



Combining the small South American genus *Androtrichum* into *Cyperus* (Cyperaceae)

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Background and aims – Molecular phylogenetic studies have provided a clearer understanding of the complex relationships within the family Cyperaceae. These studies have consistently shown that 12 allied genera are nested in the genus *Cyperus*. However, early Sanger sequencing-based phylogenies that included the two species of the small South American genus *Androtrichum* were inconclusive in placing this genus either as sister to *Cyperus* or as part of its early divergent lineages. A recent phylogenetic analysis however conclusively placed the two species of *Androtrichum* within the C₃ *Cyperus* Grade. In this study, we investigate if the morphology and anatomy of *Androtrichum* species provide additional evidence for their placement in the genus *Cyperus*. In addition, we provide descriptions and distribution data for the species.

Material and methods – Herbarium material from FLOR, FURB, GENT, ICN, and K has been studied. Samples of the culm and leaf were studied using histological methods. Taxonomic changes and typifications of names were performed according to the International Code of Nomenclature for algae, fungi, and plants.

Key results – The morphology and the non-Kranz anatomy observed in the *Androtrichum* species confirm their placement among the other C₃ *Cyperus* species. *Androtrichum* is combined into *Cyperus*. For one species, a combination in *Cyperus* is already available: *Cyperus trigynus*. For the other species, a new name in *Cyperus* is published: *Cyperus byssaceus*. Two typifications are established and morphological descriptions and distribution data are provided.

Conclusion – By integrating recent molecular phylogenetic data with additional evidence from morphology and anatomy, *Androtrichum* is combined into *Cyperus*. As a result of this taxonomic change, a single monophyletic genus *Cyperus* is now recognised in the *Cyperus* Clade of tribe Cypereae.

Keywords – Anatomy; Cypereae; new name; taxonomy.

INTRODUCTION

Evolutionary relationships in Cyperaceae, a diverse family with c. 90 genera and c. 5,600 species (Govaerts et al. 2020), have been unveiled through several molecular phylogenetic studies (e.g., Simpson et al. 2007; Muasya et al. 2009a; Escudero & Hipp 2013; Semmouri et al. 2019). Some of these studies have clarified the complex delimitation of previously unresolved genera based on morphology alone (e.g., Lar-

ridon et al. 2011a, 2018; Global Carex Group 2015; Elliott & Muasya 2017; Roalson et al. 2019). Within tribe Cypereae, Sanger sequencing-based phylogenies have consistently shown that 12 segregate genera are nested in the genus *Cyperus* L. (c. 950 species), including genera using C₃ and C₄ photosynthesis (Muasya et al. 2002, 2009a, 2009b; Larridon et al. 2011a, 2011b, 2013; Bauters et al. 2014). Among these, the C₃ species of *Cyperus* s. str., *Courtoisina* Soják,

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Kyllingiella R.W.Haines & Lye, and *Oxycaryum* Nees form a species-poor grade (hereafter C₃ Cyperus Grade with c. 190 species; Larridon et al. 2011a, 2011b); and the C₄ species of *Cyperus* s. str., *Alinula* J.Raynal, *Ascolepis* Nees ex Steud., *Kyllinga* Rottb., *Lipocarpha* R.Br., *Pycreus* P.Beauv., *Queenslandiella* Domin, *Remirea* Aubl., *Sphaerocyperus* Lye, and *Volkella* Merxm. & Czech. comprise a diverse clade (hereafter C₄ Cyperus Clade with c. 760 species; Larridon et al. 2013, 2014). However, phylogenetic placement of the small South American genus *Androtrichum* (Brongn.) Brongn. was unresolved in the genus *Cyperus* (Muasya et al. 2009a).

Androtrichum was described based on the species *Abildgaardia polyccephalum* Brongn. [= *Androtrichum trigynum* (Spreng.) H.Pfeiff.]. Although the habit of this species differs from that of *Abildgaardia* Vahl, the structure of its spikelets at the time of flowering is somewhat similar which led Brongniart (1833) to publish *Androtrichum* first as a subgenus of *Abildgaardia*: “*Abildgaardia* subg. *Androtrichum* Brongn.: Filamentis staminum in fructu elongatis, longe exsertis (an Genus proprium?)”. Since then, more specimens of this species were collected including specimens in fruit. Those specimens present a particular character, i.e., the considerable elongation of the stamen filaments. The filaments, which because of their sheer number, their whiteness, and their length have the appearance of hairs (figs 1D, 2E), arise from the glumes and they remain on the fruits when these fall from the plant when mature. This character, combined with a rhizomatous habit differing from that of *Abildgaardia*, was deemed sufficient to accept *Androtrichum* as a separate genus (Brongniart 1834).

However, other authors placed this species (*A. trigynum*) in no less than six different genera besides *Androtrichum*, i.e., *Abildgaardia*, *Comostemum* Nees, *Cyperus*, *Eriophorum* L., *Scirpus* Tourn. ex L., and *Trichophorum* Pers. From this list, it can be assumed that this species combines several more or less conspicuous characters of all these genera. Pfeiffer (1940) proposed the inclusion of a second species in *Androtrichum* (*Scirpus giganteus* Kunth [= *A. giganteum* (Kunth) H.Pfeiff.]), which also presents elongation of the stamen filaments (figs 1B, 2B). Govaerts et al. (2007, 2020) accepted the inclusion of the second species in *Androtrichum*, although Goetghebeur (1998) did not consider its inclusion to be convincingly demonstrated.

In the molecular phylogenetic study of Muasya et al. (2009a), *Androtrichum trigynum* was retrieved as sister to the *Cyperus* Clade, while *A. giganteum* was positioned in a polytomy within the *Cyperus* Clade. Using the same accessions sequenced for the chloroplast gene *rbcL* only as part of a study including a more extensive sampling of Cyperaceae, Semmouri et al. (2019) found that both species are clearly placed within the C₃ Cyperus Grade of the *Cyperus* Clade. Van der Veken (1965) and Goetghebeur (1986) both studied the embryo of *A. trigynum* and noted that it corresponds to the *Cyperus*-type (Semmouri et al. 2019). However, the C₃ photosynthetic pathway has only been confirmed for *A. trigynum* (Larridon et al. 2011a). To date, the *Androtrichum* species have not yet been formally combined in *Cyperus*, which remains paraphyletic, although a monophyletic genus *Cyperus* is supported based on molecular data. In this study,

we investigate if the morphology and anatomy of *Androtrichum* species provide additional evidence for their placement in the genus *Cyperus* to delimit it as a monophyletic group. In addition, we provide descriptions and distribution data for the species.

MATERIAL AND METHODS

The morphological study was conducted using specimens from the herbaria FLOR, FURB, GENT, ICN, and K (acronyms according to Thiers continuously updated). Images of spikelets and fruits were captured using a digital camera attached to a stereoscope microscope (Leica EZ4 D).

The anatomical study was carried out on samples of *Androtrichum trigynum* (culm) and *A. giganteum* (leaves and culm), collected in the state of Santa Catarina, Brazil. The samples were fixed in formaldehyde-acetic acid-ethanol 70% (FAA 70) (Johansen 1940) for 24 hours and were later stored in ethanol 70%. Mature middle regions of leaves and culm were sectioned free-hand with a razor blade and stained with 1% Safranin and 1% Astra Blue (Bukatsch 1972). The anatomical characters were analysed, and images were captured using a digital camera (Leica DFC 295) attached to a microscope (Leica DM 2500).

The taxonomic changes and typifications of names were performed according to the International Code of Nomenclature for algae, fungi, and plants (Turland et al. 2018).

RESULTS

The morphology of the *Androtrichum* species agrees with their placement in the C₃ Cyperus Grade of the *Cyperus* Clade. *Androtrichum* species share a combination of morphological characteristics with the C₃ *Cyperus* species such as anhelate inflorescences, bisexual flowers, trigonous achenes (fig. 2C, F), spikelets with many glumes (fig. 2A, D), and either distichous glumes (fig. 2D) as in most *Cyperus* Clade species, or spirally-arranged glumes (fig. 2A) as in species previously placed in *Kyllingiella* and *Oxycaryum*.

The anatomical study shows that both species do not exhibit Kranz anatomy. In *Androtrichum giganteum*, the leaf blade transverse section is V-shaped (fig. 3A) with an uniseriate epidermis on both sides (fig. 3A, B) and the stomata occurring only on the abaxial side (fig. 3B). While subepidermal fibre strands occur on both sides of the leaves, the ones on the abaxial side are associated with the vascular bundles (fig. 3B). The conspicuous adaxial hypodermis with rounded translucent cells and without intercellular spaces occurs throughout the leaf blade (fig. 3B). In the midrib, the hypodermis cells are elongated (fig. 3A). The mesophyll is reduced and consists of chlorophyll parenchyma with slightly elongated cells surrounding large air cavities (fig. 3B). These air cavities are filled by stellate cells (fig. 3A, B). The vascular system consists of collateral vascular bundles intercalating the air cavities (fig. 3A, B). The culm of *A. giganteum* exhibit uniseriate epidermis (fig. 3C). Several fibre strands with strongly thick-walled cells are observed below the epidermis (fig. 3C). The chlorophyll parenchyma, which is formed by a homogeneous parenchyma, is interrupted by large air cavities that are filled with stellate cells (fig. 3C),



Figure 1 – A–B. *Cyperus byssaceus*. A. Habit. B. Inflorescence with reddish brown elongated stamen filaments. **C–E.** *Cyperus trigynus*. C. Habit. D. Inflorescence with hyaline white elongated stamen filaments. E. Rhizome. Photographs by Rafael Trevisan.

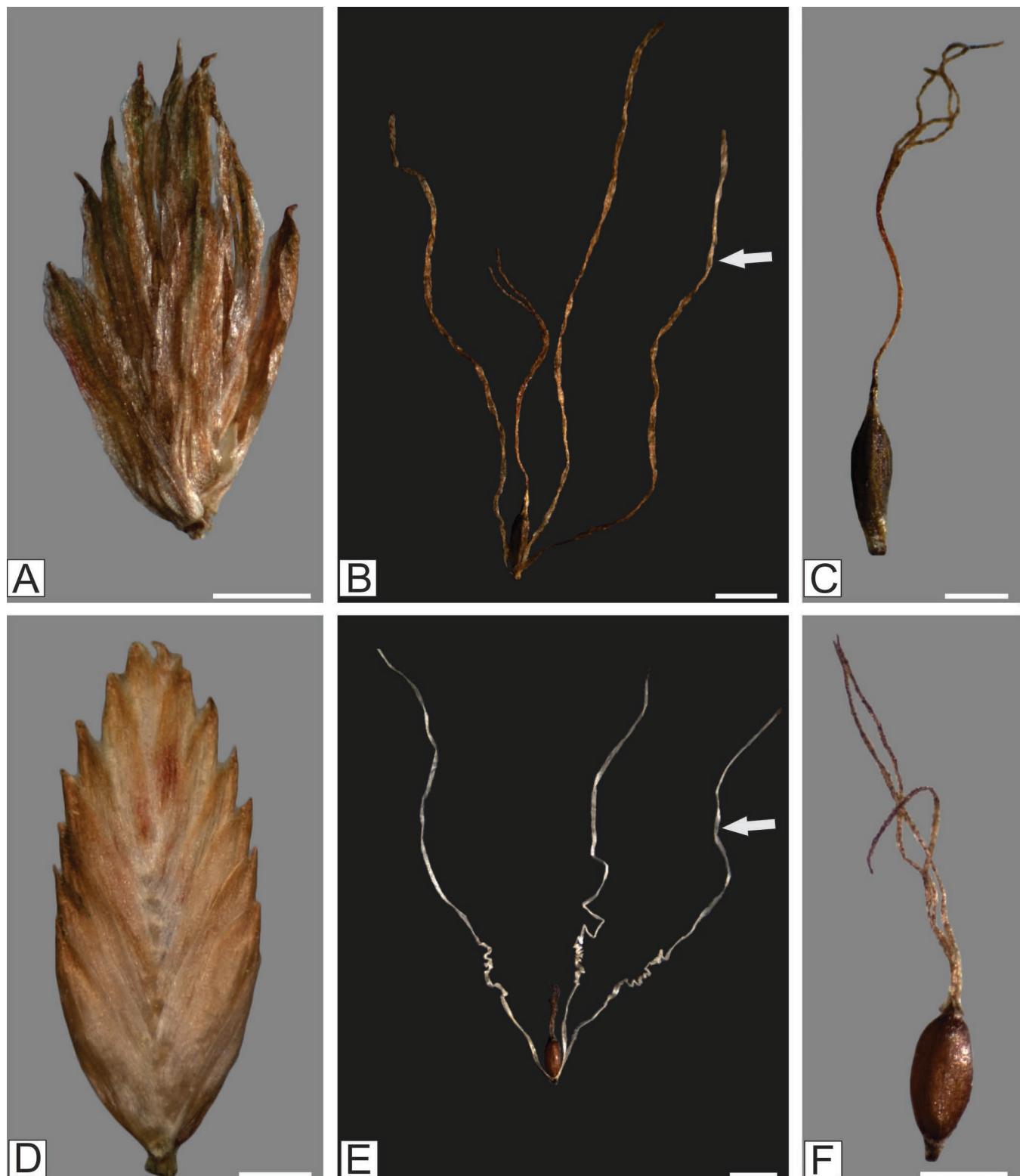


Figure 2 – A–C. *Cyperus byssaceus*. A. Spikelet. B. Elongated stamen filaments (arrow) adhered to the fruit. C. Mature fruit. **D–F.** *Cyperus trigynus*. D. Spikelet. E. Elongated stamen filaments (arrow) adhered to the fruit. F. Mature fruit. A from R. Trevisan 1673 (FLOR). B, C from S.M. Hefler & G.H. Silveira 702 (ICN). D from F. Gonzatti 276 (FLOR). E, F from R. Martins 111 (FLOR). Scale bars: A, B, D, E = 1 mm; C, F = 0.5 mm.

similar to the situation in the leaves. Stomata always occur in relation with the chlorophyll parenchyma (fig. 3C). The vascular system is formed by collateral vascular bundles of different sizes and they are surrounded by a pluricellular sheath of thickened cells (fig. 3C). The pith region consists

of ground parenchyma with relatively small cells and few intercellular spaces (fig. 3C). In *A. trigynum*, the culm has a uniseriate epidermis with the outer pericinal wall conspicuously thickened and covered by a cuticle (fig. 3D). Below the epidermis, several strongly thickened fibres strands are

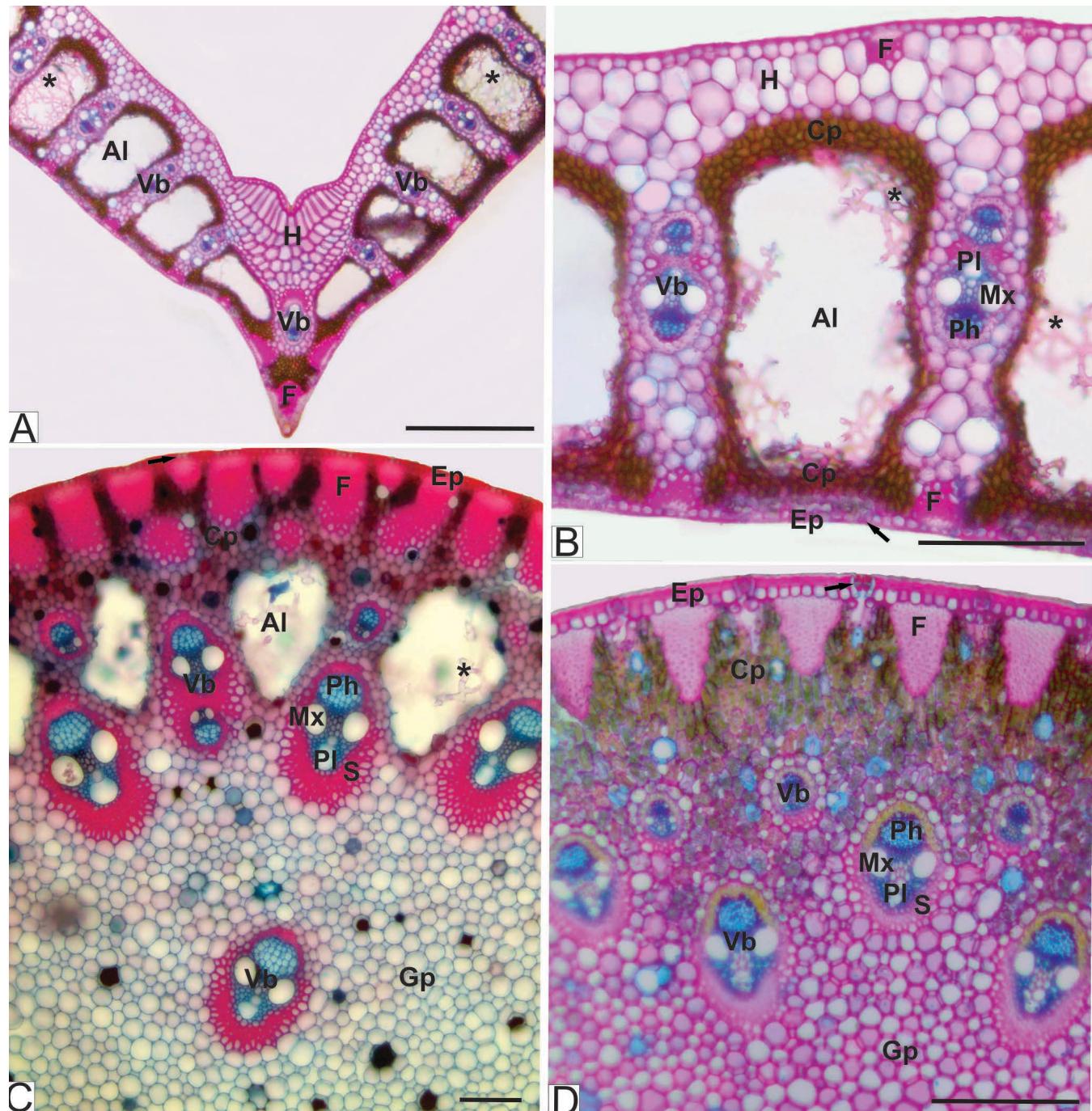


Figure 3 – Cross sections of Cyperus species. **A–C.** *C. byssaceus*. **D.** *C. trigynum*. **A–B.** Leaf. **C–D.** Culm. **A.** Midrib showing the hypodermis and large air cavities intercalated by the collateral vascular bundles. **B.** Detail showing the chlorophyll parenchyma surrounding the air cavities. **C.** Strongly thickened subepidermal fibres and air cavities. **D.** Epidermis with thickened walls, subepidermal fibres, and collateral vascular bundles. The analysed organs do not have Kranz anatomy. Ac – air cavity; Cp – chlorophyll parenchyma; Ep – epidermis; F – fibres; Gp – ground parenchyma; H – hypodermis; Mx – metaxylem; Ph – phloem; Pl – protoxylem lacuna; S – sheath; Vb – vascular bundle; arrow – stomata; * – stellate cells. A–C from *R. Trevisan 1673* (FLOR). D from *L. Pereira-Silva 420* (FLOR). Scale bars: A = 500 µm; B, D = 200 µm; C = 100 µm.

observed (fig. 3D). These fibres strands are intercalated with the chlorophyll parenchyma, which has elongated cells (fig. 3D). In the epidermis, stomata are observed with large substomatal chambers in the direction of the chlorophyll parenchyma (fig. 3D). The vascular system consists of collateral vascular bundles, which tend to increase in size towards the centre of the organ (fig. 3D). All vascular bundles are surrounded by a pluricellular sheath of thickened cells (fig. 3D). The pith region has ground parenchyma with small cells and few intercellular spaces (fig. 3D).

Based on evidence from morphology and anatomy that supported the genus *Androtrichum* as part of the C₃ *Cyperus* Grade of the Cyperus Clade, we combine the two species of the genus *Androtrichum* into *Cyperus*. For *A. trigynum*, a combination in *Cyperus* is already available: *C. trigynus* Spreng. For *A. giganteum*, a new name in *Cyperus* is published: *C. byssaceus* Pereira-Silva nom. nov. A taxonomic treatment is presented below with the relevant typifications, detailed morphological descriptions, and distribution data.

DISCUSSION

Due to its superficial resemblance to several other genera in Cyperaceae, the affinities of *Androtrichum* have long remained unclear. Since Van der Veken's (1965) embryo morphology study, we know that *A. trigynum* has an embryo of the *Cyperus*-type. In his revision of the Cyperaceae genera, Goetghebeur (1986) indicated that the inflorescence of *A. trigynum* agrees with the general inflorescence blueprint of *Cyperus*. Goetghebeur (1986) also remarked on the striking similarities between *Androtrichum* and the genus *Scirpoideas*. Thus, although the presence of strongly elongated filaments after anthesis is not observed in any other species of Cyperaceae, there was little doubt about the position of *Androtrichum* near this tribe (Goetghebeur 1986). Muasya et al. (2009a) confirmed the close relationship of *A. giganteum* and *A. trigynum* with *Cyperus*, but it remained unclear whether (1) the genus *Androtrichum* was monophyletic, and (2) whether it was sister to or nested in *Cyperus*.

Recent molecular phylogenetic hypotheses confirmed the placement of both species of *Androtrichum* in the C₃ *Cyperus* Grade and that it is a polyphyletic genus (Sembouri et al. 2019). In addition, the morphological characteristics of *Androtrichum* species agree with the general morphology of the C₃ *Cyperus* species. Our anatomical study confirms that *A. trigynum* and *A. giganteum* do not possess Kranz anatomy, which provides additional arguments for its placement among the C₃ *Cyperus* lineages. Furthermore, the two *Androtrichum* species have common anatomical features found in most *Cyperus* species, such as V-shaped leaves, large and conspicuous air cavities in the leaf blades, numerous vascular bundles embedded in the chlorenchyma or in its internal limit, and sclerenchyma as crescentiform caps of fibres at xylem poles and usually as hypodermis in the culm (e.g., Metcalfe 1971; Denton 1983; Hefler & Longhi-Wagner 2010). Based on that, we formally synonymize *A. giganteum* and *A. trigynum* into *Cyperus*. With the taxonomic changes proposed here, *Cyperus* is delimited as a monophyletic group and the only genus of the Cyperus Clade of tribe Cypereae.

TAXONOMIC TREATMENT

Cyperus L. (Linnaeus 1753: 44).

Abildgaardia subg. *Androtrichum* Brongn. (Brongniart 1833: 176). – *Androtrichum* (Brongn.) Brongn. (Brongniart 1834: 177). Type species – *Abildgaardia polyccephala* Brongn.

Comostemum Nees (Nees von Esenbeck 1834: 283). Type species – *Comostemum montevidense* (Link) Nees.

Androcoma Nees (Nees von Esenbeck 1840: 396). Type species – *Androcoma speciosa* Nees.

“*Megarrhena* Schrad. ex Nees” (Nees von Esenbeck 1842: 5), nom. nud. pro syn.

Cyperus byssaceus Pereira-Silva, nom. nov.

Scirpus giganteus Kunth, *Enumeratio Plantarum Omnit Hucusque Cognitarum* 2: 172. 1837 (Kunth 1837). – *Androtrichum giganteum* (Kunth) H.Pfeiff. (Pfeiffer 1940: 185). **Type** – Brazil: *Sellow s.n.* (holotype: B†, probably destroyed during the war). **Neotype, designated here** – Brazil: Santa Catarina, Araranguá, 17 Nov. 1971, J.C. Lindeman s.n., (neotype: ICN[ICN00010374]; isoneotype: U[U.1601303, <https://data.biodiversitydata.nl/naturalis/specimen/U.1601303>]).

Androcoma speciosa Nees (Nees 1840: 397). – *Androtrichum speciosum* (Nees) Herter (Herter 1953: 163). **Type** – Argentina: *Tweedie s.n.* (holotype: K[K000874231]).

Figs 1A–B, 2A–C

Description – Caespitose perennial 80–170 cm tall. Culm 70–130 cm × 7.5–25 mm, trigonous, smooth. Leaves 70–150(–200) cm × 13–35 mm, leathery, v-shaped, scabrous, transversal septa present. Involucral bracts 5–12; lowermost bract 35–90(–150) cm × 20–35 mm, leaf-like, scabrous margins. Inflorescence a terminal lax anthela with several capitate partial inflorescences up to third order; primary branches 10–15, lowermost branches 8–25 cm long. Spikelets 4–8 × 2–2.5 mm, with 8–15 glumes; rachilla persistent. Glumes (2.6–)2.9–4.8 mm long, spirally arranged, deciduous, slightly mucronate, mucro up to 0.7 mm long, reddish stramineous to reddish light brown. Stamens 3, filaments reddish brown, strongly elongating after flowering; anthers 1–2 mm long. Style deeply trifid; style base slightly thickened, persistent. Achenes 0.9–1.2 × 0.3–0.5 mm, elliptical to narrow obovate, trigonous, brown, surface puncticulate.

Distribution and ecology – *Cyperus byssaceus* occurs in Argentina, southern Brazil, Paraguay, and Uruguay (Govaerts et al. 2020). It is most often found in large populations in silted marshes and along the banks of creeks and small streams.

Notes – Based on Article 53 of the ICN (Turland et al. 2018), the new name *Cyperus byssaceus* is proposed for *A. giganteum*, since the name *Cyperus giganteus* Vahl (Vahl 1805) is an earlier validly published name of another species. The epithet “*byssaceus*” was given due to the filamentous appearance of the inflorescence caused by the elongation of the stamen filaments.

Additional material examined – Argentina: Buenos Aires: Campana, 27 Nov. 1938, W.J. Eyerdam & A.A. Beetle 23098 (K); Punta Lara, 29 Dec. 1946, B. Sparre s.n. (K). Corrien-

tes: Dep. San Martin, 9 Dec. 1992, S.G. Tressens et al. 4292 (K); Mburucuyá, 10 Nov. 1950, T.M. Pedersen 834 (K).

Brazil: Santa Catarina: Garopaba, 28 Jan. 2005, S.M. Hefler & G.H. Silveira 702 (ICN); Penha, 15 Nov. 1993, F. Steinbach s.n. (FURB). **Rio Grande do Sul:** Guaíba, 4 Oct. 2009, N.I. Matzenbacher 3063 (ICN); Osório, 20 Nov. 2014, M.R. Baéz-L. 190 (ICN); Porto Alegre, 10 Nov. 2008, R. Setubal & R. Trevisan 708 (ICN); Terra de Areia, 18 Mar. 2008, R. Trevisan 953 (ICN); Torres, 11 Jul. 1972, B. Irang & A. Girardi s.n. (ICN); Torres, 20 Nov. 2015, R. Trevisan 1673 (FLOR); Viamão, 4 Jan. 2007, R. Trevisan et al. 817 (ICN).

Cyperus trigynus Spreng., *Systema Vegetabilium, editio decima sexta* 1: 216. 1824 (Sprengel 1824). – *Androtrichum trigynum* (Spreng.) H.Pfeiff (Pfeiffer 1937: 10). – *Eriophorum montevidense* Link (Link 1827: 331). – *Trichophorum montevidense* (Link) G.Don (Don 1830: 468). – *Comostemum montevidense* (Link) Nees (Nees von Esenbeck 1834: 283). – *Androtrichum montevidense* (Link) Schrad. (Schrader 1835: [1]). – *Scirpus montevideensis* (Link) C.B.Clarke, nom. illeg. (Clarke 1908: 89). **Type** – Uruguay: Montevideo, Sellow s.n. (holotype: B†, probably destroyed during the war). **Lectotype, designated here:** K[K000632047]; isolectotypes: P[P00257445, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00257445>]; HAL[HAL0145793].

Cyperus preslii A.Dietr. (Dietrich 1833: 211). – *Cyperus globulifer* J.Presl & C.Presl (Presl & Presl 1828: 165), nom. illeg. – “*Comostemum globuliferum* (J.Presl & C.Presl) Nees” (Nees von Esenbeck 1842: 5), nom. inval. **Type** – Peru: “Habitat in montanis Huanoccensisibus Peruviae”, T. Haenke s.n. (holotype: probably PRC[PRC450357]).

Abildgaardia polyccephala Brongn. (Brongniart 1833: 176). – *Androtrichum polyccephalum* (Brongn.) Kunth (Kunth 1837: 250). **Type** – Brazil: Santa Catarina, Oct. 1822, J.S.C. Dumont d'Urville s.n. (holotype: P[P00257429, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00257429>]).

Cyperus abnormis Steud. (Steudel 1854: 43). **Type** – Country unknown: 1843, F.J. Chauvin 225 (holotype: P[P00257449, <http://coldb.mnhn.fr/catalognumber/mnhn/p/p00257449>]).

Figs 1C–E, 2C–D

Description – Rhizomatous perennial 30–130 cm tall; creeping rhizome. Culm 25–125 cm × (0.9–)1.3–3.5 mm, rounded, smooth. Leaves reduced to purple leaf sheaths. Involucral bracts rather short, lowermost bract 1–5 cm long, erect, boat-shaped. Inflorescence a ± pseudolateral contracted to lax anthela with several capitate partial inflorescences in first order; primary branches 4–15, lowermost branches (1.5–)3–12 cm long. Spikelets 4.5–9 × (1.7–)2.2–4 mm, with 6–20 glumes; rachilla persistent. Glumes 2.9–4.5 mm long, distichous, deciduous, slightly mucronate, mucro up to 0.5 mm long, reddish stramineous to reddish light brown. Stamens 3, filaments white, strongly elongating after flowering; anthers 1.3–2.5 mm long. Style deeply trifid; style base slightly thickened, persistent. Achenes 0.8–1.1 × (0.3–)0.4–0.5 mm, elliptical to narrow ovate, trigonous, with a short thick beak, brown, surface smooth.

Distribution and ecology – *Cyperus trigynus* occurs in Argentina, southern Brazil, and Uruguay (Govaerts et al. 2020). A halophytic plant, which is characteristic of the vegetation of coastal dunes. *Cyperus preslii* was described based on a specimen from Peru collected by Haenke. In the PRC herbarium, there is a Haenke specimen, however, the location of the collection is not mentioned, which makes it impossible to confirm whether this specimen is from Peru, since no other record of this species has been made for this country (see also Pfeiffer 1937).

Notes – Both the protologue of *Cyperus trigynus* and of *Eriophorum montevidense* state that the description was based on a specimen from Montevideo. The protologue of *E. montevidense* further details it to be a Sellow specimen. The original material was studied at the B herbarium, with duplicates (labelled as such) sent to K and P. The original material was likely destroyed during the war, leading to the name *C. trigynus* here being lectotypified with the K specimen. *Eriophorum montevidense* is here explicitly synonymised with *C. trigynus* as both species were very likely described from the same material at B.

Additional material examined – **Argentina: Buenos Aires:** General Juan Madariaga, 4 Mar. 1961, A. Burkart 22377 (K); Villa Gesell, 12 Jan. 1974, E.A. Ulbarri 563 (K); Villa Gesell, 26 Dec. 1982, P. Goetghebeur 4764 (GENT, K).

Brazil: Paraná: Paranaguá, 27 Nov. 1970, G. Hatschbach et al. 25657 (K); Paranaguá, 20 Oct. 2017, M.G. Nunes & P.C. Ferreira 88 (FLOR); Pontal do Paraná, 3 Oct. 1966, J.C. Lindeman & J.H. Hass 2623 (K). **Santa Catarina:** Balneário Arroio do Silva, 12 Nov. 2017, L. Pereira-Silva & R. Trevisan 143 (FLOR); Florianópolis, 20 Oct. 1965, Klein & Bre-solin 6307 (FLOR); Florianópolis, 27 Nov. 2014, L.A. Funez 3388 (FURB); Içara, 9 Dec. 2010, A. Korte & M.J. Rigon-Júnior 5566 (FURB); Imbituba, 7 Nov. 2007, R. Martins 111 (FLOR); Palhoça, 2 Dec. 2010, A. Korte 5387 (FLOR, FURB). **Rio Grande do Sul:** Palmares do Sul, 27 Nov. 2011, F. Gonzatti 276 (FLOR); Rio Grande, 19 Jan. 2005, S.M. Hefler 669 (ICN); Terra de Areia, 18 Mar. 2008, R. Trevisan 955 (ICN); Torres, 24 Nov. 2006, A.C. Araújo & G.S. Ven-druscolo 1691 (ICN, K); Tramandaí, 21 Jan. 2010, R. Trevisan 1047 (ICN); Viamão, 10 Nov. 2005, R. Trevisan 471 (ICN); Viamão, 20 Nov. 2006, R. Trevisan et al. 721 (ICN).

Uruguay: 1816–1821, A. de Saint-Hilaire 2359 (K).

CONCLUSION

After a long period of taxonomic uncertainty, by integrating recent molecular phylogenetic data with additional evidence from morphology and anatomy, *Androtrichum* is combined into *Cyperus*. As a result of this taxonomic change, a single monophyletic genus *Cyperus* is now recognised in the *Cyperus* Clade of tribe Cypereae.

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REFERENCES

- Bauters K., Larridon I., Reynders M., Asselman P., Vrijdaghs A., Muasya A.M., Simpson D.A., Goetghebeur P. (2014) A new classification for *Lipocarpha* and *Volkviella* as infrageneric taxa of *Cyperus* s.l. (Cypereae, Cyperoideae, Cyperaceae): insights from species tree reconstruction supplemented with morphological and floral developmental data. *Phytotaxa* 166: 1–32. <https://doi.org/10.11646/phytotaxa.166.1.1>
- Brongniart A.T. (1829–1834) Phanérogamie. In: Dupperey L.M.I. (ed.) Voyage autour du monde. Botanique. Paris, Bertrand. Available at <https://www.biodiversitylibrary.org/page/10349365#page/3/mode/1up> [accessed 15 Aug. 2020].
- Bukatsch F. (1972) Bemerkungen zur doppelfärbung astrablau-safranin. *Mikrokosmos* 6: 255.
- Clarke C.B. (1908) New genera and species of Cyperaceae. *Bulletin of Miscellaneous Information Additional Series* 8: 1–196.
- Denton M.F. (1983) Anatomical studies of the “Luzulæ” group of *Cyperus* (Cyperaceae). *Systematic Botany* 8(3): 250–262. <https://doi.org/10.2307/2418479>
- Dietrich A.G. (1833) Species Plantarum ed. 6, Tom. I, Pars. I, Sec-tio II. Berlin. Available at <https://www.biodiversitylibrary.org/page/59124007#page/761/mode/1up> [accessed 15 Aug. 2020].
- Don G. (1830) Loudon’s Hortus Britannicus. London, Longman, Rees, Orme, Brown, and Green. <https://doi.org/10.5962/bhl.title.10320>
- Elliott T.L., Muasya A.M. (2017) Taxonomic realignment in the southern African *Tetraria* (Cyperaceae, tribe Schoeneae; *Schoenus* clade). *South African Journal of Botany* 112: 354–360. <https://doi.org/10.1016/j.sajb.2017.06.011>
- Escudero M., Hipp. A.L. (2013) Shifts in diversification rates and clade ages explain species richness in higher-level sedge taxa (Cyperaceae). *American Journal of Botany* 100(12): 2403–2411. <https://doi.org/10.3732/ajb.1300162>
- Global Carex Group (2015) Making *Carex* monophyletic (Cyperaceae, tribe Cariceae): a new broader circumscription. *Botanical Journal of the Linnean Society* 179(1): 1–42. <https://doi.org/10.1111/boj.12298>
- Goetghebeur P. (1986) Genera Cyperacearum. Een bijdrage tot de kennis van de morfologie, systematiek en fylogeneze van de Cyperaceae-genera. PhD thesis. Ghent University, Belgium.
- Goetghebeur P. (1998) Cyperaceae. In: Kubitzki K. (ed.) The families and genera of vascular plants vol. 4: 141–190. Berlin, Springer-Verlag.
- Govaerts R., Simpson D.A., Goetghebeur P., Wilson K.L., Egorova T., Bruhl J.J. (2007) World checklist of Cyperaceae. Sedges. London, Kew Publishing, Royal Botanic Gardens, Kew.
- Govaerts R., Jiménez-Mejías P., Koopman J., Simpson D.A., Goetghebeur P., Wilson K.L., Egorova T., Bruhl J.J. (2020) World checklist of Cyperaceae online. Facilitated by the Royal Botanic Gardens, Kew. Available at <http://wcsp.science.kew.org/> [accessed 13 Jan. 2020].
- Heftler S.M., Longhi-Wagner H.M. (2010) A contribuição da anatomia foliar para taxonomia das espécies de *Cyperus* L. subg. *Cyperus* (Cyperaceae) ocorrentes no Sul do Brasil. *Acta Botanica Brasiliensis* 24(3): 708–717. <https://doi.org/10.1590/S0102-33062010000300014>
- Herter W.G. (1953) Flora del Uruguay V. Glumiflorae III. *Revista Sudamericana de Botanica* 9(5): 129–173.
- Johansen D.A. (1940) Plant Microtechnique. Principles and Practice. New York, McGraw-Hill.
- Kunth C.S. (1837) *Enumeratio Plantarum* vol. 2: Cyperaceae Juss., Brown, Nees ab Esenb. Stuttgart & Tübingen, Sumtibus J.G. Cottae. Available at <https://www.biodiversitylibrary.org/page/742806#page/9/mode/1up> [accessed 15 Aug. 2020].
- Larridon I., Reynders M., Huygh W., Bauters K., Van de Putte K., Muasya A.M., Boeckx P., Simpson D.A., Vrijdaghs A., Goetghebeur P. (2011a) Affinities in *C₃ Cyperus* lineages (Cyperaceae) revealed using molecular phylogenetic data and carbon isotope analysis. *Botanical Journal of the Linnean Society* 167(1): 19–46. <https://doi.org/10.1111/j.1095-8339.2011.01160.x>
- Larridon I., Reynders M., Huygh W., Bauters K., Vrijdaghs A., Leroux O., Muasya A.M., Simpson D.A., Goetghebeur P. (2011b) Taxonomic changes in *C₃ Cyperus* (Cyperaceae) supported by molecular phylogenetic data, morphology, embryology, ontogeny and anatomy. *Plant Ecology and Evolution* 144(3): 327–356. <https://doi.org/10.5091/plecevo.2011.653>
- Larridon I., Bauters K., Reynders M., Huygh W., Muasya A.M., Simpson D.A., Goetghebeur P. (2013) Towards a new classification of the giant paraphyletic genus *Cyperus* (Cyperaceae): phylogenetic relationships and generic delimitation in *C₄ Cyperus*. *Botanical Journal of the Linnean Society* 172(1): 106–126. <https://doi.org/10.1111/boj.12020>
- Larridon I., Bauters K., Reynders M., Huygh W., Goetghebeur P. (2014) Taxonomic changes in *C₄ Cyperus* (Cypereae, Cyperoideae, Cyperaceae): combining the sedge genera *Ascolepis*, *Kyllinga* and *Pycreus* into *Cyperus* s.l. *Phytotaxa* 166(1): 33–48. <https://doi.org/10.11646/phytotaxa.166.1.2>
- Larridon I., Bauters K., Semmouri I., Viljoen J.A., Prychida C.J., Muasya A.M., Bruhl J.J., Wilson K.L., Senterre B., Goetghebeur P. (2018) Molecular phylogenetics of the genus *Costularia* (Schoeneae, Cyperaceae) reveals multiple distinct evolutionary lineages. *Molecular Phylogenetics and Evolution* 126: 196–209. <https://doi.org/10.1016/j.ympev.2018.04.016>
- Link J.H. (1827–1833) Hortus regius botanicus berolinensis, descriptus. Berlin, G. Reimer. Available at <https://www.biodiversitylibrary.org/page/46937276#page/343/mode/1up> [accessed 15 Aug. 2020].
- Linnaeus C. (1753) Species Plantarum vol. 1. Stockholm, Laurentius Salvius. Available at <http://www.biodiversitylibrary.org/item/13829> [accessed 15 Aug. 2020].
- Metcalfe C.R. (1971) Anatomy of the monocotyledons. V. Cyperaceae. Oxford, Clarendon Press.
- Muasya A.M., Simpson D.A., Chase M.W. (2002) Phylogenetic relationships in *Cyperus* L. s.l. (Cyperaceae) inferred from plastid DNA sequence data. *Botanical Journal of the Linnean Society* 138(2): 145–153. <https://doi.org/10.1046/j.1095-8339.2002.138002145.x>
- Muasya A.M., Simpson D.A., Verboom G.A., Goetghebeur P., Naczi R.F.C., Chase M.W., Smets E. (2009a) Phylogeny of Cyperaceae based on DNA sequence data: current progress and future prospects. *The Botanical Review* 75: 2–21. <https://doi.org/10.1007/s12229-008-9019-3>
- Muasya A.M., Vrijdaghs A., Simpson D.A., Chase M.W., Goetghebeur P., Smets E. (2009b) What is a genus in Cyperaceae: phylogeny, character homology assessment and generic circumscription in Cyperaceae. *The Botanical Review* 75: 52–66. <https://doi.org/10.1007/s12229-008-9018-4>
- Nees von Esenbeck C.G.D. (1834) Uebersicht der Cyperaceengattungen. *Linnaea* 9: 273–306. Available at <https://www.biodiversitylibrary.org/page/2011#page/1/mode/1up> [accessed 15 Aug. 2020].

- Nees von Esenbeck C.G.D. (1840) Cyperaceae a Schomburgkio in Guiana Anglica collectae, ex herbario Lindleyano. *Journal of Botany* 2: 393–397. Available at <https://www.biodiversitylibrary.org/item/6309#page/2/mode/1up> [accessed 15 Aug. 2020].
- Nees von Esenbeck C.G.D. (1842) Flora Brasiliensis Cyperographia. In: von Martius C.F.P. (ed.) *Flora Brasiliensis* vol. 2(1). Munich & Leipzig, R. Oldenbourg.
- Pfeiffer H. (1937) *Androtrichum trigynum* (Spreng.) H.Pfeiff. Ein oft verkanntes, halophiles Sauergras Südamerikas. *Repertorium Novarum Specierum Regni Vegetabilis* 42(1–10): 10–14. <https://doi.org/10.1002/fedr.19370420105>
- Pfeiffer H. (1940) Untersuchungen an der Cyperaceengattung *Androtrichum* Brongn. *Revista Sudamerica de Botanica* 6: 179–186.
- Presl J., Presl C. (1828) Reliquiae Haenkeanae, seu descriptiones et icones plantarum quas in America Meridionali et Boreali. Prague, J.G. Calve. Available at <https://www.biodiversitylibrary.org/page/390804#page/2/mode/1up> [accessed 15 Aug. 2020].
- Roalson E.H., Prata A.P., Mesterházy A., Chase M.W., Simpson D.A., Thomas W.W., Larridon I. (2019) A broader circumscription of *Bulbostylis* including *Nemum* (Abildgaardieae: Cyperaceae). *Phytotaxa* 395: 199–208. <https://doi.org/10.11646/phytotaxa.395.3.4>
- Schrader H.A. (1835) Index Seminum Horti Academicici Gottingensis. Gottingen.
- Seemmouri I., Bauters K., Léveillé-Bourret E., Starr J.R., Goetghebeur P., Larridon I. (2019) Phylogeny and systematics of Cyperaceae, the evolution and importance of embryo morphology. *The Botanical Review* 85(1): 1–39. <https://doi.org/10.1007/s12229-018-9202-0>
- Simpson D.A., Muasya A.M., Alves M., Bruhl J.J., Dhooge S., Chase, M.W., Furness C.A., Ghamkhar K., Goetghebeur P., Hodgkinson, T.R., Marchant A.D., Reznicek A.A., Nieuwborg R., Roalson E.H., Smets E., Starr J.R., Thomas W.W., Wilson K.L., Zhang X. (2007) Phylogeny of Cyperaceae based on DNA sequence data – a new *rbcL* analysis. *Aliso* 23: 72–83.
- Sprengel C.P.J. (1824) *Systema Vegetabilium*, editio decima sexta 1. Göttingen. Available at <https://www.biodiversitylibrary.org/page/6720283#page/1/mode/1up> [accessed 15 Aug. 2020].
- Steudel E.G. von (1854–1855) *Synopsis plantarum glumacearum* 2. Cyperaceae. J.B. Metzler, Stuttgart.
- Thiers B. (continuously updated) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available at <http://sweetgum.nybg.org/ih/> [accessed 29 Jan. 2020].
- Turland N.J., Wiersema J.H., Barrie F.R., Greuter W., Hawksworth D.L., Herendeen P.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. Glashütten, Koeltz Botanical Books. <https://doi.org/10.12705/Code.2018>
- Vahl M. (1805) *Enumeratio plantarum* 2. Impenis Viduae, Copenhagen. Available at <https://www.biodiversitylibrary.org/page/546730#page/1/mode/1up> [accessed 15 Aug. 2020].
- Van der Veken P. (1965) Contribution à l'embryographie systématique des Cyperaceae-Cyphoideae. *Bulletin du Jardin Botanique de l'État à Bruxelles* 35(3): 285–354. <https://doi.org/10.2307/3667185>

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