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Research Article

Reinstatement and expansion of the genus *Anatherum* (Andropogoneae, Panicoideae, Poaceae)

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The genus *Andropogon* sensu lato is known to be polyphyletic. Accordingly, we here adjust part of the classification of the genus to reflect its evolutionary history and morphological diversity. A plastome phylogeny including 20 new plastome sequences confirms a well-supported clade of species broadly corresponding to *Andropogon* section *Leptopogon.* Morphological diversity was assessed across *Andropogon* sensu lato using specimens held at the K, MO, and A/GH herbaria, GrassBase, and photographs of spikelet pairs, with an emphasis on identifying members of this clade and their distinguishing features. The genus *Anatherum* is here reestablished, expanded to incorporate 45 of the 131 of *Andropogon* sensu lato species worldwide, and described and illustrated. Five species names in *Anatherum* are reinstated and new combinations are made for 40 species and one subspecies. *Anatherum* is most common and diverse in the Americas but also commonly found across Africa. Few species occur in Europe or Asia. *Anatherum* inflorescences generally have 2 branches, linear and slender internodes and pedicels with long trichomes, small elliptic to lanceolate spikelets, and flat to concave 2-keeled lower glumes with no intercarinal veins visible. Generic circumscription in this group is complicated by its polyploid history and limited understanding of the relationship between genomic composition and key morphological characters. Five species of doubtful generic affiliation are listed for future analysis.

Key words: Grass, grassland, large genera, phylogenomics, plastome, species, spikelet, spikelet pair, taxonomy

Introduction

Species in the large grass genus *Andropogon* L. are ubiquitous in C_4 open canopy ecosystems around the world, are significant drivers of these ecosystem functions and are commonly encountered by pastoralist farmers and range managers, ecologists, and conservation biologists (Clayton & Renvoize, 1986; Gibson, 2009). Understanding and management of grassy ecosystems depends on accurate classification of the plants on which both ecosystem function and local people's livelihoods depend. In its current circumscription, *Andropogon* (tribe Andropogoneae Dumort., subfamily Panicoideae A. Braun, family Poaceae Barnhart) includes 131 species distributed on all continents and is often common where it occurs (Nagahama & Norrmann, 2012; Welker et al., 2020). *Andropogon gerardi* Vitman is a major component of the tallgrass prairie of North America, *A. amethystinus* Steud., *A. appendiculatus* Nees, and *A. gayanus* Kunth are key components of African savannas and pastures (Acocks & Zacharias, 1990; Boonman, 1993), while *A. gayanus* has invaded and now dominates parts of Australia (Shaik et al., 2022).

Most species of *Andropogon* are classified in the monophyletic subtribe Andropogoninae J. Presl (Welker et al., 2020), although at least one species assigned to *Andropogon* falls well outside the subtribe in molecular phylogenies ("*A.*" *burmanicus* Bor sister to *Eulalia contorta* (Brongn.) Kuntze) and will ultimately need to be moved to another genus. Also in Andropogoninae are the genera *Schizachyrium* Nees, *Hyparrhenia* Andersson ex E. Fourn., and *Diheteropogon* (Hack.) Stapf, a placement that has been supported by all molecular

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phylogenetic studies to date (Arthan et al., 2017; Estep et al., 2014; Mathews et al., 2002; McAllister et al., 2018; Skendzic et al., 2007; Welker et al., 2020). However, the same studies have shown that within Andropogoninae, *Andropogon* is clearly polyphyletic, with species falling into multiple unrelated clades. The type species, *Andropogon distachyos* L., is part of a small clade of predominantly Asian species, so the generic name *Andropogon* is not applicable to the major New World or African radiations, which all have originated separately from the *Andropogon* sensu stricto clade (Arthan et al., 2017; Welker et al., 2020).

Relationships and classification of species within *Andropogon* have always been challenging. Hackel (1889) described *Andropogon* as "a vast genus, polymorphic, very varied in habit" and divided it into 13 subgenera, most of which are now recognized as separate genera. Hackel's *Andropogon* subg. *Arthrolophis* (Trin.) Hack. corresponds closely to the group now recognized as *Andropogon*. Stapf (1919) presented a concept of *Andropogon* similar to that which is followed today, although he noted that "The genus *Andropogon*, even in the restricted sense in which it is understood here, is probably more heterogeneous than any other genus of Andropogoneae". He recognized four sections in the genus–*Eu-Andropogon*, *Leptopogon* Stapf, *Piestium* Stapf, *Notosolen* Stapf–but noted that the latter three are "only loosely connected with *Eu-Andropogon* and may even be entitled to rank as distinct genera". Despite this sweeping classification, Stapf (1919) included only 43 species, all from Africa, and did not designate types, thus leaving species from other parts of the world unassigned to section. Nonetheless, his sectional classification has been widely adopted, for example by Campbell (2003) for North American species and Zanin and Longhi-Wagner (2006) for Brazilian species. In the most comprehensive treatment available, Nagahama & Norrmann (2012) extrapolated Stapf's groups to encompass 39 species from Africa and 60 from the Americas as well as varieties within some of the species. They focused particularly on chromosome numbers and, in a few instances, genomic origins of polyploids, although several dozen species were still unaccounted for.

Poaceae tribe Andropogoneae and subtribe Andropogoninae are distinguished and classified primarily on the basis of their spikelet pairs and synflorescence structures, the rapid evolution of which is responsible for disagreement between the traditional morphology-based classification and monophyletic clades inferred from DNA sequence data (Clayton, 1969; Clayton & Renvoize, 1986; Kellogg, 2015; McAllister et al., 2018). Ecological success of these grasses is likely linked to their morphological complexity and variability, enabling reproductive flexibility as the synflorescence structure can initially be challenging to interpret with up to two functionally male, female, bisexual, or sterile flowers/florets in each spikelet, with glumes, lemmas, paleas, and awns which can be reduced or absent and therefore difficult to recognize. In *Andropogon* fresh synflorescences (called inflorescences in the taxonomic literature) are digitate cylindrical structures which dry out and open as the caryopses mature, often revealing awns and multiple trichomes giving the plant a white fluffy appearance (e.g., Mashau et al., 2022). Each sessile spikelet is situated on a branch point of the inflorescence structure, subtended by an internode which gives rise to one internode and one pedicel at its base (e.g., Fish et al., 2015, pp. 68–69).

The largest single section of *Andropogon* sensu lato (s.l.) includes species that are commonly classified in sect. *Leptopogon*, which looks clearly distinct from *Andropogon* sensu stricto (s.s.). Stapf (1919) distinguished sections *Eu-Andropogon* and *Leptopogon* in tropical Africa from the other two sections by the pedicels and rachis internodes, which he described as linear, although "sometimes slightly widened upwards in sect. *Eu-Andropogon*", as well as the minute or absent palea of the seed-bearing floret. In contrast, he described the pedicels and rachis internodes as "distinctly swollen upwards, clavate or cuneate" in sections *Piestium* and *Notosolen*, and the palea well developed. Most *Andropogon* species of the Americas are in sect. *Leptopogon* with only a few from Africa (Nagahama & Norrmann, 2012). The majority are diploid or hexaploid. The same concept of *Andropogon* sect. *Leptopogon* was adopted for the genus worldwide by Clayton & Renvoize (1986), describing it as the largest section of *Andropogon* of 55 species with "lower glumes membranous, without intercarinal nerves, its keels lateral to dorsal and wingless; racemes in a compound panicle, delicate and often plumose; sometimes the sessile spikelet awnless or the pedicelled spikelet suppressed". In spite of the steady accumulation of phylogenetic data and a growing understanding of the evolution of *Andropogon* sensu lato (McAllister et al. 2018; Welker et al. 2020) no global overview has been attempted since, and the American taxa are currently better understood than the African taxa (Nagahama & Norrmann, 2012; Norrmann et al., 2004).

The polyphyly and morphological diversity in *Andropogon* s.l. make the current classification misleading, with traits ascribed to any given species often inapplicable to other species that are presumed to be related. Here we propose recognizing *Andropogon* sect. *Leptopogon* as a genus distinct from *Andropogon* s.s.

based on morphological and phylogenetic data. Even with the exclusion of *Andropogon* sect. *Leptopogon*, the remainder of *Andropogon* remains polyphyletic; to denote this component of "*Andropogon*" as a traditional taxonomic concept not representing a monophyletic group, we place the generic name in quotes. This paper reestablishes the genus *Anatherum* P. Beauv. as the oldest available generic name for the section, and transfers the accepted species and infraspecific taxa summarized by POWO (POWO, 2021) from "*Andropogon*" to *Anatherum*.

Materials and methods

Phylogenetic reconstruction

We added 20 plastome sequences of species putatively assigned to "*Andropogon*" sect. *Leptopogon* to those published by McAllister et al. (2018) (Table 1). DNA was extracted using a DNeasy® Plant Kit (Qiagen Inc., Germantown, MD), Illumina TruSeq PCR-Free or TruSeq DNA nano libraries were constructed, and samples were sequenced to a depth of approximately 1X–5X on an Illumina sequencer with paired end reads of 150 bp. Quality control of raw reads was performed by analysing overlap of paired end reads to assess DNA degradation, checking non-Poaceae contamination with Kraken (Wood & Salzberg, 2014). Placement of sequences in Andropogoneae was also validated by comparison to a custom database of select gene sequences from previously published plastomes. Plastome sequences were extracted and assembled with Fast-plast (McKain et al., unpublished) and assemblies checked manually for errors. Annotation used GE-seq (Tillich et al., 2017). New sequences were added to all putative "*Andropogon*" sect. *Leptopogon* sequences available from GenBank, aligned with MAFFT (Katoh & Standley, 2014), and a phylogeny constructed with RAxML (Stamatakis, 2014) with support assessed by 500 fast bootstrap replicates.

Morphology and taxonomy

To determine whether the "*Andropogon*" sect. *Leptopogon* clade is morphologically distinctive, we developed a list of all species of *Andropogon* s.l. in the RBG Kew (K) herbarium. Co-authors MSV and EAK then independently examined specimens of all species of *Andropogon* s.l. available at K, MO, and A/GH, which together encompassed the taxonomic diversity of the genus. We then met together to focus on the handful of species whose placement seemed unclear. In addition, we checked and compared spikelet pair length measurements reported by McAllister et al. (2018). Finally, data were retrieved from Clayton et al. (2016) for all species of "*Andropogon*" sect. *Leptopogon* to compare with other species of *Andropogon* s.l. and to compile the generic description. Photographs of spikelets for most species treated here can be retrieved from www.tropicos.org by searching on the species name.

Nomenclature

The generic name *Anatherum*, based on *A. bicorne* (L.) P. Beauv., is the oldest available name in "*Andropogon*" sect. *Leptopogon*. Accordingly, we provide formal nomenclatural transfers of members of the former "*Andropogon*" sect. *Leptopogon* to *Anatherum*. We inspected the types available in K, MO, and A/GH and verified that all were morphologically consistent with the generic realignment proposed. We have not attempted to revise species concepts or provide typification of names.

Results

Clade structure and synapomorphies

Monophyly of "*Andropogon*" sect. *Leptopogon* has been confirmed by adding 20 new plastome sequences to the 14 "*A.*" sect. *Leptopogon* sequences presented by McAllister et al. (2018) (Fig. 1). As shown in all previous studies to date, the clade of "*Andropogon*" sect. *Leptopogon* is strongly supported as monophyletic and sister to the clade of *Elymandra* Stapf plus *Monocymbium* Stapf. These clades together are sister to a clade that includes a mix of species currently classified in "*Schizachyrium*" and "*Andropogon*" but not including the type of either genus (*S. brevifolium* (Sw.) Nees ex Buse and *A. distachyos* L., respectively). Sister to these is a clade including "*A.*" *tenuiberbis* Hack., "*A.*" *brazzae* Franch., and "*A.*" *durifolius* Renvoize.

Most species of "*Andropogon*" sect. *Leptopogon* share a common set of characters although it is unclear if any are synapomorphic. The spikelet pairs commonly bear long trichomes on the callus, and in two lines along the internodes and pedicels, giving the inflorescences a characteristic fluffy appearance that can often be spotted from a distance (Figs 2–4). Most species have inflorescences with two branches (paired racemes), although a few have inflorescences with three or four branches and occasionally the branches are themselves branched. Internodes and pedicels are generally straight and often slightly flattened, a trait noted by Stapf (1919) and corroborated here. The lower glume of the sessile spikelet has two prominent veins between which the glume is hyaline and often slightly concave. The glume itself is glabrous.

Table 1. Specimens included in phylogenetic analysis and associated GenBank accession numbers for the plastome sequences.

Species	Voucher specimen and herbarium	GenBank number	Source
Anatherum aequatoriensis (Hitchc.) Voronts. & E.A.Kellogg	*Laegaard 18453* (MO)	MH181218	McAllister et al. (2018)
Anatherum africanum (Franch.) Roberty	*Vorontsova 1676* (K)	OQ439988	This study
Anatherum arenarium (Hack.) Voronts. & E.A.Kellogg	*Norrmann 139* (K)	OQ439989	This study
Anatherum bicorne (L.) P.Beauv.	*AuBuchon-Elder 110* (MO)	OQ439987	This study
Anatherum brachystachyum (Chapm.) Roberty	*AuBuchon-Elder 123* (MO)	OQ439991	This study
Anatherum capillipes (Nash) Voronts. & E.A.Kellogg	*AuBuchon-Elder 134* (MO)	OQ439990	This study
Anatherum eucomum (Nees) Voronts. & E.A.Kellogg	*Malcomber 3089* (MO)	MT610095	Welker et al. (2020)
Anatherum eucomum ssp. *huillense* (Rendle) Voronts. & E.A.Kellogg	*Razakamalala 5199* (MO)	MH181180	McAllister et al. (2018)
Anatherum floridanum (Scribn.) Voronts. & E.A.Kellogg	*Godfrey 79233* (MO)	MH181221	McAllister et al. (2018)
Anatherum glaucescens (Kunth) Voronts. & E.A.Kellogg	*Laegaard 54438* (MO)	MH181185	McAllister et al. (2018)
Anatherum glaucophyllum (Roseng., B.R.Arrill. & Izag.) Voronts. & E.A.Kellogg	*Schinini & Dematteis 33379* (MO)	OQ439993	This study
Anatherum glomeratum (Walter) Voronts. & E.A.Kellogg	*Aubuchon-Elder 15-1* (MO)	OQ439995	This study
Anatherum glomeratum	*Haber 9741* (MO)	OQ439994	This study
Anatherum glomeratum	*AuBuchon-Elder 15-4* (MO)	OQ439996	This study
Anatherum gyrans (Ashe) Voronts. & E.A.Kellogg	*Evers 21860* (MO)	MH181171	McAllister et al. (2018)
Anatherum ibityense (A.Camus) Voronts. & E.A.Kellogg	*Nanjarisoa 110* (K)	OQ439997	This study
Anatherum insolitum (A.Camus) Voronts. & E.A.Kellogg	*Harley 15771* (MO)	MH181163	McAllister et al. (2018)
Anatherum ivohibense (A.Camus) Voronts. & E.A.Kellogg	*Ratovonirina 181* (K)	OQ439998	This study
Anatherum laterale (Nees) Voronts. & E.A.Kellogg	*Morrone & Pensiero 116* (MO)	OQ440000	This study
Anatherum laxatum (Stapf) Voronts. & E.A.Kellogg	*Breteler 6785* (MO)	MH181206	McAllister et al. (2018)
Anatherum leucostachyum (Kunth) Voronts. & E.A.Kellogg	*Welker 374* (ICN)	OQ439999	This study
Anatherum liebmannii (Hack.) Voronts. & E.A.Kellogg	*Nuñez & Cortés 2357* (MO)	MH181232	McAllister et al. (2018)
Anatherum ligulatum (Stapf) Voronts. & E.A.Kellogg	*Pasquet 1270* (MO)	MH181204	McAllister et al. (2018)
Anatherum longiberbe (Hack.) Voronts. & E.A. Kellogg	*Campbell 3764* (K)	OQ440001	This study
Anatherum macrothrix (Trin.) Voronts. & E.A.Kellogg	*Morrone 178* (MO)	OQ440002	This study

(*continued*)

Table 1. Continued.

Species	Voucher specimen and herbarium	GenBank number	Source
Anatherum mohrii (Hack.) Voronts. & E.A.Kellogg	*McDaniel & Brooks 20967* (MO)	MH181216	McAllister et al. (2018)
Anatherum selloanum (Hack.) Voronts. & E.A.Kellogg	*Pohl & Davidse 12395* (MO)	MH181213	McAllister et al. (2018)
Anatherum trichozygum (Baker) Voronts. & E.A.Kellogg	*Vorontsova 1925* (K)	OQ440005	This study
Anatherum urbanianum (Hitchc.) Voronts. & E.A.Kellogg	*Davidse 2691* (MO)	MH181230	McAllister et al. (2018)
Anatherum virginicum (L.) Spreng.	*AuBuchon-Elder 16-2* (MO)	OQ440004	This study
Anatherum virginicum (L.) Spreng.	*AuBuchon-Elder 88-1* (MO)	OQ440006	This study
"*Andropogon*" *appendiculatus* Nees	*Guillarmod 164* (K)	MH181173	McAllister et al. (2018)
"*Andropogon*" *brazzae* Franch.	*Corderaux 564* (MO)	MH181236	McAllister et al. (2018)
"*Andropogon*" *durifolius* Renvoize	*Mori et al. 12550* (MO)	OQ439992	This study
"*Andropogon*" *hondurensis* (R.W. Pohl) Wipff	*Pohl & Davidse 12138* (MO)	MH181178	McAllister et al. (2018)
"*Andropogon*" *ingratus* Hack.	*Atkins et al. 14786* (K)	MH181172	McAllister et al. (2018)
"*Andropogon*" *reedei* Hitchc. & Ekman	*Ekman 1004* (K)	MH181217	McAllister et al. (2018)
"*Andropogon*" *tenuiberbis* Hack.	*Fay 6081* (MO)	OQ440003	This study
Diectomis fastigiata (Sw.) P. Beauv.	*Pasquet 1231* (MO)	MH181193	McAllister et al. (2018)
Elymandra androphila (Stapf) Stapf	*Adam 24797* (MO)	MH181166	McAllister et al. (2018)
Elymandra subulata Jacq.-Fél.	*Jacques-Felix 7306* (K)	MH181214	McAllister et al. (2018)
Monocymbium lanceolatum C.E.Hubb. ex Hutch. & Dalziel	*Adam 6762* (K)	MH181170	McAllister et al. (2018)
Schizachyrium cirratum (Hack.) Wooton & Standl.	*Lyonnet 2445* (MO)	MH181235	McAllister et al. (2018)
Schizachyrium salzmannii (Trin. ex Steud.) Nash	*Zardini & Velazquez 25831* (MO)	MH181208	McAllister et al. (2018)
Schizachyrium thollonii (Franch.) Stapf	*Pasquet 1263* (MO)	MH181189	McAllister et al. (2018)
Schizachyrium ursulus Stapf	*Davidse & Handlos 7264* (MO)	MH181183	McAllister et al. (2018)

Specimen and spikelet images are available online for most accessions through the Missouri Botanical Garden at www.tropicos.org. Herbarium abbreviations follow Index Herbariorum (Thiers, updated continuously).

Comparison within "*Andropogon*" sensu lato

Morphological data collected by McAllister et al. (2018) and the morphological characters scored and compiled in GrassBase (Clayton et al., 2016) were used to explore the following characters for their utility in diagnosing "*Andropogon*" sect. *Leptopogon*:

1. Number of branches in the inflorescence.
2. Shape of the internodes and pedicels.
3. Length of the sessile spikelet.
4. Number of veins on the lower glume of the sessile spikelet.
5. Concavity of the lower glume of the sessile spikelet.
6. Presence or absence of trichomes on the lower glume of the sessile spikelet.
7. Distribution of trichomes on the internodes and pedicels.

With a few exceptions, spikelets in most members of "*Andropogon*" sect. *Leptopogon* are smaller than those of other species classified in other clades of "*Andropogon*". We compared sizes of sessile spikelets using morphometric data from McAllister et al. (2018). Mean sessile spikelet length in "*Andropogon*" sect. *Leptopogon* was 4.39 ± 0.99 mm (range 2.6–7.02), whereas for all other species of "*Andropogon*" together

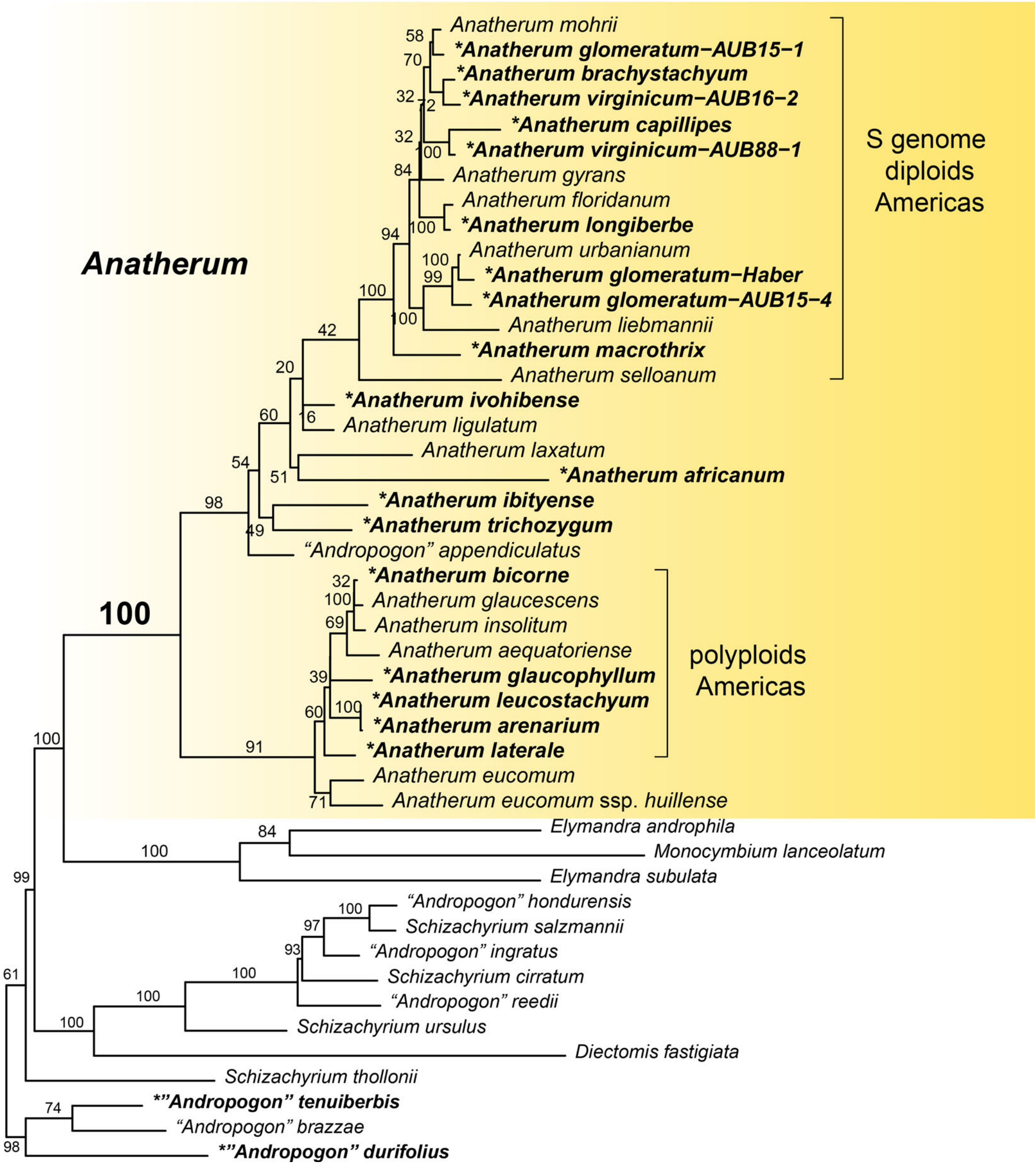

Figure 1. Plastome phylogeny of *Anatherum* and its immediate sister clades. Species with new plastomes are in bold and indicated by asterisk (*); all others were presented by McAllister et al. (2018) except for *A. eucomum* which was published by Welker et al. (2020). See also Table 1. Numbers above branches are fast bootstrap values calculated by RAxML. Sequences from *A. mohrii* and *A. laxatum* were published by McAllister et al. (2018) under those names. POWO (2021) considers them to be synonyms of *A. liebmannii* and *A. eucomum* ssp. *huillense*, respectively, but they are phylogenetically distant from their putative conspecifics and are recognized as distinct here pending further investigation.

it was 6.15 ± 1.63 mm (range 2.74–13.11). (These measurements were taken from three representative spikelets on each of three herbarium sheets per species, so the extreme values may have been missed.) In most cases, the combination of small spikelets and presence of long trichomes provide a provisional identification for "*A.*" sect. *Leptopogon*.

"*Andropogon*" sect. *Leptopogon* is distinguished from "*Andropogon*" s.l. and *Andropogon* s.s. by its sessile spikelets with lower glumes elliptic to lanceolate with two prominent veins, the glumes flat to concave, most commonly <5 mm long, although up to 6.5 mm in a few species. Other species of *Andropogon* have sessile spikelets with glumes with more than two veins, or veins indistinct, the glumes nearly flat to deeply grooved and folded into an M-shape, most commonly >5 mm long but sometimes as short as 3 mm. Inflorescence internodes and pedicels are slender and linear in "*A.*" sect. *Leptopogon*, and only slightly flared at the apex if at all. In species of "*Andropogon*" s.l. and *Andropogon*

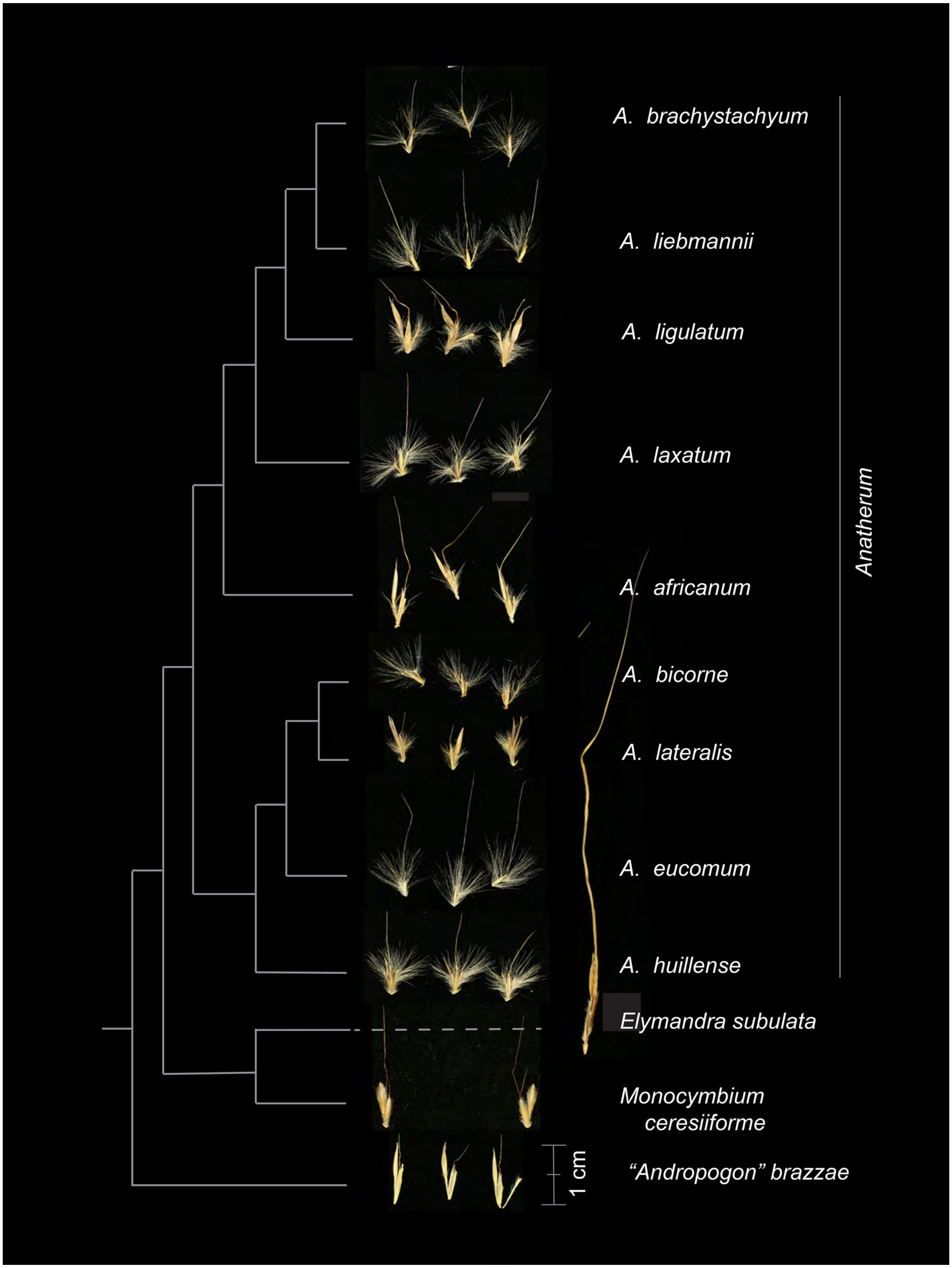

Figure 2. Spikelet morphology of selected *Anatherum* species and outgroups. Each species is represented by a single photo that includes two or three spikelet pairs from one herbarium specimen, as generated by McAllister et al. (2018), except for *Elymandra subulata*, which shows a single spikelet pair. Cladogram to the left of the images shows relationships based on the plastome tree in Fig. 1. All images to the same scale. Scale bar, 1 cm.

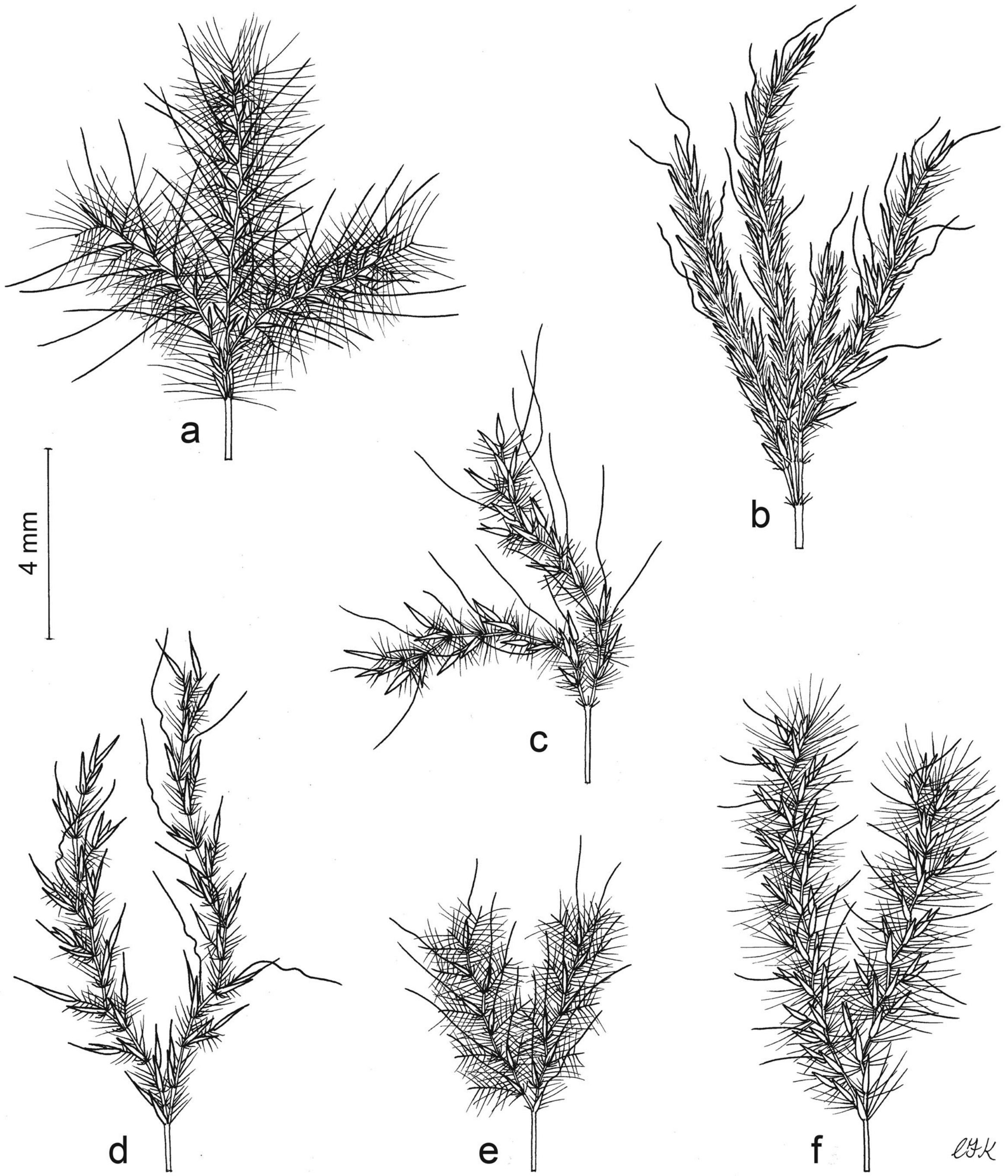

Figure 3. Inflorescences. Thicker lines indicate spikelets, internodes, pedicels, and awns; thinner lines indicate trichomes. (a) *Anatherum eucomum*, (b) *Anatherum ivohibense*, (c) *Anatherum cordatum*, (d) *Anatherum africanum*, (e) *Anatherum glomeratum*, (f) *Anatherum lindmannii*. Scale bar, 4 mm. Drawn by Christabel King.

s.s., inflorescence internodes are broadly clavate to goblet-shaped, flaring distally to a deep cup-shaped joint. "*A*." sect. *Leptopogon* inflorescences generally have two branches, rarely 3–5 or occasionally nine, whereas for "*Andropogon*" s.l. and *Andropogon* s.s. species inflorescences generally have three or more branches.

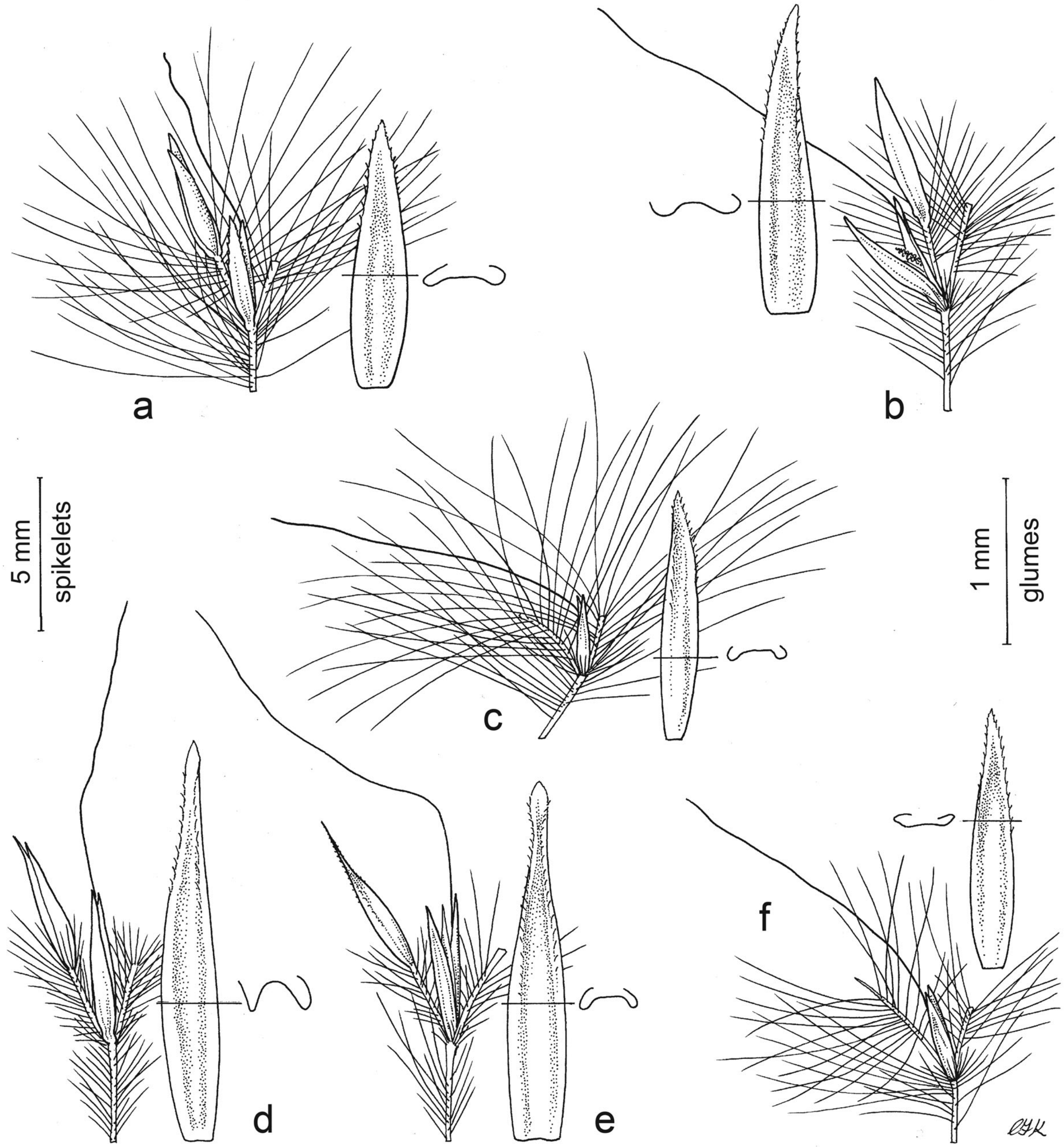

Figure 4. Spikelet pairs. Sessile spikelet on the lower internode, with the pedicel and the pedicelled spikelet where present on the left, and the upper internode on the right. Lower glume of the sessile spikelet is enlarged and the shape of its cross section is shown. Thicker lines indicate spikelets, internodes, pedicels, and awns; thinner lines indicate trichomes. (a) *Anatherum lindmannii*, (b) *Anatherum cordatum*, (c) *Anatherum eucomum*, (d) *Anatherum ivohibense*, (e) *Anatherum africanum*, (f) *Anatherum glomeratum*. Left scale bar, spikelets, 5 mm; right scale bar, glumes, 1 mm. Drawn by Christabel King.

Comparison with related genera

The closely related genus *Elymandra* has pairs of homogamous spikelets at the base of the racemes, whereas homogamous pairs are lacking in “*A.*” sect. *Leptopogon*; in addition, *Elymandra* spikelets are generally larger with longer and more robust awns (Fig. 2). “*Andropogon*” sect. *Leptopogon* is distinguished from *Monocymbium* by its glabrous glumes, whereas in *Monocymbium* the glumes are densely pubescent. Racemes of *Monocymbium* are entirely encased in reddish-brown spatheoles that are generally borne horizontally on the plant. In contrast, spatheoles in “*A.*” sect.

Leptopogon, if present, are upright (Clayton & Renvoize 1986; Clayton et al. 2016).

Discussion

Many members of Andropogoneae were initially assigned to the Linnaean genus *Andropogon*, but over time the most distinctive groups have been segregated as separate genera, leaving "*Andropogon*" sensu lato as the polyphyletic residue. As phylogenetic sampling has improved over the last couple of decades, species nominally in "*Andropogon*" have been shown clearly to belong to disparate clades. This paper represents a step toward adjusting the generic classification to align with emerging knowledge of phylogenetic relationships.

Our criteria for recognizing a clade at the generic rank include: (1) the group must be monophyletic, with as much evidence as possible from DNA sequence data and (2) the group should be morphologically homogeneous, with one or more traits shared by most members. It is ideal if the shared traits can be shown to be derived (synapomorphic) and shared by all members of the clade. However, one reason that the species of "*Andropogon*" have not already been placed in separate genera is their lack of distinctive macro-morphological characters. In addition, no formal analysis has been undertaken for the evolution of many morphological traits across the tribe, making the distinction between synapomorphy and symplesiomorphy a plausible hypothesis rather than a firm conclusion. Finally, we adopt a cautious approach with respect to ambiguous data. Species that are placed in the clade by plastome sequences but are morphologically different, and species that are morphologically similar but placed elsewhere by plastome data are left as "*Andropogon*" incertae sedis, as noted below.

The clade corresponding to "*Andropogon*" sect. *Leptopogon* is monophyletic and not directly related to *Andropogon* s.s. Several authors in the 19th and early 20th centuries, including Stapf (1919), observed that species belonging to this section were morphologically distinct from other *Andropogon* and assigned them to new genera, although Stapf failed to designate a type. The earliest available generic name was assigned by Palisot de Beauvois (1812) who established the genus *Anatherum* to accommodate *Andropogon bicornis* L., which then became *Anatherum bicorne* (L.) P. Beauv. Other relevant generic names are *Euklastaxon* Steud., [1855]1854, based on *E. tenuifolius* Steud. = *Andropogon selloanus* (Hack.) Hack., *Eriopodium* Hochst., 1846, in synonymy under *Andropogon eucomus* Nees, and *Dimeiostemon* Raf., 1825, based on *D. vaginatus* Raf. ex B.D. Jacks., an invalid synonym of *A. virginicus* L.

The name *Leptopogon* is not available as a generic name. The sectional name was raised to the rank of genus by Roberty (1960), as *Leptopogon* Roberty. Like Stapf, Roberty also failed to designate a type. *Leptopogon* Roberty is an illegitimate later homonym of *Leptopogon* Borzí (Borzí, 1907), a genus of cyanobacteria, which are covered by the same nomenclatural code as plants (Turland et al., 2018). Hereafter, we refer to "*Andropogon*" sect. *Leptopogon* as *Anatherum*.

Anatherum includes two major subclades, each of which comprise a New World clade derived from a paraphyletic group of African taxa. The diploid species with the S genome (where "S" stands for "*selloanus*") characterized by Norrmann et al. (2004) and Nagahama & Norrmann (2012) all form a monophyletic group (Fig. 1). Fluorescent *in situ* hybridization (FISH) verified that the genomes of *A. gyrans* Ashe, *A. selloanus* (Hack.) Hack., and *A. macrothrix* Trin. were indeed similar, and Norrmann et al. (2004) hypothesized that the other "*A.*" sect. *Leptopogon* diploids shared the same basic genome, a hypothesis supported by our phylogenetic data. The hexaploids *A. lateralis* Nees and *A. bicornis* bear an S genome but the other genomes are from different unknown sources (Nagahama & Norrmann, 2012).

The morphological characters compiled in GrassBase (Clayton et al. 2016) identify multiple morphological traits that are shared by all species of *Anatherum* and distinguish them from other members of Andropogoninae. These data corroborate and extend the de novo herbarium observations made by MSV and EAK. Nagahama and Norrmann (2012) suggested that the two-veined, slightly concave glume might be diagnostic, but the trait can be hard to distinguish from the concave to deeply grooved glumes of other "*Andropogon*" outside *Anatherum*, as in "*A.*" *burmanicus* Bor and "*A.*" *perligulatus* Stapf.

Several species with ambiguous morphology are not transferred here, because molecular data strongly support their placement outside *Anatherum* (Fig. 1). The species "*A.*" *tenuiberbis*, "*A.*" *brazzae*, and "*A.*" *durifolius* are large plants native to Africa, with highly branched inflorescences of small spikelets. Despite their apparent lack of relationship to *Anatherum*, they share some morphological traits with species of *Anatherum*. *Andropogon mannii* Hook. f. is phylogenetically placed in *Andropogon* s.s. (and hence not designated with quotes) but some specimens appear morphologically similar to some *Anatherum*. *Andropogon mannii* occurs in much of east Africa, from Sudan to the northern provinces of South Africa, but also has disjunct populations in equatorial west Africa. Morphologically, it varies extensively throughout its range and requires closer examination before attempting any re-classification. Our specimen of "*Andropogon*" *appendiculatus* is the same one sampled by McAllister et al. (2018) and is firmly placed within the *Anatherum* clade in our analyses and theirs. However, it has large spikelets and more racemes, which make it morphologically dissimilar to other members of the clade. The species includes complex morphological variation as well as a range of ploidy levels, which suggests that additional samples are warranted. Accordingly, we have deferred transferring it until further work can be undertaken.

"*Andropogon*" *gerardi* raises a particular problem in classification in that it is an allohexaploid of hybrid origin (Estep et al., 2014). Cytogenetic data show clearly that one of the ancestral genomes came from a species similar and possibly closely related to *Anatherum gyrans* (Nagahama & Norrmann, 2012). Using a different representative of *Anatherum* (*A. virginicum*), sequence data later confirmed this result (Estep et al., 2014). The other parent is unknown but likely to be a species similar to *Schizachyrium*. Any generic placement of an intergeneric hybrid will necessarily be arbitrary and placing the species in a new genus may be appropriate. For now, we have chosen to leave "*A.*" *gerardi* in "*Andropogon*" pending further investigation of its ancestry.

Taxonomic treatment

Anatherum P. Beauv., emend.

Type species. *Anatherum bicorne* (L.) P. Beauv.

Plants perennial, caespitose, occasionally rhizomatous, from 20 cm to 3 m tall. **Leaves** flat to filiform, 0.5–8(–22) mm wide. **Ligules** membranous to scarious, usually truncate, with or without apical trichomes. **Synflorescence** simple or complex, bracteate or not, with each axis ending in an inflorescence of 2 (3–9) racemes, sometimes branched, plumose when dry. **Each raceme** (1–)2–7(–11) cm long, **internodes** and **pedicels** slender, linear, flexuous, 2–6(–10) mm long, usually with long trichomes borne in two vertical lines, the trichomes (1–)2–10(–16) mm long, usually increasing in length distally. **Sessile spikelet** lanceolate (rarely linear or oblong), (2–)3–6.5(–12) mm long; the callus obtuse, pilose to bearded (rarely glabrous), inserted into a cup-shaped joint; lower glume lanceolate, membranous to coriaceous, glabrous (rarely pubescent), with two prominent veins (2-keeled) and no intercarinal veins, concave (rarely strongly folded or grooved); upper glume membranous to coriaceous, linear, muticous (rarely awned); lower lemma oblong to lanceolate, usually 2-veined; upper lemma lanceolate (rarely oblong), hyaline, generally bifid for a quarter to half of its length, generally with an awn from the sinus (sometimes the lemma entire with an apical awn); the awn straight or geniculate, (2–)5–20(–25) mm long, usually with a twisted column; palea reduced; anthers 1 or 3. **Pedicellate spikelet** present or absent, if absent then the pedicel ending blindly; if present then represented by one or both glumes or fully developed and staminate, linear to lanceolate, 0–6(–8) mm long; glumes thinly coriaceous to chartaceous, glabrous, apically acute to acuminate, usually mucronate or sometimes awned; awn, if present, slender, straight; stamens, if present, 3; gynoecium absent.

Distribution. North, Central, and South America to Caribbean and Africa, with limited occurrence across Asia.

Species composition

The following 45 species and one subspecies are placed in *Anatherum*, with species concepts based on the taxonomic compilation by POWO (2013), except for *A. laxatum* and *A. mohrii*, q.v. Four species names in *Anatherum* are reinstated. Thirty-nine species and one subspecies are transferred here to *Anatherum.* All the previously accepted names are in the genus *Andropogon* and these are indicated as homotypic synonyms where they differ from the basionym. For full synonymy, distributions, and bibliography see POWO (2021). Names marked with an asterisk are included in the molecular phylogeny; see also Table 1. Unmarked names are placed here based on morphology.

1. * ***Anatherum aequatoriensis*** (Hitchc.) Voronts. & E.A.Kellogg, comb. nov.
   Basionym: *Andropogon aequatoriensis* Hitchc. (Hitchcock, 1927, p. 499).
2. * ***Anatherum africanum*** (Franch.) Roberty, (Roberty, 1960, p. 207).
   Basionym: *Andropogon africanus* Franch., (Franchet, 1895, p. 325).
3. ***Anatherum arctatum*** (Chapm.) Voronts. & E.A.Kellogg, comb. nov.
   Basionym: *Andropogon arctatus* Chapm. (Chapman, 1878, p. 20).
4. * ***Anatherum arenarium*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
   Basionym: *Andropogon arenarius* Hack. (Hackel, 1885, p. 134).
5. ***Anatherum barretoi*** (Norrmann & Quarín) Voronts. & E.A.Kellogg, comb. nov.

Basionym: *Andropogon barretoi* Norrmann & Quarín (Norrmann & Quarín, 2001, p. 171).

6. * ***Anatherum bicorne*** (L.) P. Beauv., (Palisot de Beauvois, 1812, p. 128, 150, atlas t. 22, f. 11)

   Basionym: *Andropogon bicornis* L., (Linnaeus, 1753 2, p. 1046), nom et type cons., against *Andropogon glomeratus* (Walter) Britton and *Schizachyrium scoparium* (Michx.) Nash. (Davidse & Turland, 1999). The International Plant Names Index (IPNI, 2023) does not list the Linnaean name as the basionym for *Anatherum bicorne*, referring simply to *Anatherum bicorne* P. Beauv. However, Palisot de Beauvois' protologue for *Anatherum* lists *Andropogon bicornis* L. as being a species of *Anatherum*, indicating that the IPNI listing is simply incomplete.
7. ***Anatherum bourgaei*** (Hack.) Roberty, (Roberty, 1960, p. 211).

   Basionym: *Andropogon bourgaei* Hack., (Hackel, 1885, p. 134).
8. * ***Anatherum brachystachyum*** (Chapm.) Roberty, (Roberty, 1960, p. 211).

   Basionym: *Andropogon brachystachyus* Chapm., (Chapman, 1883, p. 668).
9. ***Anatherum brasiliense*** (A. Zanin & Longhi-Wagner) Voronts. & E.A.Kellogg, comb. nov., non *Anatherum brasiliense* Spreng. ex Steud., nom. inval., pro syn.

   Basionym: *Andropogon brasiliensis* A. Zanin & Longhi-Wagner (Zanin & Longhi-Wagner, 2003, p. 368).

   Anatherum brasiliense Spreng. ex Steud. was published as a synonym when Steudel listed Sprengel's previously unpublished name, but Steudel did not accept it. The name is therefore invalid.
10. ***Anatherum cabanisii*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon cabanisii* Hack. (Hackel, 1885, p. 133).
11. * ***Anatherum capillipes*** (Nash) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon capillipes* Nash (Nash, 1900, p. 431).
12. ***Anatherum cordatum*** (Swallen) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon cordatus* Swallen (Swallen, 1949, p. 274).
13. ***Anatherum cumulicolum*** (E.L. Bridges & Orzell) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon cumulicola* E.L. Bridges & Orzell (Bridges & Orzell, 2018, p. 4).
14. ***Anatherum curvifolium*** (Clayton) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon curvifolius* Clayton (Clayton, 1964, p. 465).
15. * ***Anatherum eucomum*** (Nees) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon eucomus* Nees (Nees von Esenbeck, 1841, p. 104).
16. * ***Anatherum eucomum*** (Nees) Voronts. & E.A.Kellogg subsp. ***huillense*** (Rendle) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon huillensis* Rendle (Rendle, 1899, p. 146).

    Homotypic synonym: *Andropogon eucomus* subsp. *huillensis* (Rendle) Sales 2002, p. 10).
17. * ***Anatherum floridanum*** (Scribn.) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon floridanus* Scribn. (Lamson-Scribner, 1896, p. 145).
18. * ***Anatherum glaucescens*** (Kunth) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon glaucescens* Kunth (von Humboldt et al., 1816, p. 186).
19. * ***Anatherum glaucophyllum*** (Roseng., B.R.Arrill. & Izag.) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon glaucophyllus* Roseng., B.R.Arrill. & Izag. (Rosengurtt, Arrillaga de Maffei, & Izaguirre de Artucio, 1970, p. 165).
20. ***Anatherum glaziovii*** (Hack.) Voronts. & E.A.Kellogg comb. nov.

    Basionym: *Andropogon glaziovii* Hack. (von Martius, 1883, p. 286).
21. * ***Anatherum glomeratum*** (Walter) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Cinna glomerata* Walter (Walter, 1788, p. 59).

    Homotypic synonym: *Andropogon glomeratus* (Walter) Britton, Sterns & Poggenb. (Britton et al., 1888, p. 67).
22. * ***Anatherum gyrans*** (Ashe) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon gyrans* Ashe (Ashe, 1898, p. 113).
23. * ***Anatherum ibityense*** (A.Camus) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon ibityensis* A.Camus (Camus, 1952, p. 213).
24. ***Anatherum imerinense*** (Bosser) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon imerinensis* Bosser (Bosser, 1968, p. 521).
25. * ***Anatherum insolitum*** (Sohns) Voronts. & E.A.Kellogg, comb. nov.

    Basionym: *Andropogon insolitus* Sohns (Maguire & Wurdack, 1957, p. 271).

26. * ***Anatherum ivohibense*** (A.Camus) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon ivohibensis* A.Camus (Camus, 1924 (publ. 1925), p. 922).
27. * ***Anatherum laterale*** (Nees) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon lateralis* Nees (Nees von Esenbeck, 1829, p. 329).
28. * ***Anatherum laxatum*** (Stapf) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon laxatus* Stapf (Stapf, 1919, p. 237).
    POWO (2021) considers this a synonym of *A. eucomum* ssp. *huillense* but our representatives of the two taxa are unrelated in the plastome tree (Fig. 1).
29. ***Anatherum lehmannii*** (Pilg.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon lehmannii* Pilg. (Pilger, 1899, p. 24).
30. * ***Anatherum leucostachyum*** (Kunth) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon leucostachyus* Kunth (von Humboldt et al., 1816, p. 187).
31. * ***Anatherum liebmannii*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon liebmannii* Hack. (Hackel, 1885, p. 132).
32. * ***Anatherum ligulatum*** (Stapf) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon laxatus* var. *ligulatus* Stapf (Stapf, 1919, p. 238).
    Homotypic synonym: *Andropogon ligulatus* (Stapf) Clayton, (Clayton, 1977, p. 2).
33. ***Anatherum lindmannii*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon lindmannii* Hack. (Lindman, 1900, p. 6).
34. * ***Anatherum longiberbe*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon longiberbis* Hack. (Hackel, 1885, p. 131).
35. * ***Anatherum macrothrix*** (Trin.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon macrothrix* Trin. (Trinius, 1833, p. 270).
36. ***Anatherum miamiensis*** (E.L.Bridges & Orzell) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon miamiensis* E.L.Bridges & Orzell (Bridges & Orzell, 2018, p. 13).
37. * ***Anatherum mohrii*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon liebmannii subvar. mohrii* Hack. (Hackel, 1889, p. 413).
    POWO (2021) considers this a synonym of *A. liebmannii* but our representatives of the two species are unrelated in the plastome tree (Fig. 1).
38. ***Anatherum multiflorum*** (Renvoize) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon multiflorus* Renvoize (Renvoize, 1998, p. 596).
39. ***Anatherum perangustatum*** (Nash) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon perangustatus* Nash (Small, 1903, p. 62).
40. ***Anatherum pringlei*** (Scribn. & Merr.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon pringlei* Scribn. & Merr. (Lamson-Scribner & Merrill, 1900 (publ. 1901), p. 7).
41. * ***Anatherum selloanum*** (Hack.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon leucostachyus* subsp. *selloanus* Hack. (Hackel, 1889, p. 420).
    Homotypic synonym: *Andropogon selloanus* (Hack.) Hack. (Hackel, 1904, p. 266).
42. ***Anatherum ternarium*** (Michx.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon ternarius* Michx. (Michaux, 1803, p. 57).
43. ***Anatherum tracyi*** (Nash) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon tracyi* Nash (Nash, 1900, p. 433).
44. * ***Anatherum trichozygum*** (Baker) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon trichozygus* Baker (Baker, 1883, p. 300).
45. * ***Anatherum urbanianum*** (Hitchc.) Voronts. & E.A.Kellogg, comb. nov.
    Basionym: *Andropogon urbanianus* Hitchc. (Hitchcock, 1912, p. 424).
46. * ***Anatherum virginicum*** (L.) Spreng., Pl. Min. Cogn. Pug. 2: 16. 1815
    Basionym: *Andropogon virginicus* L., (Linnaeus, 1753, p. 1046).

Incertae sedis

These species share some morphological similarity with *Anatherum*, or in the case of *A. appendiculatus* are morphologically distinct but phylogenetically placed within it. They are not transferred at this time pending more critical investigation, as noted above. However, they are distinct from *Andropogon* s.s., so the generic name is placed in quotes.

1. * "*Andropogon*" *appendiculatus* Nees, (Nees von Esenbeck, 1841, p. 105).

2. * “*Andropogon*” *brazzae* Franch., (Franchet, 1895, p. 326).
3. “*Andropogon*” *dewetii* Mashau & Fish, (Mashau et al., 2022, p. 3, 4, f. 1, 2).
4. * “*Andropogon*” *durifolius* Renvoize, (Renvoize, 1984, p. 181).
5. * “*Andropogon*” *mannii* Hook.f., (Hooker, 1864, p. 232).

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Data availability statement

Full plastome sequences used to construct the tree have been deposited at GenBank.

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