their collection in 2017.

Description

Herb saxicolous or terricolous, 65–96 cm height in bloom, rhizomatous. Rosette 39–65 cm in diameter. Leaves 47–107, slightly secund, inner ones suberect to erect, outer ones patent; blades $19\text{--}34 \times 1.3\text{--}2.3$ cm, narrow-triangular, flexible, straight or generally slightly arched; adaxial face subplane, green, sparsely lepidote at the base and the rest subglabrous or glabrous; abaxial face convex, longitudinally nerved-striate, white-lepidote between the nerves; apex spinescent; margins laxly spinose-serrate; spines $1.3\text{--}2.0 \times 1\text{--}2$ mm, aduncate, antrorse, concentrated at the base of the blade, rigid, greenish at base, yellowish-brown at apex, irregularly spaced. Inflorescence axillary, erect or erect-declined; peduncle $20\text{--}36 \times 1.2\text{--}1.6$ cm, cylindrical, slightly striate, green or reddish, densely floccose-tomentose, with white trichomes in the basal portion and ferruginous in the central-upper portion; peduncle bracts polystichous, surpassing the internodes, basal ones foliaceous, erect, $6.5\text{--}10.5$ cm long, with margins loosely serrated, abaxial face longitudinally nerved-striate, and apex spinescent, upper ones erect, slightly inflated, vinaceous in the basal portion, slightly carinate and paleaceous-whitish in the upper portion, triangular, $3.8\text{--}4.3 \times 1.5\text{--}1.8$ cm, with entire margins, and attenuate-acuminate, spinescent apex; fertile part of inflorescence simple, up to 38 cm long, or compound with 1–8 erect or suberect-arcuate branches up to 27 cm long, arranged at the base of the fertile part of the inflorescence; rachis of the main axis reddish, densely floccose-tomentose with ferruginous trichomes. Floral bracts $1.6\text{--}3.5 \times 2.5\text{--}3.0$ cm, triangular, carinate, reddish to pale brown, adpressed and densely lepidote on the abaxial surface, subglabrous or glabrous on the adaxial face, those at the base of the main axis of the inflorescence surpassing the length of the flowers, those at the apex equaling or surpassing the length of the sepals, with entire margins and attenuate-spinescent apex. Flowers $2.3\text{--}2.5$ cm long, pedicellate, polystichous, usually secund, patent or slightly suberect at anthesis; pedicels $0.3\text{--}0.5$ cm long. Calyx slightly asymmetrical; sepals $1.0\text{--}1.4 \times 0.6\text{--}0.7$ cm, oval to elliptical, orange at the base, reddish in the median region and vinaceous in the upper portion, adaxial ones slightly carinate, abaxial ones ecarinate, densely floccose-tomentose on the abaxial face with ferruginous trichomes, acuminate at apex. Corolla slightly campanulate; petals $0.8\text{--}1.1 \times 0.7\text{--}1.0$ cm, unguiculate, obtrullate; blades erect or suberect, carinate, orange, glabrous, rounded-cucullate at apex. Hypanthium ca 1.5 mm long. Stamens included, shorter than or equaling petal length; filaments up to 2 mm wide, flattened, straight, yellowish-white or

orange-yellowish, narrow-triangular to sublinear, connate for up to 2–4 mm above the hypanthium, free above the release of the petals, antesealous ones adnate by ca 2 mm to the sepals, antepetalous ones adnate by 4.0–4.5 mm to the petals; anthers before dehiscence $4.5\text{--}5.0 \times 1.5\text{--}1.6$ mm, dorsifixed, lanceoloid; thecae introrse, yellow, equal; sporangia rectilinear, divergent, sagittate at base, monorostrate at apex, with triangular rostrum and conspicuous connective, white-yellowish. Pistil 0.8–1.3 cm long; ovary $0.5\text{--}0.7 \times \text{ca } 0.2$ cm, yellowish; stigma with stigmatic segments ca 2 mm long, conduplicate, spiraled around themselves, margins lobate without trichomes. Capsule ovoid, brown to black, vernicose.

Phenology

Cultivated specimens produce inflorescences throughout all seasons of the year, with a greater abundance observed in spring and summer. Each inflorescence remains in blossom for approximately two weeks. Given that the climatic conditions under cultivation in Porto Alegre (Rio Grande do Sul) do not markedly differ from those of the natural habitat, except for slightly lower temperatures in the natural habitat, we do not believe that year-round flowering is an artifact of cultivation. However, this phenomenon has not been investigated in the natural habitat.

Distribution and habitat

The species is known only from a single population occurring on a rocky escarpment along the banks of the Touros River, in the municipality of Bom Jesus, Rio Grande do Sul, southern Brazil (Fig. 1A). Its habitat is embedded within a matrix of grassland vegetation, interspersed with patches of forest dominated by *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae). The species occurs in a region of relatively high elevation (approximately 1054 m a.s.l.), near the border between the states of Rio Grande do Sul and Santa Catarina. The climate in this area is temperate, characterized by the occurrence of frost, and snowfall during winter. For the municipality, the average temperature in July is 10.5°C, while in January it is 19.4°C (INMET 2020).

Conservation status

More data are needed to assess the degree of threat to the species, which is why it is preliminarily classified as ‘Data Deficient’ (DD) following IUCN (2022). Several sites with similar habitats in the region where it was originally found may potentially support its occurrence, requiring further investigation. The only known population is currently under pressure from cattle grazing and frequent anthropogenic fires used for grassland management in the region (Fig. 1A).

Similar species

The *D. encholirioides* complex is characterized by species bearing pedicellate flowers that do not become erect after anthesis, a well-developed hypanthium reaching up to 2.5 mm in length, sepals with ferruginous trichomes, a campanulate corolla at anthesis, and obtrullate, unguiculate, glabrous petals. Within this complex, two distinct groups of species can

be identified. The first group comprises species occurring at low elevations, relatively close to the Atlantic Ocean, on the Brazilian coast, where the climate is tropical with higher temperatures in both summer and winter. These species exhibit a taller growth habit (> 90 cm in height) and possess flowers with yellow-orange or yellow petals (*D. encholirioides*, *D. hatschbachii*, and *D. wilsonii*). The second group includes species found at higher elevations, frequently exceeding 1000 m a.s.l. in mountainous regions, where the climate is temperate, with milder summers and cold winters. These species display a smaller habit (< 80 cm in height) and have flowers with orange petals (*D. frigida*, *D. fosteriana*, *D. irmgardiae*, *D. monticola*, and *D. reitzii*). *Dyckia semperflorens* belongs to this second group of species that inhabit colder regions with higher altitude.

The new species described here is morphologically very similar to *D. monticola*, but it can be distinguished by several characteristics (Fig. 2): the basal floral bracts of the main inflorescence axis exceed the length of the flowers, while the apical bracts are equal to or longer than the sepals (Fig. 2E, G) (versus shorter than the sepals; Fig. 2F, H); the flowers are larger (2.3–2.5 versus 1.5–1.8 cm in length; Fig. 2E, F); prior to dehiscence, the anthers are smaller ($4.5\text{--}5.0 \times 1.5\text{--}1.6$ versus $5.4\text{--}5.6 \times 1.9\text{--}2.0$ mm; Fig. 2I–L); and the stigmatic margins lack trichomes (Fig. 2M) (versus with uniseriate trichomes, Fig. 2N). *Dyckia monticola* is endemic to the Quiriri mountain range, a high-altitude region in northeastern Santa Catarina, also in southern Brazil, where it occurs in grasslands with shallow soils and rocky outcrops. However, this locality is situated more than 290 km from the only known population of *D. semperflorens*.

Acknowledgements – We thank the reviewers of the manuscript. We also thank Jones Caldas da Silva for organizing the excursion in search of the new species, Rodrigo Corrêa Pontes for accompanying and helping during the collection of *Dyckia* specimens, and the Laboratório de Anatomia Vegetal (LAVeg – UFRGS) for providing space and equipment for analysis.

Funding – Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for scholarship at modality of doctorate for H.M.B. (Process 88887.648979/2021-00); Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the Productivity Research Grant for J.E.A.M. (Process 303840/2019-6).

Conflict of interest – We declare that there are no conflicts of interest.

Author contributions

Henrique Mallmann Büneker: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Project administration (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Jorge Ernesto de Araujo Mariath:** Conceptualization (supporting); Supervision (lead); Writing – original draft (supporting).

Data availability statement

This article has no additional data.

References

- Barfuss, M. H. J., Till, W., Leme, E. M. C., Pinzón, J. P., Manzanares, J. M., Halbritter, H., Samuel, R. and Brown, G. K. 2016. Taxonomic revision of Bromeliaceae subfam. Tillandsioideae based on a multi-locus DNA sequence phylogeny and morphology. – *Phytotaxa* 279: 1–97.
- Bernardello, M., Galetto, L. and Juliani, H. R. 1991. Floral nectar, nectary structure and pollinators in some Argentinean Bromeliaceae. – *Ann. Bot.* 67: 401–411.
- Büneker, H. M. 2021. Revisão taxonômica do complexo *Dyckia selloa* (Bromeliaceae, Pitcairnioideae) baseada em caracteres morfológicos. – MSc. thesis, Universidade Federal do Rio Grande do Sul, Brazil.
- Büneker, H. M. and Mariath, J. E. A. 2022. *Dyckia pseudodelicata*, a new species of the *D. selloa* complex (Bromeliaceae, Pitcairnioideae) from Rio Grande do Sul, Brazil. – *Phytotaxa* 550: 59–70.
- Büneker, H. M., Pontes, R. C., Soares, K. P., Witeck-Neto, L. and Longhi, S. J. 2013. Uma nova espécie reófito de *Dyckia* (Bromeliaceae, Pitcairnioideae) para a flora do Rio Grande do Sul, Brasil. – *Rev. Bras. Biociênc* 11: 284–289.
- Büneker, H. M., Witeck-Neto, L. and Soares, K. P. 2015. *Dyckia pontesii* (Bromeliaceae, Pitcairnioideae), uma nova espécie do Rio Grande do Sul, Brasil. – *Rodriguésia* 66: 499–504.
- Büneker, H. M., Soares, K. P. and Assis, L. de. 2016. The *Dyckia sordida* complex (Bromeliaceae, Pitcairnioideae) and a new species from Minas Gerais, Brazil. – *Phytotaxa* 244: 57–68.
- Büneker, H. M., Soares, K. P. and Witeck-Neto, L. 2018a. *Dyckia pampeana*, a new species of Bromeliaceae (Pitcairnioideae) from Pampa grasslands of Brazil and Uruguay. – *Phytotaxa* 362: 97–104.
- Büneker, H. M., Witeck-Neto, L. and Rodrigues, M. A. 2018b. Taxonomic revision of the *Dyckia tuberosa* complex (Bromeliaceae, Pitcairnioideae) in the southern cone. – In: Versieux, L. M. and Lynn, G. C. (eds.), *Abstracts of the Monocots IV*, Natal, p. 200.
- Büneker, H. M., Guarçoni, E. A. E., Santos-Silva, F. and Forzza, R. C. 2021. *Dyckia*. – In: The Brazil Flora Group (BFG) (ed.), *Coleção Flora do Brasil 2020. Jardim Botânico do Rio de Janeiro*, pp. 725–1050.
- Büneker, H. M., Pastori, T., Almeida, P. S. de. and Mariath, J. E. A. 2023. *Dyckia magnifica*, a new species of Bromeliaceae (Pitcairnioideae) from southern Brazil, and the re-establishment of *D. tomentosa*, of the *D. selloa* complex. – *Phytotaxa* 595: 169–185.
- De Queiroz, K. 2007. Species concepts and species delimitation. – *Syst. Biol.* 56: 879–886.
- Fitzhugh, K. 2009. Species as explanatory hypotheses: refinements and implications. – *Acta Biotheor.* 57: 201–248.
- Forzza, R. C. 2001. Filogenia da tribo Puyee Wittm. e revisão taxonômica do gênero *Encholirium* Mart. ex Schult. & Schult.f. (Pitcairnioideae-Bromeliaceae). – PhD thesis, Universidade de São Paulo, Brazil.
- Gomes-da-Silva, J., Santos-Silva, F. and Forzza, R. C. 2019. Does nomenclatural stability justify para/polyphyletic taxa? A phylogenetic classification in the xeric clade Pitcairnioideae (Bromeliaceae). – *Syst. Biodivers.* 17: 467–490.
- Gouda, E. J., Butcher, D. and Dijkgraaf, L. 2023. Encyclopaedia of bromeliads, ver. 5. – <http://bromeliad.nl/encyclopedia>.
- Guarçoni, E. A. E., Santos-Silva, F. and Forzza, R. C. 2025. *Dyckia*. – In: *Flora e Funga do Brasil. Jardim Botânico do Rio de Janeiro*. – <https://floradobrasil.jbrj.gov.br/FB6046>.

- INMET (Instituto Nacional de Meteorologia do Brasil). 2020. Normais climatológicas do Brasil, período: 1991–1920. – <https://portal.inmet.gov.br/normais>.
- IUCN Standards and Petitions Subcommittee. 2022. Guidelines for using the IUCN Red List categories and criteria, ver. 15.1. – https://nc.iucnredlist.org/redlist/content/attachment_files/RedListGuidelines.pdf.
- Krapp, F., Pinangé, D. S. B., Benko-Iseppon, A. M., Leme, E. M. C. and Weising, K. 2014. Phylogeny and evolution of *Dyckia* (Bromeliaceae) inferred from chloroplast and nuclear sequences. – *Plant Syst. Evol.* 300: 1591–1614.
- Leme, E. M. C., Souza, E. H. D., Till, W., Barfuss, M. H. J., Filho, J. A. S., Kollmann, L. J. C., Couto, D. R., Fraga, C. N. D., Fontana, A. P., Farias-castro, A. S. and Silva, J. B. F. D. 2025. Twenty miscellaneous new species and one new nothogenus and nothospecies in Brazilian Bromeliaceae. – *Phytotaxa* 692: 1–60.
- Pinangé, D. S. B., Krapp, F., Zizka, G., Silvestro, D., Leme, E. M. C., Weising, K. and Benko-Iseppon, A. M. 2017. Molecular phylogenetics, historical biogeography and character evolution in *Dyckia* (Bromeliaceae, Pitcairnioideae). – *Bot. J. Linn. Soc.* 183: 39–56.
- Rapini, A. 2004. Classes or individuals? The paradox of systematics revisited. – *Stud. Hist. Philos. Biol. Biomed. Sci.* 35: 675–695.
- Scharf, U. and Gouda, E. J. 2008. Bringing Bromeliaceae back to homeland botany. – *J. Bromeliad Soc.* 58: 123–129.
- Schütz, N., Krapp, F., Wagner, N. and Weising, K. 2016. Phylogenetics of Pitcairnioideae s.s. (Bromeliaceae): evidence from nuclear and plastid DNA sequence data. – *Bot. J. Linn. Soc.* 181: 323–342.
- Siqueira, S. F. H., Costa, A. F. da and Toni, K. L. G. de. 2023. Beyond SEM: stigmatic margins in Bromeliaceae. – *Flora* 298: 152195.
- Smith, L. B. and Downs, R. J. 1974. Bromeliaceae (Pitcairnioideae). – *Flora Neotrop. Monograph* 14: 1–662.
- Stamos, D. N. 2003. The species problem. Biological species, ontology, and the metaphysics of biology. – Lexington Books.
- Zachos, E. F. 2016. Species concepts in biology. Historical development, theoretical foundations and practical relevance. – Springer.