

Phylogenetic analysis and taxonomic position of section *Verrucosa* of *Panicum* and its relationship with taxa of the *Sacciolepis*–*Trichantheium* clade (Poaceae: Panicoideae: Paniceae)

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Abstract The new genus *Kellochloa* is proposed, on the basis of morphological and molecular characters, to include two North American species of *Panicum* s.l., previously classified in sect. *Verrucosa*: *P. brachyanthum* and *P. verrucosum*. Both species are annual, with decumbent culms branching divaricately at the lower nodes, and erect culms with terminal and axillary inflorescences. The spikelets are pilose, with lower glume 1/6 to 1/4 the length of the spikelet, upper glume and lower lemma subequal, 3–5-nerved, the lower antheridium reduced to the lower lemma, and upper antheridium indurate, with bicellular microhairs and simple papillae evenly distributed all over the lemma and palea. Molecular phylogenetic studies, analyzing plastid *ndhF* and *rpoA* sequences, confirmed that these morphological characters are differential. The phylogenetic position and taxonomic features of the new genus are established and compared with *Panicum* s.str. and other taxa of the *Sacciolepis*–*Trichantheium* clade. Full synonymies and descriptions, a distribution map, illustrations of both species, and a key are provided. Two new combinations are proposed. In addition, four African ungrouped species of *Panicum* s.l. were, for the first time, included in the phylogenetic analysis to analyze their relationship with the new genus and its positions in the *Sacciolepis*–*Trichantheium* clade.

Keywords *Kellochloa* · Paniceae · *Panicum* · Phylogeny · Taxonomy · *Verrucosa*

Introduction

Panicum L., as traditionally circumscribed, was one of the largest genera of the Poaceae (Webster 1988). It included approximately 450 species distributed worldwide in different tropical and subtropical habitats, such as savannas, grasslands in dry or wet areas, streamsides, and forest edges, from sea level to approximately 2500 m (Zuloaga 1987). On the basis of inflorescence and spikelet characters, Hitchcock and Chase (1910) recognized two subgenera and 13 informal species groups of *Panicum* in North America. Zuloaga (1987) provided an infrageneric classification of the New World *Panicum* species, based on morphological characters, such as ornamentation of the upper antheridium, photosynthetic type, spikelet characters, and chromosome base number. Zuloaga (1987) recognized six New World subgenera within *Panicum*: *Panicum*, *Agrostoides* (Hitchc.) Zuloaga, *Megathyrsus* Pilg., *Phanopyrum* (Raf.) Pilg., *Dichantheium* Hitchc. & Chase, and *Steinchisma* (Raf.) Zuloaga. Although the spikelets of *Panicum*, as traditionally circumscribed, are largely uniform, this feature contrasts with the variation present in several reproductive (including inflorescence type, nervation of glumes, and upper antheridium texture and ornamentation) and vegetative characters, together with the preferred habitat of the different species (Crins 1991). The infrageneric variation in vegetative characters is related to the presence of all known photosynthetic types found in grasses. *Panicum* included species with non-Kranz and Kranz physiology with all Kranz variations, i.e., NADP-me, NAD-me, and PEP-ck subtypes (Brown 1977;

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Hattersley 1987; Ellis 1988). These photosynthetic types are correlated with particular anatomical characters, e.g., number of vascular bundles, and presence of specialized chloroplasts in the parenchymatic or mestomatic bundles (Brown 1977; Ellis 1977).

Phylogenetic studies, based on morphological and molecular characters, have firmly demonstrated that *Panicum* in its traditional sense is not monophyletic (Gómez-Martínez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001, 2003; Giussani et al. 2001; Aliscioni et al. 2003). These studies allowed new delimitations within the Paniceae, such as the recognition of four genera, previously treated by Zuloaga (1987) at subgeneric level: *Dichantheium* (Hitchc. and Chase) Gould, *Phanopyrum* (Raf.) Nash, *Steinchisma* Raf., and *Megathyrsus* (Pilg.) B.K.Simon & S.W.L.Jacobs (Zuloaga et al. 1998, 2003; Aliscioni et al. 2003; Freckmann and Lelong 2003; Simon and Jacobs 2003; Barkworth 2004).

In a phylogenetic study of *Panicum* based on the *ndhF* chloroplast gene, Aliscioni et al. (2003) restricted *Panicum*, in a strict sense, to the type subgenus, which was strongly supported as a monophyletic group. Hsu (1965), Brown (1977), and Zuloaga (1987), previously treated subgenus *Panicum* as a homogeneous group clearly distinguishable from other elements of the genus. Species of subgenus *Panicum* are C₄, of the NAD-me subtype, and have a basic chromosome number of $x = 9$. Therefore, as *Panicum* is currently restricted to subg. *Panicum*, species treated by Zuloaga (1987) in subg. *Phanopyrum*, including among them section *Verrucosa*, need to be reevaluated and reclassified within the Paniceae.

The group *Verrucosa* was established by Hitchcock and Chase (1910) who included two North American species, both with tuberculate spikelets: *Panicum brachyanthum* Steud. and *P. verrucosum* Muhl. Hitchcock and Chase (1910) characterized these species as being annuals, with divaricately branching culms, panicles lax and open, and spikelets hispid, with the fruit minutely papillose. Later, Hsu (1965) raised this group to a section of *Panicum*, and Zuloaga (1987) classified *Panicum* sect. *Verrucosa* in subg. *Phanopyrum*, and characterized the section as comprising annual plants with the panicles lax and diffuse, spikelets pilose, with a minute nerveless lower glume, upper glume and lower lemma subequal, 3–5-nerved, lower palea and lower flower absent, and upper antherium longitudinally rugose, papillate and with bicellular microhairs. In the *ndhF* phylogeny of the Paniceae, Aliscioni et al. (2003) included one voucher of *Panicum verrucosum*, which appeared in a clade together with *Sacciolepis indica* (L.) Chase, *Panicum parvifolium* Lam., and *Panicum schwackeanum* Mez, the latter two species now included in the genus *Trichantheium* Zuloaga & Morrone. Zuloaga et al. (2011) treated in *Trichantheium*, on the basis of

morphological and molecular (*rpoA* and *ndhF* sequences) characters, 38 American and African species of *Panicum* sects. *Parvifolia* and *Verruculosa*; the combined phylogenetic tree (Zuloaga et al. 2011) showed *P. verrucosum* grouped in an unresolved trichotomy with the genera *Sacciolepis* Nash and *Trichantheium*, with *P. trichanthum* as the sister species of this trichotomy. *Panicum* species assigned to sections *Ovalifolia* and *Monticola* appeared as the sister group of the entire *Sacciolepis*–*Trichantheium* clade. Finally, Morrone et al. (2012) corroborated the position of *P. verrucosum*, together with *Sacciolepis*, *Trichantheium*, and species of sections *Ovalifolia* and *Monticola*, in subtribe B, an unnamed clade of Paniceae, still under revision.

The purpose of the present contribution is to test the monophyly of sect. *Verrucosa* of *Panicum* s.l and to establish the position of this section within the *Sacciolepis*–*Trichantheium* clade of the Paniceae, analyzing *ndhF* and *rpoA* sequence data and describing morphological and anatomical characters. Additionally, four “incertae sedis” African species of *Panicum*, presumably belonging to the *Sacciolepis*–*Trichantheium* clade, were included in the phylogenetic analysis: *P. aequinerve* Nees, *P. chionachne* Mez, *P. eickii* Mez, and *P. inaequilatum* Stapf. These species were studied to test their position within the *Sacciolepis*–*Trichantheium* clade and their hypothetical relationship with species of section *Verrucosa*.

Materials and methods

Molecular phylogenetic analysis

Taxa selection

Six new taxa were analyzed: two species assigned to sect. *Verrucosa* (*Panicum brachyanthum* and *P. verrucosum*) and four “incertae sedis” species of *Panicum* presumably belonging to the *Sacciolepis*–*Trichantheium* clade: *P. aequinerve*, *P. chionachne*, *P. eickii*, and *P. inaequilatum*. We added *rpoA* and *ndhF* sequences obtained for these six taxa into the combined matrix of the *Sacciolepis*–*Trichantheium* clade from Zuloaga et al. (2011). The aligned matrix was submitted to TreeBASE under the study number S16511. Details, GenBank accessions, and voucher information of taxa analyzed are shown in the “Appendix”.

DNA sequencing

All six vouchers analyzed were from herbarium material. DNA extraction was conducted using the DNeasy Plant Mini kit (Quiagen). The complete *ndhF* gene was amplified using four pairs of primers specified by Olmstead and

Sweere (1994): 5F-536R, 536F-972F, 972F-1666R, and 1666F-3R. The *rpoA* region amplified consisted of an approximately 1400 bp fragment containing the entire *rpoA* gene, the 3'-end of *petD* encoding subunit IV of the cytochrome b complex, the 3'-end of *rps11* encoding ribosomal protein S11, and the two intergenic spacers IGS between *rpoA* and *petD* and between *rpoA* and *rps11*. Two pairs of primers were used: RPOA1-RPOA6 and RPOA5-RPOA2, designed by Petersen and Seberg (1997). The PCR reactions were performed in 25 µl final volume with 50–100 ng of template DNA, 0.2 µM of each primer, 25 µM of dNTPs, 5 µM MgCl₂, 1× buffer, and 1.5 units of Taq polymerase provided by Invitrogen (Brazil). The reaction conditions were: an initial period of denaturation at 94 °C for 5 min, followed by 35 cycles of denaturation at 94 °C for 30 s., annealing at 48 °C for 1 min, and extension at 72 °C for 1 min. 30 s., and a final extension at 72 °C for 6 min terminated the reactions. PCR products were run out on a 1 % TBE agarose gel and stained.

Sequencing reactions were performed by Macrogen, Inc. (Seoul, Korea). To edit and manually align the sequences, we used the program BioEdit version 5.0.9 (Hall 1999). The sequences obtained were submitted to GenBank (KR232090–KR232100).

Data analyses

A maximum parsimony analysis was performed using TNT (Goloboff et al. 2008) with all characters equally weighted with respect to codon position and gaps scored as missing data. Searches were performed using 1000 random addition sequences (ras) followed by tree bisection–reconnection (TBR), saving 10 trees per ras. The shortest trees retained were then TBR swapped holding a maximum of 20,000 trees. A strict consensus tree was generated from the most parsimonious trees. To assess the relative support for clades, bootstrap analyses were performed using 10,000 replicates of the matrix, heuristic searches were done using 100 ras, holding 5 trees per ras and TBR swapping.

A Bayesian inference analysis was also performed with BEAUti and BEAST 1.8.1 (Drummond et al. 2012). The appropriate model of nucleotide substitution for each partition was selected by the Akaike Information Criterion (AIC) implemented in jModelTest 2.1.4 (Darriba et al. 2012). The Bayesian analysis was conducted with settings as follows: GTR+I+G and TVM+I+G substitution models for *ndhF* and *rpoA* partitions, respectively, four gamma categories, empirical base frequencies, uncorrelated rate variation with lognormal distribution, random starting tree, a Yule process as tree prior, auto-optimization option for all operators except the GTR A-G substitution parameter deactivated for the *rpoA* partition to achieve a TVM model, and default values for all other settings. Two independent

runs of 10 million generations were sampled every 1,000th generation. Convergence of the chain and effective sample size of the parameters (i.e. ESS > 200) were checked in Tracer 1.6 (Rambaut et al. 2014). The two runs were combined with LogCombiner 1.8.1 (Drummond et al. 2012) after a burn-in of 25 % of the trees from each run. Posterior probabilities of branches were calculated from a maximum clade credibility tree obtained with TreeAnnotator 1.8.1 (Drummond et al. 2012) and edited in FigTree 1.4.2 (<http://tree.bio.ed.ac.uk/software/figtree/>).

Morphological and anatomical analyses

Morphological characters were based on examination of herbarium collections and published accounts. Specimens belonging to the following herbaria were examined: MO, P, PH, SI, US, and WIS (acronyms after Thiers 2014, permanently updated).

Micromorphological observations were based on herbarium material. For anatomical studies, the second leaf below the inflorescence was selected. Specimens compared were Tryon 4547 and Moore 49-698 of *P. verrucosum* and Dale 4728 and Moore 49-714 of *P. brachyanthum*. Cross-sectional leaf anatomy was determined from hand-sectioned leaf blades of herbarium specimens rehydrated by boiling in water with soap and subsequently stored in 70 % alcohol. The materials were dehydrated in an ethanol series and embedded in Histoplast (Johansen 1940; Ruzin 1999) to obtain serial microtome sections, 10–20 µm thick. The slides were stained in Safranin-fast green (D'Ambrogio de Argüeso 1986; Ruzin 1999) and mounted in synthetic resin (Eukitt) for permanent slides.

Freehand paradermal sections were taken from each leaf surface. Half of the transverse sections and all paradermal sections were bleached in diluted household bleach until the sections became transparent, after which they were rinsed three or four times with water, stained with safranin for 30 min (Metcalf 1960), washed three times in water, and mounted gelatin–glycerin for temporary slides.

The epidermis was stained in safranin. Anatomical descriptions were prepared using the terminology of Ellis (1976, 1979).

The upper anthercia were selected and cleaned in xylene for 1.5 h with an ultrasonic cleaner (Cleanson, model CS 1106, Argentina). The material was air-dried, mounted, and coated with a gold–palladium (40–60 %) alloy by then observed using a Phillips XL 30 (Phillips, The Netherlands) Scanning Electron Microscope (SEM) at the Museo Bernardino Rivadavia (Zeiss, Germany).

The histological sections were studied and photographed with a compound microscope Wild M20, equipped with Nikon DS-U2 digital camera, and picture processing software NIC-Elements, F-package 2.30.

Results

Molecular phylogeny

The new sequences obtained for the six taxa analyzed were included in the combined *ndhF*–*rpoA* matrix of Zuloaga et al. (2011). The *rpoA* sequence of *Panicum aequinerve* could not be obtained. The combined matrix showed a total of 48 taxa and 3446 characters (2076 from *ndhF* and 1370 from *rpoA* data), being 258 parsimony-informative characters.

Parsimony analysis of the combined matrix yielded 80 trees of 457 steps (CI = 68, RI = 84). The strict consensus tree was fully congruent with the tree obtained under Bayesian inference. The Bayesian tree is shown in Fig. 1 indicating Bayesian posterior probabilities (PP) and parsimony bootstrap support (BS). The two species assigned to section *Verrucosa*, *Panicum brachyanthum* and *P. verrucosum*, form a strongly supported monophyletic group (BS = 100, PP = 100). Five molecular synapomorphies (at positions 509, 1469, 1844, 2259, and 2323 of the combined matrix) support this section.

Section *Verrucosa* appears with 100 % BS and 100 % PP as the sister group of the *Sacciolepis*–*Trichantheicum* clade; the latter including a 100 % supported clade formed by the four “incertae sedis” African species of *Panicum* (*P. aequinerve*, *P. inaequilatum*, *P. chionachne*, and *P. eickii*)

as the sister group of *Trichantheicum*. *Panicum trichanthum* appears as the sister species of the clade *Verrucosa*–*Sacciolepis*–*Trichantheicum*, while *Panicum* species of sections *Ovalifolia* and *Monticola* constitute the other clade of the subtribe B (sensu Morrone et al. 2012).

Morphology

Spikelets

Both *Panicum brachyanthum* and *P. verrucosum* have glumes and lower lemma with a distinctive coverage of hairs all over the surface, which were not analyzed previously. Both species have modified hairs on the glumes and lower lemma as follows: bracts in *P. brachyanthum* are covered by tuberculate hairs, with macrohairs arising from a cushion base, formed by thickened and modified epidermal cells (Figs. 2d, e, 4a, b), while in *P. verrucosum* prickly hairs arise from a similar cushion base (Figs. 3d, e, 4c, d). The upper antherium is indurate, with bicellular microhairs and simple papillae regularly distributed all over the surface in both species (Fig. 5c, d); *P. verrucosum* differs (Fig. 5a, b) by having thickened longitudinal and transverse walls (vs. eventually thickened on the margins of the upper lemma, otherwise smooth in *P. brachyanthum*).

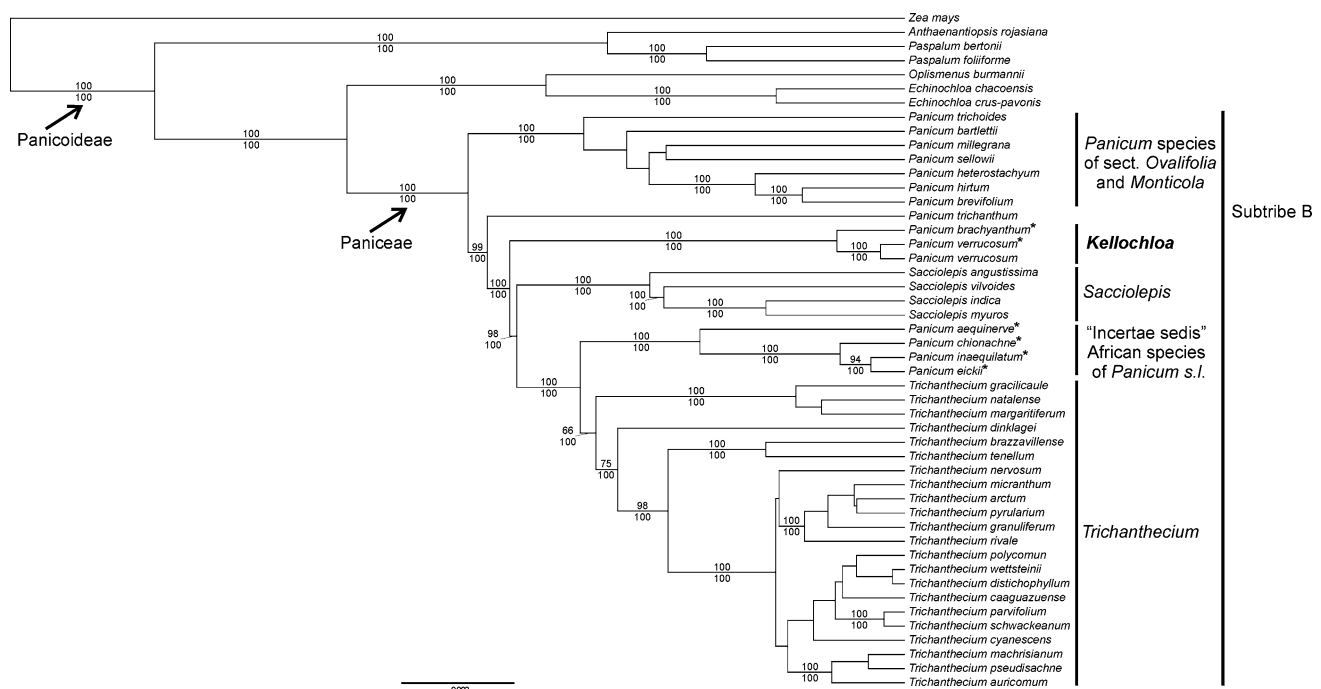


Fig. 1 Phylogenetic tree from Bayesian analysis based on the combined plastid sequences (*ndhF* + *rpoA*). Vouchers sequenced for this study are denoted by asterisks. Numbers above and below branches indicate Bayesian posterior probabilities and parsimony

bootstrap values, respectively. Vertical bars correspond to principal clades as discussed in the text. The scale bar represents substitutions per site

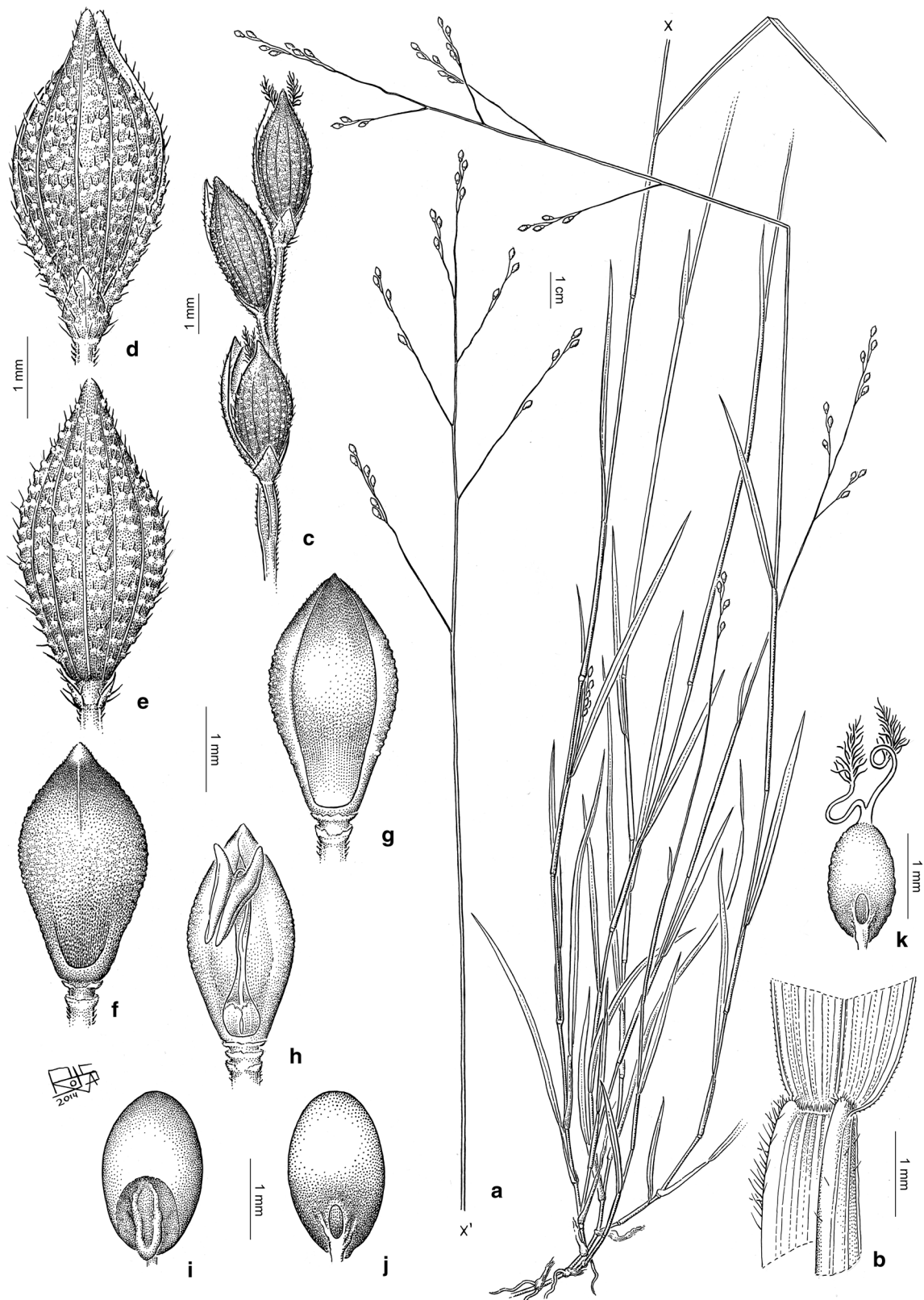


Fig. 2 *Kellochloa brachyantha* (Stued.) Lizarazu, Nicola & Scatagliini. **a** Habit; **b** detail of ligule; **c** portion of a raceme; **d** spikelet ventral view; **e** spikelet, dorsal view; **f** upper antherium, dorsal view;

g upper antherium, ventral view; **h** upper palea with lodicules and stamens; **i** caryopsis, embryo view; **j** caryopsis, hilum view; **k** caryopsis immature, hilum view (from Gould 12002)

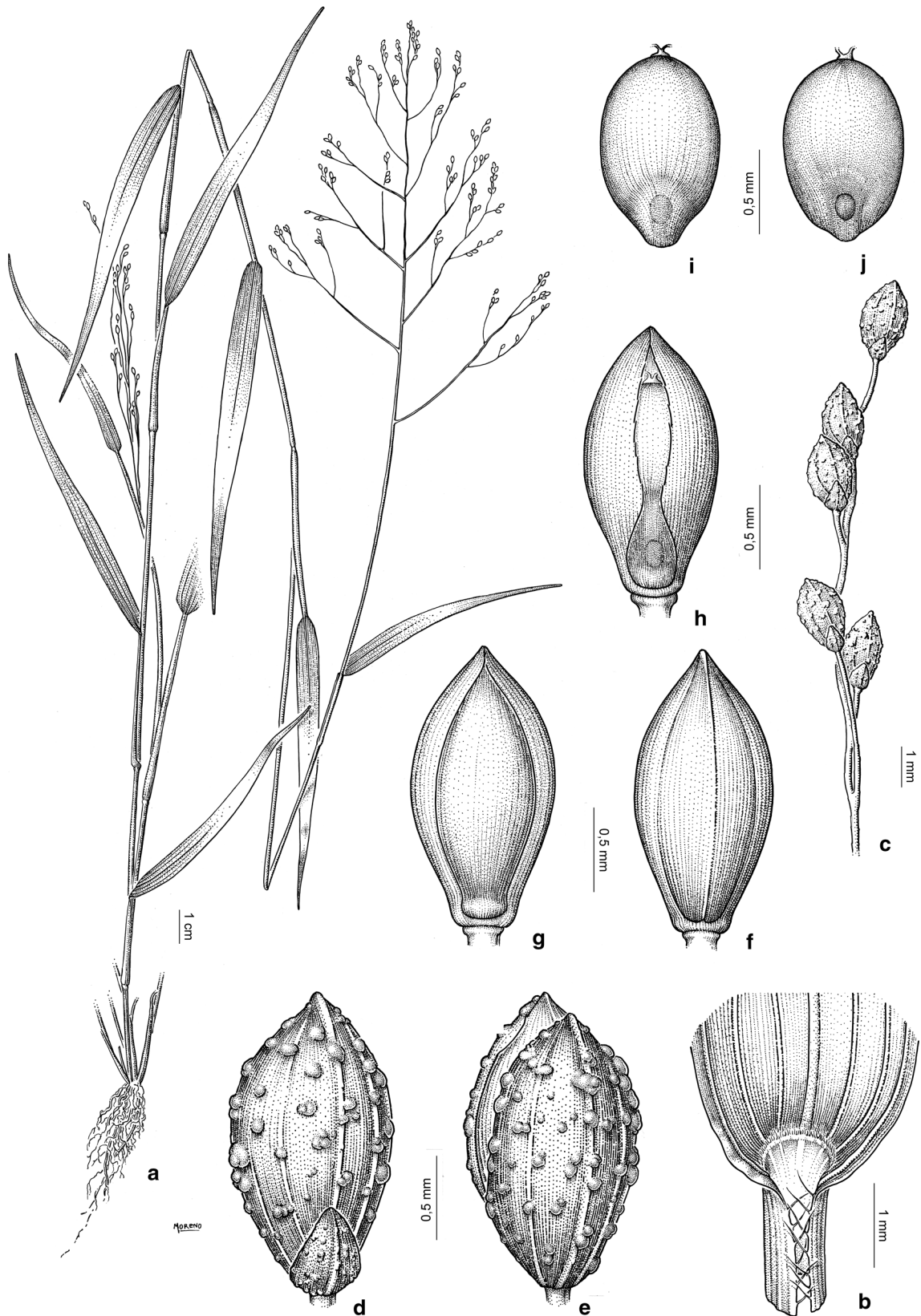
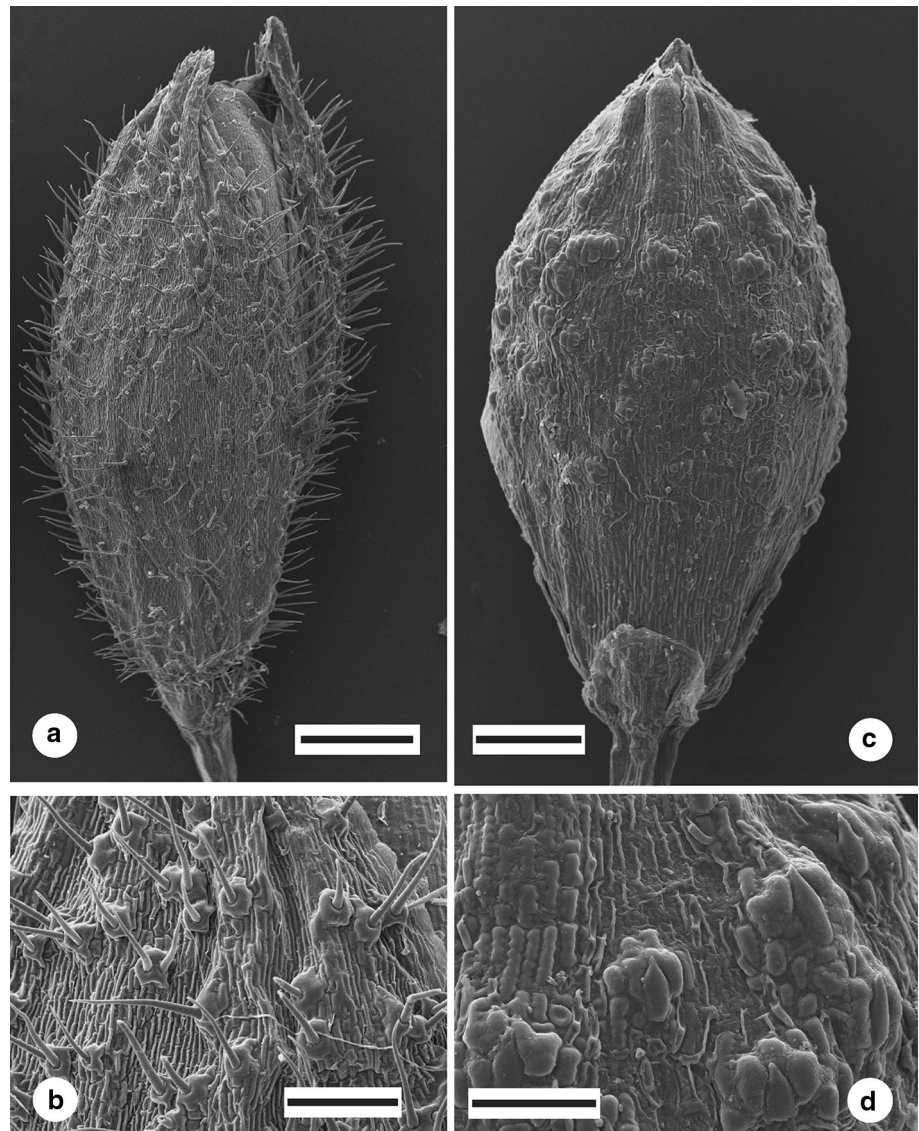


Fig. 3 *Kellochloa verrucosa* (Muhl.) Lizarazu, Nicola and Scatagliini. **a** Habit; **b** detail of ligular region; **c** spikelet ventral views; **d** spikelet ventral view; **e** spikelet, dorsal view; **f** upper antherium,

dorsal view; **g** upper antherium, ventral view; **h** upper palea with caryopsis; **i** caryopsis, embryo view; **j** caryopsis, hilum view (from Collins 114)

Fig. 4 Scanning electron micrographs of the spikelet of *Kelloggloa brachyantha* (**a**, **b**) and *K. verrucosa* (**c**, **d**). **a** Spikelet ventral view; **b** detail of the lower lemma with macrohairs, prickly hairs; **c** spikelet ventral view; **d** detail of the lower lemma with bicellular microhairs, prickly hairs. (**a**, **b** from *Hatch 1074* and **a–d** from *Brown 2698*). Scale bars **a** 500 μm ; **b** 200 μm ; **c** 250 μm ; **d** 100 μm



Anatomy

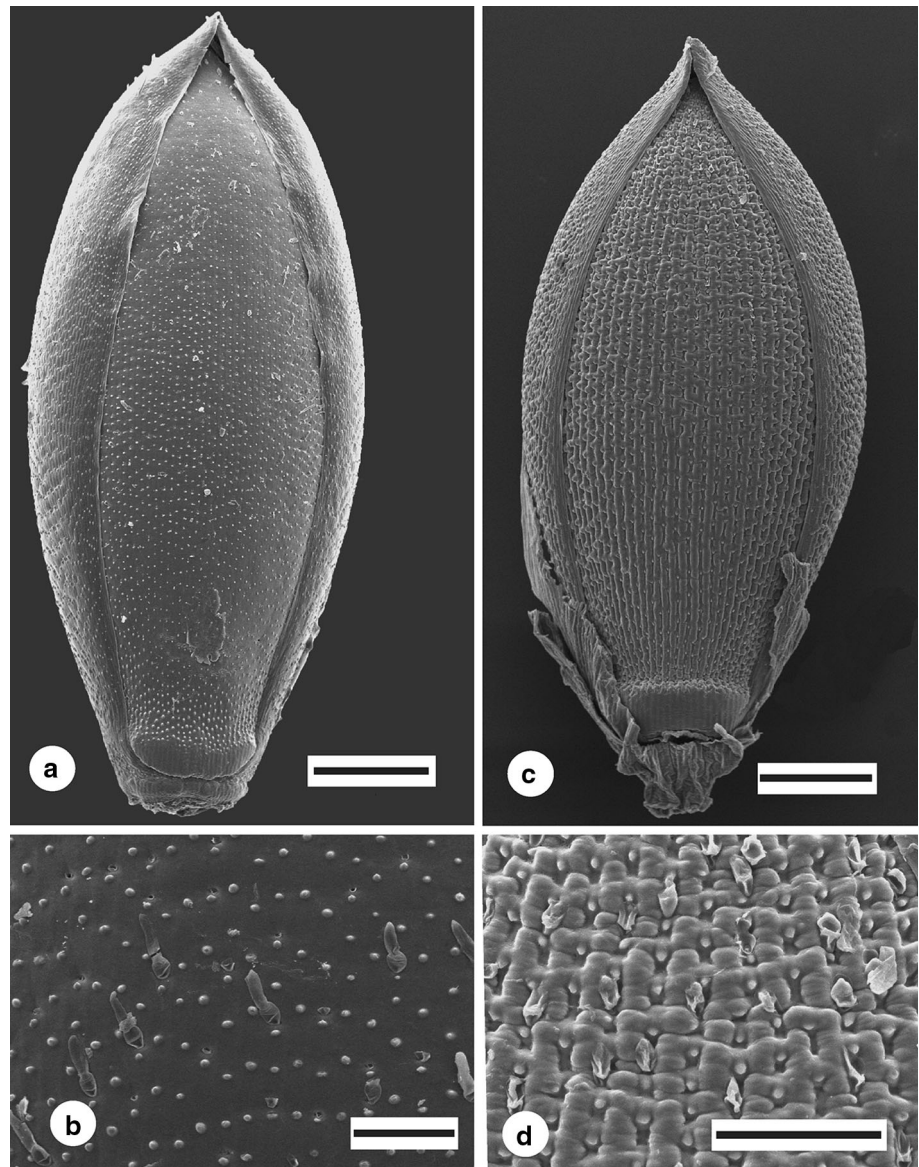
Panicum brachyanthum and *P. verrucosum* are C_3 species, with non-Kranz anatomy of the PS (XYMS+) subtype (Hattersley and Watson 1976; Brown 1977; Ellis 1977) characterized by having a parenchymatous and a mestome sheath surrounding the vascular bundles and in contact with the metaxylem vessels. The mesophyll is distinguished by the presence of more than 5 chlorenchyma cells between consecutive vascular bundles.

Leaf blade in transverse section

Outline: broadly V-shaped, with slightly involute margins; leaf thickness 320–350 μm , arms of the lamina symmetrical. Ribs and furrows: slightly rounded adaxial ribs, abaxial ribs and furrows round, rib associated with first-

and second-order vascular bundles. Keel: slightly rounded on the adaxial side and very developed on the abaxial side, 550–620 μm width in *P. verrucosum* (vs. 455–530 μm width. in *P. brachyanthum*), associated with colorless parenchyma and with vascular bundles. Vascular bundle arrangement: three or four second-order vascular bundles between contiguous first-order vascular bundles; all vascular bundles situated in the center of the blade. Vascular bundle structure: First-order vascular bundles circular in outline. Second-order vascular bundles circular in outline, with xylem and phloem tissue distinguishable. Vascular bundle sheath: non-Kranz, bundle sheaths are double with the outer sheath entire, without specialized chloroplasts; parenchyma bundle sheath of the first-order vascular bundles entire or with adaxial interruption of sclerenchyma girders, consisting of 13–18 rounded cells; parenchyma bundle sheath of the second-order vascular bundles entire,

Fig. 5 Scanning electron micrographs of upper anthercium of *Kelloggloa brachyantha* (**a**, **b**) and *K. verrucosa* (**c**, **d**). **a** Upper anthercia ventral view; **b** detail of the upper palea, with simple papillae and bicellular microhairs; **c** upper anthercia ventral view; **d** detail of the upper palea with bicellular microhairs and simple papillae. (**a**, **b** from Hatch 1074 and **c**, **d** from Brown 2698). Scale bars **a** 500 μm ; **b**, **d**, 100 μm ; **c** 250 μm



formed by 6–10 rounded cells. Sclerenchyma: small, adaxial and abaxial girders associated with the first- and second-order vascular bundles; fibers lignified, small, rounded sclerenchyma caps located in leaf margins. Mesophyll: chlorenchyma radiately arranged, 5 or more chlorenchyma cells between consecutive vascular bundles. Adaxial epidermal cells: bulliform cells fan-shaped, in restricted groups of 5–6 cells, epidermal cells small, and regular in outline. Abaxial epidermal cells: bulliform cells absent, cuticle thickened (Fig. 6a, b).

Abaxial epidermis in surface view

Zonation costal and intercostal zones distinguishable; costal zone formed by 4–6 rows of long cells; intercostal zone with

6–7 rows in *P. verrucosum* (vs. 7–9 rows in *P. brachyanthum*) of long cells. Intercostal cells elongated rectangularly, more than 3–5 times longer than wide in *P. verrucosum* (vs. 4–8 times longer than wide in *P. brachyanthum*); side walls parallel, end walls vertical, and anticlinal walls slightly thickened; rectangular cells with moderately undulated anticlinal walls. Stomata complex triangular, 1–2 rows of stomata in each intercostal zone, stomata $37.5\text{--}38.5 \times 20\text{--}26 \mu\text{m}$. Intercostal short cells absent or present, solitary, transversely elongated when present. Microhairs bicellular, finger-like, with the basal cell slightly longer than the distal cells. Macrohairs absent. Papillae absent. Prickles located in the costal zone, $54.5 \times 18 \mu\text{m}$, or absent. Silica bodies transversely elongated, intercostal silica bodies dumbbell-shaped in outline (Fig. 6c).

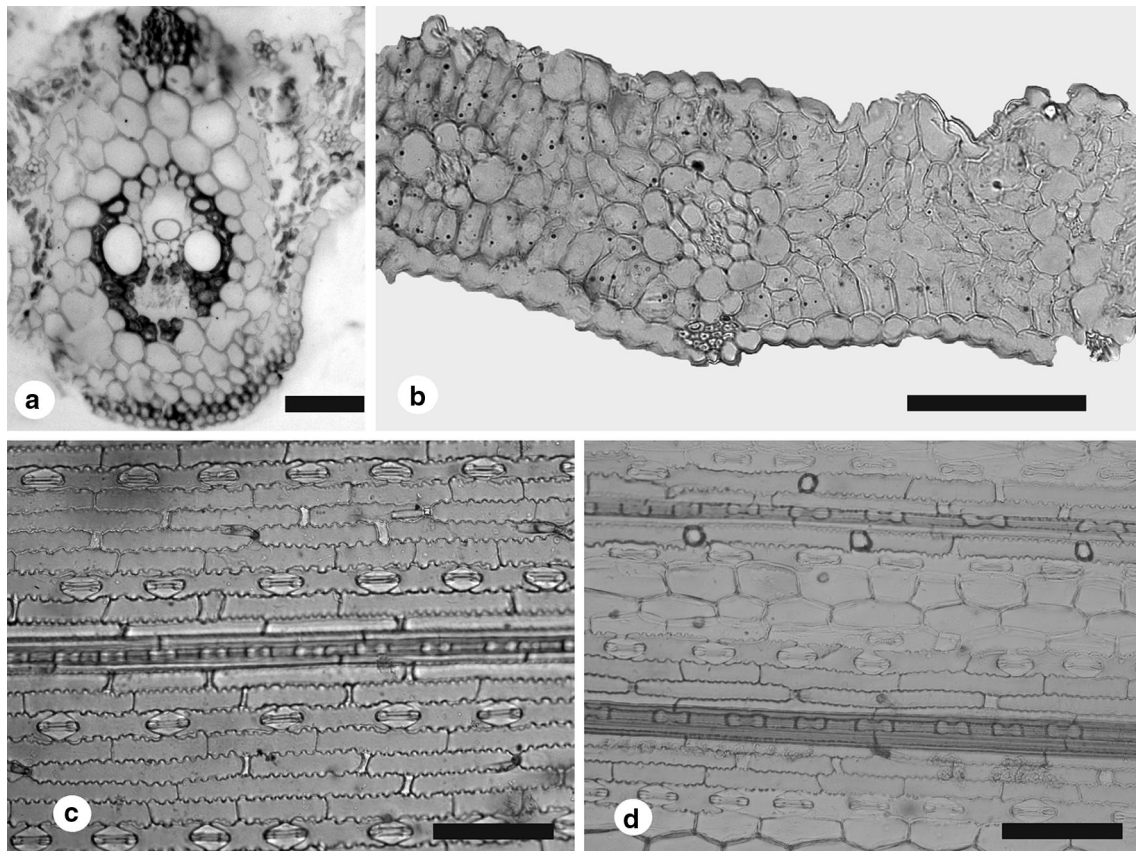


Fig. 6 Leaf blade anatomy of *Kellochloa verrucosa* (**a**, **b**) and *K. brachyantha* (**c**, **d**). Transverse leaf section. **a** General aspect of the keel; **b** portion of the leaf blade showing first-, second-, and third-order vascular bundles. Abaxial epidermis. **c** Epidermal zonation with narrow intercostal zones; detail of stomata, with triangular subsidiary cells, rectangular long cells with moderately undulating anticlinal

walls, bicellular microhairs, and short cells; silica bodies. Adaxial epidermis. **d** Detail of stomata, with triangular subsidiary cells, rectangular long cells with moderately undulating anticlinal walls, silica bodies, and short cells. (**a**, **b** from Tryon 4547 and **c**, **d** from Dale 4728). Scales bar **a–d** 100 μm

Adaxial epidermis in surface view

Epidermal cells similar to the abaxial surface, except for the presence in the costal zones of a central band of rectangular cells, 2–4 cells wide (Fig. 6d).

Discussion

In the molecular analysis *Panicum* sect. *Verrucosa* was monophyletic and related to *Sacciolepis*, *Trichanthecium*, and “incertae sedis” species of *Panicum* s.l. of the *Sacciolepis–Trichanthecium* clade; therefore, they are distinct from of *Panicum* s.str. The species of sect. *Verrucosa* share being annual plants, with the culms divaricately branching at the base, with terminal and axillary inflorescences present, spikelets hispid, with the lower glume short and nerveless, lower palea and lower flower absent, and upper anthercium with bicellular microhairs and simple papillae evenly distributed.

Section *Verrucosa* is distinguished from *Sacciolepis* by the following set of characters: panicle lax and open (vs. spiciform), spikelets biconvex (vs. gibbous), lower glume scale-like (vs. developed), lower flower and lower palea absent (vs. lower flower and lower palea present), and upper anthercium papillate with bicellular microhairs (vs. smooth, glabrous).

Section *Verrucosa* differs also from *Trichanthecium* and the clade including “incertae sedis” African species of *Panicum* s.l., i.e., *P. aequinerve*, *P. eickii*, *P. chionachne*, and *P. inaequilatum*, by the presence of terminal and axillary inflorescences, spikelets with a scale-like, nerveless lower glume, and the lower palea absent (vs. inflorescences terminal, bearing spikelets with the lower glume 1/2 to 1/1 the length of the spikelet, with the lower palea present both in *Trichanthecium* and the former “incertae sedis” species mentioned). *Panicum aequinerve*, *P. chionachne*, *P. eickii*, and *P. inaequilatum* share a spikelet with the lower glume as long as the spikelet, 3–5(–7)-nerved, lower palea present, and upper anthercium smooth and glabrous, the latter

character distinguishing these species from *Trichantheium*, a genus with the upper antherium with bicellular microhairs and simple papillae regularly distributed all over the upper lemma and palea.

Species of sect. *Verrucosa*, together with *P. aequinerve*, *P. chionachne*, *P. eickii*, and *P. inaequilatum*, are unrelated to *Panicum* s.str. as defined by Aliscioni et al. (2003). *Panicum*, as presently circumscribed, includes species with membranous-ciliate or ciliate ligules, open and lax inflorescences, spikelets ellipsoid to long ellipsoid, with the lower glume 1/3 to 3/4 the length of the spikelet, lower palea present, and upper antherium indurated, with simple or compound papillae at the top of the palea and without bicellular microhairs. In addition, all species of *Panicum* s.str. differ by C₄ carbon fixation, by having the NAD-me subtype, and a basic chromosome number of $x = 9$.

In agreement with Zuloaga et al. (2011), *Panicum trichanthum*, an American species distributed from Mexico to Argentina, appears as the sister species of the *Sacciolepis–Trichantheium* clade. Species of sect. *Verrucosa* are distinguished from *P. trichanthum* by being annual, with both terminal and axillary inflorescences, spikelets pilose, with the lower palea absent (vs. plants perennial, with terminal inflorescences with spikelets glabrous, and a lower palea present in the latter species). A summary of characters distinguishing the new genus are presented in Table 1.

Conclusions

Our analysis allowed us to conclude that both species of *Panicum* sect. *Verrucosa* should be segregated from *Panicum* and considered as a new genus within tribe Paniceae. The taxonomic position of *P. aequinerve*, *P. chionachne*, *P. eickii*, and *P. inaequilatum*, and their final relationship and possible inclusion in *Trichantheium*, should be confirmed with a detailed analysis of more related African species. A new contribution is in preparation to establish the taxonomic position of non-Kranz *Panicum* species included or related to the *Sacciolepis–Trichantheium* clade to clarify the relationships within the entire subtribe.

Key to distinguish *Kelochloa* from related taxa of the *Sacciolepis–Trichantheium* clade

1. Inflorescence spiciform with saccate spikelets, the upper glume gibbous. . . *Sacciolepis*
- 1'. Inflorescence open and lax, not spiciform; spikelets biconvex, not saccate, upper glume rounded. . . 2
2. Lower glume 1/6 to 1/4 the length of the spikelet. . . 3
- 2'. Lower glume 1/2 to 1/1 the length of the spikelet. . . 4

3. Plants annual, with terminal and axillary inflorescences, spikelets pilose, lower palea absent. United States. . . *Kelochloa*
- 3'. Plants perennial, with terminal inflorescences, spikelets glabrous, lower palea present. Mexico to Argentina. . . *Panicum trichanthum*
4. Upper antherium smooth, without bicellular microhairs and simple papillae. . . *Panicum* “*African incertae sedis*” species
- 4'. Upper antherium with bicellular microhairs and simple papillae. . . *Trichantheium*

Taxonomic treatment

Kelochloa Lizarazu, Nicola & Scataglini, **gen. nov.**—**TYPE SPECIES:** *Panicum verrucosum* Muhl. \equiv *Kelochloa verrucosa* (Muhl.) Lizarazu, Nicola & Scataglini.

= *Panicum* group *Verrucosa* Hitchc. and Chase., Contr. U.S. Natl. Herb. 15: 28, 126. 1910, **nom. inval.**

= *Panicum* unranked *Verrucosa* Hitchc., N. Amer. Fl. 3(2): 200, 205. 1915.

= *Panicum* sect. *Verrucosa* Hitchc. & Chase ex C.C. Hsu, J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 132. 1965.

Annuals, with culms rooting and divaricately branching at the lower nodes, decumbent, then erect; nodes compressed, glabrous. Ligules membranous-ciliate; collar glabrous. Blades lanceolate to linear-lanceolate, glabrous, acuminate. Inflorescences open lax, multiflowered, exserted, peduncles cylindrical, smooth, and glabrous; terminal and axillary inflorescences present; main axis cylindrical or flattened, scaberulous; pulvini short-pilose or glabrous; first-order branches ascendent, divergent, alternate, axis of the branches triquetrous, scaberulous; pedicels solitary or paired, claviform. Spikelets ellipsoid to long ellipsoid, biconvex, pilose. Lower glume 1/6–1/4 the length of the spikelet, nerveless. Upper glume and lower lemma subequal, 3–5-nerved. Lower palea and flower absent. Upper antherium ellipsoid, indurate, with bicellular microhairs and simple papillae evenly distributed all over the lemma and palea. Caryopsis obovoid to ellipsoid; hilum oblong to punctiform, embryo less than 1/2 the length of the caryopsis.

Etymology: We are pleased to name this new genus after Dr. Elizabeth A. Kellogg, who has contributed significantly to the knowledge of grasses; also, Dr. Kellogg did a great and wonderful job helping so many young students of our institution.

Key to the species

1. Blades lanceolate, flat; spikelets 1.8–2.1 mm long, glumes and lower lemma covered by tuberculate

Table 1 Comparative morphological characters between *Kelochloa* and related taxa

	<i>Kelochloa</i>	<i>Trichantheium</i>	<i>Panicum</i> s.str.	<i>Sacciolepis</i>	"Incertae sedis" African <i>Panicum</i>	<i>Panicum</i> <i>trichanthum</i>
Duration	Annual	Annual or perennial	Annual or perennial	Annual or perennial	Annual or perennial	Perennial
Inflorescence	Lax, open	Lax, open	Lax or contracted	Contracted, spiciform	Lax or contracted	Lax, open
Axillary inflorescences	Present	Absent, occasionally present	Absent	Absent	Absent	Absent
Spikelet shape	Not gibbous	Not gibbous	Not gibbous	Gibbous	Not gibbous	Not gibbous
Lower glume length	1/6 to 1/4 the length of the spikelet	1/2 to 4/5	1/3 to 4/5	1/3 to 1/2	4/5 to 1/1	1/5 to 1/4
Lower palea	Absent	Present	Present or absent	Present	Present	Present
Upper antherium pilosity	With bicellular microhairs	With bicellular microhairs	With macrohairs or glabrous	Glabrous	Glabrous	Glabrous
Upper antherium ornamentation	With simple papillae, smooth or rugose	With simple papillae, smooth	With simple or compound papillae, smooth	Without simple papillae, smooth	Smooth	Smooth
Photosynthetic pathway	C3	C3	C4	C3	C3	C3

prickle hairs, upper antherium rugose...*K. verrucosa*

- 1'. Blades linear-lanceolate, involute; spikelets 3.2–4.2 mm long, glumes and lower lemma covered by long tuberculate hairs; upper antherium smooth...*K. brachyantha*

1. *Kelochloa brachyantha* (Steud.) Lizarazu, Nicola & Scataglini, **comb. nov.**

≡ *Panicum brachyanthum* Steud., Syn. Pl. Glumac. 1: 67. 1853.—TYPE: United States. Texas. Rusk Co.: in sabulosis sylvaticus, *Vinzent 124* (holotype: P 00740934!; isotypes: US 80479!, fragment and photo ex P, W 18890237830!). Figure 2.

= *Panicum sparsiflorum* Vasey, U.S. Dept. Agric. Bot. Div. Bull. 8: 36. 1889, **nom. illeg.** (Art. 53), non Döll, 1877.—TYPE: United States. Texas. San Bernardino, Oct 1839, *J. L. Ridell 20* (lectotype, US 81288!, designated by Hitchcock & Chase, Contr. U.S. Natl. Herb. 15: 128. 1910; isolectotype, ISC 0000579!).

Plants 30–90 cm tall; internodes 1–10 cm long; nodes pale. *Sheaths* 2–6 cm long, usually shorter than the internodes, the lower ones hirsute, with short papillose-pilose hairs, the upper ones glabrous, the margins membranous, ciliate. *Ligules* 0.3–0.5 mm long. *Blades* 4–14 cm long, 0.2–0.3 cm wide, linear-lanceolate, with involute margins, narrow at the base. *Inflorescences* 5–16 cm long, 4–10 cm wide; peduncles 7–25 cm long pedicels 2–13 mm long. *Spikelets* 3.2–4.2 mm long, 1.5–2 mm wide, long ellipsoid,

green, glumes and lower lemma tuberculate, hispid, with stiff macrohairs arising from wartlike bases. *Lower glume* 0.6–0.8 mm long, 1/5–1/4 the length of the spikelet, obtuse or acute. *Upper glume* and *lower lemma* 5-nerved, acute. *Upper antherium* 2.8–3.2 mm long, 1.4–1.6 mm wide, long ellipsoid, smooth or slightly rugose toward the margins of the lemma. *Caryopsis* ellipsoid, 2 mm long, 1.1 mm wide; hilum oblong, embryo less than 1/2 the length of the caryopsis.

Phenology Flowering between August and October.

Distribution and habitat Southeastern United States, in Arkansas, Louisiana, Mississippi, Oklahoma, and Texas (Fig. 7), growing in dry, sandy soils in open areas, woodland borders, and roadsides.

Representative specimens examined United States. Arkansas. Benton, Chesney Prairie Natural Area, *McKenzie et al. 2165* (MO); E of Strong, on roadside, high file for Ouachita R bridge, *Moore 49-698* (SI). Florida. Roadbank beside Lapine Rd. 2 miles SW of jct. Of La. 34 and La. 3033, sec. 3, *Dale 4728* (WIS). Louisiana. Lake Charles, *Chase 69* (MO). Mississippi. Jones Co.: 1 mile northwest of Ellisville, at base of longleaf pine slope, common in ditch, *McDaniel 3431* (MO). Oklahoma. Sapulpa, Indian Territory, *Bush 1397* (MO). Texas. Nacogdoches Co.: about 1 mile east of Melrose, *Correll 26242* (MO); 3.7 miles of the junction of Hwy. FM 1179 and FM 2038, NE of Bryan, *Hatch 1074* (WIS); Trinity County, 5 miles northwest of Groveton, *Gould 12002* (WIS).

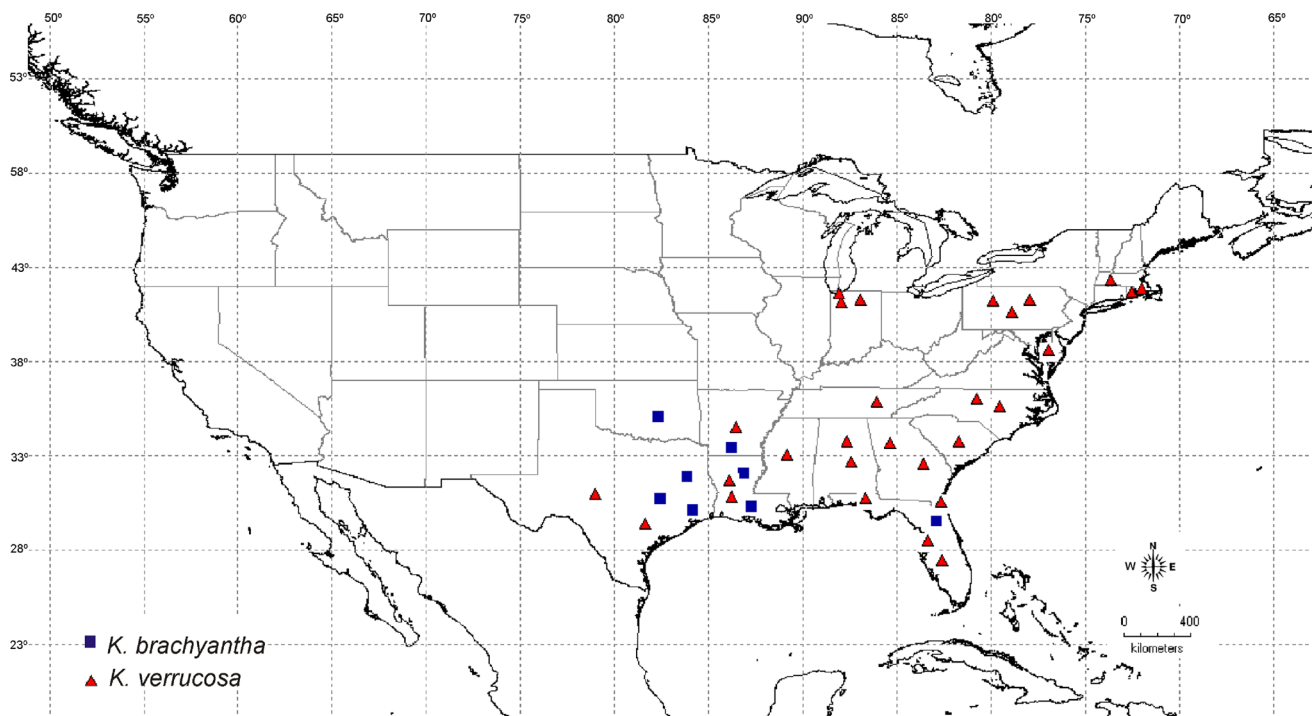


Fig. 7 Map of North America showing the distribution of *Kellochloa brachyantha* and *K. verrucosa*

2. *Kellochloa verrucosa* (Muhl.) Lizarazu, Nicola & Scataglini, **comb. nov.**

≡ *Panicum verrucosum* Muhl., Descr. Gram.: 113. 1817.—TYPE: Habitat in N. Caesarea, New Jersey, Delaware et Georgia, *Muhlenberg 107, 6* (holotype, PH 00031497!; isotype, US, fragment and photo). Figure 3.

= *Panicum debile* Elliott, Sketch Bot. S. Carolina 1: 129. 1816, **nom. illeg.** (Art. 53), non Desf., 1798.—TYPE: United States. South Carolina? (not located).

– *Panicum rugosum* Bosc ex Spreng., Syst. Veg. 1: 314. 1825, **pro syn. nom. nud.**, as a synonym of *P. verrucosum* Muhl.

– *Panicum umbraculum* Bosc ex Spreng., Syst. Veg. 1: 314. 1825, **pro syn. nom. nud.**, as a synonym of *P. verrucosum* Muhl.

Plants 20–110 cm tall; internodes 1.5–7 cm long; nodes dark, compressed, glabrous. *Sheaths* 2–7.5 cm long, shorter or longer than the internodes, the margins ciliate. *Ligules* 0.2–0.5 mm long; collar brown. *Blades* 5–18 cm long, 0.2–0.8 cm wide, lanceolate, flat, rounded at the base. *In-florescences* 7–22 cm long, 4–18 cm wide; peduncles 10–25 cm long; pedicels 1–6 mm long, scaberulous. *Spikelets* 1.8–2.1 mm long, 0.9–1 mm wide, ellipsoid, green or tinged with purple, glumes and lower lemma covered with prickle, tuberculate hairs. *Lower glume* 0.3–0.5 mm long, 1/6–1/4 the length of the spikelet, acute. *Upper glume* and *lower lemma* subequal, the upper glume shorter at maturity, 3–5-nerved, acute. *Upper anthercium* 1.7–2 mm

long, 0.8–1 mm wide, rugose, with thickened longitudinal and transverse walls. *Caryopsis* obovoid, 1.2–1.3 mm long, 0.7–0.8 mm wide; hilum punctiform, embryo 1/3 the length of the caryopsis.

Phenology Flowering between August and October.

Distribution and habitat Frequent in of eastern United States coasts, where it is present in Alabama, District of Columbia, Florida, Georgia, Louisiana, Maryland, Massachusetts, Mississippi, Missouri, New Jersey, North Carolina, Pennsylvania, Rhode Island, South Carolina, Texas, and Virginia; it can also be found in Indiana, Kentucky, and Missouri (Fig. 7); it grows in moist or wet sandy areas, occasionally can be found in open, drier woodlands.

Representative specimens examined United States. Alabama. Fayette Co.: Tupelo swamp, east side of Fayette, *Kral 48665* (MO); S of Bauxite, *Moore 49-714* (SI). Florida. Franklin Co.: at gate to Ft. Gadsden State Park, 12 mi. W of route 65, 5.8 air mi. SSW of Sumatra, *Anderson 10228* (MO). Georgia. Cook Co.: 3.3 mi. NW of Adel. Coastal Plain Province, *Faircloth 4852* (MO). Indiana. Jasper Co.: Jasper-Pulaski State Game Preserve, 12 miles southeast of Thefft, *Tryon & Tryon 4547* (MO); sloughs, Dune Park. *Umbach 4600* (SI). Kentucky. Menifee Co.: McCaurey Ridge L.O., near Frenchberg, *Reed 17496* (MO). Louisiana. Natchitoches Co.: Chopin, sandy ground, *Palmer 8830* (MO). Maryland. Caroline Co.: Smithville, edge of Community Lake, *Reed 68408* (MO). Massachusetts. Hampshire Co.: Northampton, King Street,

along railroad, *Ahles 87616* (MO); *Fernald 8509* (WIS). Mississippi. Jackson Co.: 5 miles east of Ocean Springs, common on grassy slope near pine woods, *McDaniel 3475* (MO). Missouri. Scott Co.: Unity Baptist Camp off of Rt. 77, c. 4 mi. NNE of Blodgett, *McKenzie 1838* (MO). New Jersey. Lakewood, edge of bank, *Drushel 8355* (MO). Rhode Island. *Collins 114* (WIS). Texas. Harris Co., in Eisenhower Park below dam at Lake Houston, *Brown 2680* (SI); in the Roy E. Larsen Sanctuary along Village Creek west of Silsbee, *Brown 2698* (SI).

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Appendix

List of species used in the phylogenetic analysis including the six new vouchers, in bold, and vouchers from Zuloaga et al. (2011). Voucher information and GenBank accession numbers (*ndhF*, *rpoA*) are shown.

Tribe Andropogoneae. *Zea mays* U21985, X07810.
Tribe Paspaleae. *Anthaenantiopsis rojasiana* Zuloaga 6747 AY029620, JF804815; *Echinochloa chacoensis* Zuloaga 8573 EF218711, JF804820; *E. cruspavonis* Morrone 5369 EF218710, JF804819; *Oplismenus burmanii* Morrone 3625 EF218712, JF804821; *Paspalum bertonii* Zuloaga 7186 JF804854, JF804817; *P. foliiforme* Morrone 4669 JF804853, JF804816. **Tribe Paniceae.** *Panicum aequinerve* Kellogg 109 (MO) **KR232095**; *P. bartlettii* Alvarez 152 JF804882; *P. brachyanthum* Daniel et al. 25 (MO) **KR232096**, **KR232090**; *P. brevifolium* Gereau 5315 JF804860, JF804828; *P. chionachne* Wiehe 358 (US) **KR232097**, **KR232091**; *P. eickii* Robinson 5306 (US) **KR232098**, **KR232092**; *P. heterostachyum* Greenway 14150 JF804862, JF804830; *P. hirtum* Strudwick 4389 JF804861, JF804829; *P. inaequilatum* Phillips 61 (MO) **KR232099**, **KR232093**; *P. millegrana* Zuloaga 6766 AY029660, JF804852; *P. sellowii* Zuloaga 2123 AY188484, JF804822; *P. trichanthum* Morrone 5028 JF804858, JF804827; *P. trichoides* Zuloaga 7430 JF804859, JF804826; *P. verrucosum* Wheeler s.n. AY188496; *P. verrucosum* Kral 48168 (MO) **KR232100**, **KR232094**; *Sacciolepis angustissima* Morrone 4319 JF804856, JF804824; *S. indica* Bowen 3875 AY029677; *S. myuros* Longhi-Wagner 9390 JF804857, JF804825; *S. vilvodes* Zuloaga 6745 JF804854, JF804823; *Trichantheium arctum* Liesner 15757 JF804881; *T. auricomum* Longhi-Wagner 9637 JF804870,

JF804841; *T. brazzavillense* Fay 5891 JF804880, JF804851; *T. caaguazuense* Anderson 35724 JF804875, JF804846; *T. cyanescens* Morrone 4772 JF804867, JF804837; *T. dinklagei* Jenik & Hall 1129 JF804866, JF804834; *T. distichophyllum* Longhi-Wagner 9664 JF804869, JF804840; *T. gracilicaule* Renvoize 2229 JF804864, JF804832; *T. granuliferum* Jansen-Jacobs 4064 JF804871, JF804842; *T. machrisianum* Viana 1727 JF804874, JF804845; *T. margaritifolium* Milne-Redhead 4530 JF804863, JF804831; *T. micranthum* Morrone 4770 JF804877, JF804848; *T. natalense* Kellogg 117 JF804879, JF804850; *T. nervosum* Morrone 4789 JF804876, JF804847; *T. parvifolium* Zuloaga s.n. AY188476, JF804835; *T. polycomum* Morrone 4763 JF804873, JF804844; *T. pseudisachne* Longhi-Wagner 9606 JF804868, JF804839; *T. pyrularium* Swallen 4936 JF804878, JF804849; *T. rivale* Morrone 4765 JF804872, JF804843; *T. schwackeanum* Morrone 115 AY188483, JF804838; *T. tenellum* Richards 9306 JF804865, JF804833; *T. wettsteinii* Zuloaga 6972 AY188497, JF804836.

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