

Dyckia pseudodelicata, a new species of the *D. selloa* complex (Bromeliaceae, Pitcairnioideae) from Rio Grande do Sul, Brazil

HENRIQUE MALLMANN BÜNEKER^{1,2,*} & JORGE ERNESTO DE ARAUJO MARIATH^{1,3}

¹ Laboratório de Anatomia Vegetal (LAVeg), Instituto de Biociências, Departamento de Botânica, Universidade Federal do Rio Grande do Sul (UFRGS), Av. Bento Gonçalves, 9500, Porto Alegre, RS, Brazil.

² Programa de Pós-graduação em Botânica, Instituto de Biociências, UFRGS, Av. Bento Gonçalves, 9500, Porto Alegre, RS, Brazil.

³  jorge.mariath@ufrgs.br;  <https://orcid.org/0000-0002-2776-6781>

*Author for correspondence:  henriquemallmannbuneker@gmail.com;  <https://orcid.org/0000-0003-4945-5690>

Abstract

We propose the new species *Dyckia pseudodelicata* which is described and illustrated here, and provide data on its distribution and habitat. We compare the new species to the related *Dyckia delicata* and highlight their morphological differences. Morphological features that have been little explored in *Dyckia* taxonomy proved to be diagnostic in our analysis, such as the presence and morphology of trichomes on the petal margins and the position of ovules in relation to the longitudinal axis of the ovary and their disposition in the placenta.

Keywords: bromeliads, *Dyckia delicata*, monocots, taxonomy, xerophytes

Introduction

The Brazilian subtropical region of the state of Rio Grande do Sul (extreme southern Brazil), at the border with Uruguay and Argentina, possesses great *Dyckia* Schultes & Schultes f. (1830: 65) s.s. species diversity and endemism (Gomes-da-Silva *et al.* 2017; Büneker *et al.* 2020). Thirty species are cited for Rio Grande do Sul, which represents ca. 17% of accepted species of *Dyckia* s.s., 17 of which are endemic to the state (Büneker *et al.* 2020). Many of these species have been described in recent decades and have a relatively restricted distribution in this region (e.g. *D. delicata* Larocca & Sobral (2002: 234), *D. nigrospinulata* Strehl (2008: 9), *D. rigida* Strehl (2004: 32), *D. strehliana* Büneker & Pontes (in Büneker *et al.* 2013: 285), and *D. pontesii* Büneker *et al.* (2015b: 500)), with few known populations in the rocky outcrops and escarpments (Büneker *et al.* 2020).

The most expressive group of species in Rio Grande do Sul is the *Dyckia selloa* complex, which was previously treated as the genus *Prionophyllum* by Koch (1873) and Mez (1896, 1935), *Dyckia* subg. *Prionophyllum* by Baker (1889), the *Prionophyllum* group by Leme *et al.* (2012) and Krapp & Eggli (2019), or the *D. maritima* complex by Strehl & Beheregaray (2006). According to Büneker *et al.* (2020), the *Dyckia selloa* complex currently consists of 12 spp.: *D. agudensis* Irgang & Sobral (1987: 5), *D. alba* Winkler (1982: 33), *D. delicata*, *D. hebdingii* Smith (1971: 90), *D. maritima* Baker (1889: 136), *D. myriostachya* Baker (1889: 137), *D. nigrospinulata*, *D. retardata* Winkler (1982: 42), *D. retroflexa* Winkler (1982: 44), *D. rigida* Strehl, *D. selloa* (Koch 1873: 7) Baker (1889: 136), and *D. tomentosa* Mez (1896: 515). The group is clearly distinguished from other species of the genus based on morphology. The main distinguishing characters are: inflorescences usually composed of first to third order (vs. simple or compound to first order), with numerous first order branches (usually more than 10 vs. less than 10 branches), generally small and inconspicuous floral bracts, numerous flowers (more than 100 vs. less than 80) with non-unguiculate (vs. usually unguiculate) petals, stigma during anthesis usually with erect to suberect (vs. twisted) stigmatic lobes, pauciovulate ovary locules (less than 18 vs. more than 30 ovules) and oblanceoloid (vs. flattened) seeds with a little developed wing (Büneker *et al.* 2020; Büneker 2021).

During studies for the revision of the *D. selloa* complex, we encountered a new species that is morphologically similar to *D. delicata*. Herein we propose, describe and illustrate the new species and provide data on its distribution

and habitat. Some unusual morphological features in the taxonomy of the group are explored and their importance discussed under evolutionary aspects.

Material and methods

Specimens:—Specimens from natural populations *in situ*, cultivation and herbaria were studied. Specimens for laboratory analysis were collected from living collections from: Planeta Bromélia (managed by Jones Caldas da Silva), and live collection of Laboratório de Anatomia Vegetal of Universidade Federal do Rio Grande do Sul (LAVeg UFRGS). The *Dyckia* collections of the herbaria HAS, HBR, HDCF, HUCS, HVAT, ICN, MBM, MPUC, PACA, PEL, RB, 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 (acronyms according to Thiers 2020, continuously updated).

Taxonomy:—Considering as a premise the distinction between species concept and delimitation criteria (*i.e.* operational criteria, lines of evidence in defining properties) proposed by Queiroz (2007), we adopted a variant of the taxonomic species concept with adaptations to conceptualist philosophical theory (Stamos 2003; Zachos 2016), partly following Rapini (2004) and Fitzhugh (2009). We used morphological discontinuity as main delimitation criteria. The idealization of the limits and morphological variation of the treated species was based on quantitative and qualitative data obtained through observation of the analyzed specimens. Circumscription of the studied complex was done through analysis of protologues, nomenclatural types, specimens of collections and populations in habitat of all species it comprises. The formal nomenclature follows the Shenzhen Code (Turland *et al.* 2018).

Morphology:—Macromorphologic quantitative and qualitative data of the new species description were obtained from live cultivated specimen (*H.M. Büneker 635 et al.*) and obtained from about 7 *in situ* individuals chosen at random from the type population (*Büneker 913 et al.*). The usual terminology for Bromeliaceae was used, following the model of Smith & Downs (1974), with adaptations suggested by Scharf & Gouda (2008); Bernardello *et al.* (1991) and Forzza (2001) referring to the floral pedicel and hypanthium; and Barfuss *et al.* (2016) and Brown & Gilmartin (1984, 1989) referring to stigma.

For analysis of the petal trichomes, were dissected flowers from 3 individuals of the new species (*H.M. Büneker 635 et al.* and *Büneker 913 et al.*) and two individuals of *D. delicata* (*Büneker 395 et al.*) previously fixed in a solution containing 1% glutaraldehyde and 4% formaldehyde (McDowell & Trump 1976) in 0.1M sodium phosphate buffer, pH 7.2 (Gabriel 1982), followed by rinsing in the same buffer, rinsing in distilled water and, finally, dehydration in an ethanolic series (O'Brien & McCully 1981), up to 50% ethanol. The material was stained in 0.1% Toluidine Blue in 0.1M sodium phosphate buffer pH 4.4 (Feder & O'Brien 1968) and Safranin 1% in ethanol 50% (Johansen 1940), later washed in distilled water and mounted on temporary slides with 1 : 1 ethanol/glycerin solution (Johansen 1940) for analysis in differential interferential contrast microscopy (DIC).

Imaging Technology:—Images of specimens in the field were obtained with a Nikon D5300 digital camera with a Nikon AF-S DX Nikkor 18-105mm lens. Flower detail images were obtained through a Leica M165 FC stereomicroscope with a Leica DFC 500 digital camera using LAS V4.5 software. Images of differential interferential contrast microscopy were obtained through a Leica DMR HC microscope with a Zeiss AxioCam HRc digital camera using Carl Zeiss ZEN LITE 2012 image capture software. Both microscopes are property of LAVeg UFRGS. Images in several focal planes, obtained through the microscopes mentioned above, were reconstructed using Zerene Stacker 1.04 software.

Taxonomy

Dyckia pseudodelicata Büneker & Mariath, *sp. nov.*, Figure 1A–D, 2A–J, and 3A–I.

Tantum habet haec species cum Dyckia delicata similitudinem ut primo intuitu foliis eandem diceret, nisi differt ramis inflorescentiae tenuibus (2–3.4 mm diam. vs. crassis, 4–5 mm diam.) et pluribus (usque 18 ramis vs. usque 7 ramis), floribus apicum ramorum subverticillatis (vs. laxe dispositis, numquam subverticillatis), floribus minoribus (1–1.2 cm vs. 1.4–2 cm longi), marginibus petalorum cum trichomibus trifloribus (flabelliformia, uniseriata-capitata et dendritica vs. cum trichomibus uniformibus: filiformia aut unicellularia, vel sine trichomibus), lobis stigmatibus minoribus in anthesem (1–1.4 mm vs. 2–2.5 mm longi), et seminibus rudimentis suberectis, in duas series per loculum dispositis (vs. patentibus, in 2–4 series per loculum).

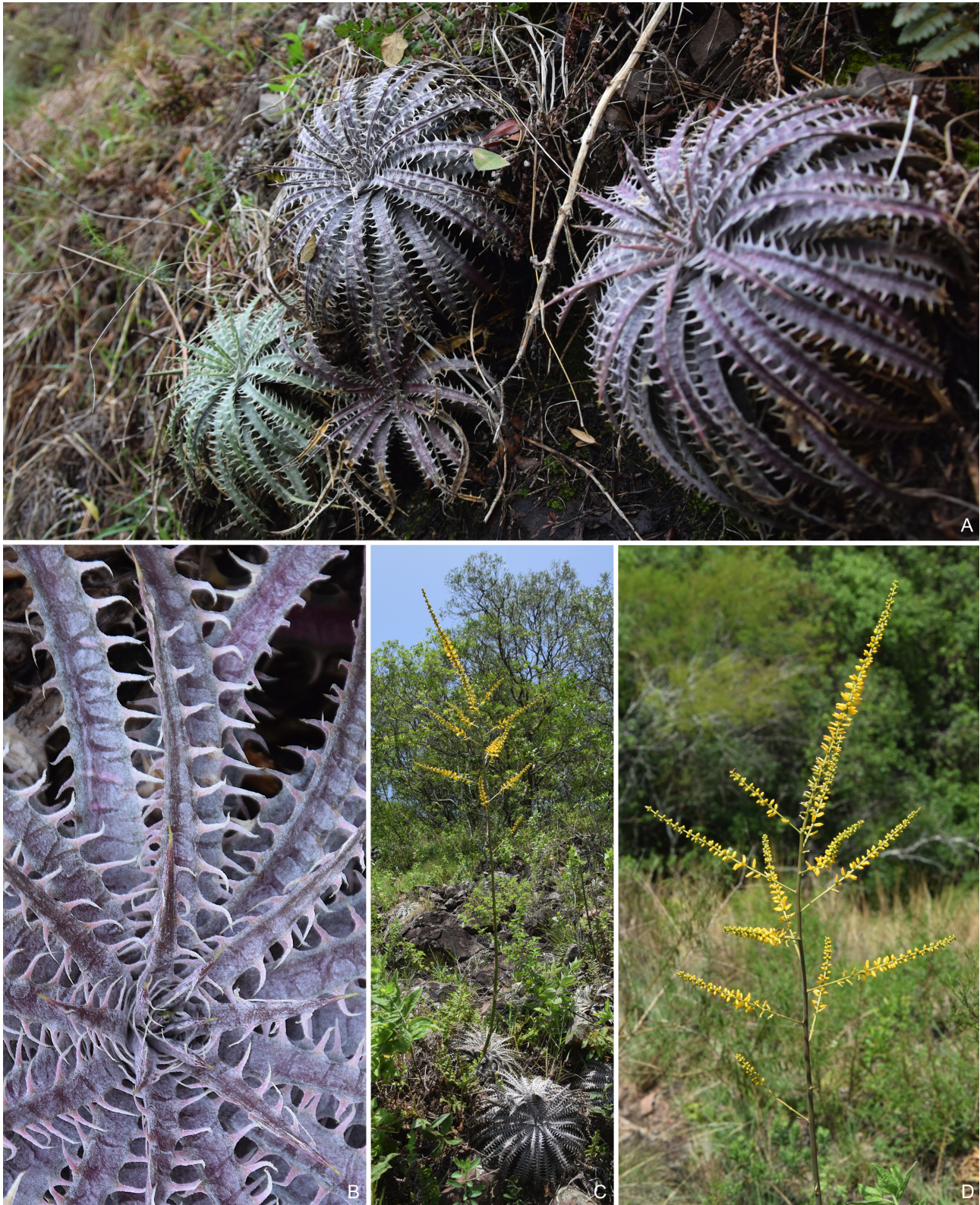


FIGURE 1. A–D. *Dyckia pseudodelicata* (A H.M. Büneker 635 et al.; B–D Büneker 913 et al.) in habitat. A. Vegetative habit. B. Leaves detail. C. Fertile habit. D. Detail of apical portion of the inflorescence.

Type:—BRAZIL. Rio Grande do Sul: **Jari**, encosta rochosa próxima ao arroio Toropi-mirim, 17 January 2020, H.M. Büneker 913, L. Witeck & J.C. Silva (holotype: ICN!, isotypes: SMDB!, RB!).

Herb saxicolous, rhizomatous, 0.47–1.19 m tall when flowering; **rosette** 15–29 cm in diameter, symmetrical. **Leaves** 50–108, the inner ones suberect, the outer ones patent to reflexed; **blade** 7–18 × 1.1–1.9 cm, arched, narrowly triangular,

flexible, adaxial surface convex, purplish-cinereous, densely lepidote, abaxial face convex, longitudinally veined-striate, cinereous, lepidote between the veins, margins densely spinose-serrate, apex terminating in a rigid, pungent spine; *spines* conspicuous, those of the blades margins narrowly triangular, patent or subpatent-retrorse, sometimes hooked at the apex, flexible, lepidote, pinkish-white at the base, whitish at the median portion and at the apex, apex not pungent. **Inflorescence** axillar, erect or suberect; *peduncle* 19–53 cm long, green to purple, devoid of trichomes and pruinose; *peduncle bracts* polystichous, those of the median portion $1.5\text{--}2.6 \times 0.5\text{--}1$ cm, stramineous, shorter than the internodes; *fertile portion of inflorescence* composed, once-branched, 28–50 cm long; *first order bracts* similar to peduncle bracts, 0.5–1.3 cm long; *branches* 4–18 in number, suberect to patent, 9–17 cm long, 2–3.7 mm diam., greenish to purple, devoid of trichomes, pruinose; *floral bracts* $1.5\text{--}3 \times 1\text{--}1.5$ mm, oval-triangular, base green, median and apical region soon dry, yellowish, the apex brown, attenuate-acuminate, ecarinate, devoid of trichomes, pruinose, shorter than the sepals. **Flowers** 1–1.2 cm long, inconspicuously pedicellate, patent, polystichous or subverticillate; *pedicels* ca. 0.7 mm long, green, pruinose; *sepals* $2.1\text{--}2.5 \times 2\text{--}2.5$ mm, suborbicular, apex obtuse to rounded, green at the base, yellow at the apex, slightly carinate, devoid of trichomes and pruinose on the abaxial surface, margins with very sparse dendritic trichomes or glabrous; *petals* $8\text{--}9 \times 3.5\text{--}4$ mm, not unguiculate, erect to incurving toward the apex, oblanceolate, yellow, glabrous on both surfaces, proximal margins exhibit sparse dendritic trichomes, median margins plicate, exhibit densely arranged uniseriate-capitate or dendritic trichomes, distally margins exhibit narrow-triangular multicellular emergences giving the margins a torn appearance and also exhibit white-hyaline trichomes densely arranged, usually alternating between uniseriate-capitate and flabelliform, apex round-cucullate; *dendritic trichomes*, those of the petal proximal margins with foot with 1–2 living cells, stalk uniseriate with 3–6 cells usually dead or living basal cells, little elongated, region of branching little expanded, with 2–7 branches formed by strongly elongate, dead cells; those of the petal median margins with foot with 1–2 living cells, stalk uniseriate with 2–6 slightly elongate dead cells, branching region expanded with (2–)3–6 anticlinally arranged cells, followed by 3–9 branches formed by elongate dead cells; *uniseriate-capitate trichomes*, those of the petal median margins with 3–6 living cells; those distal petal margins with 3–8 living cells; *flabelliform trichomes* of the petal distal margins with foot of 1–2 living cells, stalk uniseriate with 1–2(–3) hardly elongate dead cells, or live basal cells, expanded region with 3–7 anticlinally arranged dead cells, followed by (4–)6–15 branches formed by elongate dead cells; *stamens* included in the corolla during opening of the thecae, later becoming exserted; *filament* 7–9 mm long, free above the short hypanthium, the antepetalous ones adnate to the petals for ca. 0.3 mm; *anther* 1.5–2 mm long, not rostrate; *sporangia* unequal; *pistil* 0.9–1 cm long; *ovary* $1.5\text{--}2 \times 1.2\text{--}1.5$ mm, green; *locules* pauciovulate; *ovules* suberectly positioned, inserted in two rows per locule; *style* 6–7 mm long, yellowish-white; *stigma* conduplicate, stigmatic lobes 1–1.4 mm long, suberect to erect, yellow. **Capsule** ovoid, dark brown when mature. **Seeds** oblanceoloid.

Etymology:—The specific epithet “pseudodelicata” refers to the vegetative similarity between the new species and *D. delicata*. The new species was not flowering when first collected and was believed to be *D. delicata*. However, significant morphological differences found after checking its inflorescences revealed it to be a new species, which we decided to call “false” *D. delicata*.

Distribution and Habitat:—The new species occurs as a saxicolous heliophyte on a rocky basaltic escarpment facing north, near the Toropi-mirim stream. Only one population of the species was located in the municipality of Jari, state of Rio Grande do Sul, southern Brazil. Several similar environments occur in the region, and so it is possible that there are further populations of the species. Some similar environments were found within a ca. 4 km radius around the known population of *D. pseudodelicata*, but only populations of *D. selloa* (on a rocky vertical escarpment) and *D. dusenii* Smith (1932: 6) (on a hillside with shallow litholic soil) were found. Two individuals observed in the population of *D. pseudodelicata* were probably natural hybrids between *D. pseudodelicata* and *D. dusenii*, and probable hybrids of *D. selloa* and *D. pseudodelicata* were observed in vicinity to *D. selloa*.

We estimate that the population of *D. pseudodelicata* has about 200 adult individuals. The population size is being reduced due to habitat loss, as pioneer tree species, mainly *Helieta apiculata* Benth (1882: 67) (Rutaceae), are settling in the site and decreasing the availability of light. The natural reduction of the habitat of the species, and of the relictual xerophyte community to which it is associated, is worrying as some rare species of Cactaceae (*i.e.*, *Eriocephala magnifica* (Ritter 1966: 50) Guiggi (2012: 6), *Notocactus horstii* f. *purpureus* (Ritter 1970: 109) Herm (1993: 64), and *N. oxycostatus* f. *securituberculatus* (Ritter 1979: 169) Gerloff (1993: 93)) occur in association with it, in addition to other species characteristic of this environment (*e.g.* *Sinningia sellovii* (Martius 1829: 36) Wiehler (1978: 72), *S. macrostachya* (Lindley 1828: t. 1202) Chautems (1990: 386) (Gesneriaceae), *Habranthus* aff. *pedunculatus* Herbert (1837: 161) (Amaryllidaceae), and *Hatschbachiella* cf. *tweediana* (Hooker & Arnott 1835[1836]: 242) King & Robinson (1972: 394) (Asteraceae)).

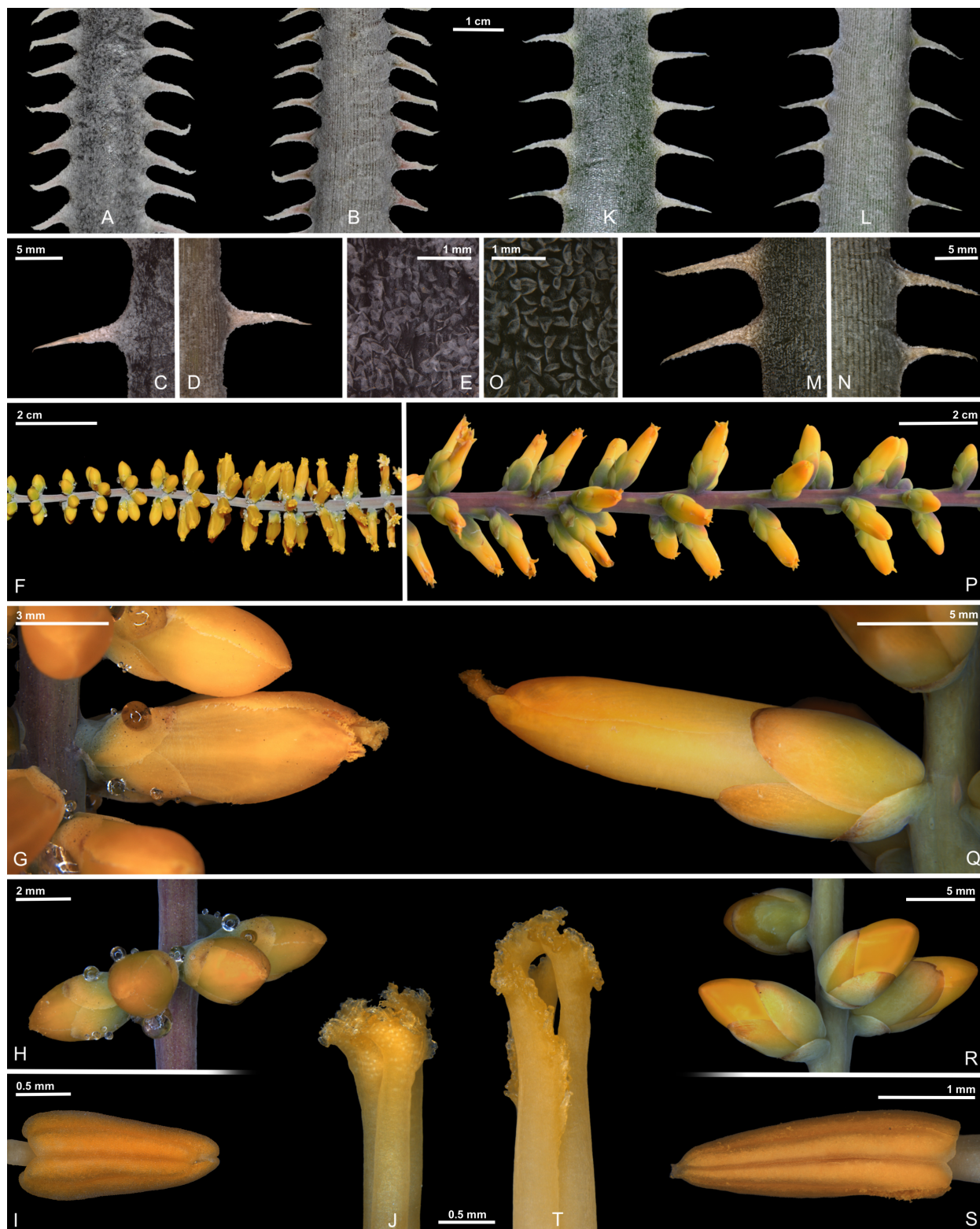


FIGURE 2. A–J. *Dyckia pseudodelicata* (Bünerker 913 *et al.*), K–T. *Dyckia delicata* (Bünerker 395 *et al.*). **A and K.** Median region of leaf adaxial face. **B and L.** Median region of leaf abaxial face. **C and M.** Detail of adaxial face leaf margin with spines. **D and N.** Detail of abaxial face leaf margin with spines. **E and O.** Details of trichomes on the surface of the leaf adaxial surface. **F and P.** Main axis of the inflorescence. **G and Q.** Detail of flower in anthesis. **H and R.** Detail of buds. **I and S.** Anther. **J and T.** Stigma.

The vegetational physiognomy in which the xerophytic relict is inserted, and where the new species occurs, is a transitional region between the Pampa grasslands and the seasonal forest of the Atlantic Forest domain. This transition is located at the edge of the Southern Brazilian Plateau, in the central region of the state of Rio Grande do Sul, in the hydrographic basin of the Toropi-mirim stream, a tributary of the Toropi river. Taxonomic studies of plants in this

region have revealed a significant number of endemic and rare (Marchiori *et al.* 2014; Büneker & Witeck-Neto 2016) or new species over the last two decades (Menezes 2009; Soares & Longhi 2011; Büneker *et al.* 2013, 2015a, 2017, 2018; Deble & Alvez 2013; Coelho & Miotto 2017; Silveira *et al.* 2019; Figueira & Schindler 2021).

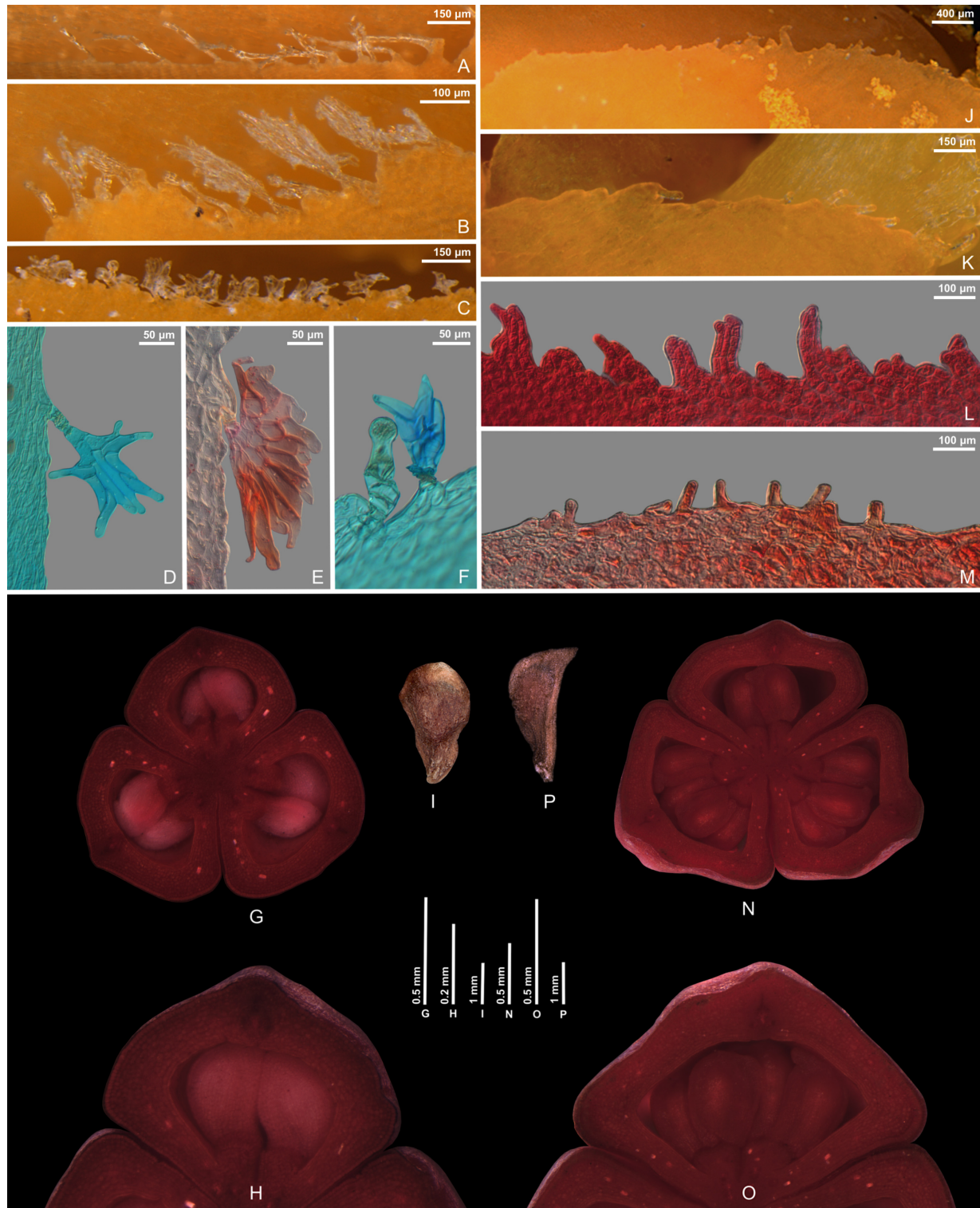


FIGURE 3. A–I. *Dyckia pseudodelicata* (Büneker 913 *et al.*), J–O. *Dyckia delicata* (Büneker 395 *et al.*). A–F and J–M. Petal margin. A. Trichomes of the proximal margin. B. Trichomes of median margin. C. Trichomes of the distal margin. D. Dendritic trichome on DIC. E. Flabelliform trichome on DIC. F. Uniseriate-capitate trichome (left) and flabelliform trichome (right) on DIC. J. Emergences of the distal margin. K. Unicellular trichomes of the apical region. L. Emergences on DIC. M. Unicellular filiform trichomes on DIC. G and N. Transverse section of the median region of ovary. H and O. Detail of transverse section of median region of ovary, where two rows of ovules can be seen in H and four in O. I and P. Seed. E, G, H, L, M, N and O. Stained with Safranin. D and F. Stained with Toluidine Blue.

Observations and discussion:—The new species is morphologically similar to *D. delicata*, mainly due to its vegetative aspect (Figs. 1A–B, and 2A–E, K–O), which is unique among the species of the *D. selloa* complex, as both species have leaf blades that resemble chilopods of the genus *Scolopendra* Linnaeus (1758: 637). The leaf blades are succulent, arched, reflexed, both faces are convex, and also possess dense conspicuous trichomes (Fig. 2E and O) and densely spiny margins with highly developed, although flexible and not pungent, spines (Fig. 2A–D, K–N). These vegetative characteristics have made *D. delicata* highly appreciated and widespread among gardeners and collectors of ornamental succulent plants (Sachs 2011) and bestow *D. pseudodelicata* with the same potential.

Dyckia delicata possesses a series of singularities among the species of the *D. selloa* complex with regards to the morphology of its inflorescences and flowers. The sparsely branched architecture of the inflorescence, being simple or compound, once-branched, with branches only at the base of the fertile portion (when compound), robust branches, relatively large flowers with spiraled stigmatic lobes in pre-anthesis, and patent ovules positioned in relation to the longitudinal axis of the ovary, are features that are absent from most of the remaining species of the *D. selloa* complex but widely observed among other *Dyckia* species. Despite the great morphological similarity between *D. delicata* and *D. pseudodelicata*, the latter does not possess the morphological singularities mentioned above, having instead various flower and inflorescence character states typical of most species of the *D. selloa* complex.

Dyckia pseudodelicata basically differs from *D. delicata* in the fertile aspect (Tab. 1) by having an inflorescence with thin (2–3.4 mm vs. robust, 4–5 mm diam. [Fig. 2F and P]) and numerous first order branches (up to 18 [Fig. 1D] vs. absent or up to 7), flowers in the apical region of the branches subverticillate (vs. flowers spaced [Fig. 2H and R]) and smaller flowers (1–1.2 cm vs. 1.4–2 cm in length [Fig. 2G and Q]), anthers without a rostrum at the apex (vs. with a rostrum [Fig. 2I and S]) and thecae with sporangia of different lengths (vs. equal [Fig. 2I and S]), stigmatic lobes that are erect (vs. spiraled) at anthesis and smaller (1–1.4 mm vs. 2–2.5 mm in length [Fig. 2J and T]). Some morphological characters of *Dyckia* have been little explored regarding their use in taxonomy, probably because they are inconspicuous, impractical for identification purposes and difficult to observe with the naked eye and/or in herborized material. Nonetheless, here we explore two unusual characters that proved to differentiate *D. delicata* and *D. pseudodelicata*: the morphology of the trichomes on the margins of the petals and the position of ovules in relation to the longitudinal axis of the ovary and their disposition in the placenta.

The margins of the upper portion of the petals of both species possess multicellular, narrowly triangular emergences; however, they are more numerous in *D. pseudodelicata*, especially in the cucullate region of the apex, giving the margin a torn appearance. The petal margins of *D. delicata* are straighter and the emergences are concentrated only in the margins of the apex (Fig. 3J and L). The margins of the petals of *D. delicata* have few trichomes, which usually occur in greater numbers at the apex and are filiform, unicellular and not very elongate (Fig. 3K and M). In contrast, *D. pseudodelicata* has numerous trichomes in the margins of the petals and possesses three patterns of morphology and distribution: well-developed, dendritic, sparse in the proximal portion of the margins (Fig. 3A–B and D); uniseriate-capitate, multicellular, sparse (and not very numerous) in the distal region of the margins and apex (Fig. 3F); and alternated by very numerous flabelliform trichomes (Fig. 3E), generally well developed, densely arranged in the margins near the apex (Fig. 3C).

The morphology and presence of these trichomes is an important diagnostic character to be analyzed in the context of the *D. selloa* complex, as it seems to be conserved among individuals of the same species and generally distinct between species. These trichomes are present in almost all species of the *D. selloa* complex, occurring in the margins and abaxial surfaces of perianth parts. However, they have been poorly characterized for most *Dyckia* species, especially those of the petals, which are absent in most species not belonging to the *D. selloa* complex (Carvalho *et al.* 2017; Büneker *et al.* 2020, Büneker 2021). Trichomes like those of the petals of species of the *D. selloa* complex can also be observed in species of the *D. ferruginea* complex (*D. excelsa* Leme (1993: 6), *D. ferruginea* Mez (1896: 533), *D. insignis* Hassler (1919: 316), *D. lymaniana* (Pereira & Martinelli 1982: 252) Forzza (*in* Gomes-Da-Silva, Santos-Silva & Forzza 2019: 486), and *D. splendida* Pereira & Gouda (2018: 137)). Species of the *D. ferruginea* complex appear related to those of the *D. selloa* complex in the phylogenies of Krapp *et al.* (2014) and Pinangé *et al.* (2017), and the presence and similarity of petal trichomes in the species of these two complexes may indicative the degree of relationship between them, even though they appear very distinguished. Thus, these trichomes have great potential to be observed in the future under evolutionary, phylogenetic, morphological and functional aspects.

The position of the ovules in relation to the longitudinal axis of the ovary and their disposition in the placenta (number of rows) have been little studied in *Dyckia* and are not covered in detail in the descriptive taxonomic literature. Mez (1935) reports that *Prionophyllum* (genus name, currently synonymous with *Dyckia*, which is equivalent to the *D. selloa* complex) has few ovules and presents an illustration with the longitudinal section of the ovary of *D. selloa* in which the ovules are suberect in relation to the axis of the ovary and inserted at the axillary base of the carpel. *Dyckia*

pseudodelicata, like *D. selloa*, possesses ovules that are suberect in relation to the longitudinal axis of the ovary (that is, oriented obliquely to the placentation region) and in a reduced number, which was also verified for most species of the *D. selloa* complex. One of the exceptions is *D. delicata*, which possesses ovules that are patent in relation to the longitudinal axis of the ovary and in a considerably larger number, as was usually verified for species of *Dyckia* that do not belong to the complex.

TABLE 1. Principal characters distinguishing *Dyckia pseudodelicata* sp. nov. and *Dyckia delicata*.

Characters		<i>Dyckia pseudodelicata</i>	<i>Dyckia delicata</i>
Inflorescence branches	Diameter	2–3.4 mm	4–5 mm
	Number	up to 18	absent or up to 7
Flowers	Arrangement in the apical region of the branches	subverticillate	spaced, not subverticillate
	Size	1–1.2 cm	1.4–2 cm
Trichomes on the margins of the petals	Cells number	multicellular	unicellular
	Shape	flabelliform, uniseriate-capitate and dendritic	filiform
Anthers	Rostrum	absent	present
	Length of thecae sporangia	unequal	equal
Stigma	Position of stigmatic lobe	erect or suberect	spiraled
	Length of stigmatic lobe	1–1.4 mm	2–2.5 mm
Ovules	Position in relation to the longitudinal axis of the ovary	suberect	patent
	Disposition	2 rows per locule	2–4 rows per locule

We hypothesize that the suberect position for the ovule was a response to carpel size reduction in the common ancestor of the *D. selloa* complex, if the *D. selloa* complex represents an evolutionary lineage. This reduction and suberect position of the ovule has yet to be widely verified among other lineages of the xeric Pitcairnioideae. However, in the earlier divergent lineages of the xeric Pitcairnioideae, such as those that compose *Encholirium* (having as references the phylogenies of Krapp *et al.* (2014) and Pinangé *et al.* (2017)), the locules of the carpels are relatively large and the position and disposition of ovules of most species are identical to that observed in species of *Dyckia* that do not belong to the *D. selloa* complex. These characters, however, need to be further investigated. A further increase in carpel size during evolution, as in *D. delicata*, could be interpreted as a reversal to the ancestral state of the xeric Pitcairnioideae. With greater availability of locular space, the position of the ovules in relation to the longitudinal axis of the ovary became clear again. Thus, the disposition of ovules in a greater number of rows may have arisen in association with this larger space, as observed in *D. delicata*.

The ovules of *D. pseudodelicata* are disposed in two rows per locule, with one row per placental attachment line (Fig. 3G and H), as is the case for most of the species of *Dyckia* studied to date. On the other hand, *D. delicata* may have ovules disposed in 2–4 rows per locule, with one or two rows per placental attachment line (Fig. 3N and O). Analysis of Endress’s (2011) review of the diversity, development and evolution of angiosperm ovules reveals that both ovule position in relation to the longitudinal axis of the ovary and ovule arrangement (number of rows) seem to be related to the proportion of available locular space and ovule size, ovule number and direction of ovule initiation sequence in placentae. Kuhn *et al.* (2020) reported that ovules arranged in a few rows per placental attachment line is an ancestral character in Bromeliaceae. Transitions toward many ovule rows occurred at least twice at the base of a clade, including all genera of Tillandsioideae, except *Catopsis*, on the one hand, and among Puyoideae and Bromelioideae on

the other hand. These transitions are followed by at least three reversals in Tillandsioideae and one, but perhaps more, in Bromelioideae. A transition from many towards lots ovule rows per each placental attachment line is observed at the base of the *Werauhia* clade within Tillandsioideae, while another transition from few to many ovule rows occurred at the base of the *Pitcairnia* clade within Pitcairnioideae.

Despite these differences in the position and disposition of ovules between *D. delicata* and *D. pseudodelicata*, their seeds are morphologically similar (Fig. 3I and P), being oblanceoloid as for other species of *Dyckia* belonging to the complex and possessing a chalazal appendix which constitutes a poorly developed wing (vs. well developed for the rest of *Dyckia*). The anatomy, number, position in relation to the longitudinal axis of the ovary and disposition of ovules are characters to be investigated more widely in the xeric Pitcairnioideae as they seem to have taxonomic importance as diagnostic characters and may be directly related to the unique morphology of the seeds of the *D. selloa* complex. They are oblanceoloid with a poorly developed chalazal appendix (vs. flated with developed chalazal appendix forming a subfalciform wing in most *Dyckia* l.s.), a characteristic that appears to be a synapomorphy of the complex. Furthermore, the study of embryological characters can be an important tool for evolutionary analysis and help in phylogenetic reconstructions.

Additional Specimen Examined (paratype):—BRAZIL. Rio Grande do Sul: **Jari**, encosta rochosa próxima ao arroio Toropi-mirim, 3 August 2017, floresceu em cultivo em January 2020, *H.M. Büneker 635 et al.* (RB).

Acknowledgments

We thank José Nicoloso, owner of the area where the only known population of the new species occurs, for our reception on his farm; Dr. Jones Caldas da Silva for organizing excursions in search for the new species; Professor Leopoldo Witeck Neto and Dr. Rodrigo Corrêa Pontes for accompanying and helping during the collection of *Dyckia* specimens; MSc. Jordano Dorval Tavares de Carvalho for help with the diagnosis; and the Laboratório de Anatomia Vegetal (LAVeg-UFRGS); Fundação Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for scholarship at modality of Master Degree for Henrique Mallmann Büneker (Process 88882.439447/2019-01); and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for the Productivity Research Grant for Jorge Ernesto de Araujo Mariath (Process 303840/2019-6). Also to editor Dr. Eric Gouda and Dr. Walter Till for their contribution in the review process.

References

- Baker, J.G. (1889) *Handbook of the Bromeliaceae*. G. Bell & Sons, London, 243 pp.
<https://doi.org/10.5962/bhl.title.51681>
- Barfuss, M.H.J., Till, W., Leme, E.M.C., Pinzón, J.P., Manzanares, J.M., Halbritter, H., Samuel, R. & Brown, G.K. (2016) Taxonomic revision of Bromeliaceae subfam. Tillandsioideae based on a multi-locus DNA sequence phylogeny and morphology. *Phytotaxa* 279: 1–97.
<https://doi.org/10.11646/phytotaxa.279.1.1>
- Bentham, G. (1882) Plate 1385, *Helietta parvifolia*. *Icones plantarum* 14: 66–67.
- Bernardello, L.M., Galetto, L. & Juliani, H.R. (1991) Floral nectar, nectary structure and pollinators in some Argentinean Bromeliaceae. *Annals of Botany* 67: 401–411.
<https://doi.org/10.1093/oxfordjournals.aob.a088174>
- Brown, G.K. & Gilmartin, A.J. (1984) Stigma structure and variation in Bromeliaceae - Neglected taxonomic characters. *Brittonia* 36: 364–374.
<https://doi.org/10.2307/2806597>
- Brown, G.K. & Gilmartin, A.J. (1989) Stigma types in Bromeliaceae - A systematic survey. *Systematic Botany* 14: 110–132.
<https://doi.org/10.2307/2419055>
- Büneker, H.M. (2021) *Revisão taxonômica do complexo Dyckia selloa (Bromeliaceae, Pitcairnioideae) baseada em caracteres morfológicos*. Masters dissertation, Universidade Federal do Rio Grande do Sul, Porto Alegre, 290 pp.
- Büneker, H.M. & Witeck-Neto, L. (2016) Levantamento de Bromeliaceae na região do curso médio do rio Toropi, Rio Grande do Sul, Brasil. *Balduinia* 52: 1–14.
<https://doi.org/10.5902/2358198022371>

- Büneker, H.M., Ferrarese, M.D. & Canto-Dorow, T.S. (2017) *Tradescantia multibracteata*, a new species of Commelinaceae from Rio Grande do Sul, Brazil. *Phytotaxa* 308: 89–96.
<https://doi.org/10.11646/phytotaxa.308.1.7>
- Büneker, H.M., Guarçoni, E.A.E., Santos-Silva, F. & Forzza, R.C. (2020) *Dyckia* in *Flora do Brasil 2020*. Jardim Botânico do Rio de Janeiro. Available from: <http://floradobrasil.jbrj.gov.br/reflora/floradobrasil/FB6046> (accessed 8 January 2021).
- Büneker, H.M., Pontes, R.C., Soares, K.P., Witeck-Neto, L. & Longhi, S.J. (2013) Uma nova espécie reófito de *Dyckia* (Bromeliaceae, Pitcairnioideae) para a flora do Rio Grande do Sul, Brasil. *Revista Brasileira de Biociências* 11: 284–289.
- Büneker, H.M., Pontes, R.C., Witeck-Neto, L. & Soares, K.P. (2015a) *Tillandsia leucopetala*, a new species of Bromeliaceae from Rio Grande do Sul, southern Brazil. *Phytotaxa* 202: 143–148.
<https://doi.org/10.11646/phytotaxa.202.2.6>
- Büneker, H.M., Soares, K.P., Assis, L.C.de & Witeck-Neto, L. (2018) Taxonomic novelties in Southern Brazilian Amaryllidaceae – III: *Hippeastrum multiflorum*, a new species from Rio Grande do Sul. *Balduinia* 64: 34–41.
<https://doi.org/10.5902/2358198035736>
- Büneker, H.M., Witeck-Neto, L. & Soares, K.P. (2015b) *Dyckia pontesii* (Bromeliaceae, Pitcairnioideae), uma nova espécie do Rio Grande do Sul, Brasil. *Rodriguésia* 66: 499–504.
<https://doi.org/10.1590/2175-7860201566217>
- Carvalho, J.D.T., Essi, L. & Oliveira, J.M.S. (2017) Flower and floral trichome morphology of species of *Dyckia* Schult. f. (Bromeliaceae, Pitcairnioideae), and their importance to species characterization and genus taxonomy. *Acta Botanica Brasilica* 31: 29–41.
<https://doi.org/10.1590/0102-33062016abb0335>
- Chautems, A.P. (1990) Taxonomic revision of *Sinningia* Nees: nomenclatural changes and new synonymies. *Candollea* 45: 381–388.
- Coelho, G.P. & Miotto, S.T.S. (2017) A new species of *Buddleja* (Scrophulariaceae) From Southern Brazil. *Systematic Botany* 42: 968–973.
<https://doi.org/10.1600/036364417X696591>
- Deble, L.P. & Alves, F.daS. (2013) *Herbertia amabilis* Deble & F.S. Alves (Iridaceae), a new species from Brazil. *Candollea* 68: 133–137.
<https://doi.org/10.15553/c2013v681a18>
- Endress, P.K. (2011) Angiosperm ovules: diversity, development, evolution. *Annals of Botany* 107: 1465–1489.
<https://doi.org/10.1093/aob/mcr120>
- Feder, N. & O'Brien, T.P. (1968) Plant microtechnique: some principles and new methods. *American Journal of Botany* 55: 123–142.
<https://doi.org/10.1002/j.1537-2197.1968.tb06952.x>
- Figueira, M. & Schindler, B. (2021) *Rhamnidium riograndense* (Rhamnaceae), a new species from southern Brazil. *Phytotaxa* 510: 53–60.
<https://doi.org/10.11646/phytotaxa.510.1.5>
- Fitzhugh, K. (2009) Species as Explanatory Hypotheses: Refinements and Implications. *Acta Biotheor* 57: 201–248.
<https://doi.org/10.1007/s10441-009-9071-3>
- Forzza, R.C. (2001) *Filogenia da tribo Puyee Wittm. e revisão taxonômica do gênero Encholirium Mart. ex Schult. & Schult.f. (Pitcairnioideae-Bromeliaceae)*. Thesis for PhD. Universidade de São Paulo, São Paulo, 208 pp.
- Gabriel, B.L. (1982) *Biological electron microscopy*. Van Nostrand Reinhold Company, New York, 264 pp.
- Gerloff, N. (1993) *Notocactus oxycostatus* Buining & Brederoo fa. *securituberculatus* (Ritter) Gerloff comb. et stat. nov. *Internoto* 14: 83–95.
- Gomes-da-Silva, J., Amorim, A.M. & Forzza, R.C. (2017) Distribution of the xeric clade species of Pitcairnioideae (Bromeliaceae) in South America: a perspective based on areas of endemism. *Journal of Biogeography* 44: 1994–2006.
<https://doi.org/10.1111/jbi.12990>
- Gomes-da-Silva, J., Santos-Silva, F. & Forzza, R.C. (2019) Does nomenclatural stability justify para/polyphyletic taxa? A phylogenetic classification in the xeric clade Pitcairnioideae (Bromeliaceae). *Systematics and Biodiversity* 17: 467–490.
<https://doi.org/10.1080/14772000.2019.1646834>
- Guiggi, A. (2012) New genera and combinations in the family of Cactaceae Jussieu (Magnoliopsida-Cactales). *Cactology* 3: 5–9.
- Hassler, E. (1919) *Bromeliacearum paraguayensiam conspectus*. *Annuaire du Conservatoire et du Jardin Botaniques de Genève* 20: 268–341.
- Herbert, W. (1837) *Amaryllidaceae*. James Ridway & Sons, London, 428 pp.
- Herm, K. (1993) *N. horstii* (Ritter) forma *purpureus* (Ritter) Herm forma *nova*. *Internoto* 14: 59–64.
- Hooker, W.J. & Arnott, G.A.W. (1836) Contributions towards a Flora of South America and the Islands of the Pacific. *Companion to the Botanical Magazine* 1: 234–244.
- Irgang, B.E. & Sobral, M. (1987) *Dyckia agudensis* (Bromeliaceae), nova espécie do Rio Grande do Sul, Brasil. *Napaea* 3: 5–7.

- Johansen, D.A. (1940) *Plant microtechnique*. MacGraw-Hill, New York, 523 pp.
- King, R.M. & Robinson, H.E. (1972) Studies in the Eupatorieae (Asteraceae). LXXXI. A new genus, *Hatschbachiella*. *Phytologia* 23: 393–394.
<https://doi.org/10.5962/bhl.part.19873>
- Koch, K. (1873) *Index seminum in horto botanico berolinensi anno 1873 collectorum. Appendix quarta ad indicem seminum horti botanici Berolinensis anni 1873*. Berlin, pp. 1–7.
- Krapp, F. & Eggli, U. (2019) *Dyckia*, Bromeliaceae. In: Eggli, U. & Nyffeler, R. (Eds.) *Illustrated Handbook of Succulent Plants: Monocotyledons*, ed. 2. Springer, Berlin, pp. 1–71.
https://doi.org/10.1007/978-3-662-56324-3_80-1
- Krapp, F., Pinangé, D.S.B., Benko-Iseppon, A.M., Leme, E.M.C. & Weising, K. (2014) Phylogeny and evolution of *Dyckia* (Bromeliaceae) inferred from chloroplast and nuclear sequences. *Plant Systematics and Evolution* 300: 1591–1614.
<https://doi.org/10.1007/s00606-014-0985-0>
- Kuhn, S.A., Nogueira, F.M., Chauveau, O. & Mariath, J.E.deA. (2020) Diversity and evolutionary trends of the ovary and ovule in Bromeliaceae. *Flora* 272: 151691.
<https://doi.org/10.1016/j.flora.2020.151691>
- Larocca, J. & Sobral, M. (2002) *Dyckia delicata* (Bromeliaceae), a new species from Rio Grande do Sul, Brazil. *Novon* 12: 234–236.
- Leme, E.M.C. (1993) Novas bromeliáceas nativas do Brasil – XI. *Pabstia* 4: 6–7.
- Leme, E.M.C., Ribeiro, O.B.C. & Miranda, Z.J.G. (2012) New species of *Dyckia* (Bromeliaceae) from Brazil. *Phytotaxa* 67: 9–37.
<https://doi.org/10.11646/phytotaxa.67.1.2>
- Lindley, J. (1828) *Gesneria macrostachya*. Long-spiked Gesneria. *Botanical Register* 14: t. 1202.
- Linnaeus, C. (1758) *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima, reformata*, vol. 1. Laurentius Salvius, Holmiae, 824 pp.
<https://doi.org/10.5962/bhl.title.542>
- Marchiori, J.N.C., Canto-Dorow, T.S., Büneker, H.M., Essi, L., Breier, T.B. & Pontes, R.C. (2014) Campos e florestas no curso médio do Rio Toropi, Rio Grande do Sul (Brasil). Retrato de um admirável patrimônio ameaçado. *Balduinia* 45: 1–16.
<https://doi.org/10.5902/2358198014685>
- Martius, C.F.P. (1829) *Nova Genera et Species Plantarum Brasiliensium*. *Nova Genera et Species Plantarum* 3: 1–198.
- McDowell, E.M. & Trump, B.F. (1976) Histologic fixatives suitable for diagnostic light and electron microscopy. *Archives of Pathology & Laboratory Medicine* 100: 405–414.
- Menezes, L.C. (2009) Uma nova espécie do Rio Grande do Sul: *Cyrtopodium witeckii*. *Boletim CAOB* 75: 58–63.
- Mez, C. (1896) Bromeliaceae. In: De Candolle, C. (Ed.) *Monographiae Phanerogamarum* 9. Sumptibus G. Masson & Cie., Paris, 990 pp.
- Mez, C. (1935) Bromeliaceae. In: Engler, A. (Ed.) *Das Pflanzenreich, regni vegetabilis conspectus* 4 (32). W. Engelmann, Leipzig, 667 pp.
- O'Brien, T.P. & McCully, M.E. (1981) *The study of plant structure principles and selected methods*. Termarcaphi Pty Ltd., Melbourne, 344 pp.
- Pereira, E. & Martinelli, G. (1982) *Species novae in brasiliana bromeliacearum* XIX. *Bradea* 3: 251–260.
- Pereira, E.E. & Gouda, E.J. (2018) A new *Dyckia* species (Bromeliaceae, Pitcairnioideae) from Brazilian Central-West region, Pantanal Mato-Grossense. *Phytotaxa* 333: 137–14.
<https://doi.org/10.11646/phytotaxa.333.1.12>
- Pinangé, D.S.B., Krapp, F., Zizka, G., Silvestro, D., Leme, E.M.C., Weising, K. & Benko-Iseppon, A.M. (2017) Molecular phylogenetics, historical biogeography and character evolution in *Dyckia* (Bromeliaceae, Pitcairnioideae). *Botanical Journal of the Linnean Society* 183: 39–56.
<https://doi.org/10.1111/boj.12489>
- Queiroz, K. de (2007) Species concepts and species delimitation. *Systematic Biology* 56: 879–886.
- Rapini, A. (2004) Classes or individuals? The paradox of systematics revisited. *Studies in History and Philosophy of Biological and Biomedical Sciences* 35: 675–695.
<https://doi.org/10.1016/j.shpsc.2004.09.006>
- Ritter, F. (1966) *Eriocactus magnificus* Ritter spec. nova. *Succulenta* 45: 50–53.
- Ritter, F. (1970) Nieuwe cactussen uit Zuid-Amerika I. *Succulenta* 49: 108–109.
- Ritter, F. (1979) *Kakteen in Südamerika. Band 1. Brasilien/Uruguay/Paraguay*. Friedrich Ritter Selbstverlag, Spangenberg, 374 pp.
- Sachs, H. (2011) Searching for *Dyckia delicata*. *Die Bromelie* 2011: 118–121.
- Scharf, U. & Gouda, E.J. (2008) Bringing Bromeliaceae back to homeland botany. *Journal of the Bromeliad Society* 58: 123–129.
- Schultes, J.A. & Schultes, J.H. (1830) *Classis VI, Hexandria*. In: Roemer, J.J. & Schultes, J.A. (Eds.) *Systema Vegetabilium* 7 (2).

Cottaem, Stuttgart, pp. 45–107.

Silveira, F.S., Bordignon, S.A.L. & Miotto, S.T.S. (2019) *Mimosa cerifera*, a new threatened species from the Pampa Biome, Southern Brazil. *Systematic Botany* 44: 133–138.

<https://doi.org/10.1600/036364419X697976>

Smith, L.B. (1932) Studies in the Bromeliaceae – III. *Contributions from the Gray Herbarium of Harvard University* 98: 3–42.

<https://doi.org/10.5962/p.336146>

Smith, L.B. (1971) Notes on Bromeliaceae, XXXII. *Phytologia* 21: 73–96.

Smith, L.B. & Downs, R.J. (1974) Bromeliaceae (Pitcairnioideae). *Flora Neotropica Monograph* 14: 1–662.

Soares, K.P. & Longhi, S.J. (2011) Uma nova espécie de *Butia* (Becc.) Becc. (Arecaceae) para o Rio Grande do Sul. *Ciência Florestal* 21: 203–208.

<https://doi.org/10.5902/198050983223>

Stamos, D.M. (2003) *The species problem. Biological species, ontology, and the metaphysics of biology*. Lexington Books, New York, 380 pp.

Strehl, T. (2004) Novas espécies de Bromeliaceae do Rio Grande do Sul, Brasil. *Vidalia* 2: 19–25.

Strehl, T. (2008) New bromeliads, genus *Dyckia*, from Rio Grande do Sul, Brazil. *Bromeliaceae* 42: 8–22.

Strehl, T. & Beheregaray, L.B. (2006) Morfologia de sementes do gênero *Dyckia* subfamília Pitcairnioideae (Bromeliaceae). *Pesquisas Botânicas* 57: 103–120.

Thiers, B. (2020 [continuously updated]) *Index Herbariorum*: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from: <http://sweetgum.nybg.org/science/ih/> (accessed 10 January 2020).

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (Eds.) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. Koeltz Botanical Books, Glashütten.

<https://doi.org/10.12705/Code.2018>

Wiehler, H. (1978) Miscellaneous transfers and new species of Neotropical Gesneriaceae. *Selbyana* 5: 61–93.

Winkler, S. (1982) Die Bromeliaceae von Rio Grande do Sul. *Documenta Naturae* 3: 1–90.

Zachos, E.F. (2016) *Species Concepts in Biology. Historical Development, Theoretical Foundations and Practical Relevance*. Springer, Cham, 220 pp.