

Phylogeny of sections *Clavelligerae* and *Pectinatae* of *Panicum* (Poaceae, Panicoideae, Paniceae): establishment of the new subtribe *Dichantheiinae* and the genus *Adenochloa*

Fernando O. Zuloaga · L. Salomón · Maria A. Scataglini

Received: 4 April 2014 / Accepted: 28 November 2014 / Published online: 31 December 2014
© Springer-Verlag Wien 2014

Abstract Taxonomic features of African species of *Panicum* sections *Clavelligerae* and *Pectinatae* are reviewed and compared with *Dichantheium* and other taxa in tribe Paniceae. The new subtribe *Dichantheiinae* is proposed on the basis of molecular and morphological characters: it includes non-Kranz species, growing at forests edges or in mountain grasslands with membranous-ciliate ligules, lax and open inflorescences, ellipsoid to oblongoid spikelets, and an indurate upper anthercium. Within the *Dichantheiinae*, the new genus *Adenochloa* is also established on the basis of chloroplast *ndhF* sequences and morphological characters, i.e., plants with clavellate multicellular, and glandular hairs present on blades, main axis, branches, and pedicels of inflorescences; ellipsoid to oblongoid, glabrous spikelets, with a lower glume 1/3 to more than 1/2 the length of the spikelet; a 7–13-nerved upper glume and a 5–9-nerved lower lemma; the upper anthercium is indurate, pilose or glabrous. *Adenochloa* includes 14 species from Africa and Madagascar. The new combinations: *Adenochloa adenophylla*, *A. adenophora*, *A. bullockii*, *A. claytonii*, *A. ecklonii*, *A. flacciflora*, *A. habrothrix*, *A. hymeniochila*, *A. lukwangulense*, *A. nigromarginata*, *A. pectinella*, *A. pole-evansii*, *A. sadinii*, and *A. squarrosa* are proposed and the new genus is compared with other genera of the tribe Paniceae. Also, lectotypes are designated for *Brachiaria sadinii*, *Panicum adenophorum*, *P. adenophyllum*, *P. ecklonii*, *P. katentaniense*, *P. kisantuense*, *P. hymeniochilum*, *P. hymeniochilum* var.

glandulosum, *P. snowdenii*, and *P. scandens*; *Panicum glanduliferum* and *P. omega* are treated as new synonyms of *Adenochloa hymeniochila* and *A. pectinella*, respectively. Finally, new illustrations are provided for 6 species of the new genus.

Keywords *Adenochloa* · *Clavelligerae* · *Dichantheiinae* · *ndhF* phylogeny · Paniceae · *Panicum* · *Pectinatae*

Introduction

Sections *Clavelligerae* and *Pectinatae*, of *Panicum* L., were established by Stapf (1920), in his treatment of grasses of Tropical Africa; the former was based on the presence of glandular hairs on the inflorescences, culms and blades, and the latter by having glumes pectinately toothed. Stapf (1920) included four species in *Clavelligerae* and two in *Pectinatae*. Renvoize (1968) reviewed both sections, mentioning that they share an oblong shape of the spikelet, and the presence of clavellate tipped hairs on the axis and branches of the inflorescence. These clavate glandular hairs were described (Kabuye and Wood 1968) as multicellular hairs, present in culms, sheaths, blades, and panicle axis and branches of species of *Clavelligerae* and *Pectinatae*; Kabuye and Wood (1968) also distinguished these hairs from those present in *P. deustum* Thunb., which in the latter species are unicellular and with swollen tips. Renvoize (1968) arranged four species in sect. *Pectinatae*, *P. ecklonii* Nees, *P. lukwangulense* Pilg., *P. pectinatum* Rendle, and *P. pectinellum* Stapf, and 10 species in *Clavelligerae*: *P. adenophorum* K.Schum., *P. claytonii* Renv., *P. deustum* Thunb., *P. flacciflorum* Stapf, *P. habrothrix* Renv., *P. hymeniochilum* Nees, *P. nigromarginatum*

Handling editor: Karol Marhold.

F. O. Zuloaga · L. Salomón · M. A. Scataglini (✉)
Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, San Isidro, Buenos Aires B1642HYD, Argentina
e-mail: ascataglini@darwin.edu.ar

Robyns, *P. pole-evansii* C.E.Hubb., *P. sadinii* (Vanderyst) Renv., and *P. snowdenii* C.E.Hubb. Later, Renvoize (1980) described *P. omega* in sect. *Pectinatae*, and *P. bullockii* (Renvoize 1989b) in sect. *Clavelligerae*. Recent floristic treatments of the flora of Africa recognized 11 and 14 species in section *Clavelligerae* (Clayton and Renvoize 1982), and section *Pectinatae* (Renvoize 1989a). It should be pointed out that *P. deustum* Thunb., placed by Renvoize (1968) in sect. *Clavelligerae* is an “incertae sedis” species of subtribe *Melinidinae* (Salariato et al. 2010). Also, *Panicum glanduliferum* K.Schum., a species from Madagascar (Bossler 1969) was included among the analyzed species of sect. *Clavelligerae*. Based on a Panicoid *ndhF* sequence analysis, Aliscioni et al. (2003) and Morrone et al. (2012) discussed the systematic position of two species of *Clavelligerae* which were included in “clade A”, together with five species of the genus *Dichanthelium*.

Polyphyly of the genus *Panicum* has been confirmed in several morphological and phylogenetic studies of Panicoideae based on chloroplast (*ndhF*, *trnL-F*, *rpoC2*) and ribosomal nuclear (ETS) sequence data (Gómez-Martínez and Culham 2000; Zuloaga et al. 2000; Duvall et al. 2001, 2003; Giussani et al. 2001; Aliscioni et al. 2003). Aliscioni et al. (2003) restricted *Panicum* to those taxa usually placed in *Panicum* subg. *Panicum* and characterized it as including caespitose plants, with ciliate or membranous-ciliate ligules, spikelets arranged in an open and lax inflorescence, with the upper glume and lower lemma (5–)7–13 nerved, the upper antherium indurate, and the upper palea with simple or compound papillae toward the apex. Based on four plastid markers, Christin et al. (2009) and Zimmermann et al. (2013) also indicated, that *Panicum* should be restricted to a set of species all using the C₄ NAD-me photosynthesis subtype. Aliscioni et al. (2003) transferred several species to other panicoid genera [such as *Dichanthelium* (Hitc. & Chase) Gould, *Hymenachne* P.Beauv., and *Steinchisma* Raf.], and recognized *Phanopyrum* (Raf.) Nash as an independent genus. Aliscioni et al. (2003) also suggested that all “incertae sedis” species of *Panicum* should be segregated from the genus and transferred to new taxa or to other extant genera. As a result, several species were transferred recently to other panicoid genera, i.e., *Aakia* (Grande Allende 2014), *Apochloa* Zuloaga & Morrone (Sede et al. 2008), *Canastra* Morrone, Zuloaga, Davidse & Filg. (Zuloaga et al. 2006), *Coleaetaenia* Griseb. (Soreng 2010), *Cyphoanthus* Zuloaga & Morrone (Morrone et al. 2007), *Hopia* Zuloaga & Morrone (Zuloaga et al. 2007), *Ocellochloa* Zuloaga & Morrone (Sede et al. 2009), *Parodiophyllochloa* Zuloaga & Morrone (Morrone et al. 2008), *Renvoizea* Zuloaga & Morrone (Sede et al. 2008), *Stephostachys* Zuloaga & Morrone (Zuloaga et al. 2010), *Trichantheicum* Zuloaga

& Morrone (Zuloaga et al. 2011), and *Zuloagaea* Bess (Bess et al. 2006).

The aims of this study are: (a) to analyze, with additional molecular and morphological data, clade A of Morrone et al. (2012) to define its taxonomic position, and (b) to evaluate the systematic positions of sects. *Clavelligerae* and *Pectinatae* using the chloroplast (*ndhF*) DNA phylogeny of Panicoideae.

Materials and methods

Morphological data

Morphological characters were recorded from herbarium specimens from BAA, BR, G, K, MA, MO, P, SI, and US (acronyms after Thiers 2013).

Molecular data and phylogenetic analyses

A total of 20 new *ndhF* sequences belonging to *Panicum* sects. *Clavelligerae* and *Pectinatae* and to genus *Dichanthelium* were obtained from herbarium specimens for the present work (GenBank accession numbers: KP173693–KP173711). The sequences obtained were added to the 123-*ndhF* Panicoid matrix of Aliscioni et al. (2003). Details of the 143 taxa analyzed and GenBank accession numbers are available in “Appendix”.

DNA sequencing. DNA was isolated, from herbarium material, using the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany) following the manufacturer’s recommendations. The plastid marker, *ndhF*, was amplified by polymerase chain reaction (PCR). The complete *ndhF* gene (ca. 2,100 bp) was amplified using primers specified by Olmstead and Sweere (1994) and Aliscioni et al. (2003). Four fragments were amplified (5F-536R, 536F-972R, 972F-1666R and 1666F-3R).

PCR reactions were performed in 25 μ L final volumes with 50–100 ng of template DNA, 0.2 μ M of each primer, 25 μ M dNTP, 5 mM MgCl₂ 1 \times buffer and 0.3 units of *Taq* polymerase provided by Invitrogen Life Technologies (Brazil). The PCR reactions were carried out using the following parameters: 1 cycle of 94 $^{\circ}$ C for 5 min, 39 cycles of 94 $^{\circ}$ C for 30 s, 48 $^{\circ}$ C for 1 min, and 72 $^{\circ}$ C for 1 min 30 s, and a final extension cycle of 72 $^{\circ}$ C for 10 min. PCR products were run out on a 1 % TBE agarose gel stained with SYBR Safe DNA gel stain (Invitrogen) and visualized in a blue light transilluminator. Automated sequencing was performed by Macrogen, Inc. (Seoul, South Korea). Forward and reverse strands were sequenced of each template to reach the complete sequence of each voucher. Alignment was manually performed, using BioEdit ver. 5.0.9

(Hall 1999). The alignment is available at Treebase under study accession S15539.

Phylogenetic analyses

A maximum parsimony (MP) analysis was performed using TNT ver. 1.1 (Goloboff et al. 2008). All characters were equally weighted, and gaps were scored as missing data. Prior to heuristic searches, all uninformative characters were deactivated. The searches involved 1000 replicates, each of which generated a Wagner tree using a random addition sequence of taxa from the data matrix, swapping the initial tree with TBR (tree bisection and reconnection) and retaining a maximum of 10 trees in each replicate. Subsequently, all optimal trees were swapped using TBR, holding a maximum of 10,000 trees. Branches with ambiguous length of 0 or 1 were collapsed, according to collapsing rules. A strict consensus tree was generated from the most parsimonious trees. Branch supports were estimated with Bootstrap (Felsenstein 1985) using a total of 10,000 replicates. Each replicate was analyzed using 10 Wagner trees as a starting point followed by TBR branch swapping, saving only one tree per replicate. Bootstrap values (BS) over 80 % are reported.

A Bayesian phylogenetic analysis was also performed. The general time reversible substitution model (GTR+I+G) was chosen using the Akaike Information Criterion (AIC) as implemented in jModeltest 2.1.1 (Darriba et al. 2012). Four Markov chains were run simultaneously in two independent runs for 5 million generations in MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2001). Trees were sampled every 1,000 generations, discarding the first 25 % of the samples as burn-in. Convergence diagnostics for log likelihood values were assessed visually using Tracer v.1.5.0 software (Rambaut and Drummond 2007); to calculate the Bayesian posterior probabilities (PP), trees prior to stability of the average standard deviation of split frequencies were excluded, and the remaining trees were used to generate a 50 % majority rule consensus tree.

Results

The analyzed matrix consisted of 143 taxa and 2074 characters, of which 445 were parsimony informative. The MP analysis resulted in more than 10,000 most parsimonious trees of 1,600 steps. The strict consensus tree is shown in Fig. 1. Parsimony and Bayesian consensus trees were fully congruent, showing the same strongly supported clades. Posterior probabilities of the Bayesian analysis are indicated in the cladogram of Fig. 1.

The consensus tree shows that clade A of Morrone et al. (2012) is supported by nine synapomorphic positions, a Bootstrap value (BS) = 84 %, and posterior probabilities (PP) = 1. Within this clade, all analyzed species of *Clavelligerae* and *Pectinatae* grouped together with BS = 87 % and PP = 0.86. Three molecular synapomorphies support this clade at positions 74, 102 and 209 of the *ndhF* Panicoid matrix, respectively. The *Clavelligerae*–*Pectinatae* clade appears as the sister group of *Dichantheleum*, which was monophyletic (BS = 77 %, PP = 1).

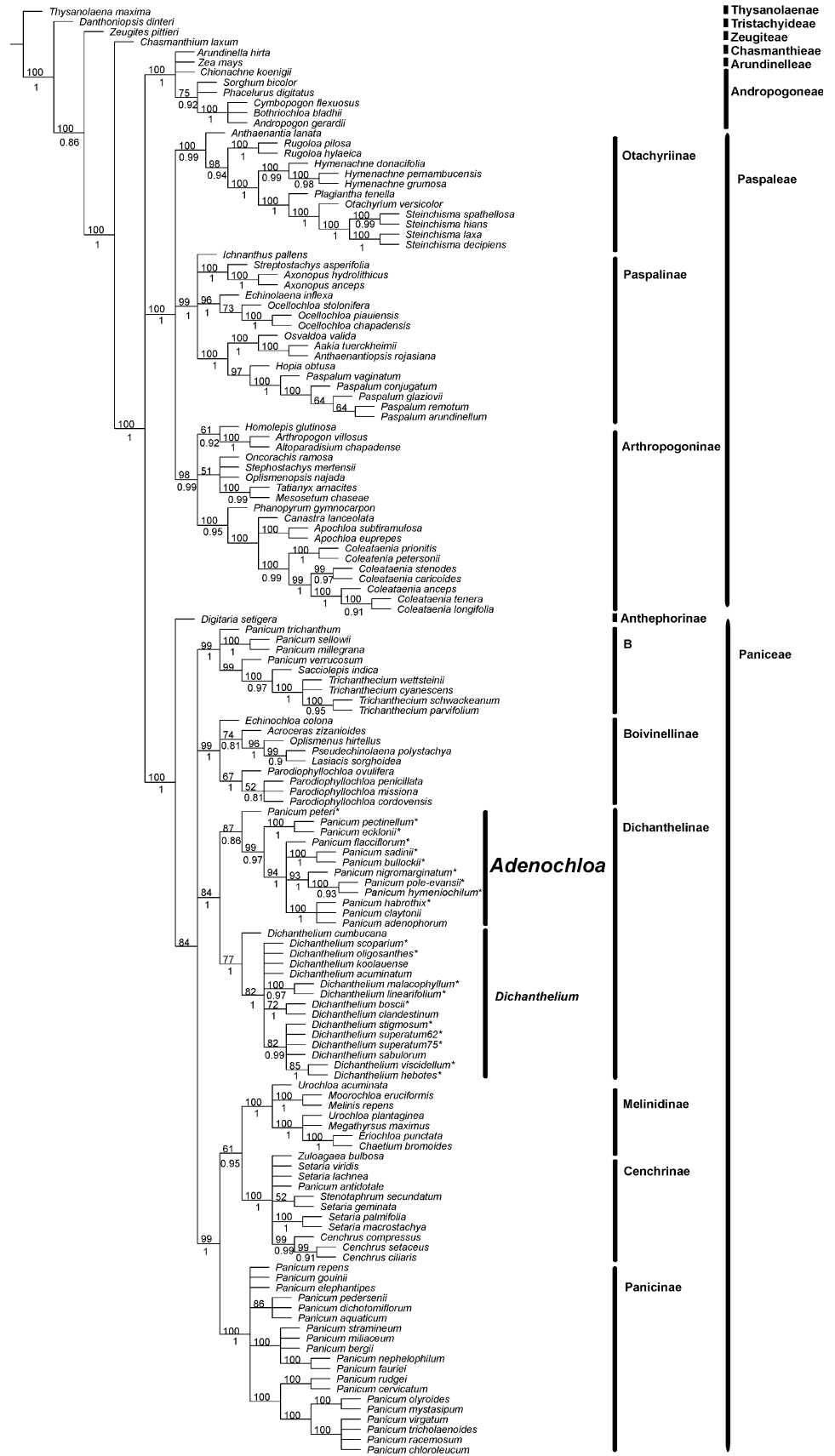
Within the *Clavelligerae*–*Pectinatae* clade, *P. peteri* appears as the sister taxon of the remaining species, which are strongly supported as a monophyletic group with 99 % of BS and 0.97 of PP. The two analyzed species, previously assigned to sect. *Pectinatae*, form a well-supported clade (BS = 100 %, PP = 1) that is the sister group of a polytomy (BS = 94 %, PP = 1). Three subclades are found within this polytomy: *P. sadinii*–*P. bullocki* (BS = 100 %, PP = 1), *P. nigromarginatum*–*P. pole-evansii*–*P. hymenochilum* (BS = 93 %, PP = 1), and *P. habrothix*–*P. claytonii*–*P. adenophorum* (BS = 100 %, PP = 1).

As previously mentioned, the sister group of the *Clavelligerae*–*Pectinatae* clade is the genus *Dichantheleum*. *Dichantheleum cumbucana* appears as the sister taxon of the remaining species of that genus, while the remaining species are supported by a BS of 82 % and PP of 1.

Discussion

Aliscioni et al. (2003) treated *Dichantheleum* (120 species approx.) as an independent, monophyletic genus, with sect. *Clavelligerae* as its sister taxon. These authors mentioned that section *Clavelligerae* should be segregated from *Panicum* s.str., its final position pending the study of more species from this section. Later, Morrone et al. (2012) stressed that *Dichantheleum* and species of *Clavelligerae*, that grouped in a well-supported clade A, still have an uncertain position within the Paniceae, due to the limited number of taxa examined. Our study allows us to conclude, after the analysis of 12 (of 14) species of *Clavelligerae*/*Pectinatae*, and 14 species of *Dichantheleum*, that this clade is well supported and morphologically coherent; all taxa share membranous-ciliate ligules, lax and open inflorescences, ellipsoid to oblongoid spikelets, the lower glume present, 1–7-nerved, a (5–)7–13-nerved upper glume and lower lemma, the upper antherium indurate, with simple papillae usually present and regularly arranged, with macrohairs present or absent. Also, species in this clade are non-Kranz (Brown 1977; Zuloaga et al. 1993; Osborne et al. 2014). Considering molecular and morphological characters, we are here describing a new subtribe within

Fig. 1 Strict consensus tree obtained in the parsimony analysis of the *ndhF* Panicoideae matrix including the new sequences belonging to sections *Clavelligerae* and *Pectinatae* and to *Dichantherium*. The new sequences are indicated with *asterisk*. Bootstrap values are shown above branches. Posterior probabilities ≥ 0.8 obtained in the Bayesian analysis are indicated below branches. *Bars* indicate tribes and subtribes according to Morrone et al. (2012)



the Paniceae to contain the members of these two clades and allied species.

Species of *Clavelligerae/Pectinatae* differ from *Dichantheium* by the presence of pedicellate multicellular glandular hairs on the culms, leaves, and inflorescences. In addition, foliar dimorphism and cleistogamy are absent (vs. pedicellate glandular hairs absent, and foliar dimorphism and cleistogamy usually present in species of *Dichantheium*).

Panicum s.str. differs from species of *Clavelligerae/Pectinatae* by including taxa without clavellate tipped hairs, all over the plants, the spikelet without pectinate glumes and lower lemma, and upper anthercium with simple or compound papillae at the top of the palea and lemma; also, all species of *Panicum* s.str. are C_4 , of the NAD-me subtype.

Based on the discussion above, and because species of *Clavelligerae/Pectinatae* cannot be included in any genus of tribe Paniceae or subtribe Panicinae (Morrone et al. 2012), we describe this taxon as a new genus.

The phylogenetic analysis has also shown several relationships within the boundaries of this taxon (Fig. 1), which agree with morphological similarities between the species, as follows:

Panicum peteri, which appears in the molecular analysis as sister to all remaining species, differs from these by its inflorescences that are partially included in the upper blades, leaves ovate lanceolate, lower glume 7–9-nerved, lower palea developed, and the upper anthercium crested and glabrous.

All species previously classified in sect. *Pectinatae*, *P. lukwangulense*, *P. pectinellum*, and *P. ecklonii* share the presence of pectinate glumes, with the upper glume shorter than the upper anthercium, lower palea and lower flower absent, and the upper anthercium pilose. *Panicum flacciflorum* is distinguished by the presence of a stipitate upper anthercium; this is an annual species with spikelets having the lower palea developed. *Panicum nigromarginatum*, *P. hymeniophilum*, and *P. pole-evansii* are annual plants, freely branching at the lower nodes, with the upper anthercium glabrous, papillose, and crested at the apex. *Panicum sadinii* and *P. bullockii* are perennials, conspicuously branching at the lower nodes, the pedicels with long macrohairs, and spikelets with the upper anthercium glabrous, smooth, and crested. Finally, *Panicum adenophorum*, *P. claytonii* and *P. habrothrix* share the presence of lower palea and lower flower developed, the upper anthercium papillose and pilose toward the apex; both *P. adenophorum* (a perennial plant) and *P. habrothrix* (annual species) have long whitish macrohairs on pedicels, these being absent in *P. claytonii*.

Taxonomic treatment

***Dichantheiinae* Zuloaga, subtribe nov.**—TYPE: *Dichantheium* (Hitchc. & Chase) Gould

Annuals or perennials, cespitose or with culms decumbent and rooting at the lower nodes, with or without foliar dimorphism; ligules membranous-ciliate; blades filiform to ovate lanceolate, with or without glandular hairs. Inflorescence lax and open, spikelets ellipsoid to oblongoid, pilose or glabrous; lower glume present, 0–9-nerved; upper glume and lower lemma (5–) 7–13-nerved; lower palea present or absent, lower flower male or absent; upper anthercium indurate; caryopsis with a punctiform to oblong hilum. C_3 photosynthetic pathway; basic chromosome number $x = 9$.

Subtribe with 2 genera, *Adenochloa* and *Dichantheium*, which are found in Africa and America, respectively.

***Adenochloa* Zuloaga, gen. nov.**—TYPE SPECIES: *Adenochloa hymeniophila* (Nees) Zuloaga = *Panicum hymeniophilum* Nees, Fl. Afr. Austral. III: 46. 1841.

= *Polyneura* Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 53. 1929, nom. illeg. (Art. 53), non (J. Agardh) Kykin.

Annuals or perennials, with or without conspicuous rhizomes, culms scrambling and slender, decumbent and rooting at the lower nodes to ascending or erect, simple or branching; internodes hollow, terete; nodes pilose or glabrous; sheaths striate, with or without clavellate glandular hairs; ligules membranous-ciliate; blades linear lanceolate to ovate lanceolate, flat, cordate and amplexicaulous to subcordate or rounded at the base, the apex acuminate, with or without clavellate glandular hairs, otherwise pilose to glabrous. Inflorescence an open panicle, subexserted to exserted from the uppermost leaves, sparsely to densely clavellate hairy, glandular hairs occasionally absent; main axis terete, first-order branches divergent; pedicels claviform, with or without clavellate hairs and with or without long macrohairs, some of them exceeding the length of the spikelet; sessile glands present or absent. Spikelets oblongoid to ellipsoid, glabrous, upper glume and lower lemma subequal or the upper glume shorter than the upper anthercium, membranous; lower glume 1/3 to 3/4 the length of the spikelet, 0–9-nerved, pectinate or not; upper glume 7–13-nerved, pectinate or not; lower lemma glumiform, 5–11-nerved, pectinate or not; lower palea as long as the upper anthercium, hyaline and with short hairs at the margins, to reduced or absent; lower flower male or absent. Upper anthercium narrowly ellipsoid, indurate, with macrohairs toward the apex of the lemma or glabrous, with or without simple papillae distributed all over the lemma and palea, the

lemma crested or not at the apex. *Caryopsis* ellipsoid; hilum oblong, embryo less than half the length of the caryopsis.

Etymology—the name of the new genus makes reference to the presence of glandular hairs on vegetative and/or reproductive portions of the plants.

Distribution and habitat—an African genus, with one species growing also in Madagascar.

Observation—genus with 14 species.

Key to the species

1. Glumes and lower lemma pectinate 2
- 1'. Glumes and lower lemma entire, not pectinate 4
2. Plants 0.7–1.6 m tall; blades 20–50 × 1–2 cm; inflorescences 13–40 cm long 3
- Adenochloa lukwangulense*
- 2'. Plants 0.15–0.8(–0.9) m tall; blades 4–14(–18) × 0.1–0.7 cm; inflorescences 5–15(–17) cm long 3
3. Spikelets 2.5–3.4 mm long 3
- Adenophora ecklonii*
- 3'. Spikelets 1.6–2 mm long 3
- Adenophora pectinella*
4. Upper anthercium glabrous, the upper lemma crested at the apex, usually greenish 5
- 4'. Upper anthercium conspicuously pilose at the apex, the upper lemma not crested, pale 11
5. Spikelets 1.2–1.8 mm long; upper glume shorter than the upper anthercium, bracts and upper anthercium with black spots at the apex 6
- Adenochloa nigromarginata*
- 5'. Spikelets 2–4.5 mm long; upper glume as long or longer than the upper anthercium, bracts and upper anthercium without black spots at the apex 6
6. Blades symmetric, linear lanceolate to lanceolate, up to 1.2 cm wide; culms herbaceous, simple or branching, plants annual; lower glume 0–3-nerved, upper glume 7–9-nerved 7
- 6'. Blades asymmetric, lanceolate to ovate lanceolate, up to 2 cm wide; culms rigid, freely branching, plants perennial; lower glume 5–9-nerved, upper glume 9–13-nerved 8
7. Lower glume 1/2 to 2/3 the length of the spikelet; upper anthercium smooth; lower palea reduced, lower flower absent 8

Adenochloa hymeniochila

Fig. 2 *Adenochloa adenophora* (K.Schum.) Zuloaga. **a** Habit; **b** ligular region; **c** portion of inflorescence; **d** spikelet, ventral view; **e** spikelet, dorsal view; **f** lower palea, ventral view; **g** upper anthercium, dorsal view; **h** upper palea, ventral view; **i** caryopsis, scutellar view with stamens and stigmas; **j** caryopsis, hilar view [a–j from *Namaganda 921* (K)]

7'. Lower glume 1/3 to 1/2 the length of the spikelet; upper anthercium with simple papillae all over its surface; lower palea developed, lower flower present

Adenochloa pole-evansii

8. Inflorescence with sessile glands on the main axis and branches, with pedicellate glandular hairs only on the main axis

Adenochloa adenophylla

8'. Inflorescence without sessile glands on the main axis and branches, with pedicellate glandular hairs all over the inflorescence, including the pedicels

9

9. Spikelets 4.3–5 mm long; lower glume less than 1/2 the length of the spikelet, 7–9-nerved

Adenochloa squarrosa

9'. Spikelets 2.5–3.5 mm long; lower glume 1/2 to 3/4 the length of the spikelet, 3–5-nerved

10

10. Plants 20–40 cm tall; blades 3.5–4.5 × 0.6–0.8 cm

Adenochloa bullockii

10'. Plants 90–140 cm tall; blades 5–14 × 1–2 cm

Adenochloa sadinii

11. Pedicels with whitish macrohairs longer than the spikelet

12

11'. Pedicels without long whitish macrohairs

13

12. Plants annual, 18–20 cm tall, spikelets 2–2.2 mm long

Adenochloa habrothrix

12'. Plants perennial, 45–90 cm tall, spikelets 2.5–3(–3.8) mm long

Adenochloa adenophora

13. Plants perennial, strongly rhizomatous; spikelets 3.5–5.5 mm long; upper anthercium non-stipitate

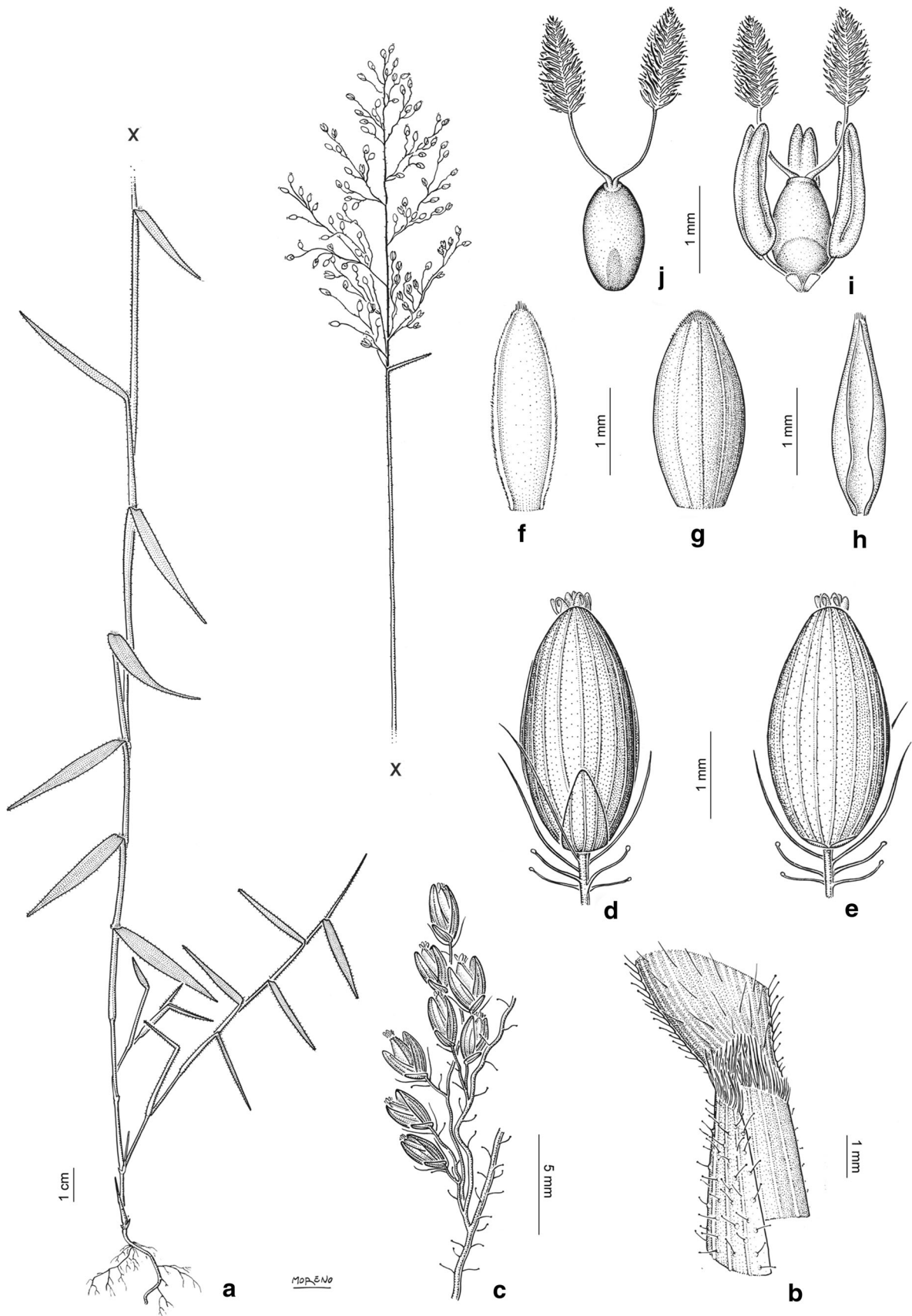
Adenochloa claytonii

13'. Plants annual; spikelets 3–4 mm long; upper anthercium stipitate

denochloa flacciflora

1. *Adenochloa adenophora* (K.Schum.) Zuloaga, **comb. nov.**

≡ *Panicum adenophorum* K.Schum., Pflanzenw. Ost-Afrikas C: 103. 1895.—TYPE: Uganda. Ankole District: Seengebiet (Ruhanga), 26 Apr 1891, *F. Stuhlmann 2143* (**lectotype designated here**, B barcode B100167793!; isolecotypes, US barcodes US1063855!, US1715360!) Fig. 2.



Distribution and habitat—this species grows in grasslands, on sandy soils, or in forest margins of Burundi, Democratic Republic of the Congo, Malawi, Tanzania, Uganda, and Zambia, between 1,800 and 2,300 m elevation.

Adenochloa adenophora is morphologically similar to *A. habrothrix*, the latter differing by being an annual species with inflorescence 3–4 cm long, and spikelets with the upper glume and lower lemma 7 nerved.

2. *Adenochloa adenophylla* (Pilg.) Zuloaga, **comb. nov.**

≡ *Panicum adenophyllum* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 13: 260. 1936.—TYPE: Tanzania. Lindi District: Bezirk Lindi, ca. 70 km NW von Lindi, Muera plateau, 24 Feb 1935, *H.J. Schlieben 6064* (**lectotype designated here**, B barcode B100167792!; isolectotypes, B barcode B100167792!, BM barcode BM000923097!, BR barcode BR0000008760807!, LISC barcode LISC003459!, M barcode M0103871!, MA barcode MA175812!, S barcode SS-G-4477!).

Distribution and habitat—Tanzania, a scrambling perennial growing in forest margins ca. 700 m elevation.

Clayton and Renvoize (1982) considered this species a synonym of *A. adenophora*, without any further explanation. Nevertheless, *A. adenophylla* can be distinguished from *A. adenophora* by having sessile glands all over the inflorescence, clavellate hairs only present on the main axis, pedicels without glands or macrohairs, and upper antherium glabrous (vs. sessile glands absent and conspicuous clavellate hairs on the main axis, branches of the inflorescence and pedicels, pedicels with clavellate hairs and long macrohairs, and upper antherium pilose toward the apex in *A. adenophora*).

Several syntypes of the specimen *Schlieben 6064* were examined, of which the collection B barcode B100167792 was selected as lectotype of the species.

3. *Adenochloa bullockii* (Renvoize) Zuloaga, **comb. nov.**

≡ *Panicum bullockii* Renvoize, Kew Bull. 44: 543. 1989.—TYPE: Zambia. Kasama, Chisimbia Falls, 25 km WNW of Kasama, 28 Feb 1970, in sandy soils pockets among rocks, *R. B. Drummond and G. Williamson 10092* (holotype, SRGH barcode SRGH109633-0!; isotype, K!).

Distribution and habitat—only known from Zambia, where it grows in mountain slopes on sandy soils between 1,700 and 2,200 m elevation.

This species is morphologically similar to *A. sadinii*, from which it differs by including plants strongly rhizomatous and 20–40 cm tall (vs. plants not strongly rhizomatous, scrambling on the vegetation and up to 1.50 m tall).

4. *Adenochloa claytonii* (Renvoize) Zuloaga, **comb. nov.**

≡ *Panicum claytonii* Renvoize, Kew Bull. 22: 484, f. 1-12. 1968.—TYPE: Zambia. Nyika Plateau, Lake Lau-lime, grassland, 2150 m, 24 Oct 1958, *N.K.B. Robson 332*

Fig. 3 *Adenochloa ecklonii* (Nees) Zuloaga. **a** Habit; **b** ligular region; **c** spikelet, lateral view; **d** lower glume; **e** upper glume; **f** lower lemma; **g** upper antherium, dorsal view; **h** upper palea with lodicules, stamens and stigmas [**a–h** from *Hepper 2116* (K)]

(holotype, K barcode K000282438!; isotypes, BR barcode BR0000008760692!, EA barcode EA000000476!, LISC barcode LISC003461!, SRGH barcode SRGH0106318-0!, WAG barcode WAG0001527!).

Distribution and habitat—this species grows in the Democratic Republic of the Congo, Malawi, Tanzania, and Zambia, where it is found climbing on shrubs along forest margins, growing in reddish laterite soils between 1800 and 2400 m elevation.

Adenophora claytonii is a species with conspicuous rhizomes and erect culms, usually unbranched. This species is morphologically similar to *A. adenophora*, differing by the absence of long whitish macrohairs on pedicels, spikelets 3.5–5.5 mm long, lower glume 7–9-nerved, and upper glume and lower lemma 9–11-nerved (vs. pedicels with long whitish macrohairs, spikelets 2.5–3 mm long, lower glume 3-nerved, and upper glume and lower lemma 7–9-nerved in *A. adenophora*).

5. *Adenochloa ecklonii* (Nees) Zuloaga, **comb. nov.**

≡ *Panicum ecklonii* Nees, Fl. Afr. Austral. Ill.: 43. 1841.—TYPE: South Africa. Katberg, *J.F. Drège s.n.* (**lectotype designated here**, P barcode P00442154!; isolectotype, LE-TRIN.689.2) Fig. 3.

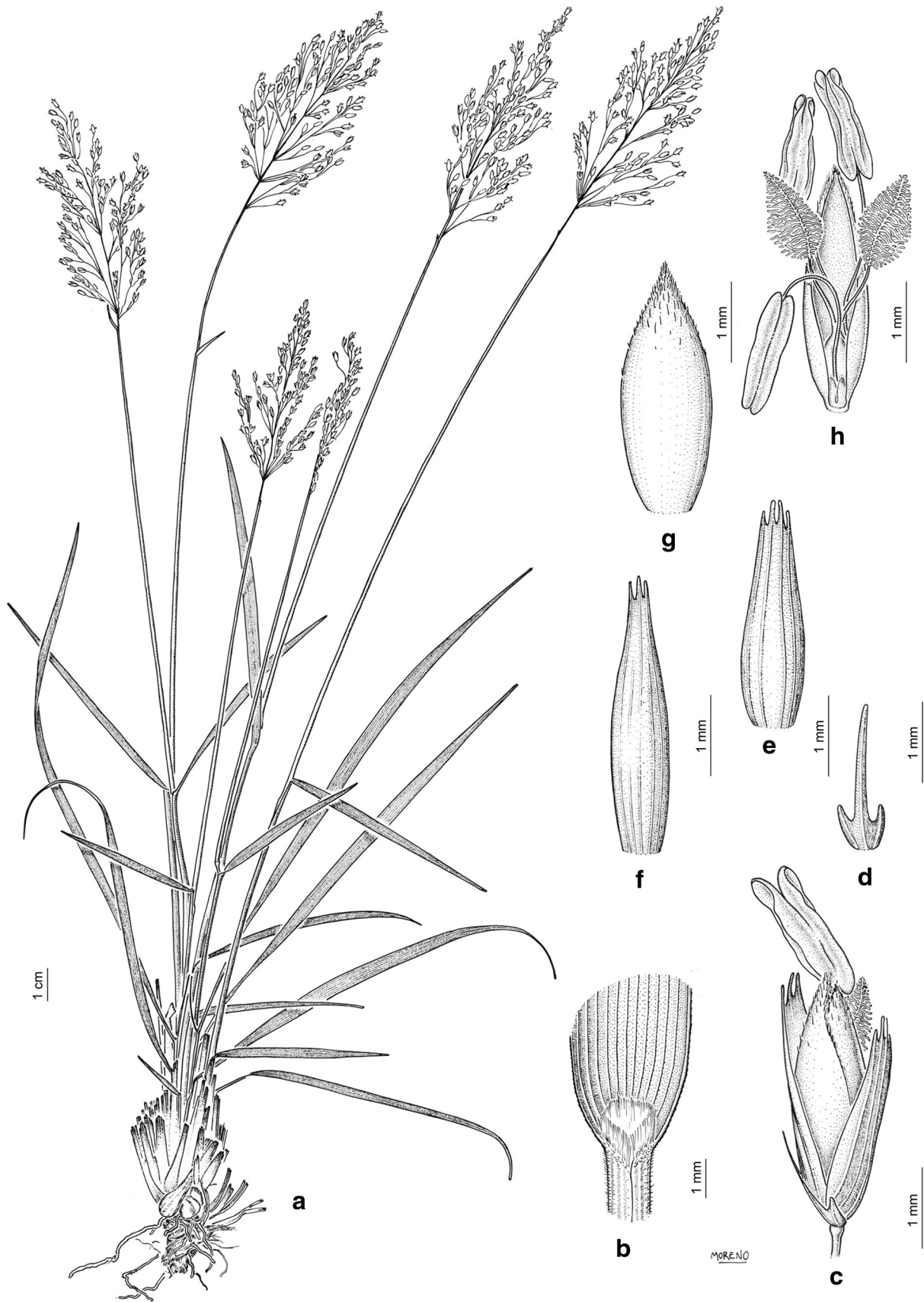
= *Panicum pectinatum* Rendle, Trans. Linn. Soc. London, Bot. 4: 54, tab. 10, Fig. 1–6. 1894.—TYPE: Malawi. Mt. Milanji, *A. White 10* (holotype, BM barcode BM000923138!; isotype, K barcode K000255542!, US barcode US1445182!, fragment).

= *Panicum catangense* Chiov., Ann. Bot. (Rome) 13: 44. 1914.—TYPE: Democratic Republic of the Congo: “Catanga, plateau bianos a Katantania”, Nov 1912, *E.A.R. Bovone 82* (holotype, TO!).

= *Panicum katentaniense* Robyns, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8vo) 1(6): 57, tab. 5, A-F. 1932.—TYPE: Democratic Republic of the Congo. Katanga: Plate des Bianos, Katentania, Nov 1912, *H.A. Homblé 706* (**lectotype designated here**, BR barcode BR0000008760814!; isolectotypes, BR barcode BR0000008761217, K, US barcode US1538736!).

Distribution and habitat—this species is present in Sierra Leone and from Cameroon, Democratic Republic of the Congo, Mozambique, Malawi and Zambia to South Africa; it grows in montane grasslands, on rocky places, between 1,100 and 2,600 m.

Adenochloa ecklonii is morphologically similar to *A. lukwangulense*, both species with pectinate glumes and lower lemma, the upper glume shorter than the spikelet, with the upper antherium pilose at the apex. It differs from



the latter by being smaller plants, 15–75 cm tall, with inflorescences 6–15 cm long; the presence of burned basal leaves indicates that this species is frequent in burned areas. Plants are characterized by being robust, caespitose perennials, densely hispid along blades and culms, with glandular hairs all over the terminal inflorescence; the spikelets are nearly 4 mm long, with the lower glume 1/2 or less the length of the spikelet, the upper glume usually not covering the upper antherium, the latter with macrohairs toward the distal portion.

Adenochloa ecklonii differs from *A. pectinella* by including plants with simple culms, blades mostly basal, blades linear to linear lanceolate, 0.2–0.5 cm wide, spikelets 2.5–3.5 mm long (vs. plants with branching culms, blades arranged along the culms, lanceolate, 0.4–0.8 cm wide, and spikelets 1.8–2 mm long in the latter species).

When describing *P. ecklonii*, Nees (1841) cited two syntypes, *Ecklon s.n.* and *Drège s.n.* The specimen *Drège* from P is selected as lectotype of the species since it agrees with the protologue and is a well preserved specimen. Also, the specimen *Homblé 706* from BR (barcode BR8760814) is selected as lectotype of *Panicum katentaniense* Robyns.

6. *Adenochloa flacciflora* (Stapf) Zuloaga, **comb. nov.**

≡ *Panicum flacciflorum* Stapf, Fl. Trop. Afr. 9: 720. 1920.—TYPE: Tanzania. Kahama-Tabora District: Miniga, 3800 ft, *J.A. Grant s.n.* (holotype, K 000255546!; isotype, US barcode US1445207) Fig. 4.

= *Panicum microcephalum* Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 44, tab. 25, Fig. 2. 1929.—TYPE: Burundi. Deutsch Ost. Afr. Avinsa: westl. von Lugufu, *G.A. Peter 36484, 36546* (syntypes, B?, not located).

= *Panicum microcephalum* fo. *nanum* Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 44. 1929.—TYPE: Burundi, without locality, *G.A. Peter 38174* (holotype, B?, not located).

Distribution and habitat—growing in open and sandy soils in Burundi, Tanzania, Zambia, and Uganda, between 1,000 and 1,500 m elevation.

Adenochloa flacciflora is characterized by being an annual, caespitose plant, with open and lax terminal inflorescences, the spikelets 3–4 mm long, and the upper antherium with a manifest, thick stipe below, being the antherium papillose, with simple papillae regularly distributed, and macrohairs toward the apex of lemma and palea.

7. *Adenochloa habrothrix* (Renvoize) Zuloaga, **comb. nov.**

≡ *Panicum habrothrix* Renvoize, Kew Bull. 22: 486, Fig. 2. 1968.—TYPE: Zambia. Mwinilunga District: just S of Matonchi Farm, in *Brachystegia* woodland, 24 Jan 1938, *E.W.B.H. Milne-Redhead 4305* (holotype, K barcode K000282440!; isotypes, BR barcode BR0000008761378!, LISC barcode LISC003462!, PRE barcode PRE0747957-0!).

Fig. 4 *Adenochloa flacciflora* (Stapf) Zuloaga. **a** Habit; **b** ligular region; **c**, portion of the inflorescence; **d**, spikelet, dorsal view; **e** spikelet, ventral view; **f** lower palea; **g** upper antherium, dorsal view; **h** upper palea with caryopsis; **i** caryopsis, embryo view; **j** caryopsis, hilum view [a–j from *Bidgood and Darbyshire 5501* (K)]

Distribution and habitat—Burundi and Zambia, where it is found in forest shade, at elevations ca. 1,000 m.

Adenochloa habrothrix is morphologically similar to *A. adenophora* and *A. claytonii*; it differs from the former by its annual habit, plants 20–40 cm tall, spikelets 2–2.2 mm long, and upper antherium glabrous (vs. perennial, 30–100 cm tall, and spikelets 2.5–3(–3.6) mm long, and upper antherium pilose in *A. adenophora*); it is distinguished from *A. claytonii* by its annual habit, the presence of long whitish macrohairs on pedicels, spikelets 2–2.2 mm long (vs. a perennial habit, absence of macrohairs on pedicels, and spikelets 3.5–5.5 mm long in the *A. claytonii*).

8. *Adenochloa hymeniochila* (Nees) Zuloaga, **comb. nov.**

≡ *Panicum hymeniochilum* Nees, Fl. Afr. Austral. III.: 46. 1841.—TYPE: South Africa: Natal, “in graminosis inter Omsamculo et Omcomas alt 500”, *J.F. Drège 4247* (**lectotype designated here**, P barcode P00444247!; isolectotype, K barcode K000282468!) Fig. 5.

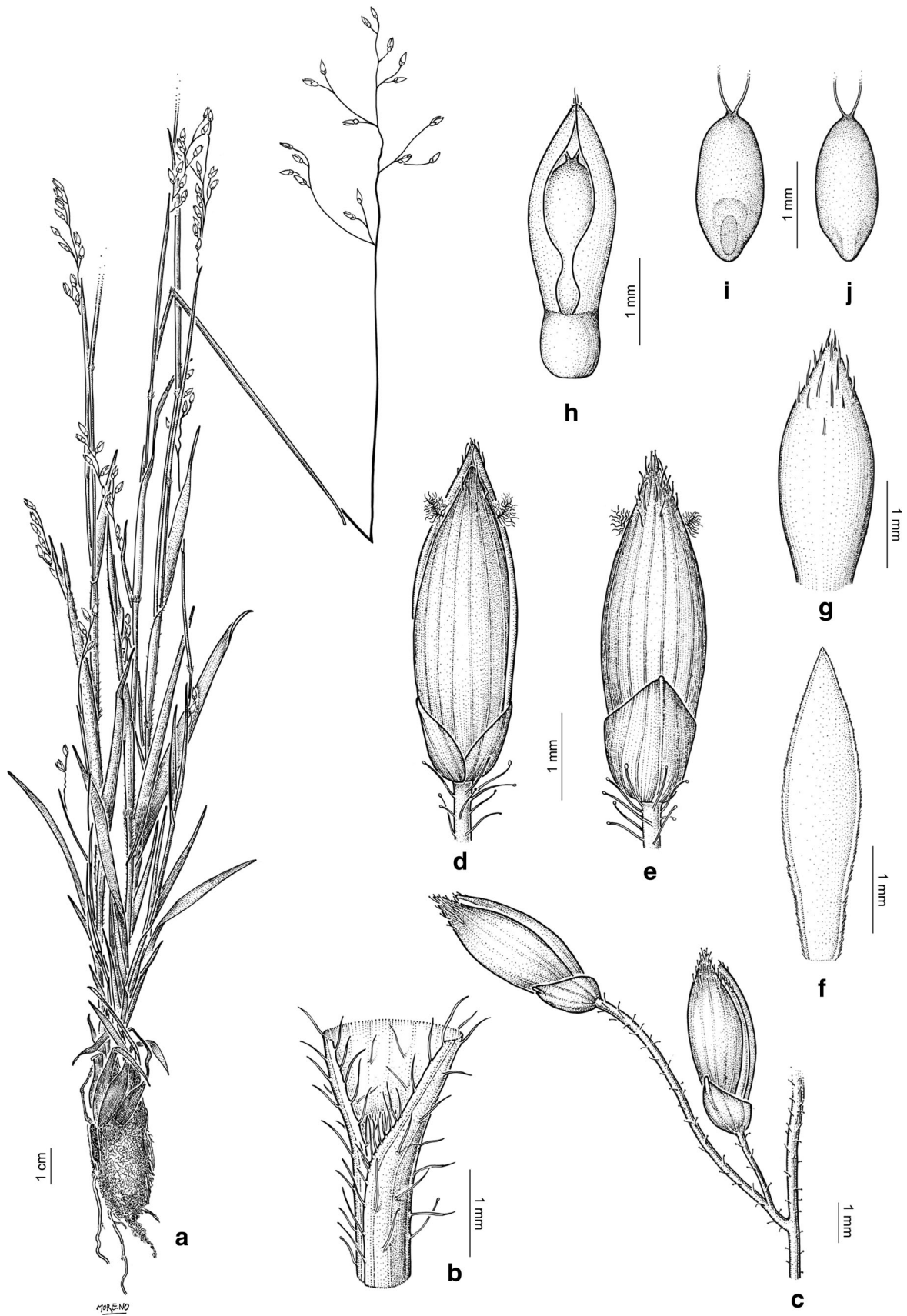
= *Panicum hymeniochilum* var. *glandulosum* Nees, Fl. Afr. Austral. III.: 47. 1841.—TYPE: South Africa. Natal: near the Umlazi river, 25 Mar 1832, *J.F. Drège s.n.* (—TYPE: P barcode P00442175!; isolectotypes, HAL barcode HAL0063367!, K barcode K000282469).

= *Panicum glanduliferum* K.Schum., Abh. Naturwill. Vereine Bremen 9: 401. 1887.—TYPE: Madagascar: “Im Sümpfen ohne genauere Standortsangabe”, 8 Nov 1877, *C. Rutenberg s.n.* (not located).

= *Panicum filiculme* Hack. ex Schinz, Bull. Herb. Boissier 3(8): 377. 1895.—TYPE: South Africa. Natal: inter Pinetown et Umbilo, *A. Rehmann 8049* (holotype, Z; isotypes, K barcode K000255480!, US-80764!).

= *Panicum schlechteri* Hack., Bull. Herb. Boissier 7(1): 24. 1899.—TYPE: South Africa. Natal: «in humidis prope Hilton Road (Terra Capens, orientalis)», 17 Feb 1895, *F.R.R. Schlechter 6759* (holotype, Z; isotype, BOL barcode BOL139355!).

= *Panicum snowdenii* C.E.Hubb., Bull. Misc. Inform. Kew 1928(4): 132–133. 1928.—TYPE: Uganda. Mt. Elgon, Butandiga, 2100–2400 m, in shade of and near bushes, following cultivation, 19 Aug 1927, *J.D. Snowden 1188* (**lectotype designated here**, K barcode K000255553!; isolectotypes, BM barcode BM000923145!, BR barcode BR0000008768186!, K barcode K000255554!, MO barcode MO1660941!, PRE barcode PRE0033229-0!, SRGH barcode SRGH0107002-0, US barcodes US140001!, US00731198!).



= *Sacciolepis semienensis* Chiov., Pl. Nov. Minus Not. Aethiopia: 25. 1928.—TYPE: Ethiopia. Semien, *E. Chiovenda* 937 (holotype, FT barcode FT000239!).

– (“*Panicum semienense* Chiov.”, Pl. Nov. Minus Not. Aethiopia: 25. 1928, pro syn. nom. nud.)

= *Panicum kisanuense* Vanderyst ex Robyns, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8vo) 1(6): 25, tab. 1, G-M. 1932.—TYPE: Zaire. Kisanu, 13 Apr 1916, *H. Vanderyst* 6010 (lectotype, BR barcode BR00000 0876513!, designated by Renzoize, Kew Bull. 22: 488. 1968; isolectotype, BR barcode BR000000876217!).

= *Panicum djalonense* A.Chev., Rev. Bot. Appl. Agric. Trop. 14: 27. 1934.—TYPE: French Guinea. Lit de la rivière Mafin à Dalaba, 1350 m, 16 Apr 1907, *O. Caille* 18139 (holotype, P!; isotypes, BR barcode BR0000008769176!, K barcode K000257019!).

Distribution and habitat—A widespread species which inhabits humid, shady areas, at river margins in Botswana, Burundi, Cote d’Ivoire, Ethiopia, Guinée, Malawi, Mozambique, Zambia, and Zimbabwe; 600–2,800 m elevation. This species is also found in Madagascar.

Adenochloa hymeniochila is included, together with *A. nigromarginata* and *A. pole-evansii*, in a group of aquatic annual species, with culms conspicuously branching at the lower nodes, blades lanceolate, lower glume 1/3 to 1/2 the length of the spikelet, nerveless to 1-nerved, and upper anthercium glabrous, papillose. *Adenochloa pole-evansii* differs from *A. hymeniochila* and *A. nigromarginata* by having a developed lower palea enclosing a lower flower (vs. lower palea reduced and lower flower absent); also, *A. nigromarginata* has 1.2–1.8 mm long spikelets, black at the upper portion, upper glume shorter than the upper anthercium, and upper anthercium black towards the apex (vs. spikelets 2–3 mm long, upper glume as long as or longer than the upper anthercium, and upper anthercium pale in *A. hymeniochila*).

The type specimen of *P. glanduliferum* is not preserved at B; nevertheless, the analysis of the original description, and additional material of the species preserved at P from Madagascar, allowed us to conclude that this species is a synonym of *A. hymeniochila*.

9. *Adenochloa lukwangulense* (Pilg.) Zuloaga, **comb. nov.**

≡ *Panicum lukwangulense* Pilg., Notizbl. Bot. Gart. Berlin-Dahlem 12: 380. 1935.—TYPE: Tanzania. Uluguru Mts., Lukwangule Plateau, 20 Feb 1933, *H.J. Schlieben* 3520 (holotype, B; isotypes, BM barcode BM000923146!, BR barcode BR0000008769183!, LISC barcode LISC003465!, M barcode M0103983!, MA barcodes MA175716!, 175716-2!, MO barcode MO1710404!, P barcode P00442181!, PRE barcode PRE0033219-0!).

Distribution and habitat—Malawi and Tanzania, where it is found in montane grasslands, between 2,300 and 2,900 m elevation.

Fig. 5 *Adenochloa hymeniochila* (Nees) Zuloaga. **a** Habit; **b** ligular region; **c** portion of the inflorescence; **d** spikelet, ventral view; **e** spikelet, dorsal view; **f** upper anthercium, dorsal view; **g** upper lemma; **h** stamens and gynoeceum [**a–h** from *Biegel and G. Russell* 3908 (K)]

This species is characterized by being a robust, caespitose perennial with culms up to 160 cm tall, densely hispid along blades and culms, with glandular hairs all over the terminal inflorescence, the panicles 10–40 cm long; the spikelets are 2.6–3.7 mm long, with the lower glume 1/2 or less the length of the spikelet, the upper glume usually not covering the upper anthercium, lower palea and lower flower absent, and upper anthercium with macrohairs toward the distal portion.

10. *Adenochloa nigromarginata* (Robyns) Zuloaga, **comb. nov.**

≡ *Panicum nigromarginatum* Robyns, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8vo) 1(6): 24, tab. 1, A-F. 1932.—TYPE: Democratic Republic of the Congo. Shaba: Welgelegen, 2 May 1912, *J.C.C. Bequaert* 385 (holotype, BR barcode BR0000008769381!; isotypes, K barcode K000256717!, K barcode K000256718!, US barcode US1538733!, fragment).

Distribution and habitat—it grows in swampy places, in forest margins, of the Democratic Republic of the Congo, Uganda, and Zambia, ca. 1400 m.

Adenochloa nigromarginata differs from *A. hymeniochila* and *A. pole-evansii* by its spikelets 1.2–1.8 mm long, dark, and also by having a dark upper anthercium (see relationships of this species under *A. hymeniochila*).

11. *Adenochloa pectinella* (Stapf) Zuloaga, **comb. nov.**

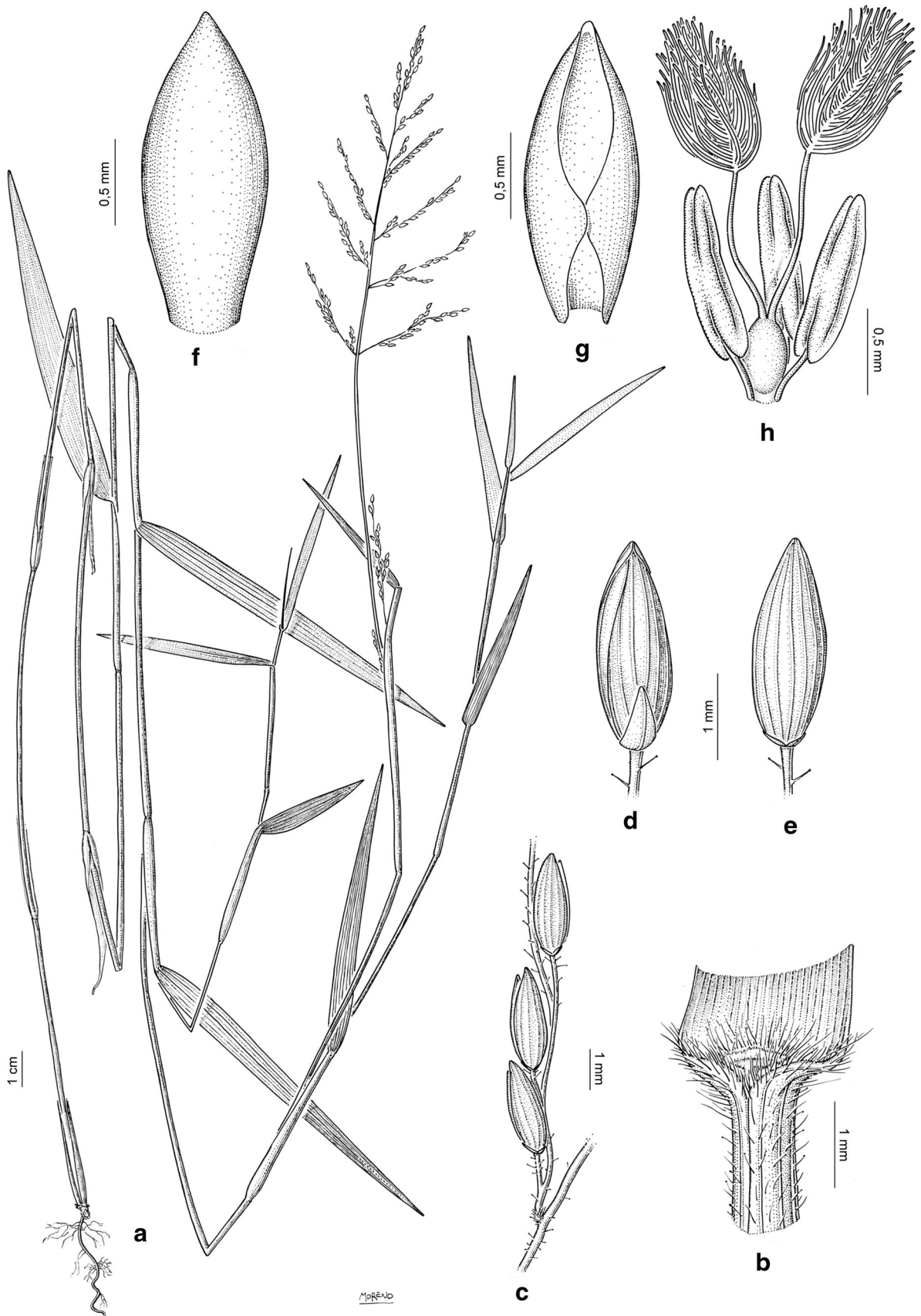
≡ *Panicum pectinellum* Stapf, Fl. Trop. Afr. 9: 720. 1920.—TYPE: Democratic Republic of the Congo. Katanga: near Elisabethville, on dry wooded ground, Feb 1912, *H. Homblé* 54 (holotype, K!; isotypes, BR barcodes BR0000008769053!, BR0000008768728!) Fig. 6.

= *Panicum omega* Renvoize, Kew Bull. 34(3): 551. 1979[1980].—TYPE: Tanzania. Mbeya District: World’s End View, 25 Dec 1969, *R. Wingfield* 512 (holotype, K barcode K000282426!; isotype, EA barcode EA000000479!).

Distribution and habitat—Angola, Democratic Republic of the Congo, Malawi, and Zambia, growing in woodlands or rocky grassland; 1100–2000 m.

When describing *P. omega*, Renvoize (1980) differentiated the species from *P. pectinellum* by its compact base, basal blades, and absence of glandular hairs. However, we consider that the single collection of *P. omega* represents a depauperate specimen of *P. pectinellum*, and therefore, we include this species in the synonymy of the latter. See relationships of *A. pectinella* under *A. ecklonii*.

12. *Adenochloa pole-evansii* (C.E.Hubb.) Zuloaga, **comb. nov.**



≡ *Panicum pole-evansii* C.E.Hubb., Bull. Misc. Inform. Kew 1934: 113. 1934.—TYPE: Zambia. At river 9 miles south of Lake Tanganyka, creeping over rocks, July 1930, I.B. Pole Evans 3039 (holotype, K).

Distribution and habitat—Democratic Republic of the Congo, Tanzania, and Zambia, in margins of streams and swamps, in areas partially shaded; 1,200–1,500 m.

Adenochloa pole-evansii is morphologically related to *A. hymeniocchila*, differing from the latter species by its reduced lower palea, without enclosing a lower flower (vs. lower palea and lower flower developed in *A. hymeniocchila*), spikelets ellipsoid (vs. spikelets lanceolate), and, as already pointed out by Clayton and Renvoize (1982), by the spikelets not appressed on the branches (vs. spikelets appressed on the branches in the latter species).

13. *Adenochloa sadinii* (Vanderyst) Zuloaga, **comb. nov.**

≡ *Brachiaria sadinii* Vanderyst, Bull. Agric. Congo Belge, 10: 244. 1919.

≡ *Panicum sadinii* (Vanderyst) Renvoize, Kew Bull. 22: 485. 1968.—TYPE: Democratic Republic of the Congo. Kitiaka, Apr 1917, *H. Vanderyst 6310* (**lectotype designated here**, BR barcode BR0000008766113!).

= *Panicum acuminatifolium* Robyns, Mém. Inst. Roy. Colon. Belge, Sect. Sci. Nat. (8vo) 1(6): 27, tab. 2 A-F. 1932.—TYPE: Democratic Republic of the Congo. District forestier Central Banalia, 8 Dec 1913, *J.C. Bequaert 1402* (holotype, BR barcode BR0000008768759!; isotypes, K barcode K000256719!, US barcode US1538738!).

= *Panicum lineatum* Trin., Sp. Gram. 2(20): tab. 233. 1829, nom. illeg. (Art. 53), non Schumach., 1828.—TYPE: Sierra Leone. Without locality, *J. Lindley s.n.* (isotype, K barcode K000257018!).

= *Panicum scandens* Mez, Bot. Jahrb. Syst. 57: 190. 1921, nom. illeg. (Art. 53), non Trin., 1826.—TYPE: Liberia. Sinoe, 24 Nov 1908, *M. Dinklage 2326* (**lectotype designated here**, B barcode B10-016891!; isolectotypes, B barcodes B10-016890!, B10-016892!).

Distribution and habitat—a species from western Africa, where it is found in Angola, the Democratic Republic of the Congo, and Zambia; it is frequent in margins of forests.

Renvoize (1968) cited the following specimens as syntypes of *Brachiaria sadinii*: *Vanderyst 5325, 5341, and 6313*, all from BR. However, the original description by Vanderyst cited the syntypes: “AR, Kitiaka, avril 1917; Kindundu (sans numéro); région d’Idiofa, 8642; Haut-Kwilu, 3356, janvier 1914. The specimen *Vanderyst 6310*, kept at BR, agrees with the protologue and is therefore designated as lectotype of the species.

14. *Adenochloa squarrosa* (Peter) Zuloaga, **comb. nov.**

≡ *Polyneura squarrosa* Peter, Repert. Spec. Nov. Regni Veg. Beih. 40 (1, Anhang): 53–54, tab. 30, Fig. 1, 1929.

Fig. 6 *Adenochloa pectinella* (Stapf) Zuloaga. **a** Habit; **b** ligular region; **c** portion of the inflorescence; **d** spikelet, ventral view; **e** spikelet, dorsal view; **f** upper antheridium, dorsal view; **g** upper lemma with caryopsis [**a–g** from *Renvoize 5713* (K)]

≡ *Panicum peteri* Pilg., Nat. Pflanzenfam. 14e: 20. 1940.

≡ *Brachiaria squarrosa* (Peter) Clayton, Kew Bull. 34(3): 559. 1979[1980].—TYPE: Tanzania. Uzuramo District: Pugu, 28 Oct 1925, *G.A. Peter 31511* (lectotype, B barcode B10-0168856!; isolectotypes, K barcode K000255545!, US barcode US00141251!, fragment) Fig. 7.

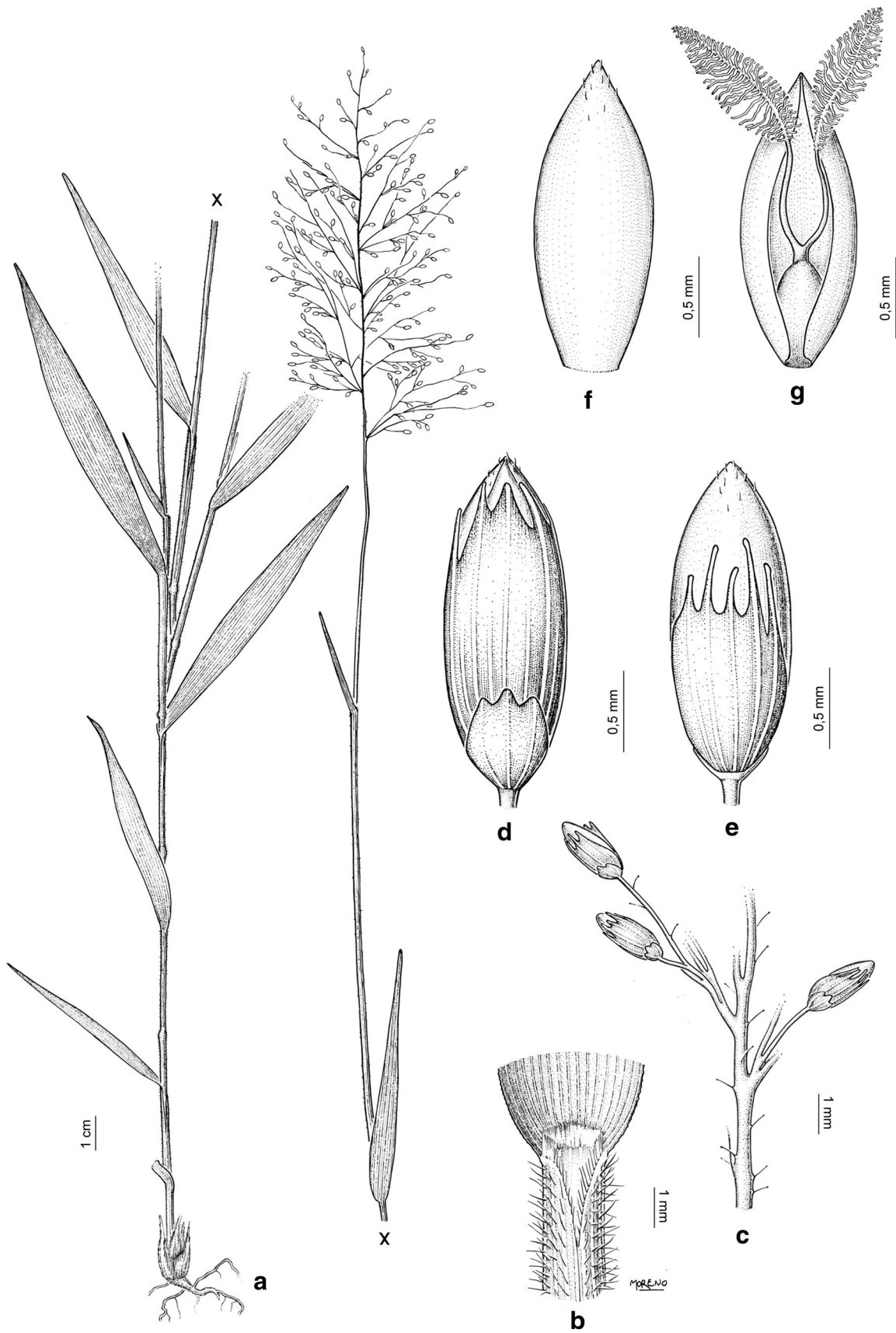
Distribution and habitat—Eastern Africa, in Mozambique, Tanzania, and Zimbabwe, where it is found in forest edges in humid habitats; 100–700 m.

This species is characterized by its rigid culms profusely branching from the lower nodes, blades ovate lanceolate, flat and asymmetric at the base, the leaves with many glandular hairs; the inflorescences are partially exerted on the culms, and the spikelets have a lower glume 1/2 the length of the spikelet, 7–9-nerved, the upper glume and lower lemma are 9–13-nerved.

Acknowledgments Funding of this research was provided by CONICET, grant 11220100100207. We like to express our deep gratitude to Francisco Rojas and Marcelo Moreno for the illustrations included in this contribution. We especially appreciate the help of the Editor-in-Chief Karol Marhold, Rob Soreng, and two additional anonymous reviewers who provided useful suggestions to improve an early version of this paper.

Appendix: List of taxa used in the molecular analysis and GenBank accession numbers. For new sequences (*) voucher information is given

Tribe Andropogoneae. *Andropogon gerardii* Vitman, AF117391; *Bothriochloa bladhii* (Retz.) S.T.Blake, AF117395; *Chionachne koenigii* (Spreng.) Thwaites, AF117397; *Cymbopogon flexuosus* (Nees ex Steud.) Will. Watson, AF117404; *Phacelurus digitatus* (Sibth. & Sm.) Griseb., AF117418. *Sorghum bicolor* (L.) Moench, U21981; *Zea mays* L., U21985. **Tribe Arundinelleae.** *Arundinella hirta* (Thunb.) Tanaka, AF117393. **Tribe Chasmanthieae.** *Chasmanthium laxum* (L.) H.O.Yates, U27296. **Tribe Paniceae.** *Acroceras zizanioides* (Kunth) Dandy, AY029618; *Cenchrus ciliaris* L., AY029625; *C. compressus* (R. Br.) Morrone, AY029672; *C. setaceus* (Forssk.) Morrone, AY029673; *Chaetium bromoides* (J. Presl) Benth. ex Hemsl., AY029626; *Dichantherium acuminatum* (Sw.) Gould & C.A.Clark, AY188485; **D. bosicii* (Poir.) Gould & C.A.Clark, United States, Missouri, Cherokee Pass Quadrangle, Brant 5442 (MO) KP173703; *D. clandestinum* (L.) Gould, AY188461; *D. cumbucana*



(Renvoize) Zuloaga, AY188464; **D. hebotes* (Trin.) Zuloaga, Brazil, Ceará, Guaramiranga, Huber s.n. (IAN); *D. koolauense* (H.St.John & Hosaka) Gould & C.A.Clark, AY029627; **D. linaerifolium* (Scribn.) Gould, United States, Missouri, Howell County, Summers 8082 (MO) KP173704; **D. malacophyllum* (Nash) Gould, United States, Missouri, Vernon County, Camp Clark, Becker 1042 (MO) KP173705; **D. oligosanthos* (Schult.) Gould, United States, Missouri, Vernon County, Camp Clark, Becker 900 (MO) KP173706; *D. sabulorum* (Lam.) Gould & C.A.Clark, AY029654; **D. scoparium* (Lam.) Gould, United States, Missouri, Stoddard County, Gust 729 (MO) KP173707; **D. stigmatosum* (Trin.) Zuloaga, Brazil, Santa Catarina, Urubici, Silva and Silva 26 (SI) KP173708; **D. superatum* (Hack.) Zuloaga, Brazil, Santa Catarina, Dalmoli et al. 62 (SI) KP173709; Brazil, Santa Catarina, Urubici, Dalmoli et al. 75 (SI) KP173710; **D. viscidellum* (Scribn.) Gould, Colombia, Norte de Santander, vicinity of Toledo, Killip and Smith 20046 (US) KP173711; *Digitaria setigera* Roth ex Roem. & Schult., AY029629; *Echinochloa colona* (L.) Link, AY029631; *Eriochloa punctata* (L.) Desv., AY029634; *Lasiacis sorghoidea* (Desv.) Hitchc. & Chase, AY029639; *Megathyrsus maximus* (Jacq.) B. K. Simon and S. W. L. Jacobs, AY029649; *Melinis repens* (Willd.) Zizka, AY029675; *Moorochloa eruciformis* (Sm.) Veldkamp, AY188452; *Oplismenus hirtellus* (L.) P.Beauv., AY029644; *Panicum*. Section *Dichotomiflora* (Hitchc.) Honda: *Panicum aquaticum* Poir., AY029658; *P. dichotomiflorum* Michx., AY188466; *P. elephantipes* Nees ex Trin., AY029647; *P. gounii* E.Fourn., AY188467; *P. pedersenii* Zuloaga, AY029646; *P. repens* L., AY029651. Section *Panicum*: *P. bergii* Arecnav., AY188457; *P. fauriei* Hitchc., AY029650; *P. miliaecum* L., AY188472; *P. nephelophilum* Gaudich., AY029645; *P. stramineum* Hitchc. & Chase, AY188489. Section *Rudgeana* (Hitchc.) Zuloaga: *P. cervicatum* Chase, AY188459; *P. rudgei* Roem. & Schult., AY029661. Section *Urvilleana* (Hitchc.) Pilg.: *P. chloroleucum* Griseb., AY188460; *P. racemosum* (P.Beauv.) Spreng., AY188481. Section *Virgata* Hitchc. & Chase ex Pilg.: *P. tricholaenoides* Steud., AY188493; *P. virgatum* L., U21986. Ungrouped. *P. mystasipus* Zuloaga & Morrone, AY188474; *P. olyroides* Kunth, AY188475. *Panicum* "incertae sedis": Section *Clavelligerae* Stapf: *P. adenophorum* K.Schum., AY188454; *P. claytonii* Renvoize, AY188462; **P. bullockii*, Zambia, Sunzu Mountain, 20 miles S of Abercorn, Phipps and Vesey-Fitzgerald 3314 (K) KP173693; **P. ecklonii*, Tanzania, Iringa, Makete, Gereau 3123 (MO) KP173694; **P. flacciflorum*, Tanzania, Mpanda, Uzondo Plateau, Bidgood et al. 5501 (K) KP173695; **P. habrothix*, Burundi, Bujumbura, Muhira, Reekmans 8890 (K) KP173696; **P. hymenochilum*, Tanzania, Rukwa,, Sumbawanga, Harder et al. 1257

Fig. 7 *Adenochloa squarrosa* (Peter) Zuloaga. **a** Habit; **b** ligular region; **c** spikelet, ventral view; **d** spikelet, dorsal view; **e-f** lower palea; **g** upper antheridium, dorsal view; **h** upper antheridium, ventral view; **i** upper palea with lodicules and stamens [a-i from Simon and Ngoni 1296 (K)]

(MO) KP173697; **P. nigromarginatum*, Tanzania, Bukoba, Minziro Forest Reserve, Bayona and Festo 9244 (K) KP173698; **P. pectinellum*, Zambia, Mporokoso, 28 miles east of Mporokoso, Fitzgerald 3124 (MO) KP173699; **P. peteri*, Mozambique, Sofala, southern tip of Chimanimani Mts., Muller and Kelly 1103 (K) KP173700; **P. pole-evansii*, Zambia, Luapula, Lake Bangweulu, Renvoize 5513 (MO) KP173701; **P. sadinii*; Zambia, Mwinilunga, river Lunga at Mwinilunga, Milne-Redhead 3339 (K) KP173702; Section *Monticola* Stapf: *P. milligrana* Poir., AY029660; *P. sellowii* Nees, AY188484; *P. trichanthum* Nees, AY188492. Section *Verrucosa* Hitchc. & Chase ex C. C. Hsu: *P. verrucosum* Muhl., AY188496. Ungrouped: *P. antidotale* Retz., AY188456; *Parodiophyllochloa cordovens* (E.Fourn.) Zuloaga & Morrone, AY188463; *P. missiona* (Ekman) Zuloaga & Morrone, AY188473; *P. ovulifera* (Trin.) Zuloaga & Morrone, AY029653; *P. penicillata* (Nees ex Trin.) Zuloaga & Morrone, AY18847; *Pseudechinolaena polystachya* (Kunth) Stapf, AY029676; *Sacciolepis indica* (L.) Chase, AY029677; *Setaria geminata* (Forssk.) Veldkamp, AY029662; *S. lachnea* (Nees) Kunth, AY029683; *S. macrostachya* Kunth, AY029678; *S. palmifolia* (J.König) Stapf, AY029680; *S. viridis* (L.) Beauv., U21976; *Stenotaphrum secundatum* (Walter) Kuntze, AY029684; *Trichantheicum cyanescens* (Lam.) Zuloaga & Morrone, AY188465. *T. parvifolium* (Lam.) Zuloaga & Morrone, AY188476; *T. schwackeanum* (Mez) Zuloaga & Morrone, AY188483; *T. wettsteinii* (Hack.) Zuloaga & Morrone, AY188497; *Urochloa acuminata* (Renvoize) Morrone & Zuloaga AY029629; *U. plantaginea* (Link) R.D.Webster, AY029693; *Zuloagaea bulbosa* (Kunth) Bess, AY029648. **Tribe Paspaleae.** *Aakia tuerckheimii* (Hack.) J.R.Grande, AY188494; *Altoparadisium chapadense* Filg. et al., AY029619; *Anthaenantia lanata* (Kunth) Benth., AY029640; *Anthaenantia rojasiana* Parodi, AY029620; *Apochloa euprepes* (Renvoize) Zuloaga & Morrone, AY029657; *A. subtiramulosa* (Renvoize & Zuloaga) Zuloaga & Morrone, AY188490; *Arthropogon villosus* Nees, AY029622; *Axonopus anceps* (Mez) Hitchc., AY029623; *Axonopus hydrolithicus* (Filg. et al.) A. López & Morrone, AY029642; *Canastra lanceolata* (Filg.) Morrone et al., AY029621; *Coleataenia anceps* (Michx.) Soreng, AY188455. *C. caricoides* (Nees ex Trin.) Soreng, GU253330; *C. longifolia* (Torr.) Soreng, AY188482. *C. petersonii* (Hitchc. & Ekman) Soreng, AY188479. *C. prionitis* (Nees) Soreng, AY029652; *C. stenodes* (Griseb.)



Soreng, GU253333; *C. tenera* (Beurr. ex Trin.) Soreng, AY188491; *Echinolaena inflexa* (Poir.) Chase, AY029633; *Homolepis glutinosa* (Sw.) Zuloaga & Soderstr., AY029637; *Hopia obtusa* (Kunth) Zuloaga & Morrone, AY029659; *Hymenachne donacifolia* (Raddi) Chase, AY029635; *H. grumosa* (Nees) Zuloaga, AY188468; *H. pernambucensis* (Spreng.) Zuloaga, AY188478; *Ichnanthus pallens* (Sw.) Munro ex Benth., AY029638; *Mesosetum chaseae* Luces, AY029641; *Ocellochloa chapadensis* (Swallen) Zuloaga & Morrone, AY188486; *O. piauiensis* (Swallen) Zuloaga & Morrone, AY029656; *O. stolonifera* (Poir.) Zuloaga & Morrone, AY18848; *Oncorachis ramosa* (Zuloaga & Soderstr.) Morrone & Zuloaga, AY029686; *Oplismenopsis najada* (Hack. & Arechav.) Parodi, AY188453; *Otachyrium versicolor* (Döll) Henrard, AY029643; *Oswaldoa valida* (Mez) J.R.Grande, AY188495; *Paspalum arundinellum* Mez, AY029663; *P. conjugatum* Bergius, AY029669; *P. glaziovii* (A.G.Burm.) S.Denham, AY029689; *P. remotum* J.Remy, AY029668; *P. vaginatum* Sw., AY029665; *Phanopyrum gymnocarpon* (Elliott) Nash, AY188469; *Plagiantha tenella* Renvoize, AY029674; *Rugoloa hylaeica* (Mez) Zuloaga, AY188470; *Rugoloa pilosa* (Sw.) Zuloaga, AY188480; *Steinchisma decipiens* (Nees ex Trin.) W. V. Br., AY188499; *S. hians* (Elliott) Nash, AY029685; *S. laxa* (Sw.) Zuloaga, AY029655; *S. spathellosa* (Döll) Renvoize, AY188500; *Stephostachys mertensii* (Roth) Zuloaga & Morrone, AY188471; *Streptostachys asperifolia* Desv., AY029687; *Tatianyx amacites* (Trin.) Zuloaga & Soderstr., AY029688. **Tribe Thysanolaenae.** *Thysanolaena maxima* (Roxb.) Kuntze, U21984. **Tribe Tristachyideae.** *Danthoniopsis dinteri* (Pilg.) C.E.Hubb., AY029695. **Tribe Zeugiteae.** *Zeugites pittieri* Hack., U21987.

References

- Aliscioni SS, Giussani LM, Zuloaga FO, Kellogg EA (2003) A molecular phylogeny of *Panicum* (Poaceae: Paniceae): tests of monophyly and phylogenetic placement within the Panicoideae. *Amer J Bot* 90:796–821. doi:10.3732/ajb.90.5.796
- Bess E, Doust ANL, Davidse G, Kellogg EA (2006) *Zuloagaea*, a new genus of neotropical grass within the “Bristle Clade” (Poaceae: Paniceae). *Syst Bot* 31:656–670
- Bosser J (1969) Graminées des paturages et des cultures a Madagascar. *Mem ORSTOM* 35:1440
- Brown WV (1977) The Kranz syndrome and its subtypes in grass systematics. *Mem Torrey Bot Club* 23:1–97
- Christin PA, Salamin N, Kellogg EA, Vicentini A, Besnard G (2009) Integrating phylogeny into studies of C₄ variation in the grasses. *Pl Physiol* 149:82–87
- Clayton WD, Renvoize SA (1982) Gramineae (Part 3). In: Polhill RM (ed.), *Fl Trop E Africa, Gram (Part 3)*, pp 461–499
- Darriba D, Taboada GL, Doallo R, Posada D (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Meth* 9:772. doi:10.1038/nmeth.2109
- Duvall MR, Noll JD, Minn AH (2001) Phylogenetics of Paniceae (Poaceae). *Amer J Bot* 88:1988–1992
- Duvall MR, Saar DE, Grayburn WS, Holbrook GP (2003) Complex transitions between C₃ and C₄ photosynthesis during the evolution of paniceae: a phylogenetic case study emphasizing the position of *Steinchisma hians* (Poaceae), a C₃–C₄ intermediate. *Int J Pl Sci* 164:949–958
- Felsenstein J (1985) Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791. doi:10.2307/2408678
- Giussani LM, Cota-Sanchez JH, Zuloaga FO, Kellogg EA (2001) A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C₄ photosynthesis. *Amer J Bot* 88:1993–2012
- Goloboff PA, Farris JS, Nixon KC (2008) TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786
- Gómez-Martínez R, Culham A (2000) Phylogeny of the subfamily Panicoideae with emphasis on the tribe Paniceae: evidence from the *trnL-F* cpDNA region. In: Jacobs SWL, Everett JE (eds) *Grasses: systematics and evolution*. Commonwealth Scientific and Industrial Research Organization (CSIRO) Publishing, Victoria, Collingwood, pp 136–140
- Grande Allende JR (2014) Novitates Agrostologicae. IV. Additional segregates from *Panicum incertae sedis*. *Phytoneuron* 22:1–6
- Hall TA (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp Series* 41:95–98
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17:754–755
- Kabuye CHS, Wood D (1968) A first record of multicellular glandular hairs in the Gramineae. *Bot J Linn Soc* 62:69–70
- Morrone O, Scataglieni MA, Zuloaga FO (2007) *Cyphonanthus*, a new genus segregated from *Panicum* (Poaceae: Panicoideae): Paniceae based on morphological, anatomical and molecular data. *Taxon* 56:521–532
- Morrone O, Denham SS, Aliscioni SS, Zuloaga FO (2008) *Parodiophyllochloa*, a new genus segregated from *Panicum* (Paniceae, Poaceae) based on morphological and molecular data. *Syst Bot* 33:66–76. doi:10.1600/036364408783887393
- Morrone O, Aagesen L, Scataglieni MA, Salariato DL, Denham SS, Chemisquy MA, Sede SM, Giussani LM, Kellogg EA, Zuloaga FO (2012) Phylogeny of the Paniceae (Poaceae: Panicoideae): integrating plastid DNA sequences and morphology into a new classification. *Cladistics* 28:333–356. doi:10.1111/j.1096-0031.2011.00384.x
- Nees von Esenbeck CGN (1841) *Fl Afr Austral Ill. I. Gramineae: 1–490*. Glogau
- Olmstead RG, Sweere JA (1994) Combining data in phylogenetic systematics: an empirical approach using three molecular data sets in the solanaceae. *Syst Biol* 43:467–481. doi:10.1093/sysbio/43.4.467
- Osborne CP, Salomaa A, Kluyver TA, Visser V, Kellogg EA, Morrone O, Vorontsova MS, Clayton WD, Simpson DA (2014) A global database of C₄ photosynthesis in grasses. *New Phytol.* doi:10.1111/nph.12942
- Rambaut A, Drummond A (2007) Tracer, version 1.4. Computer program and documentation distributed by the author, website <http://tree.bio.ed.ac.uk/software/tracer/>
- Renvoize SA (1968) Studies in the Gramineae: XVIII. *Kew Bull* 22:481–488
- Renvoize SA (1979 [1980]) New species of *Panicum* (Poaceae) from tropical Africa. *Kew Bull* 34:551–555
- Renvoize SA (1989a) *Panicum*. In: Launert E, Pope GV (eds) *Flora Zambesiaca*. pp 9–40
- Renvoize SA (1989b) New species of *Panicum* (Poaceae) from southern tropical Africa. *Kew Bull* 44:543–546

- Salariato DL, Zuloaga FO, Giussani LM, Morrone O (2010) Molecular phylogeny of the subtribe Melinidinae (Poaceae:Panicoideae:Paniceae) and evolutionary trends in the homogenization of inflorescences. *Molec Phylogen Evol* 56:355–369
- Sede SM, Morrone O, Giussani LM, Zuloaga FO (2008) Phylogenetic studies in the Paniceae (Poaceae): a realignment of section Lorea of *Panicum*. *Syst Bot* 33:284–300. doi:10.1600/036364408784571626
- Sede SM, Zuloaga FO, Morrone O (2009) Phylogenetic studies in the Paniceae (Poaceae-Panicoideae): *Ocellochloa*, a new genus from the New World. *Syst Bot* 34:684–692. doi:10.1600/036364409790139655
- Soreng R (2010) *Coleataenia* Griseb. (1879): the correct name for *Sorengia* Zuloaga and Morrone (2010) (Poaceae: Paniceae). *J Bot Res Inst Texas* 4:691–692
- Stapf O (1920) *Panicum*. In: Prain D (ed.) *Flora of Tropical Africa*, vol IX. L. Reeve & Co. Ltd, London, pp. 638–738
- Thiers B ([continuously updated]) *Index Herbariorum: A global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. <http://sweetgum.nybg.org/ih/>. Accessed 2013
- Zimmermann T, Bocksberger G, Brüggemann W, Berberich T (2013) Phylogenetic relationship and molecular taxonomy of African grasses of the genus *Panicum* inferred from four chloroplast DNA-barcodes and nuclear gene sequences. *J Pl Res* 126:363–371
- Zuloaga FO, Morrone O, Ellis RP (1993) A revision of *Panicum* subg. *Dichantheium* (Poaceae: Panicoideae: Paniceae) in Mesoamerica, the West Indies, and South America. *Ann Missouri Bot Gard* 80:119–190
- Zuloaga FO, Morrone O, Giussani LM (2000) A cladistic analysis of the Paniceae: a preliminary approach. In: Jacobs SWL, Everett JE (eds) *Grasses: Systematics and Evolution*. Commonwealth Scientific and Industrial Research Organization (CSIRO) Publishing, Victoria, Collingwood, pp 123–135
- Zuloaga FO, Giussani LM, Morrone O (2006) On the taxonomic position of *Panicum aristellum* (Poaceae: Panicoideae: Paniceae). *Syst Bot* 31:497–505. doi:10.1043/05-56.1
- Zuloaga FO, Giussani LM, Morrone O (2007) *Hopia*, a new genus segregated from *Panicum* (Poaceae: Panicoideae: Paniceae). *Taxon* 56:145–156
- Zuloaga FO, Scataglini MA, Morrone O (2010) A phylogenetic evaluation of *Panicum* sects. *Agrostoidea*, *Megista*, *Prioniitia* and *Tenera* (Panicoideae, Poaceae): two new genera. *Stephostachys Sorengia*. *Taxon* 59:1535–1546
- Zuloaga FO, Morrone O, Scataglini MA (2011) Monograph of *Trichantheium*, a new genus segregated from *Panicum* (Poaceae, Paniceae) based on morphological and molecular data. *Syst Bot Monogr* 94:1–101