JSE Journal of Systematics and Evolution

doi: 10.1111/jse.12857

Research Article

Grasses through space and time: An overview of the biogeographical and macroevolutionary history of Poaceae

Timothy J. Gallaher[1]*, Paul M. Peterson[2], Robert J. Soreng[2], Fernando O. Zuloaga[3], De-Zhu Li[4,5], Lynn G. Clark[6], Christopher D. Tyrrell[7], Cassiano A.D. Welker[8], Elizabeth A. Kellogg[9], and Jordan K. Teisher[10]

[1]Department of Natural Science, Herbarium Pacificum, Bishop Museum, 1525 Bernice St., Honolulu, HI 96817, USA
[2]Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA
[3]Instituto de Botánica Darwinion (CONICET-ANCEFN), Labardén 200, Casilla de Correo 22, San Isidro B1642HYD, Buenos Aires, Argentina
[4]Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China
[5]University of Chinese Academy of Sciences, Beijing 100049, China
[6]Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA 50011, USA
[7]Botany Department, Milwaukee Public Museum, 800 W Wells Street, Milwaukee, WI 53233, USA
[8]Instituto de Biologia, Universidade Federal de Uberlândia, Rua Ceará s/n, 38400-902, Uberlândia, MG, Brazil
[9]Donald Danforth Plant Science Center, St Louis, MO 63132, USA
[10]Missouri Botanical Garden, 4344 Shaw Blvd, St. Louis, MO 63110, USA
*Author for correspondence. E-mail: timothy.gallaher@bishopmuseum.org

Received 1 August 2021; Accepted 19 April 2022; Article first published online 27 April 2022

Abstract Grasses are widespread on every continent and are found in all terrestrial biomes. The dominance and spread of grasses and grassland ecosystems have led to significant changes in Earth's climate, geochemistry, and biodiversity. The abundance of DNA sequence data, particularly chloroplast sequences, and advances in placing grass fossils within the family allows for a reappraisal of the family's origins, timing, and geographic spread and the factors that have promoted diversification. We reconstructed a time-calibrated grass phylogeny and inferred ancestral areas using chloroplast DNA sequences from nearly 90% of extant grass genera. With a few notable exceptions, the phylogeny is well resolved to the subtribal level. The family began to diversify in the Early–Late Cretaceous (crown age of 98.54 Ma) on West Gondwana before the complete split between Africa and South America. Vicariance from the splitting of Gondwana may be responsible for the initial divergence in the family. However, Africa clearly served as the center of origin for much of the early diversification of the family. With this phylogenetic, temporal, and spatial framework, we review the evolution and biogeography of the family with the aim to facilitate the testing of biogeographical hypotheses about its origins, evolutionary tempo, and diversification. The current classification of the family is discussed with an extensive review of the extant diversity and distribution of species, molecular and morphological evidence supporting the current classification scheme, and the evidence informing our understanding of the biogeographical history of the family.

Key words: ancestral area estimation, dispersal, Gondwana, historical biogeography, molecular dating, vicariance.

1 Introduction

Recent work has provided a diverse set of evidence for piecing together the timing, geographic origins, and factors that influenced the diversification of the grass family. The phylogeny of Poaceae, at least that of the Poaceae chloroplast, is now relatively well established, with nearly 90% of grass genera represented in GenBank accessions and over 300 genera with complete or near-complete plastome sequence (Gallaher et al., 2019; Orton et al., 2021). Additional sequences are added regularly to public databases, and full phylogenetic coverage at the genus level should be achieved within the next few years. Recent studies offer a range of dates for the diversification of the family, with most studies indicating an origin of the family in the Cretaceous (145–66 mya), possibly around 100 Ma (Vicentini et al., 2008; Bouchenak-Khelladi et al., 2010; Gallaher et al., 2019; Schubert et al., 2019b; Orton et al., 2021). Further refinements of the ages of lineages will be made possible as new fossils are described, previously described fossils are re-evaluated through the lens of modern phylogenetic reconstructions, and new methods are developed to describe and classify the silica short cell phytolith microfossils which have been found on all continents, in some cases dating back to the Early

Cretaceous (Poinar, 2003; Prasad et al., 2005; Poinar et al., 2015; Wu et al., 2018).

Recent work has also given us further evidence about the habitat in which grasses first evolved. That ancestral habitat was either the deep shade of the tropical forest understory (Bouchenak-Khelladi et al., 2010) or the dynamic conditions that characterize forest margins, an important, or possibly obligatory, transition zone for shifts between full shade and open habitat (Gallaher et al., 2019). Grasses shifted to open habitats independently several times, leading to many of the most species-rich lineages. Shifts back into the forest understory from open habitats have occurred but are less frequent. Finally, the various transitions to open habitat, which began in the Paleocene (Gallaher et al., 2019), predate, by several million years, the evolution of grass-dominated ecosystems, which became widespread in the Miocene (Strömberg, 2011).

Nearly 42% of all grasses use the C_4 photosynthetic pathway and this innovation has been an important driver of the diversification of grasses into new habitats (Soreng et al., 2017; Linder et al., 2018). Our understanding of the timing and drivers of the evolution of C_4 photosynthesis has also improved in recent years. An ancestral state estimate of photosynthesis type found at least 18 and up to 24 independent origins of C_4 photosynthesis in the family (Grass Phylogeny Working Group [GPWG], 2011; Gallaher et al., 2019). However, the number could be fewer, with evidence suggesting that some lineages may have acquired the C_4 pathway through lateral gene transfer (Christin et al., 2012). Earlier studies found that the C_4 pathway began to evolve in the Oligocene (Christin et al., 2008; Vicentini et al., 2008; Bouchenak-Khelladi et al., 2010), suggesting that higher global temperatures and lower atmospheric CO_2, which has dominated the climate since that time, favored the evolution of C_4 photosynthesis (Sage, 2004). However, recent time-calibrated phylogenies estimated an older Early-Eocene (41–56 Ma) age for the origin of C_4 in the Chloridoideae (Gallaher et al., 2019) when global CO_2 levels were far higher than at present. Such a timeframe is thus at odds with physiological inferences on the drivers of C4. That subfamily evolved in Africa (Hartley & Slater, 1960; Peterson et al., 2007; Bouchenak-Khelladi et al., 2010), which experienced hot and arid conditions during the Eocene, and a savanna-like grassland may have been present (Adegoke et al., 1978; Jacobs et al., 1999; Handley et al., 2012). Open habitats, globally higher temperatures, and a regionally dry climate may have promoted the evolution of the C_4 NAD-ME subtype in the Chloridoideae (Sage, 2004; Edwards & Smith, 2010; Liu & Osborne, 2015; Rao & Dixon, 2016). C_4 photosynthesis in other PACMAD lineages occurred more recently, beginning in the Oligocene. Some evolved the NADP-ME C_4 subtype, which has been associated with greater nitrogen use efficiency, suggesting that nitrogen-limited habitats, including those characterized by frequent fire (Bond et al., 2003; Ripley et al., 2015; Schafer & Mack, 2018), may have been another potential driver for C_4 evolution. Differences in timing of the origin of C_4 photosynthesis in different lineages and a better understanding of the effects on fitness in different habitats of the various C_4 subtypes suggest that both local and global factors may have driven the evolution of the C_4 pathway.

Cold tolerance evolved at least twice in the family through different mechanisms. Cold tolerant species in the Danthonioideae appear to restrict the formation of ice crystals to leaf surfaces where the risk of tissue damage is limited (Wharton et al., 2010; Humphreys & Linder, 2013). Cold tolerance also evolved in the Pooideae, the most species-rich subfamily, through the action of ice-binding proteins, which reduces the degree of ice formation while altering the shape and size of ice crystals (Bredow & Walker, 2017; Bredow et al., 2018; Schubert et al., 2019a, 2020).

It has long been assumed that Poaceae had either a Gondwanan origin or an origin on continents derived from Gondwana (Bremer, 2002; Bouchenak-Khelladi et al., 2010). A true Gondwanan origin would implicate vicariance in the early diversification of the family and requires as evidence an origin on continents derived from Gondwana and a crown age for the family before 100 Ma, the timeframe for the complete breakup of modern continents (incl. Africa and South America) (McLoughlin, 2001). This scenario was inferred by Bouchenak-Khelladi et al. (2010) in the first family-wide geographic reconstruction of the family. That study was done before the availability of a well-resolved phylogeny estimation and recent advances in modeling ancestral areas. This paper serves to update our understanding of the spatio-temporal history of the family. We compare our results with previous findings, suggest new hypotheses that can be tested with new methods and broader sampling in the future, and provide an in-depth discussion of each subfamily, tribe, and subtribe, examining the distribution, key adaptations, and biogeography of 90 percent of the genera in the family.

2 Materials and Methods

Chloroplast DNA sequences for 700 taxa were downloaded from GenBank except for two taxa, where sequences are unpublished in GenBank but available as supplementary data from Gallaher et al. (2019) (Tables S1, S2). These represented 677 Poaceae genera and representatives from three close outgroup families: *Ecdeiocolea monostachya* F.Muell. (Ecdeiocoleaceae), *Joinvillea ascendens* Gaudich. ex Brongn. & Gris (Joinvilleaceae), and *Flagellaria indica* L. (Flagellariaceae). Complete or near-complete plastomes were used for 312 taxa. These were supplemented with available sequences from the tRNA-Leu (*trnL*) partial gene and *trnL-trnF* intergenic spacer, the NADH dehydrogenase subunit F (*ndhF*) gene, and the tRNA-Lys (*trnK-UUU*) partial gene and maturase K (*matK*) partial gene for taxa without complete genome sequence.

The trnK-*matK, trnL-trnF*, and *ndhF* loci were extracted from the complete plastomes, and separate alignments were constructed for each of the three gene regions and the partial plastomes separately. Alignments were done with MAFFT version 7 (https://mafft.cbrc.jp/alignment/server/) using the slow iterative refinement method (FFT-NS-i) (Katoh et al., 2002, 2018; Katoh & Standley, 2013). Positions with more than 10% missing data or alignment gaps were stripped from each alignment using Jalview version 2.11.1.3 (Waterhouse et al., 2009). After alignment and gap-stripping, the loci were concatenated for phylogeny estimation.

Joint Bayesian inference (BI) of phylogeny and clade divergence times was implemented in BEAST 2.6.3 (Bouckaert et al., 2019) on the CIPRES Science Gateway (Miller et al., 2010). The GTR+I+G evolution model with four gamma categories was used based on AIC results from jModelTest (Guindon & Gascuel, 2003; Darriba et al., 2012). A starting value of 0.5 was used to estimate the proportion of invariant sites. The trees were modeled under a Yule process using a random starting tree and a relaxed clock with a lognormal distribution. *Flagellaria* was constrained to be the sister to all other taxa, and the Poaceae was constrained to monophyly. The analysis was allowed to run for 100 000 000 generations and was sampled every 5000 generations. The maximum clade credibility tree was calculated and used as the start tree for a further 100 000 000 generation analysis. Tracer 1.7 (Rambaut et al., 2018) was used to determine if the sample of parameters had reached a stable distribution, to determine whether effective sample sizes were above 200, and to set the burn-in value (20%) before calculating the final maximum clade credibility tree using Treeannotator 2.6.3 (Bouckaert et al., 2019). Trees were visualized in FigTree 1.4.4 (Rambaut, 2018).

Several node time calibration priors were applied to the tree based on fossil data. For each, an exponential prior was used with an offset equal to the youngest age of the oldest fossil assigned to a clade. The mean of the exponential range was set to a value of 15% of the offset. The exponential prior reflects our assumptions that the occurrence of a fossil is unlikely to represent the first member of the clade to which it is assigned while acknowledging that the probability distribution for the actual age of the clade declines with time beyond the age of the fossil. The fossils, the clades constrained, and prior age ranges are shown in Table S3.

We inferred the biogeographical history of the Poaceae using the maximum likelihood implementation of the program BioGeoBEARS 1.1.2 (Matzke, 2013a, 2013b, 2014). Ancestral ranges were inferred using the Bayesian calibrated tree. The geographical areas of extant taxa were assessed from the Plants of the World Online Database (POWO, 2022) (Table S4). The following six areas were used, roughly corresponding to seven of the eight biogeographical realms of Udvardy (1975): (i) Nearctic (North America), (ii). Neotropical (South America through subtropical Mexico), (iii). Afrotropical (Africa+Madagascar) (excluding strictly Mediterranean taxa), (iv). Indomalayan (India through southern China, Philippines, Borneo, and Indonesia up to the Wallace Line), (v). Palaearctic (Europe, North Asia, and the Mediterranean), and (vi). Australian (combining the Australian and Oceanic realms) (see map in Fig. 2). Separate Oceanic and Antarctic realms are deemed inconsequential for our purposes. A taxon present in more than one region was coded as belonging to each region in which it is considered to be native.

We compared several models, including DEC (Dispersal-Extinction-Cladogenesis (Ree et al., 2005; Ree & Smith, 2008; Matzke, 2012), DIVALIKE, and BAYAREALIKE. The last two models use maximum likelihood to estimate parameters under the assumptions of the DIVA and BAYAREA models, which were originally estimated in a Bayesian framework (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis et al., 2013). The base models differ primarily in the types of sympatric and vicariant cladogenetic events allowed (see Matzke, 2012, 2013a). In addition to each base model, we also included models that estimate founder speciation events with the jump parameter "j," which estimates founder-event speciation (Matzke, 2013b, 2014). Since we did not have an *a priori* preference for any of the models, the best-fitting model (DEC + j) was selected by comparing the AIC criterion among all models. Nested models were compared using the likelihood ratio test (Table S5). Any ancestral range with a probability of less than 10% for a given node was combined into a group called "other" to simplify the visualization of results. Since the inference of biogeographical events is limited when using exemplar taxa (i.e., one taxon representing a genus), we did not simulate biogeographical events or compare alternate biogeographical hypotheses. Therefore, the ancestral area estimation presented here should be treated as a rough estimation to deduce overall patterns with the caveat that future studies with more comprehensive sampling will be needed to understand the biogeographical events that have produced the spatial distribution seen today.

The abbreviations following each section heading in the discussion indicate the coauthor who contributed the summary. The estimated number of species for each genus was initially taken from Soreng et al. (2017: suppl. doc. S1) before evaluation by each coauthor. An updated version of this generic summary appears in Soreng et al. (2022b).

3 Results

3.1 Phylogeny

Relationships among subfamilies, tribes, and subtribes were similar to those shown in recent whole plastome-based phylogenies (Cotton et al., 2015; Burke et al., 2016b; Duvall et al., 2016; Teisher et al., 2017; Saarela et al., 2018; Gallaher et al., 2019; Orton et al., 2021) with notable differences discussed below (Fig. 1).

Subfamilies Anomochlooideae Pilg. ex Potztal, Pharoideae L.G. Clark & Judz., and Puelioideae L.G. Clark, M. Kobay., S. Mathews, Spangler & E.A. Kellogg form a grade leading to the Core Grasses. These relationships are maximally supported except for the relationship between the two genera of Puelioideae, *Puelia* and *Guaduella*, which are united in a clade but with a posterior probability (PP) of 0.84 (Table S2).

The core grasses, which contain over 99% of the diversity of the family, are composed of two sister groups: BOP (Bambusoideae Luerss., Oryzoideae Kunth ex Beilschm., and Pooideae Benth.) and PACMAD (Panicoideae A. Braun, Aristidoideae Caro, Chloridoideae Kunth ex Beilschm., Micrairoideae Pilg., Arundinoideae Kunth ex Beilschm., and Danthonioideae H.P. Linder & N.P. Barker). Relationships among these subfamilies also have maximal support except for the relative positions of Panicoideae and Aristidoideae. In our analysis, Panicoideae was sister to the remaining members of PACMAD with a posterior probability of 0.63, with Aristidoideae sister to the remaining subfamilies (Fig. 1). Cotton et al. (2015) and others (Burke et al., 2016a; Duvall et al., 2020) have reported that the relative positions of these subfamilies shift with different alignment and gap stripping

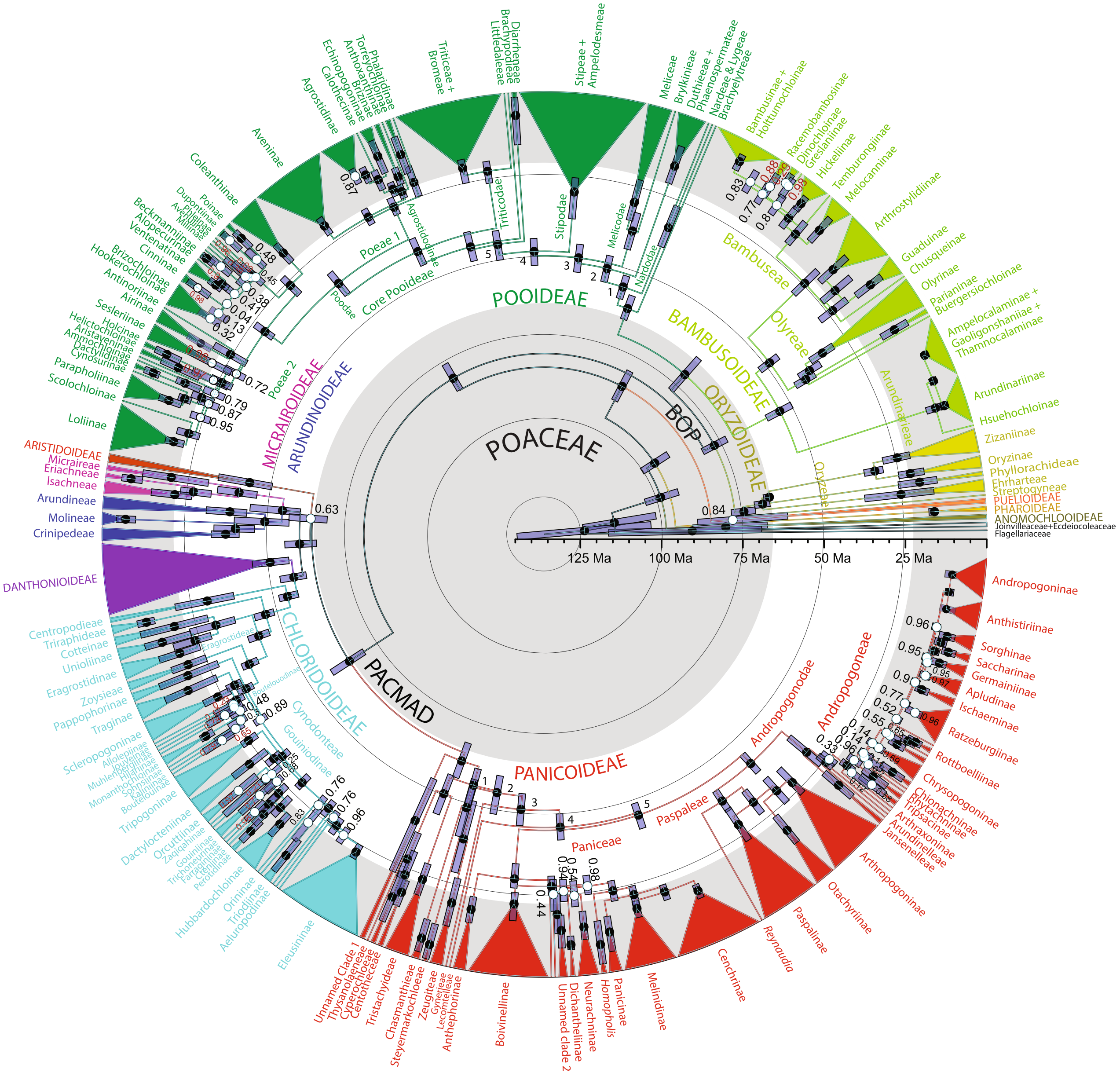

Fig. 1. Phylogenetic reconstruction and timetree of the Poaceae and close relatives (*Joinvillea*, *Ecdeioclea*, and *Flagellaria*) based on chloroplast DNA sequence from 700 samples. The branches are color-coded by subfamily and collapsed at the subtribal level. Nodes with posterior probabilities below 0.99 are marked with a white node symbol and the posterior probability is shown. Node bars represent the 95% highest posterior density of node age estimates.

strategies. In general, removing regions of the alignment with a higher proportion of gapped data yields stronger support for Panicoideae over Aristidoideae as sister to the remaining members of PACMAD (Teisher et al., 2017; Duvall et al., 2020).

3.2 Calibration results

The stem age of the Poaceae was estimated to be 114.27 Ma before present, with a 95% posterior probability density of between 101.32–124.05 Ma and a crown age of 98.54 Ma (92.88–103.5). Stem and crown ages for select clades are summarized in Tables 1, S6).

3.3 Biogeography results

The crown node of Poaceae was inferred to have occurred in a combined area consisting of the Neotropics and Afrotropics (42%) (Fig. 2). The Afrotropics was the most probable ancestral area along much of the backbone of the family, including at the crown of the Spikelet Clade (43%), Bistigmatic Clade (77%), and Core Grass Clade (69%), leading to the crown nodes of the BOP (49%) and PACMAD (87%). The common ancestor of Pooideae and Bambusoideae was estimated to have occurred in the Indomalayan region (21%), Afrotropics + Palaearctic (15%), Afrotropics (12%) or Indomalayan + Palaearctic (12%). Within PACMAD, each of the

Table 1 Summary of time-calibrated phylogenetic and ancestral area estimations for subfamilies, tribes, and select named clades of the grass family based on the DEC + J biogeographical model implemented in BioGeoBEARS

Clade	Posterior/phylogenetic summary	Mean age and 95% CI (Ma)	Highest probability ancestral area
Poaceae	1.0	98.54 (92.88–103.5)	Neotropics + Afrotropics (36%)
Anomochlooideae	1.0	80.22 (67.46–90.33)	Neotropics (100%)
Spikelet Clade	1.0	95.69 (90.77–100.28)	Afrotropics (43%)
Pharoideae	1.0	15.86 (15.17–17.58)	Neotropics + Afrotropics + Indomalayan + Australian (29%)
Bistigmatic clade	1.0	84.66 (79.47–89.6)	Afrotropics (77%)
Puelioideae	0.84	76.76 (61.02–88.76)	Afrotropics (100%)
Core Grasses	1.0	80.45 (75.44–84.55)	Afrotropics (69%)
BOP	1.0	77.09 (72.85–81.13)	Afrotropics (49%)
Oryzoideae	1.0	74.29 (70.73–78.15)	Afrotropics (72%)
Ehrharteae	1.0	25.66 (15.52–36.89)	Australian (51%)
Phyllorachideae	1.0	19.50 (14.16–26.12)	Afrotropics (100%)
Oryzeae	1.0	32.56 (30–35.89)	Cosmopolitan (25%)
Oryzinae	1.0	21.98 (17.7–25.63)	Cosmopolitan (28%)
Zizaniinae	1.0	25.01 (21.09–29.55)	Indomalayan (26%)
Bambusoideae + Pooideae	1.0	70.65 (64.09–77.04)	Indomalayan (21%)
Bambusoideae	1.0	54.35 (50.24–58.95)	Indomalayan (21%)
Arundinarieae	1.0	9.67 (7.4–12.58)	Indomalayan (53%)
Arundinariinae	1.0	6.85 (5.6–8.13)	Indomalayan (95%)
Ampelocalaminae + Gaoligonshaniinae + Thamnocalaminae	1.0	6.74 (5.55–7.74)	Afrotropics + Indomalaya (54%)
Olyreae + Bambuseae	1.0	49.01 (45.77–52.72)	Neotropics (36%)
Olyreae	1.0	42.61 (39.42–46.32)	Neotropics + Australian (63%)
Parianinae	1.0	11.37 (6.79–15.97)	Neotropics (100%)
Olyrinae	1.0	33.97 (30.02–38.39)	Neotropics (100%)
Bambuseae	1.0	24.85 (19.31–29.58)	Neotropics + Indomalayan (53%)
Neotropical woody bamboos	1.0	23.83 (18.38–28.78)	Neotropics (81%)
Guaduinae	1.0	9.8 (5.61–15.32)	Neotropics (98%)
Arthrostylidiinae	1.0	15.6 (9.97–21.09)	Neotropics (100%)
Paleotropical woody bamboos	1.0	15.72 (10.99–19.54)	Indomalayan (72%)
Melocanninae	1.0	10.02 (5.02–14.49)	Indomalayan (100%)
Hickeliinae	1.0	7.34 (4.81–9.87)	Afrotropics (100%)
Dinochloinae + Greslaniinae	0.98	5.17 (2.63–9.36)	Indomalayan + Australian (83%)
Racemobambosinae	0.88	8.03 (4.12–12.27)	Indomalayan (48%)
Bambusinae + Holtumnochloinae	1.0	6.69 (4.42–9.53)	Indomalayan (96%)
Pooideae	1.0	62.07 (57.9–65.62)	Palaearctic (67%)
Nardodae	1.0	34.35	Palaearctic (92%)

Continued

Table 1 Continued

Clade	Posterior/phylogenetic summary	Mean age and 95% CI (Ma)	Highest probability ancestral area
		(27.19–40.63)	
Duthieae + Phaenospermateae	1.0	15.92 (9.54–21.54)	Nearctic + Afrotropics + Indomalayan + Australian (15%)
Melicodae	1.0	38.92 (33.18–44.78)	Indomalaya (52%)
Stipodae	1.0	30.37 (26–38.65)	Palaearctic (87%)
Diarrheneae	1.0	6.94 (1.34–15.95)	Nearctic + Indomalayan + Palaearctic (72%)
Core Pooideae	1.0	44.80 (40.09–49.26)	Palaearctic (82%)
Triticodae + Poodae	1.0	40.78 (36.45–45.29)	Palaearctic (93%)
Triticodae	1.0	23.02 (19.99–26.74)	Palaearctic (69%)
Triticeae + Bromeae	1.0	20.64 (18.01–25.38)	Palaearctic (73%)
Poodae	1.0	36.24 (32.02–40.6)	Palaearctic (96%)
Poeae 1	1.0	25.28 (22.26–27.83)	Palaearctic (72%)
Torreyochloinae	1.0	11.22 (5.43–17.34)	Neotropical + Palaearctic (16%)
Brizinae	1.0	17.21 (14.33–19.78)	Palaearctic (96%)
Echinopogoninae	1.0	9 (3.84–14.64)	Neotropical + Australian (57%)
Agrostidinae	0.87	11.35 (9.06–13.98)	Neotropical + Palaearctic (29%)
Aveninae	1.0	19.53 (16.64–22.65)	Palaearctic (99%)
Poeae 2	1.0	29.84 (26.16–32.93)	Palaearctic (98%)
Coleanthinae	1.0	17.99 (14.45–21.75)	Palaearctic (81%)
Dupontiinae	0.96	3.44 (0.47–7.80)	Palaearctic (67%)
Beckmanniinae	0.32	1.85 (0.12–4.54)	Nearctic + Indomalayan + Palaeartic (64%)
Ventenatinae	1	9.17 (6.67–11.37)	Palaearctic (100%)
Cinninae	0.98	5.17 (1.45–9.59)	Nearctic + Neotropical +Indomalayan + Australian + Palaeartic (38%)
Hookerochloinae + Brizochloinae	0.32	3.91 (6.74–13.01)	Palaearctic (74%)
Airinae	1.0	24.72 (19.01–30.35)	Palaearctic (99%)
Sesleriinae	0.96	20.76 (13.29–27.48)	Palaearctic (86%)
Holcinae	1.0	7.37 (3.54–12.01)	Palaearctic (39%)
Helictochloinae	1.0	12.31(6.61–19.46)	Palaearctic (74%)
Dactylidinae	1.0	5.88 (3.03–7.87)	Palaearctic (34%)
Parapholiinae	1.0	13.39 (10.22–17.38)	Palaearctic (93%)
Loliinae	1.0	18.47 (15.56–21.69)	Palaearctic (55%)
PACMAD	1.0	64.44 (58.03–69.79)	Afrotropics (86%)
Panicoideae	1.0	61.78 (56.36–67.64)	Afrotropics (93%)
Unnamed Clade 1 (Alloeochaete + Dichaetaria)	1.0	39.35 (22.31–53.45)	Afrotropics + Indomalayan (73%)
Cyperochloeae	1.0	15.00 (6.98–23.32)	Australian (100%)
Centotheceae	1.0	17.49 (13.04–21.38)	Afrotropics (41%)
Tristachyideae	1.0	23.37 (18.42–28.5)	Afrotropics (98%)
Chasmanthieae	1.0	6.15 (1.92–12.18)	Nearctic + Neotropics +Afrotropics (71%)

Continued

Table 1 Continued

Clade	Posterior/phylogenetic summary	Mean age and 95% CI (Ma)	Highest probability ancestral area
Steyermarkochloeae	1.0	4.93 (0.5–11.54)	Neotropics + Afrotropics (82%)
Zeugiteae	1.0	19.1 (11.84–26.84)	Neotropics (23%)
Paniceae + Paspaleae + Andropogoneae	1.0	44.92 (40.67–48.75)	Afrotropics (39%)
Paniceae	1.0	29.96 (26.8–34.3)	Afrotropics (38%)
Anthephorinae	1.0	18.43 (14.36–22.4)	Afrotropics (21%)
Boivinellinae	1.0	21.92 (16.78–25.45)	Afrotropics (68%)
Dichantheliinae	1.0	9.5 (8.0–12.13)	Nearctic + Afrotropics (24%) or Neotropical + Afrotropical (24%)
Neurachninae	1.0	14.61(10.11–19.44)	Australian (95%)
Panicinae	1.0	12.04 (6.05–16.89)	Australian (19%)
Melinidinae	1.0	17.42 (14.66–19.77)	Afrotropics (40%)
Cenchrinae	1.0	16.63 (14.23–18.68)	Australian (81%)
Paspaleae	1.0	36.00 (33.82–41.15)	Nearctic + Neotropics (48%)
Paspalinae	1.0	28.61 (22.89–34.51)	Neotropics (100%)
Otachyriinae	1.0	18.28 (13.48–23.93)	Neotropics (85%)
Arthropogoninae	1.0	28.11 (23.61–33.91)	Neotropics (100%)
Jansenelleae	1.0	17.11 (11.66–22.96)	Indomalayan (100%)
Andropogoneae	1.0	18.89 (16.33–21.11)	Indomalayan (30%), Afrotropics (24%)
Tripsacinae	1.0	10.43 (5.28–14.21)	Nearctic (81%)
Chionachninae	1.0	6.38 (2.44–10.62)	Indomalayan (49%)
Rottboelliinae	1.0	5.26 (3.27–8.01)	Indomalayan (34%)
Ratzeburgiinae	0.96	9.43 (7.3–12.52)	Indomalayan (86%)
Apludinae	0.97	11.06 (9.47–12.86)	Indomalayan (86%)
Germainiinae	1.0	8.27 (6.08–10.86)	Indomalayan (60%)
Saccharinae	1.0	6.66 (4.33–8.66)	Indomalayan (53%)
Sorghinae	0.99	8.23 (5.83–10.75)	Indomalayan (39%)
Anthistiriinae	0.99	9.98 (8.58–11.4)	Indomalayan (89%)
Andropogoninae	0.99	9.74 (7.99–11.06)	Indomalayan (85%)
A + C + M + A + D	0.63	63.51 (57.27–69.02)	Afrotropics (88%)
Aristidoideae	1.0	17.00 (16.33–21.11)	Afrotropics (42%)
C + M + A + D	1.0	60.65 (56.08–65.81)	Afrotropics (82%)
M + A	1.0	55.10 (45.12–60.62)	Afrotropics (29%)
Micrairoideae	1.0	41.21 (34.54–46.74)	Indomalaya (34%)
Micraireae	1.0	19.89 (11.07–31.45)	Indomalayan + Australian (73%)
Eriachneae	1.0	7.72 (4.87–11.23)	Australian (43%)
Isachneae	1.0	21.66 (14.43–26.87)	Indomalaya (38%)
Arundinoideae	1.0	49.90 (40.51–57.38)	Afrotropics (32%)
Arundineae	1.0	39.01 (31.75–44.21)	Afrotropics + Indomalayan + Australian (28%)
Moliniinae	1.0	7.08 (4.23–10.17)	Cosmopolitan (67%)
Crinipinae	1.0	37.95 (33.51–42.11)	Afrotropics (97%)
C + D	1.0	57.82 (53.57–61.69)	Afrotropics (97%)
Danthonioideae	1.0	51.17	Afrotropics (86%)

Continued

Table 1 Continued

Clade	Posterior/phylogenetic summary	Mean age and 95% CI (Ma)	Highest probability ancestral area
		(45.72–56.99)	
Chloridoideae	1.0	54.71 (52.08–58.07)	Afrotropics (98%)
Centropodieae	1.0	30.27 (20.29–38.61)	Afrotropics (91%)
Triraphideae	1.0	10.62 (7.81–13.21)	Afrotropics (46%)
Eragrostideae	1.0	31.15 (22.88–37.23)	Afrotropics (50%)
Cotteinae	1.0	18.69 (8.01–29.28)	Cosmopolitan (10%)
Unioliinae	1.0	13.84 (8.35–29.28)	Nearctic + Afrotropics (26%) or Neotropics + Afrotropics (26%) or Afrotropics (24%)
Eragrostidinae	1.0	18.01 (11.41–24.56)	Afrotropics (57%)
Zoysieae	1.0	19.27 (14–25.23)	Cosmopolitan (11%)
Cynodonteae	1.0	32.66 (29.92–35.04)	Afrotropics (28%)
Pappophorinae	1.0	18.02 (8.69–28.03)	Neotropics (69%)
Traginae	1.0	16.31 (8.69–25.98)	Afrotropics (39%)
Scleropogoninae	1.0	23.73 (19.0–28.01)	Nearctic (95%)
Monanthochloinae	1.0	14.72 (13.0–17.46)	Nearctic (74%)
Tripogoninae	1.0	25.03 (22.64–28.09)	Afrotropics (79%)
Dactylocteniinae	1.0	20.96 (14.67–27.53)	Afrotropics (88%)
Orcuttiinae	1.0	13.13 (6.07–20.38)	Nearctic (100%)
Gouiniinae	1.0	17.22 (9.14–24.07)	Nearctic (93%)
Perotidinae	1.0	7.53 (3.41–11.91)	Afrotropics (73%)
Hubbardochloinae	1.0	15.28 (10.75–19.4)	Afrotropics (94%)
Triodiinae	1.0	9.18 (3.13–15.44)	Australian (100%)
Eleusininae	1.0	22.37 (20.29–24.85)	Afrotropics (90%)

All values are for the crown node of each clade. CI, confidence interval.

subfamilies had an inferred Afrotropical origin, including Panicoideae (stem 87%), Aristidoideae (stem 90%), Micrairoideae, and Arundinoideae (stem 38%, or Afrotropics + Indomalaya 14%), and Danthonioideae and Chloridoideae (stem 85%). Ancestral area estimation results for select clades are summarized in Table 1. A comparison with the results from other studies is shown in Table S7.

4 Discussion

4.1 Phylogeny and calibration (TJG)

Our analyses inferred an origin of the grasses at the Early–Late Cretaceous boundary [crown date of 98.54 Ma (92.88–103.5)] consistent with other studies that use fossil phytoliths assigned to extant internal clades of the family. A recent nuclear genome phylogeny of Poaceae (Huang et al., 2022) found a similar crown date of 101 Ma and largely corroborates the plastome phylogenetic topology presented here. Critical differences in that study are that Aristidoideae is sister to PCMAD; Micrairoideae is possibly sister to Panicoideae; Puelioideae may represent two separate subfamily lineages, and the woody bamboos form a monophyletic clade. In the current study, exponential priors give a higher likelihood to node ages closer to the fossil ages used to calibrate each clade resulting in younger age estimates than analyses that use uniform calibration priors such as in Gallaher et al. (2019) since, in the case of that strategy, the root estimate can range with an equal probability between an arbitrarily set maximum age and a minimum age established by fossil-based priors. Regardless of calibration strategy, if an Early–Late Cretaceous time frame for the origin of the grasses continues to be supported, this must be eventually reconciled with the more recent ages for the family inferred in studies that rely on calibration evidence from outside of Poaceae (Prasad et al., 2011; Christin et al., 2014; Magallón et al., 2015).

Unfortunately, due to a lack of available character data for the fossils and extant taxa, we cannot yet place many of the oldest Poaceae fossils with high confidence or precision within the family. Instead, the available fossils are placed conservatively at stem nodes of the larger clades to which they likely belong. Our low precision for fossil placement and the fact that the ages used to calibrate a phylogeny are the most recent age within the geologic strata in which the fossil was found may result in underestimation of the age of the family. For example, Crepet & Feldman (1991) described a well preserved 55–60 Ma grass spikelet from the Wilcox formation in

Tennessee, USA (North America). This fossil is used in our analysis to constrain the bistigmatic clade to be at least 55 Ma. Although assigned to the spikelet clade, the authors suggest that the fossil resembles members of the Pooideae or Arundinoideae subfamilies. If available evidence could confirm a more nested placement, the age of the family would likely be pushed farther back in time.

Similarly, if their relationships to extant clades could be better determined, silicified anthoecia from the Oligocene and Miocene of North America assigned to Stipeae Dumort. (Thomasson, 1985), and Eocene phytoliths affiliated with Bambusoideae (Strömberg, 2005), including some possibly allied with Olyreae Kunth ex Spenn. (Gallaher et al., 2020) would, if their relationship to extant clades could be better determined, similarly push back the age of Poaceae while significantly revising our understanding of the biogeographical history of the family.

4.2 Historical biogeographical estimation (TJG)

Based on the phylogeny reconstruction, time-calibration, and biogeographical models employed here, the most probable biogeographical scenario for the early evolution of the Poaceae involves an origin in West Gondwana in the Cretaceous with the first divergence in the family between Anomochlooideae and the rest of the family potentially arising through vicariance of West Gondwana into South America and Africa at approximately 100 Ma. While the Anomochlooideae in the Neotropics did not result in high extant diversity (see Section 4.3), the ancestors of the spikelet clade diverged in the Afrotropics to give rise to over 99% of the extant diversity in the family. The bistigmatic clade and core-grass clade were all inferred to have evolved in the Afrotropics, consistent with Bouchenak-Khelladi et al. (2010) (Table 1). The Afrotropics were also the likely ancestral area of the PACMAD clade, while the ancestor of the BOP clade evolved either in the Afrotropics (49%) or a combined area of the Afrotropics and Indomalaya (12%).

Fossil evidence, including 100 Ma titanosaur associated phytoliths and silicified cuticles from China (Wu et al., 2018) and 98 Ma grass spikelets and leaves in Burmese amber (Poinar, 2003, 2011; Poinar et al., 2015), suggests that Poaceae was already established in South Asia in the Early Cretaceous. However, in our model, South Asia does not hold a high probability at any ancestral node until about 20 Ma later in the stem ancestor of the Core Grasses. This suggests that these fossils either represent extinct lineages not captured within our geographic reconstruction or that the age of some Asian lineages must be older than our estimate. Under the calibration strategy employed in this study, most of the subfamilies of the core grasses begin to diversify just after the KT boundary (66 Ma).

The ancestral area analysis presented here is intended as a rough estimate of the biogeographical history of the family. Focused studies with more comprehensive species-level sampling within clades are needed to test the biogeographical hypotheses that the results here suggest.

4.3 Anomochlooideae, Pharoideae, and Puelioideae (CDT)

The early-diverging grasses comprise three species-poor lineages. The first to diverge, **Anomochlooideae**, has stem and crown dates of 98.54 and 80.22 Ma (Table 1, Fig. 1), about 11 Ma earlier than previous estimates (Burke et al., 2016a). The crown area is Neotropics (Fig. 2A). Today, the subfamily ranges across tropical Central and South America (but is only sporadically known from the Amazon basin) with the three species of *Streptochaeta* Schrad. ex Nees being the most widespread, while the single species of *Anomochloa* Brongn., the other genus in the subfamily, is endemic to southern Bahia, Brazil. These two genera have inflorescences that differ from each other and all other members of Poaceae, making interpretation of structural homologies difficult. *Anomochloa* has inflorescences with two-ranked branches, each with two bract-like structures and two additional bract-like structures below each flower, which possess four stamens and one stigma. Flowers of *Streptochaeta* are surrounded by an inner perianth whorl of three parts and an outer perianth whorl of two to three parts, subtended by several additional bracts, one of which bears a long, coiled awn (Preston et al., 2009; Reinheimer & Kellogg, 2009). Anomochlooideae possess pseudopetiolate leaf blades, a plesiomorphic character in the family retained in Pharoideae, Puelioideae, Bambusoideae, and a few members of other subfamilies. Potential synapomorphies include a pulvinus at the distal end of the pseudopetiole, large microhairs with a constriction in the mid-portion of the basal cell, adaxially and abaxially projecting midribs, and the shape and orientation of the silica cells (Kellogg, 2015).

The clade containing all other grasses, also known as the **spikelet clade** (GPWG, 2001), has a crown date of 95.69 Ma (similar to the crown date of 93.9 Ma in Schubert et al., 2019b). The crown area is Afrotropics, or less likely Afrotropics + Australian (Table 1, Fig. 2A). Members of this clade possess the conventional grass spikelet: a spicate inflorescence with two empty basal bracts called glumes subtending one–many two-ranked flowers. Each flower is subtended by a lemma (flower bracteole), palea (two connate outer tepals), and three lodicules (inner tepals) (Kellogg, 2015). **Pharoideae** diverge from this clade with a mean crown date of 15.86 Ma, which is later than the 25.0 Ma crown date of Schubert et al. (2019b). The crown area is a pantropical combined area of Neotropics + Afrotropics + Indomalaya + Australian. The three species of *Leptaspis* R. Br. and two species of *Scrotochloa* Judz. are found in Australasia, with *Leptaspis* also occurring in the Afrotropics. The seven species of *Pharus* P. Browne, in contrast, are found throughout the Neotropics, with one species also extending into subtropical North America (Florida). Given the relatively recent crown age of the subfamily, the widespread distribution on multiple continents is likely due to long-distance dispersal. Members of the Pharoideae share the synapomorphies of resupinate leaves with oblique lateral veins, leaf blades with epidermal fibers, monoecy, and uncinate microhairs on the inflorescences (Judziewicz & Clark, 2007).

The third early-diverging clade, **Puelioideae**, diverged from the remaining bistigmatic grasses 84.66 Ma ago and has a crown date of 76.76 Ma. Schubert et al. (2019b) estimated a more recent crown date of 51.6 Ma. The crown area is Afrotropics. The two genera of Puelioideae are poorly known forest grasses of tropical west Africa (Clark et al., 2000).

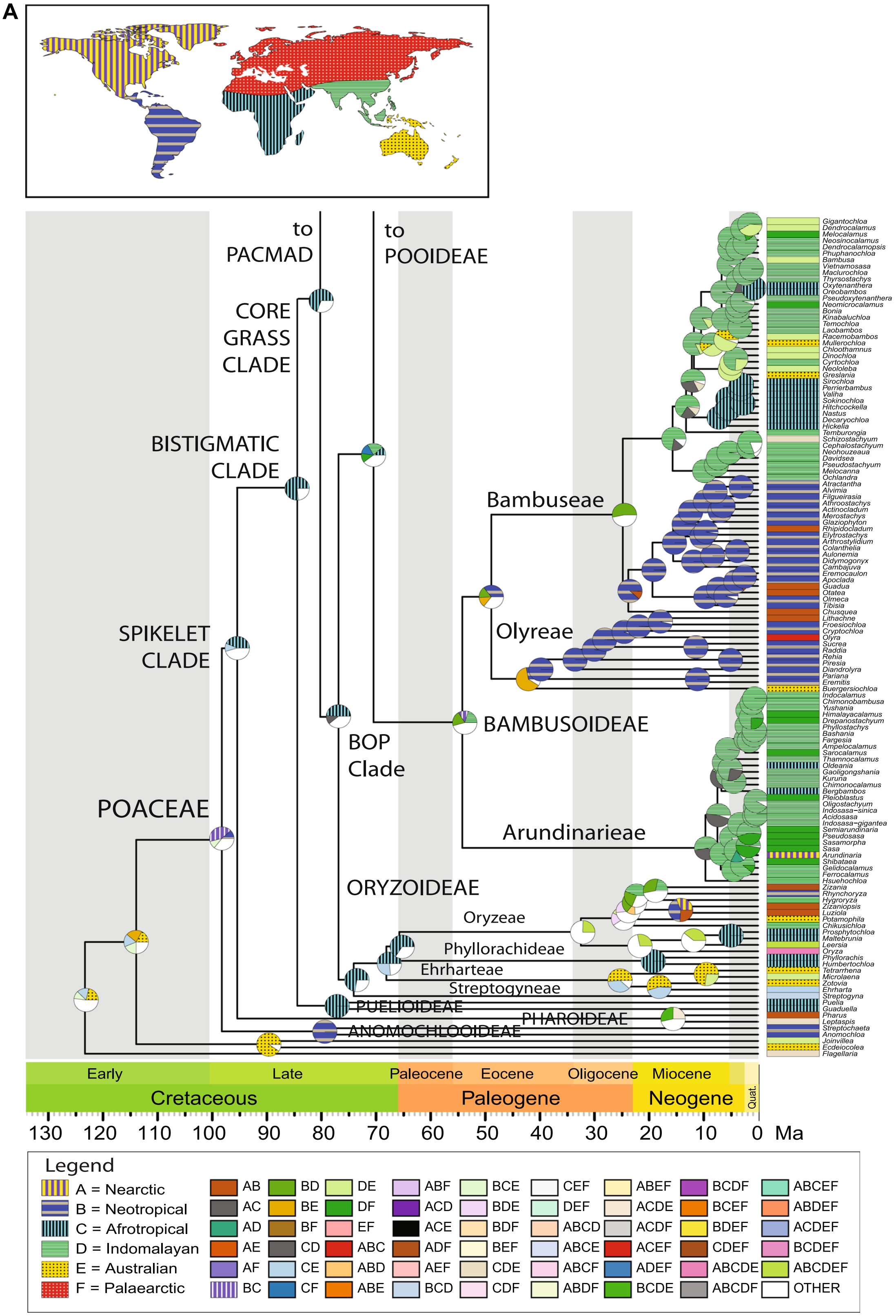

Fig. 2. Ancestral area estimation of Poaceae modeled using the modern geographic distribution of 677 Poaceae genera, three outgroup genera, and the time tree of Figure 1 with the DEC + J biogeographical model and six biogeographical realms as indicated on the inset map. **A,** Anomochlooideae, Puelioideae, Pharoideae, Oryzoideae, and Bambusoideae. **B,** Pooideae. **C,** The ACMAD clade. **D,** Panicoideae.

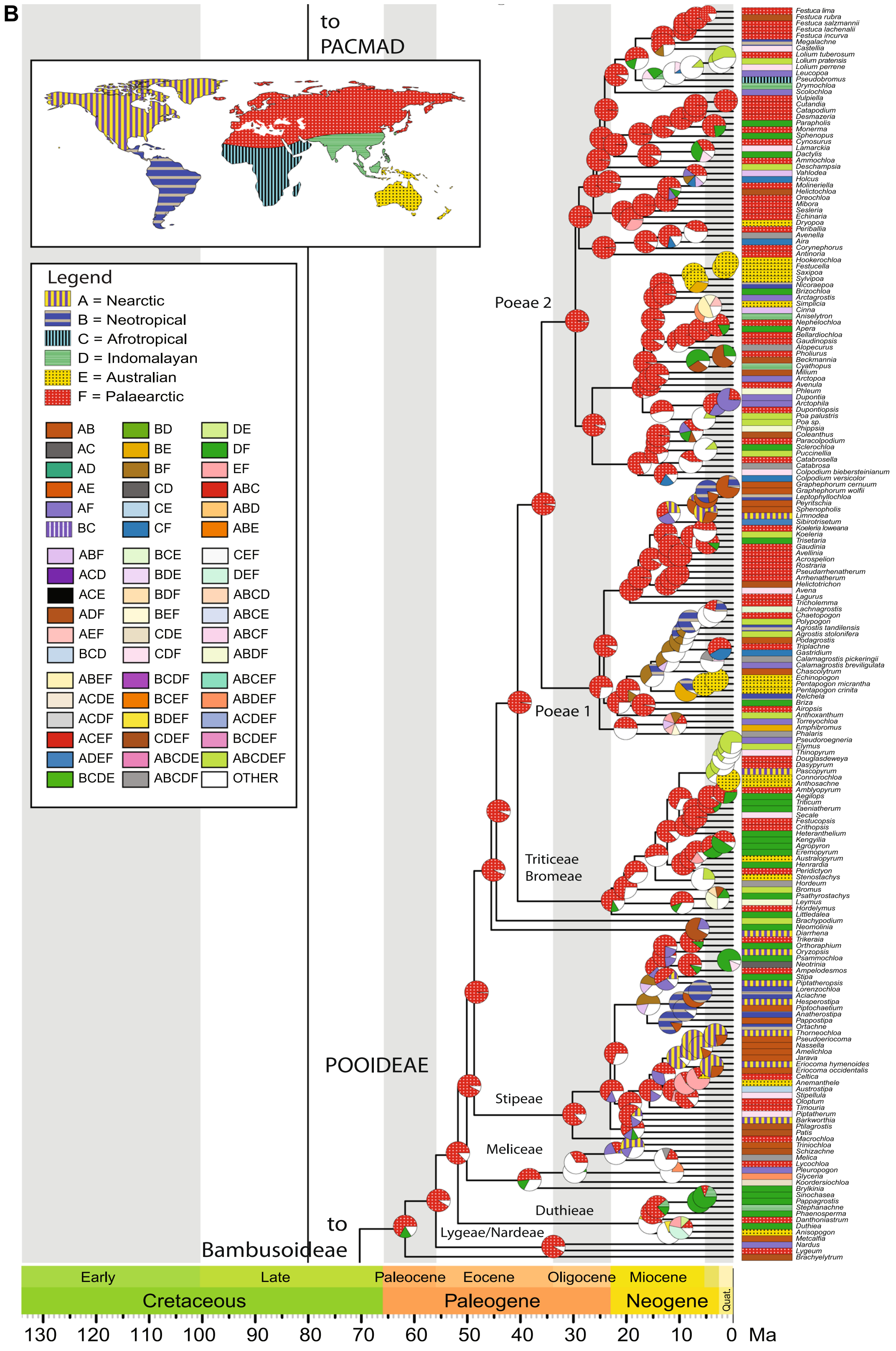

Fig. 2. Continued

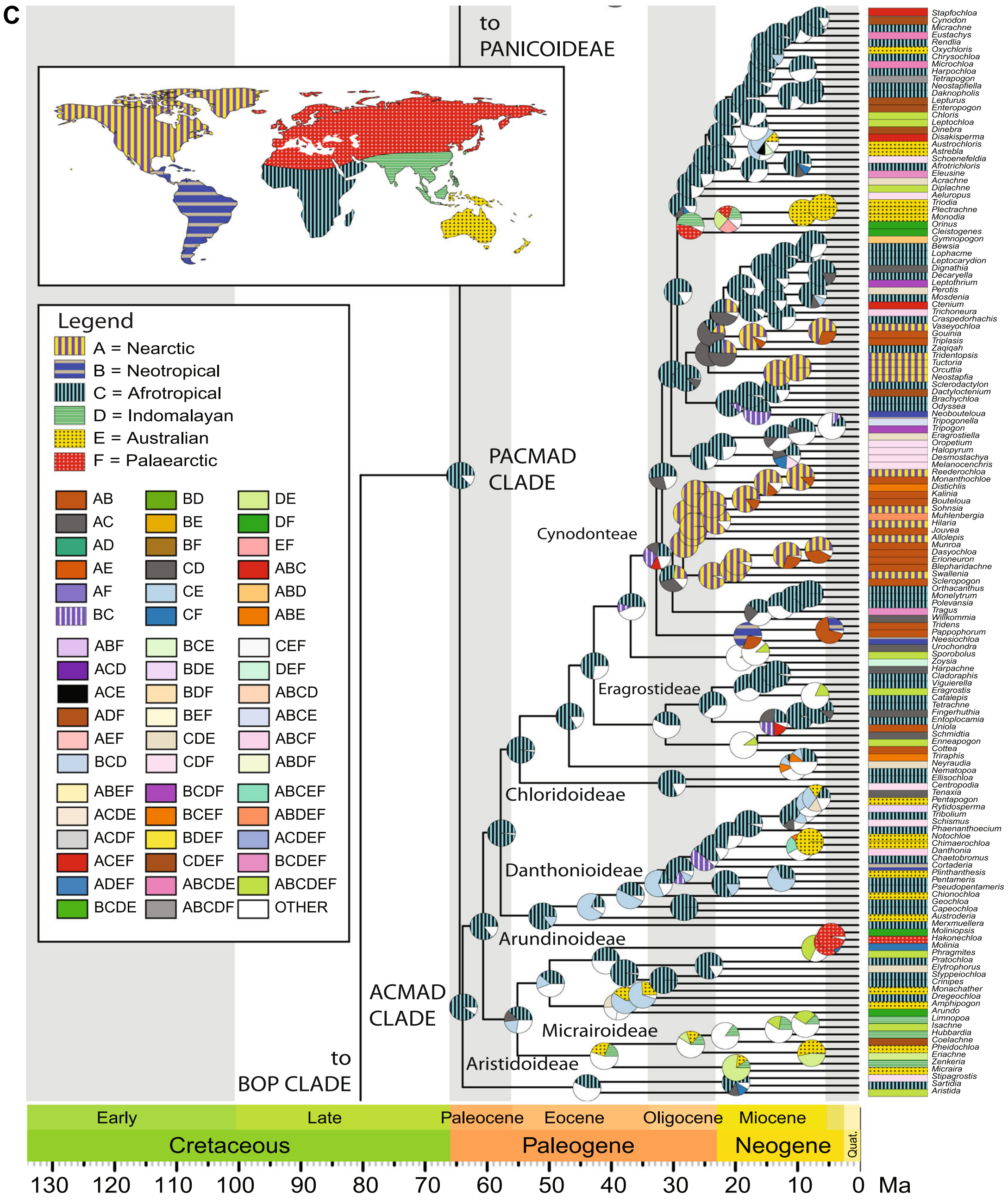

Fig. 2. Continued

Puelia Franch. has five species and *Guaduella* Franch. has six species. They share staminate or sterile basal flowers with three stigmas.

The crown grass clade consisting of the "**Core Grasses**" has stem and crown dates of 84.66 and 80.45 Ma (crown 80.2 Ma in Schubert et al., 2019b). The stem and crown areas are Afrotropics, agreeing with Bouchenak-Khelladi et al. (2010). This clade forks into two large clades: Bambusoideae + Oryzoideae + Pooideae (**BOP clade**) with a crown date of 77.09 Ma (comparable to 77.8 Ma in Schubert et al., 2019b, but differing from the 95.0 Ma of Orton et al., 2021) and Panicoideae + Aristidoideae + Chloridoideae + Micrairoideae + Arundinoideae + Danthonioideae (**PACMAD clade**) with a crown date of 64.44 Ma (compared to 55.1 Ma in Schubert et al., 2019b and 63.7 Ma in Orton et al., 2021).

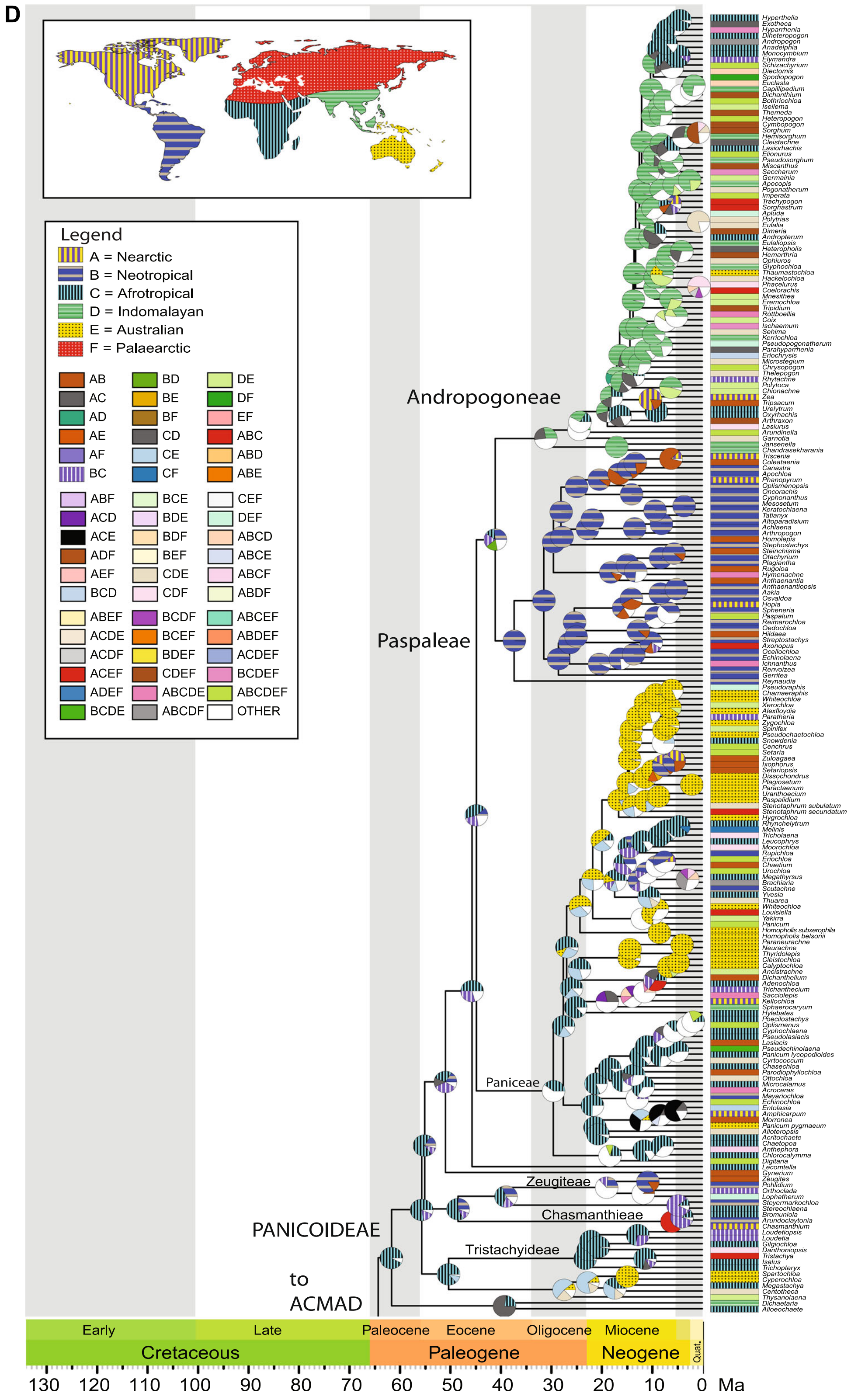

Fig. 2. Continued

4.4 Oryzoideae (CDT)

Subfamily **Oryzoideae** diverges from the other members of the BOP clade 77.09 Ma ago and has a crown date of 74.29 Ma. The crown area is Afrotropical (72%). The 18 genera of Oryzoideae are divided among four tribes and a sagittate-leaved Afrotropical genus, *Suddia* Renvoize (1 sp.), of uncertain placement. The monogeneric **Streptogyneae** C.E. Hubb. ex C.E. Calderón & Soderstr., stem age 74.29 Ma, is the first sampled lineage to diverge in Oryzoideae. *Streptogyna* P. Beauv. (2 spp.) is widespread, found in the Neotropical, Afrotropical, and western Indomalayan realms (Soderstrom & Judziewicz, 1987; Soderstrom et al., 1988). *Streptogyna* has an outer ligule, fusoid cells in the leaf mesophyll, and spikelets with two glumes, two to four fertile florets, and a rachilla extension bearing rudimentary florets. The style branches and stigmas are persistent and become entangled with the lemma awns as the fruits mature and the rachilla internodes develop into hooks. Spikelets of core Oryzoideae have zero or two glumes and three flowers, with the lower two flowers sterile (Kellogg, 2015). This pattern is pronounced in groups like Ehrharteae Nevski but is more subtle in other tribes where the glumes and/or sterile lemmas become highly reduced or lacking. Core Oryzoideae also exhibit distinctive, notched silica bodies (called "oryzoid") oriented perpendicular to the proximal-distal axis of the leaf blade.

Ehrharteae diverge next and have stem and crown dates of 68.29 and 25.66 Ma. The crown area is Afrotropics + Australian (52% and 34%, respectively), suggesting eastward range expansion via long-distance dispersal from a stem origin in the Afrotropics. Their spikelets have two glumes, two empty lemmas, and one fertile floret, and the caryopsis lacks an epiblast (Kellogg, 2015). Some members of the tribe have become highly invasive outside their native range (Calvo & Moreira-Muñoz, 2018; Sánchez-Ken, 2019; Stinca & Mei, 2019). *Ehrharta* Thunb. (27 spp.) is native to the Afrotropical realm, while the tribe's other three genera are Australasian: *Zotovia* Edgar & Connor (3 spp.), a New Zealand endemic, *Tetrarrhena* R. Br. (6 spp.), an Australian endemic, and *Microlaena* R. Br. (4 spp.) ranging throughout Australasia.

Tribes **Phyllorachideae** C.E. Hubb. **and Oryzeae** Dumort., together, form a sister clade to Ehrharteae with a crown date of 65.92 Ma. The smaller **Phyllorachideae** has a crown date of 19.5 Ma and is distributed across the Afrotropics. This tribe is poorly known but has spikelets with two glumes, one empty lemma, and one fertile floret borne on a flattened, leaf-like inflorescence axis (Kellogg, 2015). The two species of *Humbertochloa* A. Camus & Stapf are currently known from Madagascar and Tanzania, while the single species of *Phyllorachis* Trimen ranges across the tropics of continental Africa.

Oryzeae has a stem date of 65.92 Ma. The stem area is Afrotropical, and the likely crown area expands to Cosmopolitan (24%), differing from the prediction of Eurasia (Palaearctic) by Bouchenak-Khelladi et al. (2010) but indicative of the broad geographic ranges of many of the genera in the tribe. Analyses with more comprehensive sampling will be needed to better estimate the geographical origins of the clade. The tribe is diagnosed morphologically by reduced or absent glumes in the spikelets and an unusual anatomical structure of the leaf midrib, with superposed vascular bundles often also with intercellular airspace (Kellogg, 2015). All members of the tribe grow in mesic to aquatic environments. Oryzeae is classified into two subtribes: **Oryzinae** Griseb. and Zizaniinae Benth. The divergence date for these subtribes is 32.56 Ma, with the Oryzinae having a crown date of 21.98 Ma. Both Oryzinae and Zizaniinae lack diagnostic morphological characters (Kellogg, 2015), but the monophyly of each is repeatedly upheld in molecular studies (e.g., Tang et al., 2010; this study). Members of **Oryzinae** range from worldwide in distribution (*Leersia* Sw., 18 spp.) to the pan-tropical (Afrotropical + Australian + Indomalayan + Neotropical) *Oryza* L. (21 spp.), to *Maltebrunia* Kunth (4 spp.) and *Prosphytochloa* Schweick. (1 sp.), which are restricted to the Afrotropics.

Subtribe **Zizaniinae** has a crown date of 25.01 Ma. Tang et al. (2010) estimated that the subtribe underwent rapid radiation around 21 Ma, more recently than we estimate here. Of the seven genera, two are Indomalayan (*Hygroryza* Nees, 1 sp. and *Chikusichloa* Koidz., 3 spp.), Potamophila R. Br. (1 sp.), is Australian, *Rhynchoryza* Baill., (1 sp.) is Neotropical, *Zizania* L. (4 spp.) is temperate with three species in the eastern Nearctic and one in the eastern Palaearctic. The remaining two genera, *Luziola* (9 spp.) and *Zizaniopsis* Döll & Asch. (6 spp.) are distributed across the Nearctic and Neotropic realms (Martínez-y-Pérez et al., 2008). Members of the subtribe generally have branched inflorescences (except in a few species of *Luziola* Juss.).

4.5 Bambusoideae (CDT and LGC for Western Hemisphere subtribes; DZL for all other subtribes)

Within the BOP Clade, the Bambusoideae + Pooideae diverge from Oryzoideae at 77.09 Ma. The crown date for **Bambusoideae** is 54.35 Ma, differing from the crown date of approximately 38 Ma estimated by Schubert et al. (2019b). Estimates for the stem area include Indomalaya, Neotropics + Indomalaya, Afrotropics + Palaearctic, and Afrotropics with similar probabilities, while the crown area is Indomalaya, Neotropics + Indomalaya, or Neotropics + Afrotropics. Members of the Bambusoideae are generally perennial forest-associated grasses, and all share the anatomical feature of strongly asymmetrically-invaginated arm cells in the leaf mesophyll. Bambusoideae is divided into three well-supported monophyletic tribes: the Arundinarieae Asch. & Graebn. (temperate woody bamboos) and Bambuseae Kunth ex Dumort. (tropical woody bamboos), both expressing a syndrome of woody characteristics (strongly lignified culms, differentiated culm and foliage leaves, complex branching, foliage leaves with outer ligules, and gregarious monocarpy), and Olyreae with more herbaceous characteristics: weakly lignified culms, culm leaves not differentiated, limited branching, foliage leaves without outer ligules, and annual to seasonal flowering in most (Clark et al., 2015; Ruiz-Sanchez et al., 2021). Bamboo taxa are endemic to five continents: Africa, Asia, Australia, and North and South America, and also Oceania.

Arundinarieae is an allotetraploid lineage that underwent whole-genome duplication (WGD) and subsequent radiation. It has stem and crown dates of 54.35 and 9.67 Ma, notably differing from the crown date of 12.72 Ma estimated by Zhang et al. (2016) using six plastid DNA markers and

18.73 Ma estimated by Guo et al. (2021) using ddRAD data. The crown area is Indomalaya, or less likely, Afrotropics + Indomalaya and much of the diversification within the tribe occurred in the Indomalayan realm. The tribe has long been undivided because of its complex morphological and evolutionary history (Zhang et al., 2012; Kelchner & Bamboo Phylogeny Group, 2013) but was treated as 12 informal plastid-based clades by Kellogg (2015). Leptomorph rhizomes, diagnosed by basipetal branch development, could be a synapomorphy for this clade (Bamboo Phylogeny Group [BPG], 2012). Recently, five subtribes have been proposed (Zhang et al., 2020): (i) **Hsuehochloinae** D.Z. Li & Y.X. Zhang, comprising one monospecific genus, *Hsuehochloa* D.Z. Li & Y.X. Zhang, endemic to south-central China, which used to be treated as a member of *Ampelocalamus* S.L. Chen, T.H. Wen & G.Y. Sheng but was more recently resolved as an early-diverging lineage of the Arundinariinae Nees ex Lindl. in both plastome- and ddRAD- based phylogenies (Ma et al., 2014; Zhang et al., 2018; Guo et al., 2021); (ii) **Ampelocalaminae** D.Z. Li & Y.X. Zhang, distributed in southeast Asia but extending to south China with three genera, *Ampelocalamus* (14 spp., southeast Asia), *Drepanostachyum* Keng f. (10 spp., southeast Asia), and *Himalayacalamus* Keng f. (9 spp., Himalayan front ranges, northeast India to Myanmar and Tibet of China); (iii) **Gaoligonshaniinae** D.Z. Li & Y.X. Zhang, with one monospecific genus, *Galoigongshania*, endemic to the border between China and Myanmar in the Gaoligong Mountains; (iv) **Thamnocalaminae** Keng f. (the pachymorph lineage or the alpine bamboos), with eight genera, that is, *Bergbambos* Stapleton (1 sp., Lesotho, South Africa), *Chimonocalamus* Hsueh & T.P. Yi (18 spp., southeast Asia), *Fargesia* Franch. (86 spp., China to continental Southeast Asia), *Kuruna* Attigala, Kathriar. & L.G. Clark (7 spp., southern India and Sri Lanka), *Oldeania* Stapleton (7 spp., Madagascar to tropical African uplands), *Sarocalamus* Stapleton (3 spp., southwest China), *Thamnocalamus* Munro (4 spp., Himalayan front ranges, northeast India, Nepal, and Tibet of China) and *Yushania* Keng f. (86 spp., southeast Asia, to Taiwan of China), the Philippines, and Borneo); and (v) **Arundinariinae** (the leptomorph lineage), with a center of diversity in temperate to subtropical East Asia, with three species in North America. The phylogenetic taxonomy of *Fargesia* and *Yushania* remains to be settled. Stapleton (2021) favored expanding *Bashania* Stapleton (to 51 spp.) as a paraphyletic grade to *Yushania*, but the species could all be subsumed into a polymorphic *Yushania*. In any case, Stapleton's proposal results in a much reduced *Fargesia*. Stapleton (2021) also proposed a new genus, *Tongpeia* Stapleton (3 spp., southwestern China highlands). The phylogenetic estimate presented here supports Hsuehochloinae and Arundinariinae as monophyletic lineages, each a successive sister to a clade that comprises the taxa assigned to the remaining three subtribes. Within that clade, genera assigned to Ampelocalaminae, Thamnocalaminae, and Gaoligonshaniiae were intermixed, suggesting that further work is needed to confirm these relationships.

Ye et al. (2019) estimated the crown date of **Thamnocalaminae** (alpine bamboos) at 7.36 Ma. Of the 212 described species, over 93% are distributed in eastern and southeastern Asia, with less than 7% of species extending to southern India, Sri Lanka, continental Africa, and Madagascar. It spread to the Hengduan Mountains region and underwent a significant acceleration in net diversification in the Pliocene, temporally congruent with the Tibetan orogeny (Ye et al., 2019). Members of this subtribe provide the primary staple food for the giant panda, an iconic species for biodiversity conservation. Paleontological and molecular evidence suggest that pandas switched to bamboo feeding ca. 2 million years ago (Jin et al., 2007; Zhao et al., 2010).

Arundinarinae, arguably the most taxonomically challenging subtribe in the Poaceae because of long flowering cycles and, therefore, a paucity of specimens to work with, is the largest subtribe of the temperate woody bamboos with about 350 described species tentatively treated in 21 genera or so. Recent nuclear- and plastome-based phylogenies both deviate markedly from the current taxonomy based on diagnostic morphological characters (i.e., inflorescence and spikelet structures, number of stamens, and branching patterns; Guo et al., 2021). Many currently delineated genera were resolved as paraphyletic or polyphyletic. Consequently, some of the following discussions at the generic level should be treated as tentative. *Ravenochloa* D.Z. Li & Y.X. Zhang is resolved as an early-diverging clade (Zhang et al., 2020). It has only one species, endemic to south-central China at elevations of 1500-3000 m, higher than any other members of the subtribe. *Phyllostachys* Siebold & Zucc. (61 spp.) is a temperate East Asian genus with a distribution extending west to the Himalayas. The closely related *Shibataea* Makino ex Nakai (7 spp.) is found in eastern China but with a long history of cultivation in Japan (Guo et al., 2019a). *Semiarundinaria* Nakai (8 spp.) is also found in eastern China and Japan. It has close relationships with *Phyllostachys* in the ddRAD tree and forms a well-supported clade with four species of *Pleioblastus* Nakai in the chloroplast tree, implying its likely origin by hybridization (Guo et al., 2021; Triplett & Clark, 2021). *Brachystachyum* Keng (2 spp.) is found in eastern China and may also have a hybrid origin (Zhang et al., 2012).

Arundinaria Michx. (3 spp.) is the only genus of temperate woody bamboos found in the New World (temperate to subtropical eastern North America). The disjunct distribution of the genus appears to be the result of long-distance dispersal from the Indomalaya region. In temperate east Asia, the relationships among the three-branched genera, including *Pleioblastus* (25 spp.) and *Pseudosasa* Makino ex Nakai (20 spp.), and those among the one-branched, usually smaller shrubby genera of *Indocalamus* Nakai (33 spp.), *Sasa* Makino & Shibata (43 spp.), *Sasaella* Makino (12 spp.), *Sasamorpha* Nakai (5 spp.) and the newly published *Sinosasa* L.C. Chia ex N.H. Xia et al. (7 spp.) need to be resolved at both generic and species levels, together with the multi-branched *Gelidocalamus* T.H. Wen (11 spp.) and *Bashania* Keng f. & T.P. Yi (7 spp.). The other one-branched genus, the arborescent *Ferrocalamus* Hsueh & Keng f. (3 spp.), notably with fleshy fruit, is found in subtropical eastern Asia. The monophyletic *Chimonobambusa* Makino (42 spp.) is also found in the mid-elevation forest area and is closely related to the genera mentioned above but with distinct morphology, e.g., the much-reduced culm leaf blade (less than 1 cm long), often simply acicular.

Acidosasa C.D. Chu & C.S. Chao ex Keng f. (11 spp.) is found in south China and north Vietnam, together with *Indosasa* McClure (19 spp.), *Sinobambusa* Makino ex Nakai (13 spp.)

and *Oligostachyum* Z.P. Wang & G.H. Ye (17 spp.). These genera look similar in the vegetative state but differ in inflorescence (determinate vs. indeterminate) and spikelet characters (three vs. six stamens). Molecular phylogenetic studies show that these genera are not well defined and are closely related to members currently placed in *Pleioblastus* and *Pseudosasa* (Cai et al., 2012, Zeng et al., 2010).

Within Arundinarieae, *Khoonmengia* N.H. Xia, Y. H. Tong & X.R. Zheng is a monospecific genus recently found in Vietnam (Tong et al. 2020). It shows affinity with the early-diverging *Hsuehochloa* in spikelet structure and branching pattern and may prove to be a member of the Hsuehochloinae. Another monospecific genus, *Vietnamocalamus* T. Q. Nguyen, also found in Vietnam, could be a member of the Arundinariinae (Zhang et al. 2020), but its position needs to be confirmed with molecular analysis.

Sister to the Arundinarieae is a clade containing members of **Olyreae + Bambuseae** with a crown date of 49.01 Ma. The crown area is Neotropics. The Olyreae crown date is 42.61 Ma. The crown area is Neotropics+Australian, in agreement with Ruiz-Sanchez et al. (2019), but switches to Neotropics after *Buergersiochloa* Pilg. diverges. The tribe includes three subtribes: Buergersiochloinae L.G. Clark & Judz., Parianinae Hack., and Olyrinae Kromb. The earliest diverging, **Buergersiochloinae** (stem date 42.61 Ma), had, until recently, a single species endemic to the island of New Guinea. Molecular investigations by de Carvalho et al. (2021) demonstrated that the Cuban micro-endemic *Piresiella* Judz., Zuloaga & Morrone (1 sp., not sampled for this analysis) is sister to *Buergersiochloa* (1 sp.) and was thus transferred to Buergersiochloinae. Based on the morphological similarities of two other endemic Cuban genera, *Ekmanochloa* Hitchc. (2 spp.) and *Mniochloa* Chase (1 sp.), to *Piresiella*. These genera were also transferred to this subtribe. The members of Buergersiochloinae are morphologically united by (i) a lack of papillae on the abaxial subsidiary cells of the leaves, (ii) ciliolate or laciniate ligules, and (iii) dimorphic culms with the leafy reduced culm morph bearing the inflorescences.

The **Parianinae + Olyrinae** clade (stem age 42.61 Ma, crown age 40.27 Ma) is sister to the Buergersiochloinae and is supported by the shared presence of crenate (olyroid) and cruciform silica bodies (Lima et al., 2020, 2021). The less diverse **Parianinae** has a crown date of 11.37 Ma. All members of the Parianinae have fimbriate leaf sheaths, spiciform inflorescences, spikelets in whorls, disarticulation of the inflorescence axis, and male spikelets with glumes (Ferreira et al., 2019). The Parianinae have a western hemisphere distribution with *Eremitis* Döll (16 spp.) and *Parianella* Hollowell, F.M. Ferreira & R.P. Oliveira (2 spp.) restricted to tropical eastern Brazil, while the more widespread *Pariana* Aubl. (27 spp.) ranges from Amazonian South America into Panama.

Sister to Parianinae, the **Olyrinae** have a crown date of 33.97 Ma. With the transfer of the three endemic Cuban genera to Buergersiochloinae (Lima et al., 2020, 2021), the subtribe is well-supported as monophyletic in molecular analyses (Ferreira, 2019; de Carvalho, 2021; Oliveira et al., 2020a). The subtribe is Neotropical except for one species of *Olyra* L. (25 spp.), which is Neotropical +Afrotropical. In a population genetic study, Ruiz-Sanchez et al. (2019) surmised that the dispersal to Africa was a recent event, possibly anthropogenic. Still, the data are not conclusive, and this hypothesis invites further investigation. Five genera, *Agnesia* Zuloaga & Judz. (1 sp.), *Froesiochloa* G.A. Black (1 sp.), *Piresia* Swallen (6 spp.), *Raddia* Bertol. (9 spp.) and *Rehia* Fijten (1 sp.) are lowland species found in the Amazonian region of South America. *Raddia* is also known from the Atlantic forests of eastern Brazil along with four other lowland genera that are endemic to that region: *Brasilochloa* R.P. Oliveira & L.G. Clark (1 sp.), *Diandrolyra* Stapf (3 spp.), *Reitzia* Swallen (1 sp.), and *Sucrea* Soderstr. (2 spp.) (Oliveira et al., 2020a, 2020b). The distribution of *Reitzia* extends southward into subtropical Brazil. Members of the remaining Olyrinae genera are more widespread, but with some having only localized populations. *Arberella* Soderstr. & C.E. Calderón (7 spp.), *Cryptochloa* Swallen (9 spp.), *Lithachne* P. Beauv. (4 spp.), *Maclurolyra* C.E. Calderón & Soderstr. (1 sp.), *Parodiolyra* Soderstr. & Zuloaga (6 spp.) and *Raddiella* Swallen (8 spp.) have distributions that span from Central America into South America with variously sized ranges, and *Taquara* I.L.C. Oliveira & R.P. Oliveira (2 spp.) is distributed across tropical South America (Oliveira et al., 2020a). Morphologically, the subtribe is characterized by the combination of the lack of fimbriae on the leaf sheaths, paniculate or racemose inflorescences, usually un-awned female spikelets (awned only in Agnesia), and two or three stamens. Still, none of these is exclusive to Olyrinae (Lima et al., 2020).

Stem and crown dates for the divergence of **Bambuseae** (the tropical woody bamboos) are 49.01 and 24.85 Ma, respectively. The crown area is Neotropics+Indomalayan. The Bambuseae include over 1000 described species in 78 genera (Clark & Oliveira, 2018; Ruiz-Sanchez et al., 2021) and are widespread in the tropics, with some members adapted to high elevations or high latitudes (e.g., *Chusquea* Kunth in the western hemisphere or *Bambusa* Schreb. in the eastern hemisphere). This clade received strong support for its monophyly in molecular analyses (Bouchenak-Khelladi et al., 2008; Sungkaew et al., 2009; Kelchner & Bamboo Phylogeny Group, 2013; Wysocki et al., 2015; Soreng et al., 2017; Guo et al., 2019b) but the only potential morphological synapomorphy identified to date is the presence of acropetal or bidirectional branch development (Clark et al., 2015). The Bambuseae comprises two major clades, the Paleotropical woody bamboos (at least 554 spp.), crown area Indomalayan, and the Neotropical woody bamboos (448 spp.), crown area Neotropics. The stem divergence time for Paleotropical and Neotropical woody bamboos is 24.85 Ma, with a crown date of 15.72 for the Paleotropical and 23.83 Ma for the Neotropical woody bamboos.

Within the **Neotropical woody bamboos**, the stem date for the divergence of **Chusqueinae** Soderstr. & R.P. Ellis is estimated to be 23.83 Ma, consistent with the crown date for the Neotropical woody bamboos. This subtribe contains one genus, *Chusquea* Kunth (193 spp.), distributed from Mexico to Argentina and Chile, with one species in the West Indies, mostly at medium to high elevations (Ruiz-Sanchez et al., 2021). The areas of highest species diversity and endemism in *Chusquea* include Mexico, Costa Rica, the northern and central Andes, and Brazil. To date, all molecular analyses strongly support the monophyly of *Chusquea*, and diagnostic morphological characters include two papillae per subsidiary cell in the stomatal apparatus and spikelets consisting of four glumes and one fertile floret, and no rachilla extension (Ruiz-Sanchez et al., 2021).

Diverging from Chusqueinae, the **Arthrostylidiinae + Guaduinae** clade has stem and crown dates of 23.83 and 19.4 Ma. The crown of **Guaduinae** Soderstr. & R.P. Ellis is dated at 9.8 Ma. All genera of Guaduinae generally inhabit relatively low elevations, but with some species reaching 2000 m. Guaduinae are distinguished by abundant stomata on both abaxial and adaxial foliage leaf blade surfaces, oral setae on the culm and foliage leaves in most species (absent in *Apoclada* McClure), and some members of the subtribe having pseudospikelets (Ruiz-Sanchez et al., 2021). *Guadua* Kunth (33 spp.) is distributed across tropical Central and South America. Among the remaining genera, *Apoclada* (1 sp.) and *Eremocaulon* Soderstr. & Londoño (5 spp.) are found in southern and eastern Brazil, while *Olmeca* Soderstr. (5 spp.) is restricted to northern Central America (south of the Isthmus of Tehuantepec) and *Otatea* (McClure & E.W. Sm.) C.E. Calderón & Soderstr. (13 spp.) is found throughout Central America to Colombia. The Guaduinae were considered absent from the West Indies until the endemic genus *Tibisia* C.D. Tyrrell, Londoño & L.G. Clark (3 spp.) was recognized as a part of the subtribe (Tyrrell et al., 2018).

The **Arthrostylidiinae** Soderstr. & R.P. Ellis crown date, 15.6 Ma, is older than that of Guaduinae. Members of Arthrostylininae are distinguished by a combination of foliage leaf characters, including simple midribs, intercostal sclerenchyma, an abaxial, waxless green marginal stripe, and the foliage leaf blades are usually reflexed at the pseudopetiole (Ruiz-Sanchez et al., 2021). The largest genera, *Arthrostylidium* Rupr. (28 spp.), *Aulonemia* Goudot (47 spp.), *Merostachys* Spreng. (55 spp.), and *Rhipidocladum* McClure (21 spp.) are widespread throughout the tropical and subtropical Americas. There is high generic diversity in Brazil, especially in the south and east, where *Actinocladum* McClure ex Soderstr. (1 sp., also extending into Bolivia), *Alvimia* C.E. Calderón ex Soderstr. & Londoño (3 spp.), *Athroostachys* Benth. (2 spp.), *Cambajuva* P.L. Viana, Filg. & L.G. Clark (1 sp.), *Colanthelia* McClure & E.W. Sm. (10 spp., also extending into Argentina), *Filgueirasia* Guala (2 spp.), and *Glaziophyton* Franch. (1 sp.) are concentrated (Ruiz-Sanchez et al. 2021). *Myriocladus* Swallen (13 spp.) is restricted to the highlands of the Guiana Shield in northern South America. *Atractantha* McClure (5 spp.) has a disjunct distribution with one species in the Guiana Shield region and four in eastern Brazil. Three smaller genera, *Aulonemiella* L.G. Clark, Londoño, C.D. Tyrrell & Judz. (2 spp.), *Didymogonyx* (L.G. Clark & Londoño) C.D. Tyrrell, L.G. Clark & Londoño (2 spp.), and *Elytrostachys* McClure (2 spp.) form a cluster in the central and northern Andes, with *Elytrostachys* extending up the Central American cordillera.

The **Paleotropical woody bamboos** are all allohexaploids (Guo et al., 2019b) and were divided into four subtribes, Bambusinae J. Presl, Hickeliinae A. Camus, Melocanninae Benth., and Racemobambosinae Stapleton (Kellogg, 2015; Soreng et al., 2015b), with four segregates from the complex Bambusinae: Dinochloinae K.M. Wong & W.L. Goh (low support in the current analysis), Greslaniinae K.M. Wong & W.L. Goh (monogeneric), Holttumochloinae (nested in Bambusinae) and Temburongiinae K.M. Wong (monogeneric) (Soreng et al., 2017). The first-diverging lineage of the Paleotropical woody bamboos, **Melocanninae,** has estimated stem and crown dates of 15.72 and 10.02 Ma, different from the crown date of 19.68 Ma (Zhou et al., 2022, this volume). Members of the subtribe share an elongated hollow style and are distributed in tropical southeast Asia and South Asia. *Schizostachyum* Nees (62 spp.) is the largest and most widely distributed genus with distribution in Southeast Asia and the Pacific islands. *Neohouzeaua* A. Camus, a segregate genus with three species in Myanmar and Thailand, may prove to be part of it. *Cephalostachyum* Munro (13 spp.) is found in southeast Asia, including the Philippines, while *Ochlandra* Thwaites (10 spp., with numerous stamens and fleshy fruit) is endemic to south India and Sri Lanka. All other genera are monospecific or oligospecific in tropical southeast Asia, including *Melocanna* Trin. (3 spp.) and *Stapletonia* P. Singh, S.S. Dash & P. Kumari (2 spp.) both with a berry-like fruit, while *Davidsea* Soderstr. & R.P. Ellis is endemic to Sri Lanka.

Apart from Melocanninae, the monospecific *Temburongia* S. Dransf. & K.M. Wong (**Temburongiinae**) is resolved as the sister lineage to the rest of Paleotropical woody bamboos, with a stem date of 13.21 Ma. This genus is endemic to Brunei. The subtribe **Hickeliinae** is nearly endemic to Madagascar, with a stem and crown date of 11.94 and 7.34 Ma. The crown area is Afrotropics. *Hickelia* A. Camus (4 spp.) is mainly distributed in Madagascar, with one species extending to Tanzania, most likely by a recent dispersal. A recent study restricted *Nastus* Juss. to the 12 Madagascar and Reunion Island species, while the southeast Asian species belong to Bambusinae (Zhou et al., 2017). Members of *Sokinochloa* S. Dransf. (7 spp.) had been placed in the southeast Asian *Cephalostachyum*, but it proved to be a genus endemic to Madagascar. Other small genera in this subtribe are all endemic to Madagascar, including *Cathariostachys* S. Dransf. (2 spp.), *Decaryochloa* A. Camus (1 sp.), *Hitchcockella* A. Camus (1 sp.), *Perrierbambus* A. Camus (2 spp.), *Sirochloa* S. Dransf. (1 sp.), and *Valiha* S. Dransf. (2 spp.).

The relationships between the monogeneric **Greslaniinae** and genera of the **Dinochloinae** K.M. Wong & W.L. Goh need to be further clarified. They were resolved as the *Dinochloa-Greslania-Mullerochloa-Neololeba-Sphaerobambos* (DGMNS) assemblage with weak support (Zhou et al., 2017). *Greslania* Balansa (2 spp.) is endemic to New Caledonia, with none or one branch per node. Within the Dinochloinae, *Dinochloa* Buse (38 spp.) is a large genus found in tropical southeast Asia with culms spiraling around tree trunks and fleshy fruit. *Cyrtochloa* S. Dransf. (7 spp.) is endemic to the Philippines. *Parabambusa* Widjaja and *Pinga* Widjaja, both monospecific, are endemic to New Guinea. *Sphaerobambos* S. Dransf. (3 spp.) is found in Borneo, the Philippines, and Sulawesi, while the monospecific *Mullerochloa* K.M. Wong is endemic to Queensland, Australia. *Neololeba* Widjaja (5 spp.) is distributed in the Pacific islands, tropical southeast Asia, and Australia.

Racemobambos Holttum (19 spp.) is found in tropical southeast Asia and placed in its own subtribe, the **Racemobambosinae**. *Chloothamnus* Buse (11 spp.) is found in southeast Asia and northern Australasia, while *Widjajachloa* K.M. Wong & S. Dransf. (monospecific) was endemic to New

Guinea. Both genera were previously placed in *Nastus*. Their relationship with *Racemobambos* has weak support.

Holttumochloinae is nested within the Bambusinae, with three small genera: *Holttumochloa* K.M. Wong (3 spp.) in southeast Asia, *Kinabaluchloa* K.M. Wong (2 spp.) found in tropical southeast Asia, extending to Hainan Island, and the monospecific *Nianhochloa* H.N. Nguyen & V.T. Tran endemic to Vietnam.

Bambusinae is another taxonomically challenging subtribe in Bambusoideae, with more than 300 described species in 20 genera. The estimated stem and crown dates for Bambusiae are 10.01 and 6.69 Ma. The basal grade within the subtribe includes *Bonia* Balansa (5 spp.) found in southern China and adjacent Vietnam, *Neomicrocalamus* Keng f. (3 spp.) and the monospecific *Temochloa* S. Dransf. both from continental tropical southeast Asia, and the monospecific *Laobambos* Haev., Lamxay & D.Z. Li, a succulent bamboo found in central Laos. *Kinabaluchloa* and *Holttumochloa* may be part of the grade (Zhou et al., 2017).

Much work is needed to clarify generic boundaries and interspecific relationships, particularly within the BDG (*Bambusa-Dendrocalamus-Gigantochloa*) complex (Goh et al., 2013; Liu et al., 2020). The three largest genera, *Bambusa* Schreb. (153 spp.), *Dendrocalamus* Nees (66 spp.) and *Gigantochloa* Kurz ex Munro (63 spp.) are widely distributed and cultivated in tropical and subtropical Asia. They are economically important bamboos in tropical Asia and include the tallest grass species, *D. sinicus* L.C.Chia & J.L.Sun (culms up to 33 m high and 30 cm in diameter). Apart from the BDG complex, *Melocalamus* Benth., also distributed in tropical southeast Asia (14 spp.), includes individuals with scandent culms and fleshy fruits. Other genera, often with few species, are distributed in tropical southeast Asia, while the monospecific *Oxytenanthera* Munro is distributed in tropical Africa. Another monospecific genus, *Oreobambos* K. Schum., is found in central Africa. *Pseudoxytenanthera* Soderstr. & R.P. Ellis (4 spp.) is native to southern India and Sri Lanka. *Thyrsostachys* Gamble (2 spp.) is distributed in Myanmar, Thailand, and south Yunnan, China. *Maclurochloa* K.M. Wong (3 spp.) is found in Malaysia and Vietnam. *Vietnamosasa* T.Q. Nguyen (3 spp.), which used to be treated in Racemobambosinae, is found in Vietnam and Thailand. *Ruhooglandia* S. Dransf. & K.M. Wong is a monospecific genus endemic to New Guinea, whose systematic position remains unresolved.

4.6 Pooideae (RS)

The mean stem and crown ages of **Pooideae** are 70.65 and 62.07 Ma, while Schubert et al. (2019b) estimated these at 73.7 and 69 Ma, and Orton et al. (2021) estimated a crown date of 84.8 Ma. The stem area is Indomalayan, Afrotropics + Palaearctic, Afrotropics (21%, 15%, and 12%, respectively; Fig. 2b). The crown area is Palaearctic (67%), which Schubert et al. (2019b) gave that as Eurasia, with the exceptions of BrachyelytreaeOhwi, Diarrheneae C.S. Campb., Brachypodieae Harz, and Littledaleeae Soreng & J.I. Davis, the stem and crown areas remain Palaearctic along the backbone and for tribes. Members of this subfamily share, among other characters, non-woody and hollow culms, non-Kranz leaf anatomy and C_3 photosynthesis, a lack of bicellular microhairs (except in Nardodae Soreng), membranous to chartaceous ligules without ciliate apices, lodicules mostly nerveless with a membranous-hyaline apex (lodicules fused and with a fleshy apex in most Meliceae Link ex Endl.), apex mostly glabrous but without cilia, an embryo with a negligible mesocotyl internode (Reeder, 1957, 1962; Clayton & Renvoize, 1986), and an embryo shorter than 1/3 the grain. They are adapted to temperate to frigid climates (Clayton & Renvoize, 1986). Pooideae probably originated in the northern hemisphere but now range throughout tropical latitudes in high mountains and have dispersed many times to southern hemisphere temperate regions, and sometimes between Australasia and South America.

Brachyelytreae, stem age 62.07 Ma (stem of 84.4 Ma in Orton et al., 2021), with a single genus (*Brachyelytrum* P. Beauv., 3 spp., East Asia, eastern North America; revised by Saarela et al., 2003), is the sister tribe to all other Pooideae. We estimated the stem areas as Palaearctic (67%). Schubert et al. (2019b) predicted the stem area to be Eurasia (24%) and the crown area to be North America (50%), but with only one sample, we could not estimate the crown area. The species retain a bamboo-like aspect, with lanceolate blades with cross-venation. They have 1-flowered spikelets that disarticulate above the very short glumes, lemmas with long apical awns, 2 lodicules, 2 styles, and a long-linear hilum. These are temperate forest grasses with some cold tolerance already evident as populations reach 50° North.

The rest of **Pooideae 1** (in Fig. 1) have stem and crown dates of 62.07 and 56.24 Ma (crown date 66 Ma in Schubert et al., 2019b). Supertribe **Nardodae** Soreng (Soreng et al., 2017) diverged next with two monogeneric tribes with stem and crown dates of 56.24 and 34.35 Ma (65.5 and 32.1 Ma in Schubert et al., 2019b; a crown of 42.4 Ma in Orton et al., 2021). The stem and crown areas are Palaearctic. The genera (stem date 34.35 Ma) share synapomorphies of bicellular microhairs on their leaves and ovaries with a linear (possibly fused) non-plumose style. *Nardus* L., of **Nardeae** W.D.J. Koch (1 sp., Europe, western & Central Asia) is common in cool to cold moorlands and alpine wetlands of Europe eastward but is absent from east Asia. Whether it is indigenous to eastern North America, including Greenland, or not, is debatable (Chadwick, 1960; Barkworth et al., 2007). *Lygeum* Loefl. ex L., of **Lygeeae** J. Presl [1 sp.; Parodi & Calderon (1961) assessed the strange compound spikelet], is restricted to Mediterranean lowlands, in dry sandy or clayey, frequently gypseous soils (Tutin, 1980 p. 255).

The stem and crown of the rest of **Pooideae 2** (in Fig. 1) are dated at 56.24 and 52.08 Ma (65.5 and 61 Ma in Schubert et al., 2019b). The Duthieeae + Phaenospermateae diverge next with stem and crown ages of 52.08 and 15.92 Ma (61 and 30.1 Ma in Schubert et al., 2019b; stem of 60 Ma. in Orton et al., 2021). As in the previously described lineages, the young crown date may be an underestimate. The geographic distribution of the genera and paucity of species is suggestive of a much older origin and extinctions. The stem area is Palaearctic (87%), but the crown area is estimated to be Palaearctic (15%), Nearctic + IndoMalayan + Australian + Palaearctic (14%), or Neotropical + IndoMalayan + Australian + Palaearctic (14%). *Phaenosperma* Munro ex Benth. (1 sp., East Asia), the single genus of **Phaenospermateae** Renvoize & Clayton, has globose, 1-flowered spikelets that disarticulate below the glumes and is apparently reticulate in origin with Stipeae and or Meliceae (Hochbach et al., 2015). In Duthieeae, three of the eight genera are widely separated from the others: *Metcalfia* Conert (1 sp.) occurs in calcareous hills around the Chihuahuan Desert of Mexico; *Danthoniastrum* (Holub) Holub (4 spp.) occurs in the alpine of the Balkans, Greece, and the Caucasus; and *Anisopogon* R. Br. (1 sp.) occurs in southeastern Australia. The remaining five genera are distributed in and around the uplands of the Qinghai-Tibet plateau in Central Asia: *Duthiea* Hack. (3 spp.); *Pappagrostis* Roshev. (1 sp.); *Pseudodanthonia* Bor & C.E. Hubb. (1 sp.); *Sinochasea* Keng (1 sp.); and *Stephanachne* Keng (3 spp.). The genera have various combinations of two or three lodicules and two or three styles, some with multiple and others with single-flowered spikelets, all disarticulating above the glumes. It is not yet known if the 1-flowered spikelet species, *Duthiea brachypodium* (P. Candargy) Keng & Keng f., belongs in *Duthiea*, or a separate genus, *Triavenopsis* P. Candargy.

The stem and crown of the rest of the **Pooideae 3** (in Fig. 1) are dated at 52.08 and 50.38 Ma (61 and 60 Ma in Schubert et al., 2019b). The next lineage to diverge, supertribe **Melicodae** Soreng (Soreng et al., 2017; Brylkinieae + Meliceae), has stem and crown dates of 50.38 and 38.92 Ma (58 and 45.6 Ma in Schubert et al., 2019b); a crown of 34.7 Ma in Orton et al., 2021). The stem area is Palaearctic (92%), while the crown node was estimated as Palaearctic (52%) or Indomalayan+Palaearctic (15%). **Brylkinieae** Tateoka and **Meliceae** share fused sheath margins, multi-flowered spikelets (except *Triniochloa* Hitchc.), glabrous ovaries, and a caryopsis with a linear hilum nearly as long as the grain but differ in spikelet disarticulation, presence of sterile florets, and lodicule and style characteristics. Brylkinieae, comprised of *Brylkinia* F. Schmidt (1 sp., East Asia). Meliceae, with stem and crown dates of 38.92 and 30.03 Ma, has seven genera [*Glyceria* R.Br. (48 spp., worldwide; Whipple et al., 2007; Rodionov et al., 2013), *Koordersiochloa* Merr. (2 spp., low latitudes of Africa, India, Philippines, and Indonesia; Veldkamp, 2012), is perhaps sister to the rest of the tribe (Hochbach et al., 2015); *Lycochloa* Samuelsson (1 sp., Lebanon and Syria); *Melica* L. (92 spp., worldwide; Hempel, 2004, 2012); *Pleuropogon* R.Br. (5 western North America, 1 panarctic; But, 2007); *Schizachne* Hack. (3 spp., North America, Asia west to Finland; Cayouette & Darbyshire, 2007); and *Triniochloa* (6 spp., Central & South America, northern Mexico to Bolivia; Gómez-Sánchez et al., 1998).

The stem and crown dates for the remainder of **Pooideae 4** (in Fig. 1) are 50.38 and 48.99 Ma. Supertribe **Stipodae** L. Liu (Soreng et al., 2017; **Ampelodesmeae + Stipeae**) is the next to diverge. The clade stem and crown areas are Palaearctic. *Ampelodesmos* Link (1 sp., Mediterranean) has various Stipeae characteristics, including three lodicules (common but not fixed in Stipeae) long-linear hilum. Still, other features, including multiple-flowered spikelets lacking awns (beyond a mucro), and hairy ovaries, make it unrecognizable as Stipeae. Because *Ampelodesmos* is reticulate in origin (Romaschenko et al., 2014), having nuclear sequences from outside Stipeae combined with plastid and nrDNA derived within Stipeae, we maintain it in a separate monogeneric tribe.

Stipeae has stem and crown dates of 48.99 and 33.37 Ma (60 and 38.6 Ma in Schubert et al., 2019b; a crown of 43.5 Ma in Orton et al., 2021). The tribe has a phylogenetic history complicated by reticulation and convergent gross morphologies (Romaschenko et al., 2008, 2011, 2012, 2014; Hamasha et al., 2012) and contains at least 32 genera (Peterson et al., 2019a): *Achnatherum* P. Beauv. (25 spp., Eurasia); *Aciachne* Benth. (3 spp., Andes); *Amelichloa* Arriaga & Barkworth (5 spp., western hemisphere); *Anemanthele* Veldkamp (1 sp., New Zealand); *Austrostipa* S.W.L. Jacobs & J. Everett (64 spp., Australia [1 shared with South Africa], New Zealand; Syme et al., 2012); *Barkworthia* Romasch., P.M. Peterson & Soreng (1 sp., California); *Celtica* F.M. Vázquez & Barkworth (1 sp., western Mediterranean); *Eriocoma* Nutt. (26 spp., North America; Peterson et al., 2019a); *Hesperostipa* (M.K. Elias) Barkworth, 5 spp., North America); *Jarava* Ruiz & Pav. (30 spp., Central & South America; Sclovich et al., 2015); *Lorenzochloa* Reeder & C. Reeder (8 spp., South America, including *Anatherostipa* s.s., leaving four spp. unplaced; Romaschenko, 2021, pers. comm.); *Macrochloa* Kunth (2 spp., western Mediterranean); *Nassella* (Trin.) E. Desv. (117 spp., western hemisphere; Cialdella et al., 2014); *Neotrinia* (Tzvelev) M. Nobis, P.D. Gudkova & A. Nowak (1 sp., Central Asia; Nobis et al., 2019); *Oloptum* Röser & H. R. Hamasha (2 spp., Mediterranean, Eurasia); *Ortachne* Nees in Steud. (2 spp., Argentina & Chile); *Orthoraphium* Nees (1 sp., Central Asia); *Oryzopsis* Michx. (1 sp., North America); *Pappostipa* (Speg.) Romasch., P.M. Peterson & Soreng (31 spp., western hemisphere; Romaschenko et al., 2008); *Patis* Ohwi (3 spp., 2 East Asia, one eastern North America); *Piptatheropsis* Romasch., P.M. Peterson & Soreng (5 spp., North America); *Piptatherum* P. Beauv. (32 spp., Eurasia); *Piptochaetium* J. Presl (35 spp., western hemisphere; Cialdella et al., 2007); *Psammochloa* Hitchc. (1 sp., sands of East Asia); *Pseudoeriocoma* Romasch., P.M. Peterson & Soreng (6 spp., southern North American arid lands, possibly additionally including some bushy "*Jarava*" species of South America; Peterson et al., 2019a); *Ptilagrostiella* Romasch., P.M. Peterson & Soreng (1 sp., California; Peterson et al., 2019a); *Ptilagrostis* Griseb. (9 spp., 8 of Central & East Asia, 1 of western North America); *Stipa* L. (120 spp., Eurasia; Krawczyk et al., 2017; Nobis et al., 2019); *Stipellula* Röser & H.R. Hamasha (3 spp., annuals, Mediterranean, Southwest Asia); *Thorneochloa* Romasch., P.M. Peterson & Soreng (1 sp., southwestern North America; Peterson et al., 2019a); *Timouria* Roshev. (5 spp., Central Asia); *Trikeraia* Bor (2 spp., Central Asia).

The rest of **Pooideae 5** (in Fig. 1) has stem and crown dates of 48.99 and 45.75 Ma (58 and 46 Ma in Schubert et al., 2019b). The numbers of lodicules and styles are consistently two. **Diarrheneae**, with two genera with few-flowered spikelets and short glumes (*Diarrhena* P. Beauv., 2 spp., eastern North America, *Neomolinia* Honda, 3 spp., northeastern Asia), have stem and crown dates of 45.75 and 6.94 Ma (54 and 13.5 Ma in Schubert et al., 2019b; stem of 36.7 Ma in Orton et al., 2021). In our analysis, the stem area is Palaearctic, and the crown spreads to Nearctic + Indomalayan + Palaearctic (72%) or Nearctic + Palaearctic (20%). Bouchenak-Khellardi et al. (2010) predicted the stem area to be North America + Eurasia.

Core Pooideae (i.e., included in Pooideae without reservations in most second-half of the 20th-century classifications) has stem and crown dates of 45.75 and 44.8 Ma. Although Diarrheneae is commonly placed outside the core (e.g., in Bambusoideae by Clayton & Renvoize, 1986; but within Pooideae in most accounts), in this analysis, clades consisting of *Diarrhena* + *Neomolinia* and *Brachypodium* (Brachypodieae is always in the core) are well-supported as successive sister groups to the rest of the subfamily. Interestingly, Orton et al. (2021) and Saarela et al. (2015) resolved a clade of Diarrheneae + Brachypodieae in all analyses, with or without all alignment gaps removed. However, maximum likelihood bootstrap value support dropped from 100% with gaps to 54% without gaps (Orton et al., 2021). Long-branch-attraction is one possible explanation for this union in some analyses.

Brachypodieae is the next tribe to diverge and has a stem date of 44.8 Ma. Schubert et al. (2019b) estimated stem and crown dates of 52 and 18.9 Ma (crown of 22.2 Ma in Orton et al., 2021). The crown area is cosmopolitan. *Brachypodium* P. Beauv. (22 spp.; Catalán et al., 1997; Catalán & Olmstead, 2000; Catalán et al., 2015; Sancho et al., 2018) species have several- to many-flowered spikelets arranged in racemose synflorescences. They occur worldwide in temperate to subtropical climates, but only two species are native and endemic to the western hemisphere (one ranging from Mexico to Bolivia).

The rest of Pooideae, a clade of supertribes **Poodae** + **Triticodae**, has stem and crown dates of 44.8 and 40.78 Ma (52 and 49 Ma in Schubert et al., 2019b). These supertribes share $x = 7$ medium to large chromosomes, whereas the previous tribes frequently have other base numbers (9, 10, 11, 12) and/or small chromosomes. Supertribe **Triticodae** (Littledaleeae + Bromeae + Triticeae) has stem and crown dates of 40.78 and 23.02 Ma (49 and 37 Ma in Schubert et al., 2019b; a crown of 25.6 Ma in Orton et al., 2021).

The stem date for the one genus of **Littledaleeae**, *Littledalea* Hemsl. (4 spp., alpine of Central Asia), is 23.02 Ma, and the crown area is Indomalayan + Palaearctic. Using whole plastomes of three species of the genus, Orton et al. (2021) confirmed *Littledalea* as sister to the rest of Triticodae. The species have elongated lemmas that aid in wind dispersal.

In our plastid analysis, **Bromeae** Dumort. (*Bromus* L., 165 spp., worldwide) is nested within **Triticeae** as sister to *Psathyrostachys* Nevski + *Leymus* Hochst. It is unclear if *Bromus* is derived within Triticeae or if some reticulation event led to this topology. In Schubert et al. (2019b) *Leymus arenarius* (L.) Hochst. + *Hordelymus* (Jess.) Harz + the three *Psathyrostachys* species sampled are separated from the rest of Triticeae, including three other *Leymus* species, by the species of *Bromus* sampled. Orton et al. (2021) had a similar result (see also Bernhardt et al., 2017). The stem and crown ages of Bromeae + Triticeae are 23.02 and 20.64 Ma, and for the core of Triticeae, 18.65 and 14.71 Ma (49 and 37 Ma in Schubert et al., 2019b). *Bromus* differs from the genera of Triticeae in having paniculate synflorescences, sheath margins fused (versus spicate or racemose with brief pedicels, and sheaths open to the base). More work is needed to resolve the origin and classification of *Bromus* (Saarela et al., 2007; Alonso, 2015; Pourmoshir et al., 2019). The two tribes share abundant, simple, rounded starch grains in their endosperm. Generic concepts in Triticeae are troublesome due to extensive reticulation and recognition of diploid lineages as separate from perennials derived between those and other parents. Triticeae genera (27 in all) are derived from Eurasia, with four endemic to Australia and New Zealand and one to North America (*Pascopyrum* Á. Löve —reticulate in origin between *Elymus* L. and *Leymus*). *Elymus*, *Hordeum* L., and *Leymus* have speciated widely in the western hemisphere, with *Hordeum* dispersing back to Africa and Eurasia (Blattner, 2004; Pleines & Blattner, 2008). The tribe includes *Aegilops* L., 28 spp., annuals, Eurasia [except East Asia] (Van Slageren, 1994); *Agropyron* Gaertn., 13 spp., Eurasia; *Amblyopyrum* (Jaub. & Spach) Eig, 1 sp., annual, Southwest Asia (Van Slageren, 1994); *Anthosachne* Steud., 10 spp., New Zealand; *Australopyrum* (Tzvelev) Á. Löve, 5 spp., Australasia; *Connorochloa* Barkworth, S.W.L. Jacobs & H.Q. Zhang, 1 sp., New Zealand; *Crithopsis* Jaub. & Spach, 1 sp., annual, Eurasia [except East Asia]; *Dasypyrum* (Coss. & Durieu) T. Durand, 2 spp., annuals, southeastern Europe, Southwest Asia; *Douglasdeweya* C. Yen, J.L. Yang & B.R. Baum, 2 spp., East Asia (better in *Agropyron*?); *Elymus*, 241 spp., worldwide; *Eremopyrum* (Ledeb.) Jaub. & Spach, 4 spp., annuals, Eurasia [except East Asia]; *Festucopsis* (C.E. Hubb.) Melderis, 1 sp., southeastern Europe; *Henrardia* C.E. Hubb., 2 spp., annuals, Southwest and western Central Asia; *Heteranthelium* Hochst., 1 sp., annual, Southwest Asia; *Hordelymus*, 1 sp., Europe, Southwest Asia; *Hordeum*, 43 spp., some annuals, worldwide; *Kengyilia* C. Yen & J.L. Yang, 27 spp., Asia; *Leymus*, 55 spp., Eurasia, North & South America; *Pascopyrum*, 1 sp., North America; *Peridictyon* Seberg, Fred. & Baden, 1 sp., southeastern Europe; *Psathyrostachys*, 10 spp., eastern Europe, Asia; *Pseudoroegneria* (Nevski) Á. Löve, 15 spp., eastern Europe, Asia, 1 in western North America; *Secale* L., 8 spp., annuals, Eurasia [except East Asia]; *Stenostachys* Turcz., 4 spp., New Zealand; *Taeniatherum* Nevski, 1 sp., annual, Eurasia [except East Asia]; *Thinopyrum* Á. Löve, 7 spp., Europe, western & Central Asia; *Triticum* L., 18 (5—25) spp., annuals, southeastern Europe, western and Central Asia.

Supertribe **Poodae** L. Liu has one tribe, **Poeae** R. Br., with stem and crown dates of 40.78 and 36.24 Ma (49 and 44.3 Ma in Schubert et al., 2019b; a crown age of 55.1 Ma in Orton et al., 2021). Tkach et al. (2020) proposed dividing Poeae (sensu Soreng et al., 2015b, 2017, and here) into Aveneae, Festuceae, and Poeae, leaving seven subtribes unaffiliated that represent possible grades and reticulation among the lineages as is evident in nrDNA trees when compared to plastid trees. In contrast, plastid phylogenies show two well-marked clades: Chloroplast groups 1 (Aveneae type) and 2 (Poeae type). There are many genera once placed in Aveneae based on morphology (glumes equaling or exceeding the proximal lemma, spikelets often single-flowered, lemmas often with dorsal, geniculate awns) (Clayton & Renvoize, 1986, etc.) but with Poeae type chloroplasts and Poeae nrDNA or nrDNA intermediate between Aveneae and Poeae or within Aveneae. In addition, there are several more genera once placed in Poeae on morphology (glumes shorter than or equaling the proximal lemma, spikelets rarely single-flowered, lemma awns terminal or subterminal, not geniculate) with Aveneae type plastids and nrDNA. Thus, we do not believe splitting at the tribal level is helpful (Soreng & Davis, 2000). Compared to the rest of Pooideae, many Poodae lines exhibit extreme cold tolerance (Zhong et al., 2018; Schubert et al., 2019a; Soreng et al., 2022a). The stem and crown areas of groups 1 and 2 are all Palaearctic, but various internal clades have expanded around the world.

Poeae chloroplast group 1 (Aveneae type) has stem and crown dates of 36.24 and 25.28 Ma and contains ten subtribes, with six classified in supersubtribe **Agrostidodinae** Soreng. If we consider only plastid data, Torreyochloinae + Phalaridinae are the first subtribes to diverge, with stem and crown dates of 25.28 and 20.59 Ma.

Torreyochloinae Soreng & J.I. Davis has stem and crown dates of 20.59 and 11.22 Ma. There are two genera: *Amphibromus* Nees (12 spp., Australia, southern South America) and *Torreyochloa* G.L. Church (4 spp., 1 East Asia, 3 North America).

Phalaridinae Fr. has a stem date of 20.59 Ma and contains one genus, *Phalaris* L. (20 spp., Eurasia, western hemisphere; Voshell et al., 2015). Voshell & Hilu (2014) concluded the genus evolved in the Mediterranean basin and radiated from there. The remainder of the Group 1 plastid clade has stem and crown dates of 25.28 and 24.44 Ma and includes two subtribes and one supersubtribe with six subtribes.

Aveninae J. Presl (stem and crown dates of 24.44 and 17.5 Ma) contains 20 genera and is extraordinarily complex due to internal reticulation (Hochbach et al., 2015; Wölk & Röser, 2017; Barberá et al., 2019a; Tkach et al., 2020). There are four basal genera in the subtribe: *Arrhenatherum* P. Beauv. (7 spp., Europe, Southwest Asia); *Avena* L. (25 spp., Mediterranean and Eurasia); *Helictotrichon* Besser (37 spp., Eurasia, 1 North America); and *Tricholemma* (Röser) Röser (2 spp., northwestern Africa). These are followed by *Lagurus* L. (1 sp., western Eurasia) and the Koeleriinae clades 1 and 2. Koeleriinae clade 1 includes the genera *Acrospelion* Besser s.l. (10 spp., Eurasia; Barberá et al., 2017, 2020); *Avellinia* Parl. (2 spp., Mediterranean; Romero-Zarco & Sáez Goñalons, 2018); *Gaudinia* P. Beauv. s.l. (8 annual spp., Mediterranean); *Koeleria* Pers. (96 spp., worldwide, Barberá et al., 2019); *Rostraria* Trin. s.l. (10 annual spp., Mediterranean, Southwest Asia); *Sibirostrisetum* Barberá, Soreng, Romasch., Quintanar & P.M. Peterson (6 spp., eastern Europe, Asia to New Guinea, Alaska & Yukon, Barberá et al., 2019); *Trisetaria* Forssk. (7 annual spp., Mediterranean); *Trisetum* Pers. (1 sp., Eurasia). Koeleriinae clade 2 is primarily American and includes five genera: *Cinnagrostis* Griseb. (70 spp., Central & South America, Peterson et al., 2019b), includes many Latin American species formerly placed in *Calamagrostis* or *Deyeuxia* Clarion ex P. Beauv.; *Limnodea* L.H. Dewey (1 annual sp., south-central North America); *Peyritschia* E. Fourn. (31 spp., Central & South America, Peterson et al., 2019b); *Sphenopholis* Scribn. (6 spp., North America). Three Aveninae genera are notably reticulate (Hochbach et al., 2015; Wölk & Röser, 2017; Barberá et al., 2020): *Trisetopsis* Röser & A. Wölk (28 spp., Africa, southern Asia; Wölk & Röser, 2017) is reticulate with *Cinnagrostis* or the *Sphenopholis*/*Peyritschia* clade); *Tzveleviochloa* Röser & A. Wölk (3 spp., Central Asia), is reticulate between *Acrospelion* s.l., and *Helictotrichon* and *Arrhenatherum*); *Graphephorum* Desv. s.l. (8 spp., western hemisphere, reticulate between Koeleriinae clades 1 and 2).

Anthoxanthinae A. Gray has a stem date of 21.9 Ma, with one genus, *Anthoxanthum* L. (42 spp., worldwide). Pimentel et al. (2013) presented DNA phylogenetic results for a broad sample of species, in which a grade from *Hierochloe* R.Br. to *Anthoxanthum* s.s. is evident. All the species contain notable concentrations of coumarins, which give them a sweet smell and licorice-vanilla-like taste and probably serve as protection against predation.

Supersubtribe **Agrostidodinae Soreng** (Soreng et al., 2017) has stem and crown dates of 12.58 and 11.35 Ma and includes at least the following six subtribes, only two with multiple-flowered spikelets, these having glumes shorter than proximal lemmas and short, subterminal non-geniculate awns (Brizinae and Calothecinae).

Hypseochloinae Röser & Tkach (Tkach et al., 2020, not sampled in our phylogenetic analysis) includes *Hypseochloa* C.E. Hubb. (2 spp., rare in African highlands of Cameroon, Tanzania).

Brizinae Tzvelev has stem and crown dates of 20.13 and 17.21 Ma, including *Airopsis* Desv. (1 sp., annual, Mediterranean) and *Briza* L. (5 spp., annuals and perennials, Europe, western and Central Asia).

Echinopogoninae Soreng (Soreng et al., 2017) has stem and crown dates of 15.56 and 9 Ma and has a peculiar split in distribution, *Relchela* in Patagonian South America, *Greeneochloa* in North America and Hawaii (Peterson et al., 2019b, 2022c), and the rest in Australasia, with a few species more widespread in the Pacific Ocean basin. It includes *Echinopogon* P. Beauv. (7 spp., Australasia; Weiller et al., 2009), *Greeneochloa* P.M. Peterson, Soreng, Romasch. & Barberá (3 spp.), *Pentapogon* R. Br. (at least 22 spp., Australasia, Peterson et al., 2022c), *Relchela* Steud. (1 sp., South America, Patagonia, sister to the rest of Echinopogoninae). Generic boundaries are unsettled as the group contains Australasian species often placed in *Deyeuxia*, but species sampling is limited (Peterson et al., 2022c). Based on a phylogeny using four DNA markers, Peterson et al. (2022c) subsume all 11 species of *Dichelachne* Endl. (Edgar & Connor, 1982; Simon et al., 2009) into *Pentapogon* (Kodela et al., 2009). All DNA tested species of Australian "*Deyeuxia*" align within Echinopogoninae.

Calothecinae Soreng (Soreng et al., 2015b) has a stem date of 12.58 Ma and contains 10 genera (Da Silva et al., 2022; Peterson et al., 2022c), with all species occurring in South America and one reaching Central America. The monograph by Matthei (1975) covered many of the genera. Da Silva et al. (2022) found that *Trisetum brasiliense* Louis-Marie and *T. bulbosum* Hitch. belong to this subtribe but needed further study to place them more precisely. Peterson et al. (2022c) placed these two species, and *T. juergensii* Hack., in *Condilorachia* P.M. Peterson, Soreng & Romasch. Da Silva et al. (2022) revised the other genera: *Boldrinia* L.N.Silva (1 sp., Uruguay), *Calotheca* Desv. (1 sp., Argentina to Brazil, and disjunct in Chile); *Chascolytrum* Desv. (6 spp., all of South America, 1 reaching Central America; (Essi et al., 2017; Da Silva et al., 2020, 2022); *Condilorachia* (3 spp., Argentina, Brazil, and Chile; Peterson et al., 2022c), *Erianthecium* Parodi (1 sp., Brazil and Uruguay); *Lombardochloa* Roseng. & B.R. Arrill. (1 sp., pampas with disjunct occurrences in Peru); *Microbriza* Parodi ex Nicora & Rúgolo (1 sp., Bolivia, Paraguay, and Brazil to Argentina); *Poidium* Nees (9 spp., southern South America to Brazil); *Rhombolytrum* Link (3 spp., Brazil, Chile); *Rosengerttia* L.N.Siva (1 sp. of the Andes of Argentina to Colombia, and disjunct in Brazil). The genera differ from

Brizinae s.s. in their fibrous basal sheaths and distribution in the western hemisphere (Soreng et al., 2015b; Persson & Rydin, 2016).

Paramochloinae L.N. Silva & Saarela (Da Silva et al., 2022, not sampled in our phylogenetic analysis) contains two genera sister to Calothecinae: *Laegaardia* P.M. Peterson, Soreng, Romasch. & Barberá (1 sp., Andes), and *Paramochloa* P.M. Peterson, Soreng, Romasch. & Barberá (2 spp., northern Andes). Both genera were formerly placed in *Calamagrostis* Adans. s.l. (Sylvester et al., 2019).

Agrostidinae Fr. has stem and crown dates of 12.58 and 11.35 Ma and includes 10 genera. The genera include many annuals in the Mediterranean region. *Calamagrostis* (130 spp., worldwide, but mainly in Eurasia and North America) is the sister to the rest. The number of species in *Calamagrostis* s.l. has been reduced by Saarela et al. (2017) and Peterson et al. (2019b, 2022c). Peterson et al. (2022c) found four major clades within *Calamagrostis*, the first split comprising species from South America. The remaining species from the northern hemisphere were placed in three clades; two of these include species primarily from Eurasia, and one clade is composed of species from North America. However, there is incongruence between the placement of some species derived from their plastid and nrDNA ITS signals, often obfuscating the biogeographical composition of these clades. *Agrostis* L. (200 spp., worldwide) is the other large genus in the subtribe. It is separable into two major clades. Subgenus *Agrostis* is the most diverse, and *Agrostis* subgenus *Vilfa* is decidedly Eurasian. The *Vilfa* group seems to have arisen through reticulation between subgenus *Agrostis* and *Polypogon* and *Lachnagrostis*, leaving some traces in subgenus *Agrostis* (Romaschenko et al., in prep.). Peterson et al. (2020b) separated two new European genera from *Agrostis*. *Agrostula* P.M. Peterson, Romasch., Soreng & Sylvester (1 sp., western Mediterranean); *Alpagrostis* P.M. Peterson, Romasch., Soreng & Sylvester (4 spp., western Europe); *Gastridium* P. Beauv. (4 annual spp., western Eurasia), *Lachnagrostis* Trin. (40 spp., Africa, Asia, Australasia; Brown, 2013, 2015), some of these from Africa may be better placed in *Anomolotis* Steud. (not recognized here), possibly as a section or subgenus of *Agrostis*; *Podagrostis* (Griseb.) Scribn. & Merr. (12 spp., western hemisphere, possibly some in Southeast Asia and East Asia); *Polypogon* Desf. (22 spp., worldwide) here includes the 10 species of *Chaetotropis* Kunth; *Triplachne* Link (1 annual sp., Mediterranean, could be merged with *Gastridium* (Scoppola & Cancellieri, 2019).

Poeae Chloroplast Group 2 (Poeae type) has stem and crown dates of 36.24 and 29.84 Ma (44.3 and 38.5 in Schubert et al., 2019b) and contains 24 subtribes. The relationships inferred between many of the subtribes in this clade were poorly supported in our phylogenetic analysis (Figs. 1,2). The chloroplast 2 group subtribes are weekly supported in two subclades. The first includes 12 subtribes assigned to the PPAM clade, and the second consists of 12 subtribes, including five assigned to the supersubtribe Loliodinae Soreng.

The **PPAM clade** (Gillespie et al., 2008, 2022; Soreng et al., 2022a), including supersubtribe **Poodinae Soreng** (Soreng et al., 2017) together with subtribe **Coleanthinae Rouy**, has stem and crown dates of 29.84 and 26.65 Ma (calculated dates reported in Soreng et al., 2022a, table 3) and contains 13 subtribes. The biogeography of this clade is addressed in Soreng et al. (2022a, in this issue), where younger dates of 24.19 and 21.81 Ma (±2.6 Ma) were calculated. Soreng et al. (2022a) narrow the PPAM stem area to southwestern Asia, with several subtribes spreading around the world.

Avenulinae Röser & Tkach contains one monotypic genus, *Avenula* (Dumort.) Dumort. (1 sp., Eurasia) (Tkach et al., 2020). Although confirmed to belong to the supersubtribe Poodinae, its relationships with other subtribes and clades in the Poodinae are uncertain.

Coleanthinae has stem and crown dates of 26.65 and 17.99 Ma (crown roughly 23 Ma in Schubert et al., 2019b) and contains 10 genera (see Gillespie et al., 2022; Soreng et al., 2022a): *Catabrosa* P. Beauv. (3 spp., 7 more described by Tzvelev 2013 and Punina et al., 2016, worldwide); *Catabrosella* (Tzvelev) Tzvelev (6 spp., Southwest Asia); *Coleanthus* Seidl (1 sp., northern Eurasia, and northwestern North America); *Colpodium* Trin. (9 spp., some annuals, Africa, Southwest Asia, including *Zingeria* P.A. Smirn., (Gnutikov et al., 2020; Rodionov et al., 2020; Tkach et al., 2020); *Hyalopoa* (Tzvelev) Tzvelev (6 spp., Southwest Asia); *Hyalopodium* Röser & Tkach (2 spp., Southwest Asia); *Paracolpodium* (Tzvelev) Tzvelev (7 spp., Southwest & Central Asia); *Phippsia* (Trin.) R. Br. (3 spp., arctic and alpine northern Eurasia and North America); *Puccinellia* Parl. (116 spp., few annuals, worldwide); *Sclerochloa* Stapf (3 spp., annuals, Eurasia).

Miliinae Dumort., with a stem date of 10.87 Ma, contains *Milium* L. (6 spp., or more, some annuals, Eurasia and northeastern North America; Tzvelev & Probatova, 2019). The genus is mainly restricted to Asia, with one perennial species reaching across northern Eurasia with disjunct populations in eastern North America.

Phleinae Dumort., with a stem date of 14.21 Ma, contains *Phleum* L. (16 spp., some annuals, predominantly Eurasian with one worldwide perennial; Stewart et al., 2011) (Stewart et al., 2011).

Poinae Dumort., *sensu* Soreng et al. (2017), with a stem date of 5.73 Ma, contains one genus, *Poa* L. (570 spp., 29 annuals, worldwide; Giussani et al., 2016; Gillespie et al., 2018, 2022; Soreng et al., 2020).

Two genera are problematic to place for different reasons. *Arctopoa* (Griseb.) Prob. (8 spp., Central & East Asia, northern North America; Probatova, 2003; Gillespie et al., 2022; Soreng et al., 2022a) is an ancient hybrid between *Poa* and probably some element of Cinninae Caruel. *Agrostopoa* Davidse, Soreng & P.M. Peterson (3 spp., South America, Davidse et al., 2009) possibly belongs in *Poa*. Still, the DNA results are tentative (Romaschenko, pers. comm.), and morphologically, it seems more similar to Cinninae.

These are followed by the **Alopecurinae** Dumort. superclade (Gillespie et al., 2022; Soreng et al., 2022a, 2022b) with seven subtribes.

Cinninae (sensu Gillespie et al., 2022) has stem and crown dates of 9.91 and 5.17 Ma and contains four genera: *Aniselytron* Merr. (2 spp., southeastern and East Asia, Australasia); *Cinna* L. (3 spp., Eurasia, North America); *Cinnastrum* E. Fourn. (1 sp., Central to South America); *Cyathopus* Stapf (1 sp., Southeastern Asia); *Simplicia* Kirk (3 spp., New Zealand; de Lange et al., 2016; Gillespie et al., 2022).

Brizochloinae Röser & Tkach (Tkach et al., 2020) includes *Brizochloa* V. Jirásek & Chrtek (1 sp., annual, Southwest Asia), which is probably related to Beckmanniinae.

Dupontiinae Soreng & L.J. Gillespie (sensu Gillespie et al., 2022; "DAD clade" of Soreng et al., 2015a) contains *Arctohyalopoa* Röser & Tkach (5 spp., northeastern Asia; Tkach et al., 2020), *Arctophila* (Rupr.) Rupr. ex Andersson (1 sp., Eurasia, North America), *Dupontia* R. Br. (1 sp., Eurasia, North America), and *Dupontiopsis* Soreng, L.J. Gillespie & Koba (1 sp., Japan; Soreng et al., 2015a). This subtribe is postulated to be reticulately derived in northeastern Asia within the Alopecurinae superclade (Gillespie et al., 2022).

Hookerochloinae Soreng & L.J. Gillespie (Gillespie et al., 2022; "HSAQN clade" of Gillespie et al., 2009, 2010) contains *Arctagrostis* Griseb. (2 spp., Eurasia and North America), occurring in sub-Arctic and Arctic wetlands while all the rest are from the southern hemisphere: *Hookerochloa* E.B. Alexeev (2 spp., Australia), *Nicoraepoa* Soreng & L.J. Gillespie (7 spp., South America; Soreng & Gillespie, 2007; Finot et al., 2018), some reticulation has occurred with *Poa* sect. *Parodiochloa* (C.E. Hubb.) Soreng (Gillespie et al., 2022), *Saxipoa* Soreng, L.J. Gillespie & S.W.L. Jacobs, and *Sylvipoa* Soreng, L.J. Gillespie & S.W.L. Jacobs (with 1 sp. each, Australia; Gillespie et al., 2009; Soreng et al., 2009).

Beckmanniinae Nevski, sensu Soreng et al. (2017) has stem and crown dates of 6.44 and 1.85 Ma and contains *Beckmannia* Host (2 spp., 1 annual, Eurasia, North America); *Pholiurus* Host ex Trin. (1 sp., annual, eastern Europe); *Pseudophleum* Doğan (2 spp., annuals, Southwest Asia; Doğan et al., 2015); *Rhizocephalus* Boiss. (1 sp., annual, Southwest Asia). These wetland genera do resolve as a clade (presumably due to very long branches for the annuals, *Pseudophleum* and *Rhizocephalus*) but share morphological, e.g., saccate glumes and ecological characteristics. *Pholiurus* seems quite odd here but has DNA sequences nearly matching *Beckmannia* (Schneider et al., 2012).

Alopecurinae Dumort. has a stem date of 10.5 Ma and contains two genera: *Alopecurus* L. [42 spp., some annuals, worldwide; Cabi et al., 2017; including *Cornucopiae* L. (Soreng et al., 2022a, 2022b)]; and *Limnas* Trin. (3 spp., northeastern Asia).

Ventenatinae Holub ex L.J. Gillespie, Cabi & Soreng (Soreng et al., 2015b, 2017) has stem and crown dates of 10.5 and 9.17 Ma and contains six genera. *Bellardiochloa* Chiov. (5 spp., southern Europe, Southwest Asia, Cabi et al., 2015) is perennial, and the rest are annual: *Apera* Adans. (5 spp., Eurasia [except East Asia]); *Gaudinopsis* (Boiss.) Eig (5 spp., southeastern Europe to Southwest Asia); *Nephelochloa* Boiss. (1 sp., Southwest Asia); *Parvotrisetum* Chrtek (1 sp., northeastern Mediterranean); *Ventenata* Koeler (3 spp., southern Europe, Southwest Asia). This is a well-resolved clade centered in Southwest Asia (Soreng et al., 2015b).

The second subclade of Poeae Chloroplast Group 2 includes the following subtribes.

Antinoriinae Röser & Tkach (Tkach et al., 2020) contains *Antinoria* Parl. (2 spp., usually annual, Mediterranean) and was well supported as sister to Airinae.

Airinae Fr. has stem and crown dates of 27.5 and 24.72 Ma and contains four genera. The three annual genera are decidedly Mediterranean, while the perennial, *Avenella* Drejer (1 sp.; Chiapella & Zuloaga, 2010; Veldkamp, 2015), is widespread. The annual genera are *Aira* L. (9 spp., Africa, Europe, Southwest Asia), *Corynephorus* P. Beauv. (6 spp., western Eurasia), and *Periballia* Trin. (1 sp., Mediterranean).

Sesleriinae Parl. has a stem and crown date of 20.76 and 26.42 Ma and contains six genera. The subtribe apparently arose in northern Europe from reticulation between a Poeae plastid type parent (related to Loliodinae) and an Aveninae nrDNA parent (Kuzmanović et al., 2015, 2017; Di Pietro et al., 2017). The six genera are: *Echinaria* Desf. (1 sp., annual, Mediterranean), *Mibora* Adans. (2 tiny annual spp., Mediterranean), *Oreochloa* Link (4 spp., Europe), *Psilathera* Link (1 sp., Europe), *Sesleria* Scop. (30 spp., Europe, Southwest Asia), *Sesleriella* Deyl (1 sp., Europe). This subtribe is sister to a clade consisting of Holcinae Dumort., Helictochloinae Röser & Tkach, Aristaveninae F. Albers & Butzin, and supersubtribe Loliodinae Soreng.

Holcinae has stem and crown dates of 23.68 and 7.37 Ma and contains two genera, *Holcus* L. (12 spp., some annuals, Europe, Southwest Asia), with annuals and perennials of temperate and Mediterranean climates, and *Vahlodea* Fr. (2 spp., northern Europe and far northeastern Asia, North America), perennial of subalpine and alpine and low arctic habitats.

Helictochloinae, with a crown date of 12.31 Ma, contains two genera, *Helictochloa* Romero Zarco (30 spp., Eurasia, northwestern North America; Romero-Zarco, 2011; Winterfeld et al., 2014) is a speciose and perennial, and *Molineriella* Rouy (3 spp., Mediterranean) is annual.

Aristaveninae has a stem date of 25.24 Ma and includes a single genus, *Deschampsia* P. Beauv. (51 spp., worldwide, with several annuals in the western hemisphere), mainly of wetlands.

Supersubtribe **Loliodinae** (Soreng et al., 2017) contains five subtribes with a crown date of 24.28 Ma. **Loliinae** Dumort. has a stem and crown date of 22.34 and 18.47 Ma and contains nine genera, most of which align in one of two clades (Inda et al., 2008, 2014; Minaya et al., 2017). The "narrow leaf clade" includes only *Festuca* L. (600 spp., annuals and perennials, worldwide; Díaz-Pérez et al., 2014), where *Megalachne* Steud. and *Podophorus* Phil. are new synonyms (Tkach et al., 2020). The "broad-leaf clade" includes *Drymochloa* Holub (6 spp., western Eurasia); *Leucopoa* Griseb. (27 spp., Eurasia, North America); *Locajonoa* Soreng (2 spp., Mediterranean); *Lolium* L. (28 spp., some annuals, western Eurasia; Banfi et al., 2017); *Patzkea* G.H. Loos (2 spp., western Eurasia); *Xanthochloa* (Krivot.) Tzvelev (2 spp., eastern Europe, west & Central Asia); *Pseudobromus* K. Schum. (10 spp., Africa). *Castellia* Tineo (1 sp., annual Mediterranean Europe and Southwest Asia) has not been well supported in either clade. The generic taxonomy of the broad-leaf clade is still unsettled, but the clade is decidedly African and Eurasian, with some species of *Leucopoa* in North America.

Dactylidinae Stapf has stem and crown dates of 16.07 and 5.88 Ma, and two genera, *Dactylis* L. (3 spp., Eurasia and East Asia), and *Lamarckia* Moench (1 sp., Mediterranean), an annual. **Ammochloinae Tzvelev** is sister to Dacylidinae and has one genus of annuals, *Ammochloa* Boiss. (3 spp., Mediterranean).

Cynosurinae Fr. is sister to Parapholiinae, has a stem date of 17.79 Ma, and includes *Cynosurus* L. (10 spp., Eurasia [except East Asia]), with annuals and perennials.

Parapholiinae Caro has stem and crown dates of 17.79 and 13.39 Ma and contains seven genera, six are annuals, and *Agropyropsis* (Trab.) A. Camus is perennial. The genera are *Agropyropsis* (1 sp., Libya); *Catapodium* Link (4 spp., western Eurasia); *Cutandia* Willk. (7 spp., Mediterranean); *Desmazeria* Dumort. (3 spp., Mediterranean); *Parapholis* C.E. Hubb. (7 spp., Mediterranean); *Sphenopus* Trin. (2 spp., Mediterranean); *Vulpiella* (Batt. & Trab.) Burollet (2 spp., Mediterranean).

Scolochloinae Tzvelev (not dated) is resolved as monophyletic only in nrDNA trees (Saarela et al., 2017; Tkach et al., 2020; Gillespie et al., 2022). The two genera have similar Poeae type plastids but with nrDNA align as sisters with basal Aveneae type plastid subtribes (Phalaridinae and Torreyochloinae). One genus is from cool, temperate wetlands in the northern hemisphere (*Scolochloa* Link, 2 spp., Eurasia, North America), the other from wet mountain forests in southeastern Australia (*Dryopoa* Vickery, 1 sp.). Although not assigned to the supersubtribe, *Scolochloa* was found to be nested within Loliodinae in our analysis.

4.7 Panicoideae (CADW and EAK for Andropogoneae, Arundinelleae, Jansenelleae; FOZ for the rest)

The stem and crown age of the **Panicoideae** in our analysis is 64.44 and 61.78 Ma, respectively. The crown area is decidedly Afrotropical (Table 1, Fig. 2D). Spikelet structure is characteristic of the subfamily in a strict sense, with spikelets dorsally compressed, disarticulating above or below the glumes; glumes two, indurate or hyaline, with or without awns, the upper flower usually hermaphrodite and the lower flower male or neuter (Kellogg, 2015; Soreng et al., 2017), although basal tribes have laterally compressed spikelets and multiflowered spikelets. Kellogg (2015) pointed out that "chromosome numbers are generally consistent within major clades and are synapomorphic for some." Gynerieae, Chasmanthieae, Centotheceae, and Tristachyideae have base chromosome numbers of 11, 12, 12, and 10–12, respectively. Andropogoneae and Paspaleae share a base chromosome number of 10, while Paniceae has a base chromosome number of 9. All known photosynthetic types are present in the subfamily, C_3, $C_{4,}$ and intermediate C_3-$C_{4,}$ corresponding to non-Kranz and Kranz leaf anatomy, the latter with several subtypes. Entirely C_3 tribes include the Chasmanthieae W.V. Br. & B.N. Smith ex Sánchez-Ken & L.G. Clark, Centotheceae Ridl., Cyperochloeae L. Watson & Dallwitz ex Sánchez-Ken & L.G. Clark, Gynerieae Sánchez-Ken & L.G. Clark, Jansenelleae Voronts., Lecomtelleae Pilg. ex Potztal, Steyermarkochloeae Davidse & R.P. Ellis, Thysanolaeneae C.E. Hubb., and Zeugiteae Sánchez-Ken & L.G. Clark. Andropogoneae Dumort., Arundinelleae Stapf, and Tristachyideae Sánchez-Ken & L.G. Clark are C_4, while the Neurachninae Clayton & Renvoize includes C_4, C_3, and intermediate C_3–C_4 genera. At the same time, there is a mix of C_4 and C_3 lineages in the Paniceae R.Br. and Paspaleae J. Presl (including C_3–C_4 intermediates in this tribe). Regarding anatomical patterns related to the photosynthetic pathway, all known Kranz subtypes are present in the C_4 taxa. However, the NADP-ME is dominant, while the NAD-ME and PCK subtypes are synapomorphic for Panicinae Fr. and Melinidinae Pilg., respectively (Kellogg, 2015).

The incertae sedis genera tentatively placed in this family are *Schmidiella* Veldkamp and two basal genera, *Alloeochaete* C.E. Hubb. and *Dichaetaria* Nees ex Steud. *Schmidiella* is a monotypic genus (Veldkamp, 2018) described from a single collection from Laos, characterized by its laterally compressed spikelets, two stamens, and absent glumes and lodicules. There is no DNA data for it, and its relationship even to Panicoideae is uncertain. *Alloeochaete* and *Dichaetaria* are basal in the Panicoideae, with a stem and crown age of 61.78 and 39.35 Ma, the first one with six tropical African species, defined by having spikelets (4−)5−10-flowered, the glumes unequal and shorter than the lower lemma. *Dichaetaria*, a monotypic genus from India and Sri Lanka, has laterally compressed spikelets that are uniflowered, the upper ones reduced, lower glume persistent, the upper glume deciduous. Their crown area is Intomalayan + Afrotropical.

In order of divergence, the next split in our cladogram (Panicoideae 1 in Fig. 1) includes a clade with a crown age of 50.44 Ma, which comprises the Thysanolaeneae, Centotheceae, Cyperochloeae, and Tristachyideae. Thysanolaeneae, Centotheceae, and Cyperochloeae are in a clade with a crown age of 27.55 Ma, sister to the Tristachyideae. Next, the Thysanolaeneae is sister to the Centotheceae and Cyperochloeae. Thysanolaeneae includes a monotypic, non-Kranz genus, *Thysanolaena* Nees, defined by its spikelets 2(3–4)-flowered, the lower floret and the uppermost neuter, and fertile lemma membranous; the genus grows across the tropical and subtropical Indomalayan region to northwestern Australasia. Tribe Centotheceae, stem and crown age of 22.84 and 17.49 Ma respectively, is sister to the Cyperochloeae; it is mainly defined by its laterally compressed spikelets with (1 –)2–15(–32) florets and a membranous fertile lemma. It includes two non-Kranz genera: *Centotheca* Desv., with four species native to the eastern Afrotropics, Indomalaya, and northwestern Australasia, with spikelets laterally compressed and uniflowered, and; *Megastachya* P. Beauv., with two species from tropical Africa and Madagascar, defined by its laterally compressed spikelets and with 8−20 florets, breaking up between them at maturity. The final branch within this clade includes the Cyperochloeae L. Watson & Dallwitz ex Sánchez-Ken & L. G. Clark, stem and crown age of 22.84 and 15 Ma, with two C_3 genera, with spikelets laterally compressed, sterile glumes below and several fertile florets, endemic to Western Australia: *Cyperochloa* Lazarides & L. Watson, defined by its spikelets, carrying four to nine florets, the glumes persistent at maturity, and *Spartochloa* C.E. Hubb., monotypic, the spikelets, bearing four to eight fertile florets, each one disarticulating at maturity.

Finally, the latter tribe of this clade is the Tristachyideae, stem and crown age of 50.44 and 23.37 Ma, with Afrotropic stem and crown areas. It is characterized by its bi-flowered spikelets, the lower male or neuter, and the upper floret fertile, the lemma awned. This tribe consists of the following 8 genera: *Danthoniopsis* Stapf, with 16 native species in Africa, the Arabian Peninsula, and Pakistan is defined by its laterally compressed spikelets with glumes persistent and one fertile floret, the lemma awned. *Dilopotriche* (C.E. Hubb.)

Jacq.-Fél. has three west tropical African species, with laterally compressed spikelets, persistent glumes, one fertile floret, and a 3-awned lemma. *Gilgiochloa* Pilg. is a monotypic genus from east tropical Africa (Burundi, Malawi, Mozambique, Rwanda, Tanzania, and Zambia), with a spiciform panicle, the lower flower with the palea thickened, and the upper lemma pilose, bilobed and awned. *Loudetia* Hochst. ex Steud. is a genus with 25 accepted species, widely distributed in tropical South America, Africa, and the Arabian Peninsula (and introduced in Myanmar). *Loudetiopsis* Conert, a pantropical genus present in west tropical Africa (up to Chad) and tropical South America, has 11 species and is defined by its spikelets laterally compressed, with one male floret and a perfect upper floret, the glumes persistent, and the upper lemma awned from a sinus. *Trichopteryx* Nees, a genus from Africa and Madagascar, includes 11 species, with spikelets laterally compressed, the lower floret male or neuter, the upper one perfect, with the upper lemma with a transverse row of hair tufts, 3-awned. *Tristachya* Nees, a genus with 22 species, is widely distributed across the Afrotropics. It has a disjunct distribution in Latin America, with species growing from Mexico to Costa Rica in Mesoamerica and taxa in Brazil and Paraguay. Its species have spikelets disarticulating beneath each floret, the upper lemma bilobed, awned, and a conspicuous conical and pungent callus. Finally, *Zonotriche* (C.E. Hubb.) J.B. Phipps, with three species, is an African genus (Angola, Malawi, Mozambique, Tanzania, Zambia, Zaïre, Zimbabwe), with spikelets arranged on triads on the inflorescence, the triads falling entire, the upper lemma with a geniculate awn, and the callus short, rounded.

The next split (**Panicoideae 2** in Fig. 1) includes a clade of Chasmanthieae, Steyermarkochloeae, and Zeugiteae, with a crown age of 48.57 Ma, which is sister to a clade that includes Gynerieae, Lecomtelleae, the Panicodae, and Andropogonae. The Chasmanthieae, stem and crown ages of 48.57 and 6.15 Ma, respectively, with spikelets many-flowered and paleas winged, comprises a single C_3 genus, *Chasmanthium* Link, with seven species distributed from Northern Canada, central, eastern, and southeastern United States, and northeastern Mexico. The genus has spikelets laterally compressed, with one to many florets, reduced toward the apex, and disarticulating below each fertile floret. The **Steyermarkochloeae** is a tribe of a doubtful taxonomic position and may not be monophyletic (Davidse & Ellis, 1984; Morrone et al., 2012; Kellogg, 2015; Soreng et al., 2015b) with two C_3 genera: *Arundoclaytonia* Davidse & R.P. Ellis, a monotypic genus from northern Brazil with spikelets dorsally compressed and two flowered, with male spikelets distinct from the female ones, female flowers with the lower floret neuter and without palea, the upper one female. *Steyermarkochloa* Davidse & R.P. Ellis is a South American genus (Colombia, Venezuela, and northern Brazil) with two species, distinguished by being monoecious, with male spikelets below in the spiciform panicle and female spikelets at the upper branches, the spikelets dorsally compressed and both the male and female spikelets similar, although male spikelets are smaller; the caryopsis has a linear hilum. The positions of *Arundoclaytonia* and *Stereochlaena* (Cenchrinae) + *Steyermarkochloa* are in doubt, as they are based only on *ndhF* sequences, which are located at the endpoints of the IR and SSC and are known for inversions.

Tribe **Zeugiteae**, with stem and crown ages of 39.04 and 19.01 Ma, consists of four C_3 genera, *Chevalierella* A. Camus (1 sp., Africa, in Congo and Zaire, spikelets laterally compressed, with 1 fertile floret, the lemma awned), *Lophatherum* Brongn. (2 spp., present in subtropical and tropical Asia, Australasia, and the Pacific Islands, with spikelets arranged in racemes with 1 fertile floret, with reduced florets toward the apex), *Orthoclada* P. Beauv., a genus with a disjunct distribution (Sánchez-Ken & Clark, 2010), with one species restricted to tropical Africa, and *O. laxa* (Rich.) P. Beauv. growing from Mesoamerica to northern South America up to Bolivia and southern Brazil, including spikelets laterally compressed, 1–5-flowered and falling entire at maturity), and *Zeugites* P. Browne (12 spp., an American genus, distributed from Mexico, Mesoamerica, and the Caribbean to South America, i.e., Colombia, Venezuela, Ecuador, Peru, and Bolivia, and distinguished by having 1 or 2 female fertile florets at the base of the spikelet and 1 to many male florets toward the apex).

At the next node along the backbone of the subfamily (Panicoideae 3 in Fig. 1), tribe **Gynerieae**, stem age of 51.07 Ma, is sister to the Lecomtelleae and the remaining Panicodae and Andropogonae. It includes a monotypic C_3 genus, *Gynerium* Willd. ex P. Beauv., widely distributed in the Neotropics from the southeastern United States to Mexico, Mesoamerica, the Caribbean, and South America, with its southernmost distribution in northwestern Argentina, Paraguay, and southern Brazil. Plants are dioecious and robust, the female spikelets with two fertile florets with the lemma plumose, the male spikelets distinct.

Tribe **Lecomtelleae**, stem age of 45.78 Ma, crown area Afrotropics, is sister to the rest of the Panicodae and Andropogonae (see Panicoideae 4 and 5 in Fig. 1) and includes a single monospecific C_3 genus. *Lecomtella* A. Camus, endemic to Madagascar. The genus is characterized by its spikelets dorsally compressed with a lower male floret and an upper female, indurate floret (Besnard et al., 2013).

Paniceae, with stem and crown ages of 44.92 and 29.96 Ma, and Afrotropical stem and crown areas, dispersed and diversified pantropically. They combine a basic chromosome number of $x = 9$ and spikelets typically bi-flowered, the lower floret male or neuter, and the upper floret hermaphrodite and indurated. It includes five subtribes and three groups of taxa with uncertain affinities in the subfamily. The first incertae sedis group consists of five genera: *Cnidochloa* Zuloaga (1 C_3 species restricted to Brazil, in an unresolved position in the Paniceae; Zuloaga et al., 2020); *Hydrothauma* C.E. Hubb., (a monotypic C_3 genus native to Zambia and Zaire in Africa, with a spiciform panicle, a saccate upper glume, and a cartilaginous upper lemma, with flat margins over the palea); *Hylebates* Chippin. [with 2 C_3 species from east tropical Africa (Kenya, Mozambique, Tanzania, Zambia, and Zimbabwe), both species with spikelets dorsally compressed, the lower lemma awned, and upper anthecium not indurate, the margins of the upper lemma flat over the upper palea]; *Oryzidium* C.E. Hubb. & Schweick. [an African C_4 genus (Angola, Botswana, Namibia, Zambia, and Zimbabwe), with one species characterized by being a floating perennial, the spikelets dorsally compressed, with the upper glume awned, the lower floret male, the upper one female]; and *Thedachloa* S.W.L. Jacobs [a monotypic C_4 genus (Osborne et al., 2014) endemic to Western Australia, with plants stoloniferous, annual, spikelets laterally compressed, the lower floret male or neuter, and upper floret perfect].

Subtribe **Anthephorinae** Benth. is sister to the remaining Paniceae and has a stem and crown age of 29.96 and 18.43 Ma. Members of this subtribe share modified inflorescences with involucral bracts, possibly derived from the lower glume or sterile spikelets (Clayton & Renvoize, 1986). The subtribe includes eight C_4 genera: *Anthephora* Schreb., 11 spp., Mexico, Mesoamerica, the Caribbean, northern South America, Africa, Saudi Arabia, and Iran; *Chaetopoa* C.E. Hubb., 2 spp., east tropical Africa: Tanzania; *Chlorocalymma* Clayton, 1 sp., east tropical Africa, Tanzania; *Digitaria* Haller, 271 spp., a cosmopolitan genus, widespread in North and South America, Eurasia, Africa, and Australasia; *Taeniorhachis* Cope, a monotypic genus restricted to Somalia; *Tarigidia* Stent, 2 spp., a genus with a disjunct distribution, one species growing in southern Africa and the other one endemic of Puerto Rico; *Thyridachne* C.E. Hubb., with 1 species restricted to tropical Africa (Central African Republic and Zaire); and *Trachys* Pers., with 4 species native to India and Sri Lanka and Southeast Asia (Myanmar).

Subtribe **Boivinellinae** Pilg., previously known as "the forest shade clade" (Giussani et al., 2001; Hackel et al., 2018), with stem and crown ages of 27.65 and 21.92 Ma, is basal to the rest of the Paniceae and comprises grasses found predominantly in shaded locations. According to Hackel et al. (2018), this subtribe appears to have originated in Madagascar and later dispersed to Asia and America. It comprises the following 16 genera: *Acroceras* Stapf, a C_3 genus (including *Setiacis* S.L. Chen & Y.X. Jin), with 24 species, a pantropical genus present in Central and South America, the Caribbean, Africa, Asia, and the Pacific Islands; *Alloteropsis* J. Presl, a genus with 5 C_4 and C_3 species, distributed from Africa, Madagascar, Asia, Australia, and the Pacific Islands; *Amphicarpum* Kunth, a C_3 genus with two species, peculiar by having cleistogenes (underground cleistogamous flowers), and restricted to the eastern United States; *Chasechloa* A. Camus, a recently reinstated endemic, C_3 genus of Madagascar with 2 species (Silva et al., 2015, 2017); *Cyphochlaena* Hack. (2 C_3 species, endemic from Madagascar); *Cyrtococcum* Stapf, 14 C_3 species, distributed in Africa, temperate, and Southeast Asia, Australia, and Pacific Islands; *Echinochloa* P. Beauv., a cosmopolitan C_4 genus with 34 species present in tropical, subtropical and temperate areas of the World (several species of the genus are noxious weeds); *Entolasia* Stapf (C_3, 6 spp., tropical Africa up to Namibia, New Guinea, and Australia); *Lasiacis* (Griseb.) Hitchc. (C_3, 15 spp., distributed from southeastern United States, Mexico, Mesoamerica, and the Caribbean, and in South America from Colombia and Venezuela to northern Argentina and Paraguay); *Mayariochloa* Salariato, Morrone & Zuloaga (1 C_4 species, segregated from *Scutachne* Hitchc. & Chase, endemic of Cuba); *Microcalamus* Franch. (1 C_3 species, restricted to west tropical Africa); *Morronea* Zuloaga & Scataglini, a C_3 genus with 6 American species, ranging from Mexico, Mesoamerica, the Caribbean, and South America (Colombia, Venezuela, Ecuador, Peru, Brasil, Paraguay, and northeastern Argentina); *Oplismenus* P. Beauv. (C_3, 7 spp., with a pantropical distribution, in America, Africa, Eurasia, Australia, and the Pacific Islands); *Ottochloa* Dandy, a C_3 genus with 3 species, east tropical Africa, temperate, and Southeast Asia, Australia, and Pacific Islands; *Parodiophyllochloa* Zuloaga & Morrone (C_3, 6 spp., America, from Mexico, Mesoamerica and the Caribbean to South America, from Colombia and Venezuela to Bolivia, Paraguay, and northern Argentina); *Poecilostachys* Hack. (C_3, ca. 31 spp., Africa and Madagascar); *Pseudechinolaena* Stapf (C_3, 6 spp., pantropical: Mesoamerica, South America, from Colombia and Venezuela to Uruguay and Argentina, Africa, Madagascar, Asia, and the Pacific Islands); *Pseudolasiacis* (A. Camus) A. Camus (C_3, with 4 species endemic to Madagascar). Also, the Boivinellinae includes 10 C_3 species of *Panicum* L. to be segregated from this genus (Zuloaga et al., 2018; Hackel et al., 2018) growing in Africa, Madagascar and neighboring islands, and Australia, together with seven C_3 species currently in the genus *Brachiaria* (Trin.) Griseb., also to be segregated from the latter genus.

The **second group of incertae sedis taxa** diverges next, together with the Dichantheliinae and Neurachninae as sister taxa. Within this incertae sedis group, we find *Sacciolepis* Nash with 26 species, a cosmopolitan, primarily pantropical, C_3 genus present in America, Africa, Asia, Australia, and the Pacific Islands, characterized by its usually spiciform panicles with gibbous spikelets. *Kellochloa* Lizarazu, M.V. Nicola & Scataglini is a small C_3 genus recently segregated from *Panicum* (Nicola et al., 2015), with two species growing in eastern North America. *Trichanthecium* Zuloaga & Morrone has nearly 45 C_3 species (some of which are still in need of transfer from the genus *Panicum*), distributed in Mesoamerica, the Caribbean, and South America, and also widespread in Africa and Madagascar. Finally, this incertae sedis group includes 18 C_3 species of "*Panicum,*" from America, Africa, and Asia, still with an unresolved generic position within the tribe.

Subtribe **Dichantheliinae** is sister to the **Neurachninae** and has stem and crown ages of 24.66 and 8.5, respectively. It includes two genera. The first is *Adenochloa* Zuloaga, C_3, with 13 species growing in Africa and Madagascar, defined by the presence of clavellate hairs on the inflorescence (Zuloaga et al., 2015). The second, *Dichanthelium* (Hitchc. & Chase) Gould, is a C_3 genus with approximately 62 species with foliar or floral dimorphism, distributed from North America, and Hawaii in the Pacific, through Mexico, Mesoamerica, the Caribbean, and South America (Colombia and Venezuela to Argentina, Chile, and Uruguay). The remnant subtribe of this clade is the Neurachninae, stem and crown ages of 24.66 and 14.61, crown area Australasia, with the following six genera from Australia and the Pacific Islands: *Ancistrachne* S.T. Blake, with four C_3 species of Eastern Australia, the Philippines, and New Caledonia; *Calyptochloa* C.E. Hubb., with three C_3 species from Queensland, Australia; *Cleistochloa* C.E. Hubb., three C_3 species endemic to New Guinea and Eastern Australia; *Neurachne* R. Br., with seven C_4 and mixed C_3–C_4 species endemic of Australia; *Paraneurachne* S.T. Blake, one C_4

species of Australia, and *Thyridolepis* S.T. Blake, with three C_3 species endemic of Australia. See also Thompson and Fabillo (2021).

The next split in our cladogram, and basal to the rest of Paniceae, includes a genus of uncertain position within the tribe, ***Homopholis*** C.E. Hubb. (Teerawatananon et al., 2011), with a crown mean age of 8.64 Ma, a genus with four C_4 and C_3 species endemic to Australia.

Next, subtribe **Panicinae** Fr., stem and crown age of 21.08 and 12.04 Ma, respectively, is basal to the remaining subtribes of the Paniceae, that is, Cenchrinae Dumort. and Melinidinae Pilg. This subtribe includes two genera: *Louisiella* C.E. Hubb. & J. Léonard, with two C_4 species has a disjunct distribution, *L. fluitans* C.E. Hubb. & J. Léonard, endemic to Africa (Cameroon, Central African Republic, Sudan, and Zaire), and *L. elephantipes* (Nees ex Trin.) Zuloaga, widely distributed in the Americas, from Mexico, Mesoamerica, and the Caribbean to South America (Colombia and Venezuela to Paraguay and Argentina) (Scataglini et al., 2014). *Panicum*, as presently circumscribed, consists of nearly 163 C_4 species worldwide and is classified in seven sections (Zuloaga et al., 2018). Of these sections, one is endemic to Australia, another is present in Australia and Southeast Asia, one is restricted to the Neotropics, and the other four are pantropical. Zuloaga et al. (2018) suggested that the Neotropics was the most probable ancestral area of the genus.

The following branch of the cladogram includes two sister subtribes, the Melinidinae Pilg. and the Cenchrinae. Their stem area is most likely Australasia. **Melinidinae** (13 genera and ungrouped species of "*Panicum*," all C_4) has a stem and crown age of 19.95 and 17.42 Ma and a crown area in the Afrotropics. The subtribe includes *Chaetium* Nees, which comprises three American species, *C. bromoides* (J. Presl) Benth. ex Hemsl. in Mesoamerica, *C. cubanum* (C. Wright) Hitchc., an endemic of Cuba, and *C. festucoides* Nees, present in northern South America. *Eccoptocarpha* Launert, includes one species in Africa (Tanzania and Zambia). *Eriochloa* Kunth is either a pantropical genus (America, Africa, Asia, Australia, and the Pacific Islands) with nearly 34 species or is possibly polyphyletic (Salariato et al., 2010; Kellogg 2015) and restricted to its type species. *Leucophrys* Rendle, with 1 species is endemic to Africa); *Megathyrsus* (Pilg.) B.K. Simon & S.W.L. Jacobs includes two species in Africa, Madagascar, West Indian Ocean, and the Arabian Peninsula). *Megathyrsus maximus* (Jacq.) B.K. Simon & S.W.L. Jacobs is an important crop and an invasive weed introduced in North, Central–South America, Eurasia, Australia, and Pacific Islands). *Melinis* P. Beauv. includes 22 species native to Africa, Madagascar and nearby Islands, and the Arabian Peninsula, with several weedy species, such as *M. minutiflora* P. Beauv. and *M. repens* (Willd.) Zizka introduced in the Americas, Eurasia, and the Pacific Islands. *Moorochloa* Veldkamp has three spp., native to Africa, Madagascar, and Eurasia, with *M. eruciformis* (Sm.) Veldkamp introduced in America, Australia, and the Pacific Islands. *Rupichloa* Salariato & Morrone includes 2 species endemic to eastern Brazil). *Scutachne* Hitchc. & Chase is a monotypic genus endemic to the Caribbean. *Thuarea* Pers. has two species present in Madagascar, Sri Lanka, southeast Asia, Australia, and Pacific Islands. *Tricholaena* Schrad. has four spp., distributed in Africa and the Mediterranean, the Arabian Peninsula through Iran and India. *Urochloa* P. Beauv. is pantropical (North, Central, and South America, Africa and Madagascar, Asia, Australia, and the Pacific Islands) with nearly 100 species; however, the genus is paraphyletic (Salariato et al., 2010). *Yvesia* A. Camus is a monotypic genus endemic to Madagascar. Additionally, two "*Panicum*" unresolved species belong to the Melinidin ae, *P. trichocladum* Hack. ex K. Schum., growing in Africa and Madagascar, and *P. deustum* Thunb., from Africa and temperate Asia.

Cenchrinae, stem and crown age of 19.95 and 16.63 Ma, crown area Australasia, gathers 24 C_4 genera, which usually share the presence of persistent setae on the inflorescence. These genera are *Acritochaete* Pilg. (1 sp., tropical Africa); *Alexfloydia* B.K. Simon, with one species restricted to southeastern Australia; *Cenchrus* L., a cosmopolitan genus, including *Pennisetum* Rich., with approximately 120 species; *Chamaeraphis* R. Br., a monotypic genus restricted to northern Australia; *Dissochondrus* (Hillebr.) Kuntze, with one species from the Hawaiian Islands; *Holcolemma* Stapf & C.E. Hubb. (3 spp., eastern Africa, India, Sri Lanka, and Australia); *Hygrochloa* Lazarides, with two species restricted to Australia (Northern Territory, Queensland, Western Australia); *Ixophorus* Schltdl., with a single species present in Mexico, Mesoamerica, Cuba, and reaching Colombia in South America; *Paractaenum* P. Beauv., monotypic and endemic of Australia; *Paratheria* Griseb., one species from Africa and another one distributed in tropical America, Africa, and Madagascar; *Plagiosetum* Benth. (1 sp., Australia); *Pseudochaetochloa* Hitchc. (1 sp., Australia); *Pseudoraphis* Griff., eight Old World species (India, Sri Lanka, southeast Asia, Australia, and the Pacific Islands); *Setaria* P. Beauv., a non-monophyletic and difficult genus, still in need of additional phylogenetic studies (Kellogg et al., 2009; Morrone et al., 2013), consists of approximately 115 species and has a cosmopolitan distribution, being present in all continents; *Setariopsis* Scribn. (2 spp., southern United States, Mexico, Mesoamerica up to Colombia and Venezuela); *Spinifex* L., with four species from India, Sri Lanka, southeast Tropica Asia, Australia, and the Pacific Islands; *Stenotaphrum* Trin., a pantropical genus with seven species, distributed in America, Africa, Asia, Australia, and the Pacific Islands; *Stereochlaena* Hack. (4 spp., Africa); *Streptolophus* Hughes, with one species restricted to Angola; *Uranthoecium* Stapf, a monotypic genus of Australia; *Whiteochloa* C.E. Hubb., with six species present in Australia and the Pacific Islands [the genus was classified in the Panicinae (Burke et al., 2016b), but later confirmed, although persistent setae are absent in its species, in the Cenchrinae (Zuloaga et al., 2018)]; *Xerochloa* R. Br., with three species from southeast Asia, Java, and Australia; *Zuloagaea* Bess, one species ranging from the southern United States, Mexico, Mesoamerica and South America (Colombia and Ecuador), another genus without setae on the inflorescence (Bess et al., 2006); *Zygochloa* S.T. Blake, with one species endemic of Australia. Finally, within the Cenchrinae, another "*Panicum*" species without setae on the spikelet, *P. antidotale* Retz., remains in an unresolved position within this subtribe.

For the supertribe **Andropogonodae**, the stem and crown ages are 44.92 and 41.16 Ma, and the stem area is Afrotropical, but the crown area is either Neotropics and

Afrotropics or a mixture of these. The tribe **Paspaleae**, with stem and crown ages of 41 and 36 Ma, and a Neotropical crown area, mostly remains centered in the Neotropics. Paspaleae consists of three subtribes and a monotypic genus isolated in a basal position, ***Reynaudia*** Kunth, growing in the Caribbean (Cuba, Dominican Republic, Haiti, and Jamaica), and characterized by having spikelets awned, with bilobed glumes and fertile floret with two stamens (Morrone et al., 2012; GPWG II Grass Phylogeny Working Group II, 2011). All subtribes of the Paspaleae have a base chromosome number of $x = 10$ and are predominantly American (with a few representatives of *Ichnanthus* P. Beauv., *Axonopus* P. Beauv., and *Paspalum* L. growing in Old World areas). Subtribe **Paspalinae** Griseb. is sister to subtribes Otachyriinae Butzin and Arthropogoninae Butzin; it has a stem and crown age of 31.52 and 28.61 Ma, respectively, and includes the following 16 genera: *Aakia* J.R. Grande, with 1 C_4 species, segregated from *Panicum*, ranging from Mexico to Belize, Guatemala, and Nicaragua; *Acostia* Swallen, 1 C_4 species restricted to Ecuador, either treated as a valid genus or considered under *Axonopus* (Webster et al., 1989); *Anthaenantiopsis* Mez ex Pilg., 4 C_4 species in South America, found in open savannas of Brazil, Bolivia, and northern Argentina; *Axonopus* P. Beauv., a C_4 genus with nearly 105 species, growing in America from southeastern United States, Mexico, Mesoamerica, the Caribbean, and South America, from Colombia and Venezuela to Argentina, Chile, and Uruguay [the presence of *Axonopus flexuosus* (Peter) C.E. Hubb. in Africa is considered the result of secondary speciation, following the introduction of *A. compressus* (Sw.) P. Beauv. to this continent (Gledhill, 1968)]; *Echinolaena* Desv. (2 C_3 species, present in Mesoamerica and northern South America); *Gerritea* Zuloaga, Morrone & T. Killeen, 1 C_3 species, endemic to tropical areas of Bolivia; *Hildaea* C. Silva & R.P. Oliveira, a C_3 genus, segregated from *Ichnanthus* P. Beauv., with 14 species growing from Mexico, Mesoamerica, and the Caribbean to South America (Colombia and Venezuela to northern Argentina), with one variety, *H. pallens* var. *major* (Nees) C. Silva & R.P. Oliveira in Africa, Asia, and Australia, (according to Silva et al. (2020), "*Hildaea* apparently colonized the Old World via distinct long-distance dispersal events from the New World, at least one to the western coast of Africa and another to eastern Asia and Australia"); *Hopia* Zuloaga & Morrone, 1 C_4 species restricted to the United States and Mexico; *Ichnanthus* P. Beauv., with 22 C_3 species inhabiting Tropics of the New World, from Mexico, Mesoamerica and the Caribbean and South America (Colombia and Venezuela to northern Argentina and Paraguay); *Ocellochloa* Zuloaga & Morrone, with 12 C_3 species, growing in Mesoamerica, the Caribbean and South America (Colombia and Venezuela to northeastern Argentina; Sede et al., 2009); *Oedochloa* C. Silva & R.P. Oliveira, a C_3 genus with 9 species confined to the Neotropics, from Mesoamerica and the Caribbean to South America; *Osvaldoa* J.R. Grande, one C_4 species segregated from *Panicum* (southern Brazil, Uruguay and eastern Argentina); *Paspalum* L., a cosmopolitan C_4 genus with approximately 311 species, most of them growing in the Americas, from Canada to Chile, Argentina and Uruguay, with a few species present in Africa, Asia, Australia and the Pacific Islands; *Renvoizea* Zuloaga & Morrone, with 10 C_3 species found in Eastern Brazil; *Streptostachys* Desv., with two C_3 species from Trinidad and Tobago, Venezuela, the Gui anas, and northeastern Brazil.

Sister to the Arthropogoninae is the **Otachyriinae** (stem and crown age of 29.61 and 18.28 Ma), a subtribe with 6 C_4, C_3, and intermediate C_3-C_4 genera (Acosta et al., 2014, 2019); *Anthenantia* P. Beauv., with 4 C_4 species, southern United States, Mexico, Mesoamerica, and the Caribbean, South America; *Hymenachne* P. Beauv., a pantropical C_3 genus with 17 species; *Otachyrium* Nees, with 8 C_3 species ranging from Trinidad and Tobago, Colombia, Venezuela and the Guyanas to Paraguay and northern Argentina; *Plagiantha* Renvoize, a monotypic C_3 genus endemic of northeastern Brazil; *Rugoloa* Zuloaga (3 C_3 species, America, from Mexico, Mesoamerica and the Caribbean to South America, in all countries except Chile; and *Steinchisma* Raf., with 9 C_3 and intermediate C_3–C_4 species, present in tropical and subtropical America, from the United States to Argentina, with *S. laxa* (Sw.) Zuloaga introduced in Africa, Asia, and Australia.

Subtribe **Arthropogoninae**, with a stem and crown age of 29.61 and 28.11 Ma, includes 16 C_3 and C_4 American genera, as follows: *Achlaena* Griseb., 1 C_4 species of Cuba and Jamaica; *Altoparadisium* Filg., Davidse, Zuloaga & Morrone, a South American C_4 genus with two species, present in Central Brazil and Bolivia; *Apochloa* Zuloaga & Morrone, 15 C_3 species of savannas, and rocky slopes, of Venezuela, Guyana and Brazil; *Arthropogon* Nees (5 C_4 species, present in the Caribbean, Colombia, Brazil and Bolivia); *Canastra* Morrone, Zuloaga, Davidse & Filg., 2 C_3 species endemic of Southeast and Southern Brazil; *Coleataenia* Griseb., with 9 C_4 species ranging from Canada and United States, Mexico, Mesoamerica and the Caribbean and South America; *Cyphonanthus* Zuloaga & Morrone, a monotypic C_4 genus present in Mesoamerica, the Caribbean and South America (Colombia, Venezuela, the Guyanas, Brazil, and Bolivia); *Homolepis* Chase, a C_3 genus with five tropical and subtropical species, ranging from Mexico, Mesoamerica and the Caribbean to all South America (except Chile); *Keratochlaena* Morrone, a monotypic C_4 genus endemic of northeastern Brazil; *Mesosetum* Steud., a C_4 genus with 28 species, growing from Mesoamerica and the Caribbean to South America (Colombia and Venezuela to Paraguay and northeastern Argentina; *Oncorachis* Morrone & Zuloaga, a C_4 genus with 2 species characteristic of cerrados of Brazil and northern Paraguay; *Oplismenopsis* Parodi, a monotypic C_3 genus of humid areas of southern Brazil, Paraguay, Uruguay, and northeastern Argentina; *Phanopyrum* (Raf.) Nash, also a monotypic C_3 genus from the eastern United States; *Stephostachys* Zuloaga & Morrone, a tropical and subtropical genus with a single C_3 species, usually found in inundated areas of Mesoamerica and South America (from Colombia, Venezuela, and the Guyanas to Bolivia, Paraguay, and northern Argentina); *Tatianyx* Zuloaga & Soderstr., a monotypic C_4 genus restricted to "cerrados" and "campos rupestres" of Brazil; and *Triscenia* Griseb., with 1 C_3 species growing in Cuba.

The crown area of the remainder of Andropogonodae is Indomalayan or Indomalayan+Afrotropical. Tribe **Jansenelleae**, stem and crown age of 31.17 and 17.11 Ma, crown area Indomalaya, is sister to Arundinelleae + Andropogoneae and consists of two C_3 genera, *Chandrasekharania* V.J. Nair, V.S.

Ramach. & Sreek. (one sp., only present in SW India), and *Jansenella* Bor (2 spp., native to India, Sri Lanka, Assam, and Myanmar).

Tribe **Arundinelleae** is basal to the Andropogoneae and includes 2 C_4 genera, *Arundinella* Raddi, with 55 species and a cosmopolitan distribution, present in America, Africa, temperate and tropical Asia, Australia, and the Pacific Islands, and *Garnotia* Brongn., with 29 species growing in islands of the Indian Ocean, the Arabian Peninsula, tropical and subtropical Asia, Australia, and islands of the Pacific Ocean. In our analysis, the two genera did not form a monophyletic clade but rather a poorly supported grade leading to the Andropogoneae.

The tribe **Andropogoneae** is distributed worldwide, primarily in tropical regions, although a few species have ranges that extend into the north temperate zone (Lehmann et al., 2019). Members of this tribe share the spikelets arranged in pairs (one sessile and the other pedicellate) at each node of the disarticulating rachis (Clayton & Renvoize, 1986; Kellogg, 2015). All species use the C_4 photosynthetic pathway (Sage et al., 2011; Grass Phylogeny Working Group II [GPWG II], 2011). While C_4 photosynthesis is often associated with drought and many Andropogoneae are indeed native to areas of low precipitation, the tribe also includes many species (e.g., members of the genera *Vossia* Wall. & Griff., *Oxyrhachis* Pilg., some *Eulalia* Kunth) from moist or even inundated habitats indicating an ability to tolerate submergence (Clayton, 1972; Gibbs-Russel et al., 1990). The major grasslands of Africa, South America, and North America are all dominated by species of Andropogoneae (Lehmann et al., 2019), many of which are tall plants with massive root systems that sequester appreciable carbon (Weaver, 1954, 1968). The African species, in particular, are highly flammable and contribute to an ecosystem that depends on frequent fires (Simpson et al., 2016).

The mean stem and crown ages of **Andropogoneae** are estimated to be 24.03 and 18.89 Ma, respectively, while Welker et al. (2020) determined stem and crown dates of 17.5 and 13.89 Ma. The crown area is either Indomalayan (30%) or Afrotropics (24%), but the backbone of the clade is predominantly Indomalayan (Table 1, Fig. 2d), while lineages disperse widely throughout the tropics and subtropics. According to Welker et al. (2020), Andropogoneae likely originated in East Asia, with many later independent dispersal events, especially to Africa and the New World, resulting in a cosmopolitan distribution. Most subtribes and several genera of Andropogoneae are also widely distributed in the Old World and the New World. Polyploidy and reticulate evolution are common in many clades of Andropogoneae, increasing the complexity of their phylogenetic relationships (Estep et al., 2014; Welker et al., 2015).

The genus *Lasiurus* Boiss. (1 sp.; distributed across deserts of northern Africa to India) is the first lineage within Andropogoneae in our study. In Welker et al. (2020), *Lasiurus* formed a clade with *Thelepogon* Roth (2 spp.; tropical Africa, Southeast Asia, and Australia), which was not recovered in our analyses. Neither genus has been studied extensively, so most details of their physiology and ecology are unknown, although the former genus occurs in deserts and the latter in moist or wet sites (Clayton, 1972; Watson & Dallwitz, 1992; Naz et al., 2014). The two genera are also quite distinct morphologically, hinting that one or both may be misplaced.

The early-diverging subtribe **Arthraxoninae Benth**. (stem and crown ages of 13.4 and 5.44 Ma in Welker et al., 2020) includes only the genus *Arthraxon* P. Beauv., which comprises 27 species distributed in Old World tropics, mainly India. *Arthraxon* is a genus of decumbent annuals and perennials with leaves broadly lanceolate to ovate with a cordate base. Although Kellogg (2015) suggested that the latter character might be synapomorphic, it also appears in *Thelepogon*. Depending on the ultimate resolution of the base of the Andropogoneae phylogeny, it could be a plesiomorphy for the tribe. The position of the lemma awn is diagnostic, originating from a position below the midpoint on the back (abaxial) side of the lemma. In most species, neither of the two florets of the spikelet bears a palea. Here and throughout this section, statements about morphological characters are based on Kellogg (2015), which in turn is based on Clayton & Renvoize (1986) and Watson & Dallwitz (1992). The morphological data are also confirmed by the personal observations of the authors. For a careful and detailed comparison of the morphology and micromorphology of *Arthraxon* and *Thelepogon*, see Thompson (2019).

The New World **Tripsacinae Dumort**., which includes the genera *Tripsacum* L. (16 spp.; North America to northern South America) and *Zea* L. (7 spp.; Central America in origin), is sister to the remaining Andropogoneae. The stem and crown ages of Tripsacinae are estimated to be 15.44 and 10.43 Ma in this study (12.58 and 4.42 Ma in Welker et al., 2020). Most members of this subtribe are large (well over 1 m tall) with broad leaves. All species are monoecious with separate staminate and pistillate spikelets and lack awns. The spikelets are paired in early development (the ancestral character state for the tribe), but in the pistillate pairs, only one of the spikelets develops (see, e.g., Sundberg et al., 1995; Sundberg & Orr, 1996; Orr & Sundberg, 2007). The genus *Zea* includes *Zea mays* L., which is among the world's most valuable crops for food, feed, and many industrial applications (Edmeades et al., 2017).

Chionachninae Clayton and the recently described subtribe Rhytachninae Welker & E.A. Kellogg form a clade that is sister to the remaining Andropogoneae. All members of this clade lack awns. **Chionachninae** has stem and crown ages of 13.06 and 6.38 Ma (11.85 and 5.27 Ma in Welker et al., 2020) and includes three genera: *Chionachne* R. Br. (9 spp.; southern Asia to eastern Australia), *Polytoca* R. Br. (2 spp.; Indomalayan region), and *Trilobachne* M. Schenck ex Henrard (1 sp.; India to Myanmar). All species in the subtribe are monoecious, as in Tripsacinae, but the two subtribes appear unrelated (e.g., Estep et al., 2014; Welker et al., 2020). Other than their overall morphology, members of *Chionachne* have not been studied extensively (but see Jannink & Veldkamp, 2002), and taxonomic revisions are needed to validate and document generic limits.

Rhytachninae (stem and crown ages of 11.85 and 8.99 Ma in Welker et al., 2020) comprises five genera distributed mainly in the Old World: *Loxodera* Launert (5 spp.; tropical Africa), *Oxyrhachis* (1 sp.; tropical Africa to Madagascar), *Rhytachne* Desv. ex Ham. (12 spp.; tropical Africa and America), *Urelytrum* Hack. (7 spp.; tropical Africa to Madagascar), and *Vossia* (1 sp.; tropical Africa and Asia). Members of the clade are morphologically disparate. While none have awns on the lemma, several members of the subtribe have awned glumes, and in *Vossia*, the glumes are long and caudate. *Oxyrhachis* and *Rhytachne* grow in swamps or wet grasslands, *Loxodera* is reported to grow along riverbanks, and *Vossia* is aquatic; only *Urelytum* is reported from dry woodland sites (Clayton, 1972; Gibbs-Russel et al., 1990). Rhytachninae was not recovered as monophyletic in our study.

The subtribe **Chrysopogoninae** Welker & E.A. Kellogg (stem and crown ages of 10.53 and 6.16 Ma in Welker et al., 2020) was recently described by these authors to accommodate the genus *Chrysopogon* Trin., which includes 49 species distributed in tropical and subtropical regions of the world, especially in Asia and Oceania. *Chrysopogon* has a complex evolutionary history involving reticulation. It forms a clade with *Eriochrysis* P. Beauv. (11 species; tropical America and Africa, and India) and *Parahyparrhenia* A. Camus (6 spp; west tropical Africa to mainland Southeast Asia) in plastome trees (Arthan et al., 2017; Welker et al., 2020) but is sister to *Thelepogon* in nuclear trees (Estep et al., 2014; Welker et al., 2015, 2016). *Eriochrysis* and *Parahyparrhenia* were provisionally placed *incertae sedis* by Welker et al. (2020), pending additional phylogenetic investigation.

The next lineage to diverge includes the genera *Kerriochloa* C.E. Hubb. (1 sp.; mainland Southeast Asia), *Microstegium* Nees (27 spp.; tropical and subtropical Africa and Asia), and *Sehima* Forssk. (5 spp.; Old World tropics), which are currently placed incertae sedis. The three genera have little in common, morphologically or ecologically. Although Welker et al. (2020) found them to form a well-supported clade, this result should be confirmed by including additional species of *Microstegium* and *Sehima*. Subtribes Ratzeburgiinae Hook. f. and Rottboelliinae J. Presl formed a clade together with the genera *Elionurus* Humb. & Bonpl. ex Willd. and *Tripidium* H. Scholz in Welker et al. (2020), although their internal relationships were not completely clear. This clade was not recovered in our study. The stem and crown ages of **Ratzeburgiinae** are 13.31 and 9.43 Ma (9.59 and 8.21 Ma in Welker et al., 2020). The circumscription of this subtribe was recently expanded by Welker et al. (2020) and comprises 11 genera traditionally placed in Rottboelliinae: *Eremochloa* Buse (12 spp.; southern Asia to eastern Australia), *Glyphochloa* Clayton (9 spp.; India), *Hackelochloa* Kuntze (2 spp.; worldwide), *Hemarthria* R. Br. (14 spp.; Old World tropics), *Heteropholis* C.E. Hubb. (6 spp.; tropical Africa to Madagascar, and Sri Lanka), *Manisuris* L. (1 sp.; India), *Mnesithea* Kunth (26 spp., including *Coelorachis* Brongn.; worldwide), *Ophiuros* cf. Gaertn. (4 spp.; tropical Africa to China and Australia), *Ratzeburgia* Kunth (1 sp.; Myanmar), *Thaumastochloa* C.E. Hubb. (8 spp.; Maluku to northern Australia), and *Thyrsia* Stapf (4 spp.; tropical Africa and Asia). As a consequence, **Rottboelliinae** was drastically reduced and now includes only three genera: *Chasmopodium* Stapf (3 spp.; tropical Africa), *Coix* L. (4 spp.; tropical Asia), and *Rottboellia* Naezén (6 spp. in this strict sense; worldwide). The genus *Coix* has traditionally been placed in its own subtribe (e.g., Clayton & Renvoize, 1986; Soreng et al., 2017) but was transferred to Rottboelliinae by Welker et al. (2020). The stem and crown dates of Rottboelliinae are 7.4 and 5.26 Ma (9.07 and 5.11 Ma in Welker et al. (2020).

Members of Ratzeburgiinae and Rottboelliinae all have spikelets that lack awns (Clayton, 1973). In many species, the spikelets are embedded in concavities in the rachis with the indurate glume forming a sort of trap door; in this regard, they are morphologically similar to Tripsacinae and Rhytachninae. Generic limits in Ratzeburgiinae and Rottboelliinae are famously ill-defined, with many species having names in two or more genera; the group has been described as a "botanical black hole" (Veldkamp et al., 1986).

Elionurus (17 spp.; worldwide) and *Tripidium* (7 spp.; southern Europe to Indonesia, mainly India) were provisionally placed *incertae sedis* by Welker et al. (2020). *Elionurus* does not have a well-supported position in any recent phylogenies. There is some evidence that it may be an allopolyploid formed from particularly distant parents (McKain et al., unpublished data). In this study, *Elionurus* grouped within the subtribe Sorghinae. The most distinctive feature of the genus is the lower glume, which is keeled with hairs in tufts or lines on the keels. *Tripidium* has traditionally been considered a synonym of *Saccharum* L. and thus included in the subtribe Saccharinae Griseb. However, recent nuclear and plastome trees unequivocally showed that *Tripidium* is not closely related to *Saccharum* and other members of that subtribe (Welker et al., 2015, 2019, 2020; Lloyd Evans et al., 2019).

Ischaeminae J. Presl is the next subtribe to diverge and has stem and crown dates of 9.66 and 7.94 Ma, according to Welker et al. (2020). It includes four genera: *Andropterum* Stapf (1 sp.; tropical Africa), *Dimeria* R. Br. (61 spp.; India, southeastern Asia, Australia, and Polynesia), *Eulaliopsis* Honda (2 spp.; Afghanistan to Taiwan of China), and *Ischaemum* L. (88 spp.; worldwide). In both *Dimeria* and *Ischaemum*, the intercostal epidermal cells of the leaf have multiple papillae per cell, a character that is not otherwise common in the tribe (Watson & Dallwitz, 1992). The subtribe as a whole has no obvious synapomorphy. Ischaeminae was not recovered as monophyletic in our study.

The remaining Andropogoneae are divided into two main clades in our analyses. The first one includes subtribes Apludinae, Germainiinae, Saccharinae, and Sorghinae; the second one is formed by the "core Andropogoneae clade," which includes subtribes Anthistiriinae J. Presl and Andropogoninae J. Presl.

The subtribe **Apludinae** Hook. f. was recovered in this study as sister to the clade formed by Germainiinae, Saccharinae, and Sorghinae, but had an unclear position in the phylogeny of Welker et al. (2020). Apludinae has stem and crown ages of 11.85 and 11.06 Ma (9.02 and 8.4 Ma in Welker et al., 2020) and comprises seven genera: *Apluda* L. (1 sp.; tropical Asia to Australia), *Asthenochloa* Buse (1 sp.; Malesia), *Eulalia* (34 spp.; Old World tropics), *Homozeugos* Stapf (6 spp.; tropical Africa), *Polytrias* Hack. (1 sp.; tropical Asia and Africa), *Sorghastrum* Nash (21 spp.; tropical and subtropical America and Africa), and *Trachypogon* Nees (4 spp.; tropical and subtropical America and Africa). Even though few species of *Eulalia* have been sampled, the genus is polyphyletic in all recent phylogenetic studies (e.g., Estep et al., 2014; Welker et al., 2016, 2020; Arthan et al., 2017). However, the type of the genus (*Eulalia aurea* (Bory) Kunth) is placed within the Apludinae clade, so the genus sensu stricto will fall here (Welker et al., 2020). The phylogeny and morphology of this clade are poorly studied. Although subsets of the genera have been placed together in some studies (e.g., *Homozeugos* and *Trachypogon* by Kellogg, 2015), the circumscription of Apludinae reflects only recent studies such as the work of Welker et al. (2020). In many members of the clade, both the sessile and pedicellate spikelets are bisexual, although, in others (e.g., some species of *Sorghastrum*), the pedicellate spikelet is absent. A species-level phylogeny and morphological study of this group would shed light on the evolution of variation in sex expression and spikelet pair morphology in the tribe.

Germainiinae Clayton is sister to Saccharinae + Sorghinae and has stem and crown ages of 10.88 and 8.27 Ma (7.8 and 5.37 Ma in Welker et al., 2020). The subtribe comprises five genera: *Apocopis* Nees (16 spp.; Indian subcontinent to southern China and Malesia), *Germainia* Balansa & Poitr. (10 spp.; tropical and subtropical Asia to northern Australia), *Imperata* Cirillo (13 spp.; worldwide), *Lophopogon* Hack. (2 spp.; India), and *Pogonatherum* P. Beauv. (3 spp.; Arabian Peninsula to Japan). All members of Germainiinae lack lodicules and have a reduced number of stamens (1 or 2). Four of the genera (all except for *Imperata*) were also inferred to be related by Kellogg (2015) based on having glumes with a truncate apex and papillae of intercostal epidermal cells overarching the stomata. *Imperata cylindrica* (L.) Raeusch. (cogon grass) is highly invasive in some parts of the world (Holzmueller & Jose, 2011).

The subtribe **Saccharinae** has stem and crown dates of 9.64 and 6.66 Ma (4.91 and 3.89 Ma in Welker et al., 2020). Its circumscription was recently reduced (Welker et al., 2020), comprising now three genera: *Miscanthus* Andersson (30 spp., including *Miscanthidium* Stapf, *Narenga* Bor, and *Sclerostachya* (Andersson ex Hack.) A. Camus; Africa to southeastern Asia), *Pseudosorghum* A. Camus (2 spp.; China to tropical Asia), and *Saccharum* (32 spp., including *Erianthus* Michx.; worldwide). The generic delimitation of this group is complex, primarily due to polyploidization and reticulate evolution (Hodkinson et al., 2002; Welker et al., 2015, 2019), requiring more studies to define the circumscription of its genera (Vasquez et al., 2022). In species of *Miscanthus* and *Saccharum*, the spikelets of the spikelet pair are identical in morphology and sex expression, presumably representing a reversal from the ancestral character state for the relatives of the tribe (Kellogg, 2015). In contrast, *Pseudosorghum* is more similar to other Andropogoneae in having the sessile and pedicellate spikelets differentiated. The genus *Saccharum* includes sugarcane (*Saccharum officinarum* L.), the primary source of sugar for human consumption and a valuable source of ethanol for biofuel (Boddey et al., 2008; Cheavegatti-Gianotto et al., 2011).

Sorghinae has stem and crown ages of 9.64 and 8.23 Ma (6.63 and 4.68 Ma in Welker et al., 2020) and includes four genera: *Cleistachne* Benth. (1 sp.; tropical Africa, Arabian Peninsula, and India), *Lasiorhachis* (Hack.) Stapf (3 spp.; Madagascar), *Sarga* Ewart (9 spp.; Africa, southern Indonesia, Australia, Mexico, and Central America), and *Sorghum* Moench (24 spp.; worldwide). *Lasiorhachis* has been traditionally considered closely related to *Saccharum* in subtribe Saccharinae, but Vorontsova et al. (2020) showed that the genus is a close relative of *Sorghum*. This subtribe has no obvious morphological synapomorphy. Phylogenetic studies have found different placements of Sorghinae relative to Saccharinae (Estep et al., 2014; Vorontsova et al., 2020; Welker et al., 2020), with the differences possibly reflecting incomplete species sampling. *Sorghum* includes the economically important species *Sorghum bicolor* (L.) Moench, a species with a complex history of domestication in Africa (Fuller & Stevens, 2018; Smith et al., 2019).

The well-supported "**core Andropogoneae**" clade includes about half of the species of the tribe and is recovered in all recent phylogenies of Andropogoneae (e.g., Estep et al., 2014; Welker et al., 2016, 2020; Arthan et al., 2017). The clade has stem and crown ages of 12.09 and 10.29 Ma (8.63 and 7.84 Ma in Welker et al., 2020) and is formed by two subtribes, Anthistiriinae and Andropogoninae, both with a worldwide distribution. **Anthistiriinae** has stem and crown dates of 10.29 and 9.98 Ma (7.84 and 7.38 Ma in Welker et al., 2020) and includes 11 genera: *Agenium* Nees (4 spp.; Bolivia and Brazil to Argentina), *Bothriochloa* Kuntze (37 spp.; worldwide), *Capillipedium* Stapf (18 spp.; Old World tropics and subtropics), *Cymbopogon* Spreng. (59 spp.; Old World tropics and subtropics), *Dichanthium* Willemet (22 spp.; Old World tropics and subtropics), *Eremopogon* Stapf (4 spp.; tropical Africa and Asia), *Euclasta* Franch. (2 spp.; tropical America and tropical Africa to Myanmar), *Heteropogon* Pers. (6 spp.; worldwide), *Iseilema* Andersson (24 spp.; Indomalayan region and Australia), *Pseudanthistiria* (Hack.) Hook. f. (4 spp.; India to Thailand), and *Themeda* Forssk. (32 spp.; Old World tropics and subtropics). *Agenium* and *Pseudanthistiria* were not sampled in the phylogenetic study of Welker et al. (2020) and were placed *incertae sedis* by these authors. However, Arthan et al. (2021) demonstrated that both genera belong to Anthistiriinae. This subtribe was also recognized by Clayton & Renvoize (1986) but included quite a different set of genera.

Anthistiriinae, in its current circumscription, has no obvious synapomorphy. However, it includes several well-marked internal clades. Among these is the clade of *Bothriochloa*, *Capillipedium*, and *Dichanthium*. While diploid members of the genera are morphologically distinct and intersterile, tetra- and hexaploids are interfertile and form a species complex that was documented first by cytogenetic data (de Wet & Harlan, 1970) and more recently by DNA sequence data (Estep et al., 2014). Surprisingly, many of the allopolyploid plants are morphologically indistinguishable and are all classified as *Bothriochloa intermedia* (R. Br.) A. Camus (now *B. bladhii* (Retz.) S.T. Blake) despite having parents from all three genera. Harlan & de Wet (1963) called *B. intermedia* a compilospecies, reflecting this peculiar history. The genera *Themeda*, *Heteropogon*, *Cymbopogon*, and *Iseilema*, share the characters of homogamous spikelet pairs at the base of the inflorescence branches. Species of *Themeda* and *Heteropogon* are intermixed phylogenetically and form a clade in the work of Arthan et al. (2021), although in Welker et al. (2020), *H. triticeus* (R. Br.) Stapf ex Craib falls within *Cymbopogon*. Both Arthan et al. (2021) and Welker et al. (2020) agree that *Heteropogon* is not monophyletic.

Andropogoninae has stem and crown dates of 10.29 and 9.74 Ma (7.84 and 7.24 Ma in Welker et al., 2020) and is the largest subtribe of Andropogoneae, with about 300 species.

Its stem area is Indomalayan, but its crown area is clearly Afrotropical. It includes 11 genera: *Anadelphia* Hack. (14 spp.; tropical Africa), *Andropogon* (125 spp.; tropical and subtropical America, Africa, and Asia), *Bhidea* Stapf ex Bor (3 spp.; India), *Diectomis* Kunth (1 sp.; tropical America, Africa, and Asia), *Diheteropogon* (Hack.) Stapf (4 spp.; tropical and subtropical Africa), *Elymandra* Stapf (6 spp.; tropical Africa and southeastern Brazil), *Exotheca* Andersson (1 sp.; tropical Africa and mainland Southeast Asia), *Hyparrhenia* Andersson ex E. Fourn. (58 spp.; Old World tropics and subtropics), *Hyperthelia* Clayton (7 spp.; tropical and southern Africa), *Monocymbium* Stapf (3 spp.; tropical and southern Africa), and *Schizachyrium* Nees (70 spp.; worldwide). This subtribe lacks an obvious morphological synapomorphy, and unlike in Anthistiriinae, there are few well-marked internal clades. The genus *Andropogon* is polyphyletic (McAllister et al., 2018; Welker et al., 2020), although the individual "*Andropogon*" clades correspond reasonably well to sections of the genus (cf. Nagahama & Norrmann, 2012). Assuming the plastome tree topology is upheld by nuclear genes, it seems likely that *Andropogon* s.s. will include many fewer species than are currently assigned to the genus. *Schizachyrium* is also polyphyletic and will require taxonomic rearrangements as well (Welker et al., 2020, 2021; Peichoto et al., 2022). Species in *Andropogon* and *Schizachyrium* make up a major portion of the plants in the tallgrass prairie of North America and, along with *Hyparrhenia*, are a substantial component of the tropical African grasslands as well (Gould, 1967; Clayton, 1969; Gibson, 2009).

4.8 Aristidoideae (PMP)

The crown age for the **Aristidoideae** in our analysis is 43.99 Ma (stem age of 63.51 Ma), while Cerros-Tlatilpa et al. (2011) estimated 32.21 Ma (mean) for analysis 2, their oldest estimate. In our biogeographical analysis, the ancestral area for the stem (90%) and crown (43%) is Afrotropical (Fig. 2c). The subfamily consists of a single tribe, **Aristideae** C.E.Hubb, with three genera: *Aristida* L. (305 spp., 100 South American, 70 African, 59 Australasian, 48 Asian, 50 North American, and 5 Pacific); *Sartidia* De Winter (6 spp., African); and *Stipagrostis* Nees (56 spp., 48 African, 29 Asian, and 2 European; Clayton et al., 2016; Soreng et al., 2017). *Sartidia* (glabrous awns, 3-veined upper glume, lower glume 3–7-veined, all plants C_3) is sister to *Stipagrostis* (at least one awn plumose, C_4) plus *Aristida* (glabrous awns, 1-veined upper glume, lower glume usually 1-veined, most C_4) are derived (Cerros-Tlatilpa et al., 2011). The subfamily most likely arose in open and mesophytic habitats in Africa before radiating to other arid regions of the western hemisphere, Asia, and Australia (Bouchenak-Khelladi et al., 2010).

4.9 Arundinoideae (JKT)

The mean stem and crown ages of the **Arundinoideae** in our analysis are 55.1 and 49.9 Ma. These ages are only slightly older than the corresponding ages of ca. 48 and 46 Ma estimated for the subfamily in Hardion et al. (2017) using five plastid DNA loci. The stem area for the Arundinoideae in our biogeographical analysis is Afrotropical (38%) or Afrotropic + Indomalayan (14%), whereas the crown area is Afrotropical (39%) or Afrotropical + Australian (17%) (Fig. 2c). Despite considerable recent progress in removing taxa that were misplaced in Arundinoideae (Hardion et al., 2017; Teisher et al., 2017; Hardion et al., 2021), the remaining monophyletic assemblage is still highly heterogeneous. The reed habit that united members of the subfamily in early classifications is apparently the result of convergent evolution in two of its three tribes. Ecologically, most species occupy at least seasonally wet habitats, often on rocky substrates. The subfamily has a mostly Gondwanan distribution, though presumably resulting from dispersal if the estimated ages of the group are accurate.

Arundineae Dumort. comprises four genera (*Amphipogon* R.Br., *Arundo* L., *Dregeochloa* Conert, and *Monachather* Steud.) and has a mean stem and crown age of 39.01 and 49.9 Ma, respectively. The stem area for the Arundineae is Afrotropical (39%) or Afrotropics + Indomalayan (17%), whereas the crown area is Afrotropics + Indomalayan + Australian (24%), Afrotropics + Australian + Palaearctic (22%) or Indomalayan + Australian (15%). The tribe is characterized by glumes as long as or longer than the spikelets. *Arundo* (four species) is the earliest diverging and has a native distribution throughout warmer parts of the eastern hemisphere. The remaining three genera form a clade of xerophytic plants. *Dregeochloa* (two species) is restricted to southern Africa, while its monotypic sister genus *Monachather* is endemic to Australia. *Amphipogon* is the most diverse genus in the Arundinoideae, with nine accepted species also endemic to Australia.

The clade that is sister to the Arundineae has a mean stem and crown age of 49.9 and 40.93 Ma in our analysis. The members of this clade have glumes that are shorter than their spikelets and are divided into two distinct tribes.

Tribe **Crinipedeae** Hardion has a mean stem and crown age of 40.93 and 37.95 Ma. The stem area for the Crinipedeae is Afrotropical (50%), and the crown area is also Afrotropical (98%). This clade contains twelve species in six genera and corresponds roughly to the crinipoid group of Linder et al. (1997). An analysis of morphology in the Arundinoideae by Hardion et al. (2021) found that this tribe is the most homogenous cluster in the subfamily, possessing a caespitose habit, solid culms, paleas that are bifid or winged, and a unique (bi-)trilobate long silica body on the veins. All species in the group except for *Elytrophorus spicatus* (Willd.) A.Camus are restricted to Sub-Saharan Africa, including Madagascar, where they occupy mesophytic to helophytic habitats. *Elytrophorus* P.Beauv. contains two species and is sister to the former "*Eragrostis walteri*," now formalized as a new genus *Pratochloa* Hardion (Ingram et al., 2011; Hardion et al., 2018). Sister to these genera is a clade containing *Styppeiochloa* De Winter (three currently accepted species, with four additional species from Madagascar soon to be published (Teisher et al., in prep.) and *Crinipes* Hochst. (four species) (Teisher et al., 2017; Hardion et al., 2017). Hardion et al. (2021) found close relationships to *Crinipes* for two potentially extinct monotypic genera, *Leptagrostis* C.E.Hubb. and *Piptophyllum* C.E.Hubb., based on plastome and morphological analyses, respectively. *Piptophyllum* is now the only putative arundinoid genus that has not been included in molecular analysis.

Tribe **Molinieae** Jirásek has a mean stem and crown age of 40.93 and 7.08 Ma. This crown age is younger than the 15 Ma age found in Hardion et al. (2017), but that study noted a similarly long stem for this group and argued for a possible East Asian origin of its three or four genera. In our biogeographical analysis, the stem area is Afrotropical (50%), and the probable crown area is Cosmopolitan (68%). *Phragmites* Adans. is the most diverse of the four genera with four recognized species. *Phragmites australis* subsp. *americanus* Saltonstall, P.M. Peterson & Soreng is the only member of subfamily Arundinoideae with a native distribution in the New World (Saltonstall et al., 2004), with other *P. australis* subspecies occurring naturally on every continent except Antarctica. *Hakonechloa* Makino ex Honda is monotypic and native to Japan, while *Molinia* Schrank contains two species native to Europe, westernmost Asia, and parts of Northern Africa. Both genera are popular ornamentals and have been introduced in North America. *Moliniopsis* Hayata (one sp., far East Asia), with long hairs around the callus and elongated spikelets (versus callus glabrous or with short lateral lines of hairs and compact spikelets), is sometimes treated as a synonym of *Molinia*, but may be sister to *Hakonechloa* (Fig. 2c). All members of the Molinieae prefer wet habitats, while *Phragmites* and *Molinia* represent the only cold-tolerant taxa in the subfamily.

4.10 Micrairoideae (JKT)

The mean stem and crown ages of the **Micrairoideae** in our analysis are 55.1 and 41.21 Ma. The subfamily consists of three tribes as well as the Indian and Sri Lankan genus *Zenkeria* Trin. (Hardion et al., 2017) containing five species and treated here as *incertae sedis*. The inclusion of this Indian endemic in Micrairoideae complicates biogeographical interpretations in the subfamily, which would otherwise appear to have originated in northern Australia given the high levels of endemism of two of the three tribes on that continent. In our biogeographical analysis, the Micrairoideae stem area is Afrotropical (38%) or Afrotropic + Indomalayan (14%), whereas the crown area is Australasia (26%) or Indomalayan (19%) (Fig. 2c). Micrairoideae lack distinct synapomorphies, as evidenced by their inconsistent taxonomic history (Sánchez-Ken et al., 2007). However, most species in the group possess spikelets with two bisexual florets or with the proximal floret sterile or staminate. They typically occupy mesophytic to wet habitats or microhabitats within more xerophytic areas.

The **Micraireae** Pilg. is sister to *Zenkeria* in our analysis, and the combined clade has an estimated mean stem and crown age of 41.21 and 19.89 Ma. *Micraira* F.Muell. is the only genus in the tribe and contains 15 accepted species of Australian endemics. The Micraireae probable stem area is Australian (26%) or Indomalayan (19%), whereas the crown area is Australian + Indomalayan (77%), Australian (13%), or Indomalayan (10%). This genus is unique in possessing spiral phyllotaxis (Philipson, 1935) and forms dense mats capable of resurrecting after drought (Gaff & Latz, 1978). Carbon isotope ratios from two species of *Micraira* show that the genus uses C_3 photosynthesis (Teisher et al., 2019).

The clade sister to Micraireae plus *Zenkeria* contains tribes Eriachneae Eck-Borsboom and Isachneae Benth. and has a mean crown age of 27.25 Ma. The two tribes have mean crown ages of 7.72 and 21.66 Ma, respectively. Members of this clade share a germination flap in the spikelet and indurate florets. However, both characters can be found in the Panicoideae, accounting for the frequent placement of the genera of both tribes in that subfamily by previous authors (Sánchez-Ken et al., 2007).

Eriachneae consists of 51 accepted species in a single genus *Eriachne* R.Br. (treating *Pheidochloa* S.T.Blake as a synonym based on results in Teisher et al. 2019). This genus represents one of at least 22 independent origins of C_4 photosynthesis in the grasses (GPWG II, 2011). It occurs in open savannahs throughout Southeast Asia, the Malay Archipelago, and Australia, with all but a handful of species endemic to the latter country. Teisher et al. (2019) measured carbon isotope ratios for 27 species of Eriachneae and found that all were in the C_4 range and nonoverlapping with the typical C_3 values for Isachneae and Micraireae.

Six genera are recognized in **Isachneae**, based initially on leaf anatomy (reviewed in Iskandar & Veldkamp, 2004) and later supported by molecular data (Duvall et al., 2017; Teisher et al., 2017). Members of the Isachneae possess radiate chlorenchyma in the leaves, but carbon isotope data thus far have confirmed the tribe as entirely C_3 (Duvall et al., 2017; Teisher et al., 2017). *Isachne* R.Br. is the largest genus with 105 accepted species; however, phylogenetic analyses of plastomes by Duvall et al. (2017) and Teisher et al. (2017) suggest the genus may be paraphyletic, at least with respect to *Hubbardia* Bor (20 species) and monotypic *Limnopoa* C.E.Hubb., both of which are endemic to India. *Coelachne* R.Br. is the next most diverse genus with 12 recognized species and appears sister to the *Isachne-Hubbardia-Limnopoa* clade. The monotypic genus *Sphaerocaryum* Nees ex Hook. f. was recovered with members of the subfamily Panicoideae in this study and in a five-gene phylogeny of Chinese plants by Chen et al. (2016), but this result should be confirmed before removing the genus from the Micrairoideae; the sole species of *Heteranthoecia* Stapf has yet to be included in molecular analysis. The center of diversity for the tribe would appear to be Southeast Asia, with exceptions, including *Heteranthoecia* in central and western Africa, *Coelachne* extending throughout the Old World tropics, and *Isachne* occupying tropical habitats around the globe. Most species in the group are helophytes, in contrast to the upland grasslands favored by *Zenkeria*, the savannas inhabited by Eriachneae, and the rocky habitats of Micraireae. A worldwide revision of *Isachne* is currently lacking and needed to assess patterns of diversification and biogeography in the subfamily.

4.11 Danthonioideae (PMP)

The crown age of the **Danthonioideae** in our analysis is 51.17 Ma (stem age of 57.82 Ma), quite a bit older than earlier estimates of 30 Ma, where it was hypothesized the subfamily first occupied southern Africa and dispersed to the other areas primarily in the southern hemisphere, that is, New Zealand, Australia, and South America before eventually colonizing North America and Europe (Linder et al., 2013). The subfamily contains 292 species in 19 genera (Linder et al., 2010; Soreng et al., 2017). The Danthonioideae stem area is Afrotropical (85%), and the crown area is Afrotropical (97%) (Fig. 2C). Bouchenak-Khelladi et al. (2010) previously estimated the crown area as Africa/Madagascar (84%).

Merxmuellera Conert (7 spp., African, all with leaf blades disarticulating above the ligule) is basal and sister to all remaining members of the subfamily (Pirie et al., 2008;

Linder et al., 2010, 2013). The next split includes *Capeochloa* H.P. Linder & N. P. Barker (3 spp., African) + *Geochloa* H.P. Linder & N.P. Barker (3 spp., African) sister to the remaining members of the subfamily (Linder et al., 2010, 2013). *Pentameris* P. Beauv. (84 spp., 81 spp. African, 2 spp. Australasian, 1 sp. Asian, 1 sp. Antarctica; Clayton et al., 2016) is the next split followed by *Chionochloa* Zotov (25 spp., 22 endemic to New Zealand; 3 Australasian; Connor, 1991), each as sister to remaining members of the subfamily (Linder et al., 2010, 2013). The species of *Chionochloa* (tussock grasses often found at higher elevations) are hard to differentiate, and it has been suggested that hybridization among members is prevalent (Connor, 1991). The next split sister to the remaining species in the subfamily is the South American *Cortaderia* Stapf (21 spp.) (Linder et al., 2010, 2013). *Chaetobromus* Kunth (monotypic, African) + *Pseudopentameris* K. Schum. (2 spp., African) is the next split sister to the remaining species in the subfamily (Linder et al., 2010, 2013). There are only two major remaining clades left in the subfamily: *Rytidosperma* (76 spp., temperate and cool-temperate habitats in Australia, New Zealand, New Guinea, and South America) + *Schismus* P. Beauv. (5 spp., African with two species weedy and widespread) + *Tenaxia* N.P. Barker & H.P. Linder (8 spp., African and Asian) + *Tribolium* Desv. (16 spp., African and Australasia); and the *Danthonia* DC. clade that includes *Austroderia* N.P. Barker & H.P. Linder (5 spp., restricted to New Zealand) + *Chimaerochloa* H.P. Linder (monotypic, high elevations of New Guinea) + *Danthonia* (26 spp., western hemisphere and Europe) + *Notochloe* Domin (monotypic, Australia, alignment in this clade is based on plastid DNA sequences) + *Plinthanthesis* Steud. (3 spp., Australia) (Linder et al., 2010, 2013).

4.12 Chloridoideae (PMP)

The crown age of the **Chloridoideae** in our analysis is 54.71 Ma (stem age of 57.82), while Schubert et al. (2019b) determined 77.8 Ma. The subfamily stem and crown areas are Afrotropical (97%) which was earlier confirmed by Bouchenak-Khelladi et al. (2010) as Africa/Madagascar (82.5%) (Fig. 2c). Members of this subfamily share a single synapomorphy in having bicellular microhairs (Peterson et al., 2007, 2010a). Based on the Triraphideae being the basal lineage, Peterson et al. (2010a) indicated the Chloridoideae might have originated in Africa and/or Asia 60 million years ago. Hartley & Slater (1960) concluded the subfamily probably originated on the African continent. Since the Centropodieae P.M. Peterson, N.P. Barker & H.P. Linder, and Triraphideae P.M. Peterson include species currently distributed in Africa and southwestern Asia. Our data support these earlier hypotheses of origin for the Chloridoideae. The following seven genera have not yet been tested in a DNA sequence study and remain incertae sedis: *Gossweilerochloa* Renvoize, *Indopoa* Bor, *Lepturopetium* Morat, *Myriostachya* (Benth.) Hook.f., *Pogonochloa* C.E. Hubb., *Pseudozoysia* Chiov., and *Silentvalleya* V.J. Nair, Sreek, Vajr. & Bhargavan.

The **Centropodieae**, composed of two genera (*Centropodia* Rchb. and *Ellisochloa* P.M. Peterson & N.P. Barker), is sister to all other chloridoids with a crown age of 30.27 Ma and a stem age of 54.71 Ma (Peterson et al., 2011). The stem (97%) and crown (81%) area for the Centropodieae is Afrotropical. The two species of *Ellisochloa* are endemic to southern Africa (Namibia and South Africa) and are the only C_3 members of the subfamily, while all other species of Chloridoideae are C_4. The four species of *Centropodia* are found in Angola, Equatorial Guinea, Ethiopia, Kenya, Pakistan, Saudi Arabia, South Africa, and Sudan.

The next split in our cladogram, in order of divergence, is the **Triraphideae** P.M. Peterson (crown age 10.62 Ma, stem age 46.76 Ma) which includes three genera: *Nematopoa* C.E. Hubb. (monotypic), *Neyraudia* Hook. f. with four species, and *Triraphis* R. Br. with eight species. In our previous classifications (Soreng et al., 2015b, 2017), we placed *Nematopoa longipes* (Stapf & C.E. Hubb.) C.E. Hubb. as a synonym of *Triraphis* as originally described, and additionally, we include *Habrochloa* C.E. Hubb. (monotypic) in the Triraphideae. However, in our current tree, *Nematopoa longipes* (African) is sister to *Triraphis mollis* R. Br. (Australian, although most species in the genus occur in Africa) + *Neyraudia. reynaudiana* (Kunth) Keng ex Hitchc. (Asian) rendering *Triraphis* paraphyletic. In a molecular tree using plastid and ITS markers, Peterson et al. (2022a) found, *Habrochloa* + Nematopoa sister to *Neyraudia* + five species of *Triraphis. Nematopoa* can be separated from *Triraphis* in having 1-veined lemmas with a single awn, whereas species of *Triraphis* have 3-veined lemmas with each vein extending in an awn or mucro (Clayton et al., 2016). Hubbard (1935, 1957a, 1957b) transferred *Triraphis longipes* Stapf & C.E. Hubb. to *Crinipes* Hochst. (Arundinoideae) since it possessed a bearded callus, then later moved it to *Nematopoa*. The stem area for the Triraphideae is Afrotropical (83%) and the crown area is Afrotropical (35%), Afrotropical + Australian (11%) or Neotropics + Afrotropics + Australian + Palaearctic (11%). Members of the Triraphideae have long, slender bicellular microhairs, whereas all other species of Chloridoideae have bicellular microhairs with a broad, short terminal cell of the same thickness as the basal cell (Watson & Dallwitz, 1992; Peterson et al., 2010a).

Eragrostideae Stapf. (sister to Zoysieae + Cynodonteae) has a crown age of 31.15 Ma (stem age of 42.75) and contains three subtribes: Cotteinae Reeder (crown age of 18.69 Ma, stem age of 31.15 Ma) sister to Eragrostidinae J.Presl (crown age of 18.01 Ma, stem age of 23.68 Ma) + Uniolinae (crown age of 13.84 Ma, stem age of 23.68 Ma). The Eragrostideae probable stem (73%) and crown (43%) areas are Afrotropical.

Cotteinae contains four genera: *Cottea* Kunth (monotypic, western hemisphere); *Enneapogon* P. Beauv. (24 spp., 16 native to Australia, 8 spp. native to Africa, 1 sp. worldwide, probably naturalized in the western hemisphere; *Kaokochloa* de Winter (monotypic, Africa); and *Schmidtia* Steud. ex J.A. Schmidt (2 spp., Africa and Pakistan) (Weller & Lazarides, 2005; Peterson et al., 2010a; Clayton et al., 2016). Members of the Cotteinae have long, slender bicellular microhairs and 7–11-veined glumes (Renvoize, 1985; Clayton & Renvoize, 1986). The **Unioliinae** Clayton contains four genera: *Entoplocamia* Stapf, with a single spp., *Fingerhuthia* Nees with two species, and *Tetrachne* Nees with a single species, all distributed in Africa extending to Arabia and Pakistan; and *Uniola* L. with five species found in the western hemisphere. Species in the Uniolinae have chartaceous to coriaceous, 3–9-veined lemmas, disarticulation below the glumes, and spiciform panicles often with racemose branches (Clayton & Renvoize, 1986; Clayton et al., 2016).

Eragrostidinae includes *Eragrostis* Wolf and only two other genera, *Richardsiella* Elffers & Kenn.-O′Byrne and *Steirachne* Ekman, since we now recognize *Cladoraphis* Franch. and *Stiburus* Stapf as synonyms of *Eragrostis* (Barrett et al., 2020). *Richardsiella* and *Steirachne* have yet to be included in a molecular DNA study, although they will probably be subsumed within *Eragrostis*. Historically, the characters used to recognize the two species of *Cladoraphis* from other genera include 2- or 3-veined glumes (found in numerous species of *Eragrostis*), fruits with a free pericarp (found in at least two other species of *Eragrostis*), leaves that are needle-like and pungent, and panicles with a hard, woody rachis (Phillips, 1982; Clayton & Renvoize, 1986; Gibbs-Russel et al., 1990; Barrett et al., 2020). Based on a phenetic analysis of morphological traits, Phillips (1982) provided names in *Eragrostis* for the two species of *Stiburus*, and this was followed by Clayton and Renvoize (1986). In our tree, we sampled five species within the Eragrostidinae; four of these were once placed in other genera (*Catalepis* Stapf & Stent, *Cladoraphis*, *Harpachne Hochst. ex A.Rich.* and *Viguierella* A. Camus) and these are now subsumed into *Eragrostis* based on molecular studies (Barrett et al., 2020; Vorontsova, pers. comm.). *Eragrostis* is a large (448 species) and old (mid-Eocene) genus, perhaps derived from African ancestors now distributed throughout the world with centers of diversity in Africa, the western hemisphere, and Australia (Barrett et al., 2020; Peterson & Romaschenko, in prep.). *Eragrostis* is characterized by having multi-flowered spikelets, usually with 3-veined lemmas typically apically entire and rarely muticous or 1-awned (Lazarides, 1997; Veldkamp, 2002; Palmer et al., 2005; Barrett et al., 2020).

Zoysieae Benth. (sister to the Cynodonteae Dumort.) has a crown age of 19.27 Ma (stem age of 36.82 Ma) and consists of two subtribes, the Sporobolinae represented by two genera, *Sporobolus* R. Br. (220 species) and *Psilolemma* S.M. Phillips (monotypic), and the Zoysiinae with two genera, *Zoysia* Willd. (11 spp.) and *Urochondra* C.E. Hubb. (monotypic) (Peterson et al., 2014b, 2017b; Soreng et al., 2015b, 2017). The probable stem area for the Zoysieae is Afrotropical (46%) and Neotropics + Afrotropics (11%), whereas the crown area is Cosmopolitan (11%). *Sporobolus* is distributed worldwide, with centers of diversity in Africa, the western hemisphere, and Australia (Clayton et al., 1974; Lazarides, 1994; Simon & Jacobs, 1999; Simon, 2005; Peterson et al., 2007, 2014b). *Sporobolus* is characterized by single-flowered spikelets, 1-veined lemmas, fruit with free pericarps, and ligules a ciliate membrane or line of hairs (Peterson et al., 2014b).

Cynodonteae has a crown age of 32.66 Ma (stem age of 36.82 Ma) and consists of 25 subtribes, two supertribes, and 125 genera (Peterson et al., 2014a, 2015b, 2016, 2017a; Soreng et al., 2017). Earlier DNA sequence-derived phylogenies depict low resolution among the subtribes, perhaps indicating rapid radiation, so the order of our discussion addressing the subtribes is somewhat arbitrary

(Peterson et al., 2010a, 2014a, 2015b, 2016, 2017a). In our biogeographical analysis, the Cynodonteae probable stem area is Afrotropical (46%) and Neotropics + Afrotropics (11%), whereas the crown area is Neotropics + Afrotropics (28%), Afrotropics (23%), or Nearctic + Afrotropics (15%). Africa might have been the area of origin for the Cynodonteae since the basal clades in each of the lineages after the first split into two poorly supported clades consists of species with primarily African or Asian distribution (Peterson et al., 2014a, 2016, 2017b). In previous studies, two strongly supported and derived clades in the Cynodonteae, the supersubtribe Boutelouodinae P.M. Peterson & Romasch. (Allolepiinae P.M. Peterson, Romasch. & Y. Herrera, Boutelouinae Stapf, Jouveinae P.M. Peterson, Romasch. & Y. Herrera, Kaliniinae P.M. Peterson, Romasch. & Y. Herrera, Monanthochloinae Pilg. ex Potztal, Muhlenbergiinae Pilg., Scleropogoninae Pilg., Sohnsiinae P.M. Peterson, Romasch. & Y. Herrera, and Traginae P.M. Peterson & Columbus) is composed almost entirely of western hemisphere species while the supersubtribe Gouiniodinae P.M. Peterson & Romasch. (Cteniinae P.M. Peterson, Romasch. & Y. Herrera, Farragininae P.M. Peterson, Romasch. & Y. Herrer, Gouiniinae P.M. Peterson & Columbus, Hubbardochloinae Auquier, Perotidinae P.M. Peterson, Romasch. & Y. Herrera, Trichoneurinae P.M. Peterson, Romasch. & Y. Herrera, and Zaqiqahinae P.M. Peterson, Romasch. & Y. Herrera) includes primarily African and some western hemisphere species (Peterson et al., 2014a, 2016, 2017a, 2020a). Six genera within the Cynodonteae have not yet been included in a DNA sequence study (incertae sedis): *Kampochloa* Clayton, *Lepturidium* Hitchc. & Ekman, *Pommereulla* L.f., *Rheochloa* Filg., P.M. Peterson & Y. Herrera, *Sclerodactylon* Griseb., and *Vietnamochloa* Veldkamp & Nowack.

Within **Boutelouodinae** (crown age of 30.04 Ma, stem age of 31.71 Ma), subtribe Traginae (*Monelytrum* Hack., monotypic, African; *Orthacanthus* P.M. Peterson & Romasch., monotypic, African; *Pogononeura* Napper, monotypic, African; *Polevansia* De Winter, monotypic, African; *Tragus* Haller, 8 spp., African and one species in Australia; *Willkommia* Hack., 4 spp., western hemisphere and African) has a crown age of 16.31 Ma (stem age of 30.04 Ma) and is basal to other subtribes in this supertribe. Muhlenbergiinae (*Muhlenbergia* Gmel. with 183 spp., western hemisphere with a stem age of 21.69 Ma; a crown age of 9.3 Ma was found in Peterson et al. (2022d) is the next split and is basal to remaining subtribes (listed here in alphabetical order): Allolepiinae (*Allolepis* Soderstr. & H.F. Decker, monotypic, North American), Boutelouinae (*Bouteloua* Lag., 60 spp., western hemisphere with a stem age of 17.75 Ma), Hilariinae (*Hilaria* Kunth, 10 spp., North and Central America with a stem age of 21.69 Ma), Jouveinae (*Jouvea* E. Fourn., two spp., Mexico and Central America), Kaliniinae (*Kalinia* H.L. Bell & Columbus, monotypic, North American), Monanthochloinae (crown age of 14.72 Ma; *Distichlis* Raf., 11 spp., all western hemisphere and one species Australian), Scleropogoninae (crown age of 23.73 Ma, stem age of 28.31 Ma; *Blepharidachne* Hack., 4 spp., western hemisphere; *Dasyochloa* Willd. ex Rydb., monotypic, western hemisphere; *Erioneuron* Nash, 3 spp., western hemisphere; *Munroa* Torr., 5 spp. western hemisphere; *Scleropogon* Phil., monotypic, western hemisphere; and *Swallenia* Soderstr. & H.F. Decker, monotypic, California); and Sohnsiinae (*Sohnsia* Airy Shaw, monotypic, Mexico) (Peterson et al., 2010a, 2010b, 2015a, 2016, 2017a, 2018; Amarilla et al., 2015).

Sister to Boutelouodinae is subtribe **Pappophorinae** Dumort. (crown age of 18.02 Ma, stem age of 32.66 Ma) which includes three genera: *Pappophorum* Schreb. (8 spp., western hemisphere), *Neesiochloa* Pilg. (monotypic, Brazil), and *Tridens* Roem. & Schult. (16 spp., western hemisphere) as treated in Peterson et al. (2016). In our analysis, which is based on a much smaller sample and with missing genera representing all subtribes, Pappophorinae is sister to all other subtribes and supersubtribes in the Cynodonteae Dumort. Sister to Pappophorinae + Boutelouodinae is **Tripogoninae** Stapf. with a crown age of 25.03 Ma (stem age of 30.24 Ma) in Peterson et al. (2016), the latter subtribe includes seven genera: *Desmostachya* (Stapf) Stapf (monotypic, African and Asian), *Eragrostiella* Bor (6 spp., Asian, African, one species in Australia), *Halopyrum* Stapf (monotypic, African and Asian), *Melanocenchris* Nees (3 spp., African and Asian), *Oropetium* Trin. (6 spp., African and Asian), *Tripogon* Roem. & Schult. (46 spp., Asian and African), and *Tripogonella* P.M. Peterson & Romasch. (3 spp., *T. minima* (A. Rich.) P.M. Peterson & Romasch. from Africa, *T. loliiformis* (F. Muell.) P.M. Peterson & Romasch. from Australia, and *T. spicata* (Nees) P.M. Peterson & Romasch. from the western hemisphere). In our current treatment the Tripogoninae is sister to Dactylocteniinae + Orcuttinae + Gouinodinae + Eleusininae + Orininae + Triodiinae + Aleuropodinae.

Within **Gouiniodinae** (crown age of 27.86 Ma, stem age of 29.27 Ma), **Zaqiqahinae** a (stem age of 14.44 Ma) includes a single genus, *Zaqiqah* P.M. Peterson, Romasch. & Y. Herrera (monotypic, East Africa and the Arabian Penninsula, *Z. mucronata* (Forssk.) P.M. Peterson & Romasch.) that is sister to remaining members of the supertribe (Peterson et al., 2014b, 2016). The next split in the Gouiniodinae is the Gouiniinae P.M. Peterson & Columbus (crown age of 17.22 Ma, stem age of 21.57 Ma) that includes six genera: *Gouinia* E. Fourn. ex Benth. & Hook. (14 spp., western hemisphere), *Schenckochloa* J.J. Ortiz (monotypic, South American), *Tridentopsis* P.M. Peterson (2 spp., North American), *Triplasiella* P.M. Peterson & Romasch. (monotypic, *T. eragrostoides* (Vasey & Scribn.) P.M. Peterson & Romasch., western hemisphere), *Triplasis* P. Beauv. (2 spp., western hemisphere), and *Vaseyochloa* Hitchc. (monotypic, Texas) (Peterson et al., 2014b, 2016). Sister to Gouiniinae are the remaining subtribes in the Gouiniodinae where Cteniinae + Trichoneurinae form a clade sister to Hubbardochloinae (Farragininae + Perotidinae) (Peterson et al., 2016, 2017a).

The **Cteniinae** (stem age of 14.00 Ma) includes a single genus, *Ctenium* Panz. with 20 species primarily distributed in Africa, the western hemisphere, and Asia (Peterson et al., 2014b; Soreng et al., 2017). Sister to Cteniinae is the Trichoneurinae (stem age of 12.44 Ma) represented by a single genus, *Trichoneura* Anderrson (8 spp., African, western hemisphere, Asian). Both Cteniinae and Trichoneurinae have nearly equal representations of the number of species occurring in Africa and the western hemisphere. In an earlier DNA sequence-derived phylogeny of seven species of *Trichoneura*, species of African distribution appear in two successive basal clades indicating a possible origin in Africa (Peterson et al., 2014a).

Farragininae contains two genera, *Craspedorhachis* Benth. (3 spp., African) and *Farrago* Clayton (monotypic, African), and **Perotidinae** (crown age of 7.53 Ma, stem age of 14.0 Ma) contains three genera, *Mosdenia* Stent (monotypic, African), *Perotis* Aiton (16 spp., African and Asian), and *Trigonochloa* P.M. Peterson & N. Snow (2 spp., African and Asian) (Snow & Peterson, 2012; Peterson et al., 2014a, 2020a). Peterson et al. (2014b) found *Trigonochloa* basal and sister to *Mosdenia* + *Perotis*.

Sister to Farragininae and Perotidinae is **Hubbardochloinae** (crown age of 15.28 Ma, stem age of 19.12 Ma) with nine genera: *Bewsia* Gooss. (monotypic, African), *Decaryella* E. Camus (monotypic, African), *Dignathia* Stapf (5 spp., African and Asian), *Gymnopogon* P. Beauv. (14 spp., western hemisphere), *Hubbardochloa* Auquier (monotypic, African), *Leptocarydion* Hochst. ex Stapf (monotypic, African), *Leptothrium* Kunth (3 spp., African and western hemisphere), *Lophachne* Stapf (2 spp., African), and *Tetrachaete* Chiov. (monotypic, African) (Peterson et al., 2014a, 2020a). The Hubbardochloinae probably originated in Africa since most species of *Dignathia* and *Leptothrium* (sister to the *Dignathia-Tetrachaete* clade in Peterson et al., 2020a) are distributed in Africa or temperate Asia (Clayton & Renvoize, 1986; Clayton et al., 2016). The Gouiniodinae also probably originated in Africa or Asia, since *Zaqiqah* P.M. Peterson & Romasch. (basal and sister to all other genera in the supersubtribe, see Peterson et al., 2020a) occurs in Ethiopia, Saudi Arabia, Somalia, Socotra, and Yemen (Peterson et al., 2016).

In Peterson et al. (2016), **Gouiniodinae** is sister to Orcuttiinae (crown age of 13.13 Ma, stem age of 24.26 Ma) with two genera: *Neostapfia* Burtt Davy (monotypic, California) and *Orcuttia* Vasey (8 spp., North American), and this was found in our study. Sister to Orcuttiinae + Gouiniodinae is Triodiinae (Aeluropodinae + Orininae). The Triodiinae (crown age of 9.18 Ma, stem age of 21.18 Ma) is represented by a single genus, *Triodia* R. Br. (69 spp., Australasia excluding New Zealand) (Edgar & Connor, 2010).

Aeluropodinae P.M. Peterson includes two genera *Aleuropus* Trin. (6 spp., Eurasian and African) and *Odyssea* Stapf (monotypic, African). *Odyssea paucinervis* (Nees) Stapf might have had multiple or reticulate origins since plastid DNA sequences place it sister to *Neobouteloua* Gould in the Dactylocteniinae P.M.Peterson, Romasch. & Y.Herrera while nuclear ITS and At103 sequences place it sister to *Aeluropus* Trin. (Peterson et al., 2016). Morphologically, *Odyssea* is similar to *Aeluropus* in having elongated rhizomes, stiff and pungent leaf blades, inflorescences composed of racemes borne on a central axis, multiple-flowered spikelets, and mucronate lemmas (Peterson et al., 2016). In our study, the Dactylocteniinae is sister to the Gouiniodinae.

Sister to Aeluropodinae is **Orininae** P.M.Peterson, Romasch. & Y.Herrer, which consists of two genera, *Cleistogenes* Keng (14 spp., Asian with 2 spp. that extend to Europe) and *Orinus* Hitchc. (3 spp., Asian) (Peterson et al., 2016). The crown age for *Orinus* was estimated to be 2.85 Ma based on a study of plastid, nrITS, and AFLPs of 88 populations representing all three species found in the dry grasslands of the Qinghai-Tibet Plateau (Liu et al., 2018).

Sister to all subtribes in the Cynodonteae, Peterson et al. (2016) found Dactylocteniinae + Eleusininae pair. **Dactylocteniinae** (crown age of 20.96 Ma, stem age of 27.86 Ma) consists of four genera: *Acrachne* Wight & Arn. ex Chiov. (3 spp., African and Asian), *Brachychloa* S.M. Phillips (2 spp., African), *Dactyloctenium* Willd. (13 spp., African, Asian, and Australasian), and *Neobouteloua* (2 spp., South American) (Peterson et al., 2016; Soreng et al., 2017). *Acrachne racemosa* (B. Heyne ex Roem. & Schult.) Ohwi might have had multiple origins since the plastid DNA sequences place it within the Eleusininae Dumort., while nuclear ITS and At103 sequences indicate it is sister to *Dactyloctenium* (Peterson et al., 2015b, 2016, unpubl.). The other two species of *Acrachne* have not yet been tested in a DNA-based phylogeny.

Eleusininae [crown age of 25.85 Ma, stem age of 27.38 Ma, and an inferred ancestral crown area in the Afrotropics (90%)] currently consists of 212 species in 28 genera, and evolutionary relationships among the genera are, at best, tentatively understood (Peterson et al., 2015b Soreng et al., 2017). In our newest analysis, *Diplachne* P. Beauv. (2 spp., African, Asian, and Australian) is basal to the remaining genera (Snow et al., 2018; Peterson et al., 2022b). As documented previously, *Dinebra* Jacq. (21 spp., African, Australasian, North American) is unresolved and, based on nuclear DNA signal, appears outside of the Eleusininae, whereas the plastid DNA signal places it inside the subtribe (Peterson et al., 2012, 2015b, 2016). This appears to be another case of hybridization and subsequent genomic introgression (Peterson et al., 2016). Strongly supported clades within the subtribe include *Coelachyrum* Hochst. & Nees (5 spp., African and Asian; includes *Apochiton* C.E. Hubb.; Peterson et al., 2022b) sister to *Eleusine* Gaertn. (11 spp., African, Asian, Australasian, and South America; Liu et al., 2011; Peterson et al., 2015b, 2022b). *Leptochloa* P.Beauv. (8 spp., North American, South American, Central America, and Australian) is strongly supported in a clade sister to *Dinebra* + the remaining genera in the subtribe (Peterson et al., 2022b; Snow et al., in prep.). *Astrebla* F. Muell. (4 spp., Australasian) + *Austrochloris* Lazarides (monotypic, Australian) is sister to the remaining genera in the subtribe (Peterson et al., 2022b). *Disakisperma* Steud. (4 spp., African and western hemisphere) is then sister to remaining genera (Peterson et al., 2022b). The next basal split includes a strongly supported clade with *Schoenefeldia* Kunth (monotypic, African and Asian) + *Schoenefeldiella* P.M. Peterson (monotypic, African) + *Afrotrichloris* Chiov. (2 spp., African) (Peterson et al., 2022b). Of the remaining genera in the Eleusininae, *Enteropogon* Nees (17 spp., African, Asian, Australasian, Pacific, and South American), *Chloris* Sw. (57 spp., South American, African, North America, Asian, Australasian, and Pacific), and *Tetrapogon* Desf. (10 spp., African, Asian, North American, and South American) are the next three successive basal splits to the remaining genera (Peterson et al., 2015b). Based on molecular DNA markers for six species of *Lepturus* R. Br. (16 spp., African, Asian, Australasia, and Pacific), *Lepturus* + *Daknopholis* Clayton (monotypic, African) is the next basal split to the remaining genera (Peterson et al., unpubl.). Morphologically, *Daknopholis* seems far removed from *Lepturus* in having exerted, laterally compressed spikelets and laterally compressed caryopses versus embedded (in the rachis), dorsally compressed spikelets, and terete to dorsally compressed caryopses (Peterson et al., 2015b; Clayton et al., 2016). *Oxychloris* Lazarides (monotypic, Australian) + *Harpochloa* Kunth (2 spp., African) with *Microchloa* R. Br. (6 spp., African, Asian, Australasia, and western hemisphere) is the next basal split to the remaining genera (Peterson et al., 2015b, 2022b). The next two successive basal splits include *Micrachne* P.M. Peterson, Romasch. & Y. Herrera (5 spp., African and Australasian) and *Eustachys* Desv (16 spp., South American, North American, Asian, Australasia, and Pacific) (Peterson et al., 2015b). The most derived split in the Eleusininae includes *Chrysochloa* Swallen (4 spp., African) (Peterson et al., 2015b) sister to *Cynodon* Rich. (25 spp., African, western hemisphere, Asian, Australasian, Pacific, and European) + *Stapfochloa* H. Scholz (6 spp., western hemisphere and African) (Peterson et al., 2015b). The species of *Cynodon s.l.* appear to be undergoing rapid speciation since many morphological forms do not always segregate in shared lineages in our DNA studies (Peterson et al., 2015b). Therefore, any estimate of the number of species in *Cynodon* is tentative since the taxonomy is poorly understood. The exact alignment of *Neostapfiella* A. Camus (3 spp., African), *Pommereulla* L.f. (monotypic, Asian), and *Rheochloa* Filg, P.M. Peterson & Y. Herrera (monotypic, Goiás, Brazil) within Eleusininae has not yet been confirmed by molecular analyses.

Conflict of Interest

The authors have no conflicts of interest concerning the information presented in this manuscript.

References

Acosta JM, Scataglini MA, Reinheimer R, Zuloaga FO. 2014. A phylogenetic study of subtribe Otachyriinae (Poaceae, Panicoideae, Paspaleae). *Plant Systematics and Evolution* 300: 2155–2166.

Acosta JM, Zuloaga FO, Reinheimer R. 2019. Nuclear phylogeny and hypothesized allopolyploidization events in the subtribe Otachyriinae (Paspaleae, Poaceae). *Systematics and Biodiversity* 17: 277–294.

Adegoke OS, Jan du Chene RE, Agumanu AE, Ajayi PO. 1978. Palynology and age of the Kerri-Kerri formation, Nigeria. *Revista Espanola de Micropaleontologia* 10: 267–283.

Alonso A. 2015. *Multi-genomic evolution, ancestral reconstruction, dating, and design of microsatellites in the tribe Bromeae (Pooideae, Poaceae)*. Dissertation. León: University of León. 1–302.

Amarilla LD, Chiapella JO, Sosa V, Moreno NC, Anton AM. 2015. A tale of North and South America: Time and mode of dispersal of the amphitropical genus *Munroa* (Poaceae, Chloridoideae). *Botanical Journal of the Linnean Society* 179: 110–125.

Arthan W, Mckain MR, Traiperm P, Welker CAD, Teisher JK, Kellogg EA. 2017. Phylogenomics of Andropogoneae (Panicoideae: Poaceae) of Mainland Southeast Asia. *Systematic Botany* 42: 418–431.

Arthan W, Dunning L, Besnard G, Manzi S, Kellogg EA, Hackel J, Lehmann CER, Mitchley J, Vorontsova MS. 2021. Complex evolutionary history of two ecologically significant grass genera, *Themeda* and *Heteropogon* (Poaceae: Panicoideae: Andropogoneae). *Botanical Journal of the Linnean Society* 196: 437–455.

Bamboo Phylogeny Group (BPG). 2012. An updated tribal and subtribal classification of the bamboos (Poaceae: Bambusoideae). *The Journal of the American Bamboo Society* 24: 1–10.

Banfi E, Galasso G, Foggi B, Kopecký D, Ardenghi NMG. 2017. From *Schedonorus* and *Micropyropsis* to *Lolium* (Poaceae: Loliinae): New combinations and typifications. *Taxon* 66: 708–717.

Barberá P, Romero-Zarco C, Aedo C. 2017. Taxonomic revision of Trisetum section *Acrospelion* (Poaceae: Pooideae: Aveninae) from Eurasia. *Systematic Botany* 42: 754–781.

Barberá P, Soreng RJ, Peterson PM, Romaschenko K, Quintanar A, Aedo C. 2020. Molecular phylogenetic analysis resolves *Trisetum* (Poaceae: Pooideae: Koeleriinae) polyphyletic: Evidence for a new genus, *Sibirotrisetum* and resurrection of *Acrospelion*. *Journal of Systematics and Evolution* 58: 517–526.

Barberá P, Quintanar A, Peterson PM, Soreng RJ, Romaschenko K, Barberá P, Quintanar A, Peterson PM, Soreng RJ, Romaschenko K, Aedo C. 2019. New combinations, new names, typifications, and a new section, sect. *Hispanica*, in *Koeleria* (Poeae, Poaceae). *Phytoneuron* 46: 1–13.

Barkworth ME, Anderton LK, Capels KM, Long S, Piep MB, Roché CT, Vorobik LA, Miller A, Gunn BF, Roberts C, Blankenship MS. 2007. *Manual of grasses for North America*. Logan: Intermountain Herbarium and Utah State University Press.

Barrett RL, Peterson PM, Romaschenko K. 2020. A molecular phylogeny of *Eragrostis* (Poaceae: Chloridoideae: Eragrostideae): Making lovegrass monophyletic in Australia. *Australian Systematic Botany* 33: 458–476.

Bernhardt N, Brassac J, Kilian B, Blattner FR. 2017. Dated tribe-wide whole chloroplast genome phylogeny indicates recurrent hybridizations within Triticeae. *BMC Evolutionary Biology* 17: 141.

Besnard G, Christin PA, Malé PJG, Coissac E, Ralimanana H, Vorontsova MS. 2013. Phylogenomics and taxonomy of Lecomtelleae (Poaceae), an isolated panicoid lineage from Madagascar. *Annals of Botany* 112: 1057–1066.

Bess EC, Doust AN, Davidse G, Kellogg EA. 2006. *Zuloagaea*, a new genus of neotropical grass within the 'bristle clade' (Poaceae: Paniceae). *Systematic Botany* 31: 656–670.

Blattner FR. 2004. Phylogenetic analysis of *Hordeum* (Poaceae) as inferred by nuclear rDNA ITS sequences. *Molecular Phylogenetics and Evolution* 33: 289–299.

Boddey RM, Soares LHDB, Alves BJR, Urquiaga S. 2008. Bio-ethanol production in Brazil. In: Pimentel, D ed. *Biofuels, solar and wind as renewable energy systems: Benefits and risks*. Dordrecht: Springer Netherlands. 321–356

Bond WJ, Midgley GF, Woodward FI. 2003. The importance of low atmospheric CO_2 and fire in promoting the spread of grasslands and savannas. *Global Change Biology* 9: 973–982.

Bouchenak-Khelladi Y, Salamin N, Savolainen V, Forest F, Bank M, van der, Chase MW, Hodkinson TR. 2008. Large multi-gene phylogenetic trees of the grasses (Poaceae): Progress towards complete tribal and generic level sampling. *Molecular Phylogenetics and Evolution* 47: 488–505.

Bouchenak-Khelladi Y, Verboom GA, Savolainen V, Hodkinson TR. 2010. Biogeography of the grasses (Poaceae): A phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society* 162: 543–557.

Bouckaert R, Vaughan TG, Barido-Sottani J, Duchêne S, Fourment M, Gavryushkina A, Heled J, Jones G, Kühnert D, De Maio N, Matschiner M, Mendes FK, Müller NF, Ogilvie HA, Du Plessis L, Popinga A, Rambaut A, Rasmussen D, Siveroni I, Suchard MA, Wu CH, Xie D, Zhang C, Stadler T, Drummond AJ. 2019. BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLoS Computational Biology* 15: e1006650.

Bredow M, Walker VK. 2017. Ice-binding proteins in plants. *Frontiers in Plant Science* 8: 2153.

Bredow M, Tomalty HE, Smith L, Walker VK. 2018. Ice and anti-nucleating activities of an ice-binding protein from the annual grass, *Brachypodium distachyon*. *Plant Cell and Environment* 41: 983–992.

Bremer K. 2002. Gondwanan evolution of the grass alliance of families (Poales). *Evolution* 56: 1374–1387.

Brown AJ 2013. *Delimitation, diversification and adaptation in* Lachnagrostis. Dissertation. Adelaide: University of Adelaide.

Brown AJ. 2015. A morphological search for *Lachnagrostis* among the South African *Agrostis* and *Polypogon* (Poaceae). *Muelleria* 34: 23–46.

Burke SV, Lin C-S, Wysocki WP, Clark LG, Duvall MR. 2016a. Phylogenomics and plastome evolution of tropical forest grasses (*Leptaspis, Streptochaeta*: Poaceae). *Frontiers in Plant Science* 7: 1–12.

Burke SV, Wysocki WP, Zuloaga FO, Craine JM, Pires JC, Edger PP, Mayfield-Jones D, Clark LG, Kelchner SA, Duvall MR. 2016b. Evolutionary relationships in Panicoid grasses based on plastome phylogenomics (Panicoideae; Poaceae). *BMC Plant Biology* 16: 1–11.

But P. 2007. *Pleuropogon* R. Br. In: Flora of North America Editorial Committee ed. *Flora of North America*. New York: Oxford University Press. 24: 103–109.

Cabi E, Soreng RJ, Çingay B, Karabacak E. 2015. A new species of *Bellardiochloa, B. doganiana* (Poaceae), from the Taurus Mountains of Turkey. *Phytotaxa* 205: 123–128.

Cabi E, Soreng RJ, Gillespie LJ, Boudko E. 2017. *Alopecurus goekyigitiana* (Poaceae, subtribe Alopecurinae *sensu stricto*), a new species from Turkey based on morphological and molecular investigation. *Turkish Journal of Botany* 41: 189–199.

Cai ZM, Zhang YX, Zhang LN, Gao LM, Li DZ. 2012. Testing four candidate barcoding markers in temperate woody bamboos (Poaceae: Bambusoideae). *Journal of Systematics and Evolution* 50(6): 527–539.

Calvo J, Moreira-Muñoz A. 2018. First record of *Ehrharta longiflora* Sm. (Poaceae, Ehrharteae) for South America. *Check List* 14: 475–478.

Catalán P, Kellogg EA, Olmstead RG. 1997. Phylogeny of Poaceae subfamily Pooideae based on chloroplast ndhF gene sequences. *Molecular Phylogenetics and Evolution* 8: 150–166.

Catalán P, López-Álvarez D, Díaz-Pérez A, Sancho R, López-Herránz ML. 2015. Phylogeny and Evolution of the Genus *Brachypodium*In: Vogel Jed. *Genetics and genomics of Brachypodium. Plant genetics and genomics: Crops and models*. ChamSpringer9–38.

Catalán P, Olmstead RG. 2000. Phylogenetic reconstruction of the genus *Brachypodium* P. Beauv. (Poaceae) from combined sequences of chloroplast ndhF gene and nuclear ITS. *Plant Systematics and Evolution* 220: 1–19.

Cayouette J, Darbyshire S. 2007. *Schizachne* Hack. In: Flora of North America Editorial Committee ed. *Flora of North America*. New York: Oxford University Press. 24: 103–104.

Cerros-Tlatilpa R, Travis Columbus J, Barker NP. 2011. Phylogenetic relationships of *Aristida* and relatives (Poaceae, Aristidoideae) based on noncoding chloroplast (TRNL-F, RPL16) and nuclear (ITS) DNA sequences. *American Journal of Botany* 98: 1868–1886.

Chadwick MJ. 1960. *Nardus stricta* L. *The Journal of Ecology* 48: 255.

Cheavegatti-Gianotto A, de Abreu HMC, Arruda P, Bespalhok Filho JC, Burnquist WL, Creste S, di Ciero L, Ferro JA, de Oliveira Figueira AV, de Sousa Filgueiras T, Grossi-de-Sá M, de F, Guzzo EC, Hoffmann HP, de Andrade Landell MG, Macedo N, Matsuoka S, de Castro Reinach F, Romano E, da Silva WJ, de Castro Silva Filho M, César Ulian E. 2011. Sugarcane (*Saccharum x officinarum*): A Reference Study for the Regulation of Genetically Modified Cultivars in Brazil. *Tropical Plant Biology* 4: 62–89.

Chen ZD, Yang T, Lin L, Lu LM, Li HL, Sun M, Liu B, Chen M, Niu YT, Ye JF, Cao ZY, Liu HM, Wang XM, Wang W, Zhang JB, Meng Z, Cao W, Li JH, Wu SD, Zhao HL, Liu ZJ, Du ZY, Wang QF, Guo J, Tan XX, Su JX, Zhang LJ, Yang LL, Liao YY, Li MH, Zhang GQ, Chung SW, Zhang J, Xiang KL, Li RQ, Soltis DE, Soltis PS, Zhou SL, Ran JH, Wang XQ, Jin XH, Chen YS, Gao TG, Li JH, Zhang SZ, Lu AM, Chen ZD, Lu AM, Kong HZ, Wang XQ, Wang YZ, Zhou SL, Zhang SZ, Wang XM, Liu ZJ, Wang QF, Li JH, Li DZ, Yi TS, Hong MA, Soltis DE, Soltis PS, Li JH, Fu CX, Liu QX. 2016. Tree of life for the genera of Chinese vascular plants. *Journal of Systematics and Evolution* 54: 277–306.

Chiapella J, Zuloaga FO. 2010. A revision of *Deschampsia, Avenella*, and *Vahlodea* (Poaceae, Poeae, Airinae) in South America. *Annals of the Missouri Botanical Garden* 97: 141–162.

Christin PA, Besnard G, Samaritani E, Duvall MR, Hodkinson TR, Savolainen V, Salamin N. 2008. Oligocene CO_2 decline promoted C_4 photosynthesis in grasses. *Current Biology* 18: 37–43.

Christin PA, Edwards EJ, Besnard G, Boxall SF, Gregory R, Kellogg EA, Hartwell J, Osborne CP. 2012. Adaptive evolution of C4 photosynthesis through recurrent lateral gene transfer. *Current Biology* 22: 445–449.

Christin PA, Spriggs E, Osborne CP, Strömberg CAE, Salamin N, Edwards EJ. 2014. Molecular dating, evolutionary rates, and the age of the grasses. *Systematic Biology* 63: 153–165.

Cialdella AM, Giussani LM, Aagesen L, Zuloaga FO, Morrone O. 2007. A phylogeny of *Piptochaetium* (Poaceae: Pooideae: Stipeae) and related genera based on a combined analysis including trnL-F, rpl16, and morphology. *Systematic Botany* 32: 545–559.

Cialdella AM, Sede SM, Romaschenko K, Peterson PM, Soreng RJ, Zuloaga FO, Morrone O. 2014. Phylogeny of *Nassella* (Stipeae, Pooideae, Poaceae) based on analyses of chloroplast and nuclear ribosomal DNA and morphology. *Systematic Botany* 39: 814–828.

Clark LG, Kobayashi M, Mathews S, Spangler RE, Kellogg EA. 2000. The Puelioideae, a new subfamily of Poaceae. *Systematic Botany* 25: 181–187.

Clark LG, Londoño X, Ruiz-Sanchez E. 2015. Bamboo taxonomy and habitat. In: Liese W, Köhl M eds. *Bamboo: The plant and its uses*. Switzerland: Springer International Publishing. 10: 1–30.

Clark LG, Oliveira R 2018. Diversity and evolution of the new world bamboos (Poaceae: Bambusoideae: Bambuseae, Olyreae). In: Lucas S ed. *11th World Bamboo Congress Proceedings*. Plymouth: World Bamboo Organization. 35–47.

Clayton WD. 1969. A revision of the genus *Hyparrhenia*. *Kew Bulletin Additional Series* 2: 1–196.

Clayton WD. 1972. Gramineae. In: Hepper FN ed. *Flora of West Tropical Africa*. London: Crown Agents for Oversea Governments and Administrations. 349–512

Clayton WD. 1973. The awnless genera of Andropogoneae: Studies in the Gramineae: XXXIII. *Kew Bulletin* 28: 49.

Clayton WD, Phillips SM, Renvoize SA. 1974. *Flora of Tropical East Africa. Gramineae (Part 2)*. London: Crown Agents for Oversea Governments and Administrations.

Clayton WD, Renvoize SA. 1986. Genera graminum. Grasses of the World. *Kew Bulletin Additional Series* 13: 1–389.

Clayton WD, Vorontsova MS, Harman KT, Williamson H. 2016. *GrassBase—The Online World Grass Flora*: The Board of Trustees,Royal Botanic Gardens [online]. Available from http://www.kew.org/data/grasses-db.html [accessed 23 July 2021]

Connor HE. 1991. *Chionochloa* Zotov (Gramineae) in New Zealand. *New Zealand Journal of Botany* 29: 219–282.

Cotton JL, Wysocki WP, Clark LG, Kelchner SA, Pires JC, Edger PP, Mayfield-Jones D, Duvall MR. 2015. Resolving deep relationships of PACMAD grasses: A phylogenomic approach. *BMC Plant Biology* 15: 1–11.

Crepet WL, Feldman GD. 1991. The earliest remains of grasses in the fossil record. *American Journal of Botany* 78: 1010–1014.

Da Silva LN, Essi L, Iganci JRV, De Souza-Chies TT. 2020. Advances in the phylogeny of the South American cool-season grass genus *Chascolytrum* (Poaceae, Pooideae): A new infrageneric classification. *Botanical Journal of the Linnean Society* 192: 97–120.

Da Silva LN, Saarela JM, Essi L, De Souza-chies TT. 2022. [2021]. A comprehensive species sampling sheds light on the molecular phylogenetics of Calothecinae (Poaceae, Pooideae, Poeae): Evidence for a new subtribe and multiple genera within the *Chascolytrum* clade. *Journal of Systematics and Evolution* 60: 691–712.

Darriba D, Taboada GL, Doallo R, Posada D. 2012. JModelTest 2: More models, new heuristics and parallel computing. *Nature Methods* 9: 772.

Davidse G, Ellis RP. 1984. *Steyermarkochloa unifolia*, a new genus from Venezuela and Colombia (Poaceae: Arundinoideae: Steyermarkochloeae). *Annals of the Missouri Botanical Garden* 71: 994–1012.

Davidse G, Soreng RJ, Peterson PM. 2009. *Agrostopoa* (Poaceae, Pooideae, Poeae, Poinae), a new genus with three species from Colombia. *Novon* 19: 32–40.

de Carvalho MLS, de Jesus ISD, Bezerra HB, Oliveira ILC, van den Berg C, Schnadelbach AS, Clark LG, Oliveira RP. 2021. Phylogenetics of *Piresia* (Poaceae: Bambusoideae) reveals unexpected generic relationships within Olyreae with taxonomic and biogeographic implications. *Taxon* 70: 492–514.

de Lange PJ, Smissen RD, Rolfe JR, Ogle CC. 2016. Systematics of *Simplicia* Kirk (Poaceae, Agrostidinae)—An endemic, threatened New Zealand grass genus. *PhytoKeys* 75: 119–144.

de Wet JMJ, Harlan JR. 1970. Apomixis, polyploidy, and speciation in *Dichanthium*. *Evolution* 24: 270–277.

Di Pietro R, Kuzmanović N, Iamonico D, Lakušić D. 2017. Nomenclatural and taxonomic notes on *Sesleria* sect. Argenteae (Poaceae). *Phytotaxa* 309: 101–117.

Díaz-Pérez AJ, Sharifi-Tehrani M, Inda LA, Catalán P. 2014. Polyphyly, gene-duplication and extensive allopolyploidy framed the evolution of the ephemeral *Vulpia* grasses and other fine-leaved Loliinae (Poaceae). *Molecular Phylogenetics and Evolution* 79: 92–105.

Duvall MR, Burke SV, Clark DC. 2020. Plastome phylogenomics of Poaceae: Alternate topologies depend on alignment gaps. *Botanical Journal of the Linnean Society* 192: 9–20.

Duvall MR, Fisher AE, Columbus JT, Ingram AL, Wysocki WP, Burke SV, Clark LG, Kelchner SA. 2016. Phylogenomics and plastome evolution of the chloridoid grasses (Chloridoideae: Poaceae). *International Journal of Plant Sciences* 177: 235–246.

Duvall MR, Yadav SR, Burke SV, Wysocki WP. 2017. Grass plastomes reveal unexpected paraphyly with endemic species of Micrairoideae from India and new haplotype markers in Arundinoideae. *American Journal of Botany* 104: 286–295.

Edgar E, Connor HE. 1982. *Dichelachne* (Gramineae) in New Zealand. *New Zealand Journal of Botany* 20: 303–309.

Edgar E, Connor HE. 2010. *Flora of New Zealand, Vol. V, Gramineae*. Lincoln: Manaaki Whenua Press.

Edmeades GO, Trevisan W, Prasanna BM, Campos H. 2017. Tropical maize (*Zea mays* L.). In: Campos H, Caligari PDS eds. *Genetic* *improvement of tropical crops*. Springer International Publishing. 57–109

Edwards EJ, Smith SA. 2010. Phylogenetic analyses reveal the shady history of C4 grasses. *Proceedings of the National Academy of Sciences of the United States of America* 107: 2532–2537.

Essi L, Longhi-Wagner HM, Chies TTDS. 2017. A synopsis of *Briza, Brizochloa*, and *Chascolytrum* (Poaceae, Pooideae, Poeae). *Annals of the Missouri Botanical Garden* 102: 466–519.

Estep MC, McKain MR, Diaz DV, Zhong J, Hodge JG, Hodkinson TR, Layton DJ, Malcomber ST, Pasquet R, Kellogg EA. 2014. Allopolyploidy, diversification, and the Miocene grassland expansion. *Proceedings of the National Academy of Sciences of the United States of America* 111: 15149–15154.

Ferreira FM, Oliveira RP, Welker CAD, da Costa Dórea M, de Carvalho Lima AL, Oliveira ILC, dos Santos F, de AR, van den Berg C, Clark LG. 2019. Phylogenetic relationships within Parianinae (Poaceae: Bambusoideae: Olyreae) with emphasis on *Eremitis*: Evidence from nuclear and plastid DNA sequences, macromorphology, and pollen ectexine patterns. *Molecular Phylogenetics and Evolution* 139: 1–17.

Finot VL, Soreng RJ, Giussani LM, Muñoz RG. 2018. A multivariate morphometric delimitation of species boundaries in the South American genus *Nicoraepoa* (Poaceae: Pooideae: Poeae). *Plant Systematics and Evolution* 304: 679–697.

Fuller DQ, Stevens CJ. 2018. *Sorghum* domestication and diversification: A current archaeobotanical perspective. In: Mercuri A, D'Andrea A, Fornaciari R, Höhn A eds. *Plants and people in the African Past: Progress in African Archaeobotany*. Springer International Publishing. 427–452

Gaff DF, Latz PK. 1978. The occurrence of resurrection plants in the Australian flora. *Australian Journal of Botany* 26: 485–492.

Gallaher TJ, Adams DC, Attigala L, Burke SV, Craine JM, Duvall MR, Klahs PC, Sherratt E, Wysocki WP, Clark LG. 2019. Leaf shape and size track habitat transitions across forest–grassland boundaries in the grass family (Poaceae). *Evolution* 73: 927–946.

Gallaher TJ, Akbar SZ, Klahs PC, Marvet CR, Senske AM, Clark LG, Strömberg CAE. 2020. 3D shape analysis of grass silica short cell phytoliths: a new method for fossil classification and analysis of shape evolution. *New Phytologist* 228: 376–392.

Gibbs-Russel GE, Watson L, Koekemoer M, Smook L, Barker NP, Anderson HM, Dallwitz MJ. 1990. Grasses of Southern Africa. *Memoirs of the Botanical Survey of South Africa* 58: 1–437.

Gibson DJ. 2009. *Grasses and grassland ecology*. New York: Oxford University Press.

Gillespie LJ, Soreng RJ, Bull RD, de Lang PJ, Smissen RD. 2022. Morphological and phylogenetic evidence for subtribe Cinninae and two new subtribes, Hookerochloinae and Dupontiinae (Poaceae tribe Poeae PPAM clade). *Taxon* 71: 52–84.

Gillespie LJ, Soreng RJ, Cabi E, Amiri N. 2018. Phylogeny and taxonomic synopsis of *Poa* subgenus *Pseudopoa* (including *Eremopoa* and *Lindbergella*) (Poaceae, Poeae, Poinae). *PhytoKeys* 111: 69–102.

Gillespie LJ, Soreng RJ, Jacobs SWL. 2009. Phylogenetic relationships of Australian *Poa* (Poaceae: Poinae), including molecular evidence for two new genera, *Saxipoa* and *Sylvipoa*. *Australian Systematic Botany* 22: 413–436.

Gillespie LJ, Soreng RJ, Bull RD, Jacobs SWL, Refulio, Rodrıguez NF. 2008. Phylogenetic relationships in subtribe Poinae (Poaceae, Poeae) based on nuclear ITS and plastid *trnT-trnL-trnF* sequences. *Botany. An International Journal for Plant Biology* 86: 938–967.

Gillespie LJ, Soreng RJ, Paradis M, Bull RD. 2010. Phylogeny and Reticulation in Subtribe Poinae and Related Subtribes (Poaceae) Based on nrITS, ETS, and trnTLF data. In: Seberg O, Petersen G, Barfod AS, Davis JI eds. *Diversity, phylogeny, and evolution in the Monocotyledons*. Aarhus: Aarhus University Press. 589–617

Giussani LM, Cota-Sánchez JH, Zuloaga FO, Kellogg EA. 2001. A molecular phylogeny of the grass subfamily Panicoideae (Poaceae) shows multiple origins of C_4 photosynthesis. *American Journal of Botany* 88: 1993–2012.

Giussani LM, Gillespie LJ, Scataglini MA, Negritto MA, Antón AM, Soreng RJ. 2016. Breeding system diversification and evolution in American *Poa* supersect. *Homalopoa* (Poaceae: Poeae: Poinae). *Annals of Botany* 118: 281–303.

Gledhill D. 1968. *Axonopus*: an African relict or an introduction from America. *Journal of the West African Scientific Association* 11: 20–27.

Gnutikov AA, Nosov NN, Punina EO, Probatova NS, Rodionov AV. 2020. On the placement of *Coleanthus subtilis* and the subtribe Coleanthinae within Poaceae by new molecular phylogenetic data. *Phytotaxa* 468: 243–274.

Goh WL, Chandran S, Franklin DC, Isagi Y, Koshy KC, Sungkaew S, Yang HQ, Xia NH, Wong KM. 2013. Multi-gene region phylogenetic analyses suggest reticulate evolution and a clade of Australian origin among paleotropical woody bamboos (Poaceae: Bambusoideae: Bambuseae). *Plant Systematics and Evolution* 299: 239–257.

Gómez-Sánchez M, González-Ledesma M, Koch SD. 1998. *Triniochloa gracilis* (Gramineae: Pooideae), a new species from the Sierra Madre del sur, Mexico, and a key to the species of the genus. *Novon* 8: 144–146.

Gould FW. 1967. The grass genus *Andropogon* in the United States. *Brittonia* 19: 70–76.

Grass Phylogeny Working Group (GPWG). 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Annals of the Missouri Botanical Garden* 88: 373–457.

Grass Phylogeny Working Group II (GPWG II). 2011. New grass phylogeny resolves deep evolutionary relationships and discovers C_4 origins. *New Phytologist* 193: 304–312.

Guindon S, Gascuel O. 2003. A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* 52: 696–704.

Guo C, Guo ZH, Li DZ. 2019a. Phylogenomic analyses reveal intractable evolutionary history of a temperate bamboo genus (Poaceae: Bambusoideae). *Plant Diversity* 41: 213–219.

Guo C, Ma P-F, Yang G-Q, Ye X-Y, Guo Y, Liu J-X, Liu Y-L, Eaton DAR, Guo Z-H, Li D-Z. 2021. Parallel ddRAD and genome skimming analyses reveal a radiative and reticulate evolutionary history of the temperate bamboos. *Systematic Biology* 70: 756–773.

Guo ZH, Ma PF, Yang GQ, Hu JY, Liu YL, Xia EH, Zhong MC, Zhao L, Sun GL, Xu YX, Zhao YJ, Zhang YC, Zhang YX, Zhang XM, Zhou MY, Guo Y, Guo C, Liu JX, Ye XY, Chen YM, Yang Y, Han B, Lin CS, Lu Y, Li DZ. 2019b. Genome sequences provide insights into the reticulate origin and unique traits of woody bamboos. *Molecular Plant* 12: 1353–1365.

Hackel J, Vorontsova MS, Nanjarisoa OP, Hall RC, Razanatsoa J, Malakasi P, Besnard G. 2018. Grass diversification in Madagascar: In situ radiation of two large C_3 shade clades and support for a Miocene to Pliocene origin of C_4 grassy biomes. *Journal of Biogeography* 45: 750–761.

Hamasha HR, von Hagen KB, Röser M. 2012. *Stipa* (Poaceae) and allies in the Old World: Molecular phylogenetics realigns genus circumscription and gives evidence on the origin of American and Australian lineages. *Plant Systematics and Evolution* 298: 351–367.

Handley L, O'Halloran A, Pearson PN, Hawkins E, Nicholas CJ, Schouten S, McMillan IK, Pancost RD. 2012. Changes in the hydrological cycle in tropical East Africa during the Paleocene-Eocene Thermal Maximum. *Palaeogeography, Palaeoclimatology, Palaeoecology* 329–330: 10–21.

Hardion L, Peterson PM, Soreng RJ. 2018. Validation of *Pratochloa* (Poaceae: Arundinoideae) and a new combination, *P. walteri* based on *Eragrostis walteri*. *Phytoneuron* 31: 1–3.

Hardion L, Verlaque R, Haan-Archipoff G, Cahen D, Hoff M, Vila B. 2017. Cleaning up the grasses dustbin: Systematics of the Arundinoideae subfamily (Poaceae). *Plant Systematics and Evolution* 303: 1331–1339.

Hardion L, Verlaque R, Kaymak E, Vila B, Haan-Archipoff G, Martinez Martin M, Tournay F, Migliore J. 2021. Plastome sequencing of a 167-year-old herbarium specimen and classical morphology resolve the systematics of two potentially extinct grass species. *Botanical Journal of the Linnean Society* 195: 115–123.

Harlan JR, de Wet JMJ. 1963. The compilospecies concept. *Evolution* 17: 497–501.

Hartley W, Slater C. 1960. Studies on the origin, evolution, and distribution of the Gramineae III. The tribes of the subfamily Eragrostoideae. *Australian Journal of Botany* 8: 256–276.

Hempel W. 2004. Die infragenerische Gliederung der Gattung *Melica* L. *Haussknechtia* 10: 169–198.

Hempel W. 2012. Revision und Phylogenie der Arten der Gattung *Melica* L. (Poaceae) in Eurasien und Nordafrika. *Feddes Repertorium* 122: 1–253.

Hochbach A, Schneider J, Röser M. 2015. A multi-locus analysis of phylogenetic relationships within grass subfamily Pooideae (Poaceae) inferred from sequences of nuclear single-copy gene regions compared with plastid DNA. *Molecular Phylogenetics and Evolution* 87: 14–27.

Hodkinson TR, Chase MW, Lledó MD, Salamin N, Renvoize SA. 2002. Phylogenetics of *Miscanthus, Saccharum*, and related genera (Saccharinae, Andropogoneae, Poaceae) based on DNA sequences from ITS nuclear ribosomal DNA and plastid trnL intron and trnL-F intergenic spacers. *Journal of Plant Research* 115: 381–392.

Holzmueller EJ, Jose S. 2011. Invasion success of cogongrass, an alien C_4 perennial grass, in the southeastern United States: Exploration of the ecological basis. *Biological Invasions* 13: 435–442.

Huang W, Zhang L, Columbus JT, Hu Y, Zhao Y, Tang L, Guo Z, Chen W, McKain M, Bartlett M, Huang CH, Li DZ, Ge S, Ma H. 2022. A well-supported nuclear phylogeny of Poaceae and implications for the evolution of C4 photosynthesis. *Molecular Plant* 15: 755–777.

Hubbard CE. 1935. Notes on African Grasses: XVIII. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 5: 306–311.

Hubbard CE. 1957a. Notes on African Grasses: XXVII. *Crinipes* Hochst., a Genus of Grasses from North East Tropical Africa. *Kew Bulletin* 12: 54–58.

Hubbard CE. 1957b. Notes on African grasses: XXV. *Nematopoa*, a new genus from Southern Rhodesia. *Kew Bulletin* 12: 51–52.

Humphreys AM, Linder HP. 2013. Evidence for recent evolution of cold tolerance in grasses suggests current distribution is not limited by (low) temperature. *New Phytologist* 198: 1261–1273.

Inda LA, Sanmartín I, Buerki S, Catalán P. 2014. Mediterranean origin and Miocene-Holocene Old World diversification of meadow fescues and ryegrasses (*Festuca* subgenus *Schedonorus* and *Lolium*). *Journal of Biogeography* 41: 600–614.

Inda LA, Segarra-Moragues JG, Müller J, Peterson PM, Catalán P. 2008. Dated historical biogeography of the temperate Loliinae (Poaceae, Pooideae) grasses in the northern and southern hemispheres. *Molecular Phylogenetics and Evolution* 46: 932–957.

Ingram AL, Christin P-A, Osborne CP. 2011. Molecular phylogenies disprove a hypothesized C_4 reversion in *Eragrostis walteri* (Poaceae). *Annals of Botany* 107: 321–325. https://doi.org/10.1093/aob/mcq226

Iskandar EAP, Veldkamp JF. 2004. A Revision of Malesian *Isachne* sect. *Isachne* (Gramineae, Panicoideae, Isachneae). *Reinwardtia* 12: 159–179.

Jacobs BF, Kingston JD, Jacobs LL. 1999. The origin of grass-dominated ecosystems. *Annals of the Missouri Botanical Garden* 86: 590–643.

Jannink TA, Veldkamp JF. 2002. Revision of Chionachninae (Gramineae: Andropogoneae). *Blumea: Journal of Plant Taxonomy and Plant Geography* 47: 545–580.

Jin C, Ciochon RL, Dong W, Hunt RM, Liu J, Jaeger M, Zhu Q. 2007. The first skull of the earliest giant panda. *Proceedings of the National Academy of Sciences of the United States of America* 104: 10932–10937.

Judziewicz EJ, Clark LG. 2007. Classification and biogeography of new world grasses: Anomochlooideae, Pharoideae, Ehrhartoideae, and Bambusoideae. *Aliso: A Journal of Systematic and Evolutionary Botany* 23: 303–314.

Katoh K, Misawa K, Kuma KI, Miyata T. 2002. MAFFT: A novel method for rapid multiple sequence alignment based on fast Fourier transform. *Nucleic Acids Research* 30: 3059–3066.

Katoh K, Rozewicki J, Yamada KD. 2018. MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20: 1160–1166.

Katoh K, Standley DM 2013. MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. Molecular Biology and Evolution 30: 772–780.

Kelchner SA, Bamboo Phylogeny Group. 2013. Higher-level phylogenetic relationships within the bamboos (Poaceae: Bambusoideae) based on five plastid markers. *Molecular Phylogenetics and Evolution* 67: 404–413.

Kellogg EA. 2015. Flowering plants. Monocots Poaceae. In: Kubitski K. ed. *The families and genera of vascular plants*. St. Louis, Cham: Springer International. 1–416

Kellogg EA, Aliscioni SS, Morrone O, Pensiero J, Zuloaga F. 2009. A phylogeny of *Setaria* (Poaceae, Panicoideae, Paniceae) and related genera based on the chloroplast gene ndhF. *International Journal of Plant Sciences* 170: 117–131.

Kodela P, Weiller C, Thompson I. 2009. *Pentapogon*. In: Wilson A ed. *Flora of Australia*. 44A (Poaceae 2): Melbourne: ABRS, Canberra/CSIRO Publishing. 233–236.

Krawczyk K, Nobis M, Nowak A, Szczecińska M, Sawicki J. 2017. Phylogenetic implications of nuclear rRNA IGS variation in *Stipa* L. (Poaceae). *Scientific Reports* 7.

Kuzmanović N, Barina Z, Šída O, Lakušić D. 2015. Typification of names in the group Coerulans of the genus *Sesleria* (Poaceae). *Phytotaxa* 202: 103–120.

Kuzmanović N, Lakušić D, Frajman B, Alegro A, Schönswetter P. 2017. Phylogenetic relationships in Seslerieae (Poaceae) including resurrection of *Psilathera* and *Sesleriella*, two monotypic genera endemic to the Alps. *Taxon* 66: 1349–1370.

Landis MJ, Matzke NJ, Moore BR, Huelsenbeck JP. 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* 62: 789–804.

Lazarides M. 1994. 119. Sporobolus. In: Dassanayake MD ed. *A revised handbook of the flora of Ceylon, vol. 8, Poaceae*. New Delhi: Amerind Publishing Company. 8: 419–429.

Lazarides M. 1997. A Revision of *Eragrostis* (Eragrostideae, Eleusininae, Poaceae) in Australia. *Australian Systematic Botany* 10: 77–187.

Lehmann C, Griffith D, Simpson K, Anderson TM, Archibald S, Beerling D, Bond W, Denton E, Edwards E, Forrestel E, Fox D, Georges D, Hoffmann W, Kluyver T, Mucina L, Pau S, Ratnam J, Salamin N, Santini B, Smith M, Spriggs E, Westley R, Still C, Strömberg C, Osborne C. 2019. Functional diversification enabled grassy biomes to fill global climate space. *bioRxiv*: 583625.

Lima JF, Leite KRB, Clark LG, Oliveira RP. 2021. Notes on leaf micromorphology of the rare herbaceous bamboo *Buergersiochloa bambusoides* Pilg. (Olyreae, Poaceae) from New Guinea and its taxonomic implications. *PhytoKeys* 172: 135–143.

Lima JF, Leite KRB, Clark LG, de Oliveira RP. 2020. Leaf micromorphology in Poaceae subtribe Olyrinae (Bambusoideae) and its systematic implications. *Botanical Journal of the Linnean Society* 192: 184–207.

Linder HP, Antonelli A, Humphreys AM, Pirie MD, Wüest RO. 2013. What determines biogeographical ranges? Historical wanderings and ecological constraints in the danthonioid grasses. *Journal of Biogeography* 40: 821–834.

Linder HP, Baeza M, Barker NP, Galley C, Humphreys AM, Lloyd KM, Orlovich DA, Pirie MD, Simon BK, Walsh N, Verboom GA. 2010. A generic classification of the Danthonioideae (Poaceae). *Annals of the Missouri Botanical Garden* 97: 306–364.

Linder HP, Lehmann CE, Archibald S, Osborne CP, Richardson DM. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.

Linder HP, Verboom GA, Barker NP. 1997. Phylogeny and evolution in the *Crinipes* group of grasses (Arundinoideae: Poaceae). *Kew Bulletin* 52: 91–110.

Liu H, Osborne CP. 2015. Water relations traits of C_4 grasses depend on phylogenetic lineage, photosynthetic pathway, and habitat water availability. *Journal of Experimental Botany* 66: 761–773.

Liu JX, Zhou MY, Yang GQ, Zhang YX, Ma PF, Guo C, Vorontsova MS, Li DZ. 2020. ddRAD analyses reveal a credible phylogenetic relationship of the four main genera of *Bambusa-Dendrocalamus-Gigantochloa* complex (Poaceae: Bambusoideae). *Molecular Phylogenetics and Evolution* 146: 106758.

Liu Q, Triplett JK, Wen J, Peterson PM. 2011. Allotetraploid origin and divergence in *Eleusine* (Chloridoideae, Poaceae): Evidence from low-copy nuclear gene phylogenies and a plastid gene chronogram. *Annals of Botany* 108: 1287–1298.

Liu YP, Ren ZM, Harris AJ, Peterson PM, Wen J, Su X. 2018. Phylogeography of *Orinus* (Poaceae), a dominant grass genus on the Qinghai-Tibet Plateau. *Botanical Journal of the Linnean Society* 186: 202–223.

Lloyd Evans D, Joshi SV, Wang J. 2019. Whole chloroplast genome and gene locus phylogenies reveal the taxonomic placement and relationship of *Tripidium* (Panicoideae: Andropogoneae) to sugarcane. *BMC Evolutionary Biology* 19: 1–20.

Ma PF, Zhang YX, Zeng CX, Guo ZH, Li DZ. 2014. Chloroplast phylogenomic analyses resolve deep-level relationships of an intractable bamboo tribe Arundinarieae (Poaceae). *Systematic Biology* 63: 933–950.

Magallón S, Gómez-Acevedo S, Sánchez-Reyes LL, Hernández-Hernández T. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* 207(2): 437–453.

Martínez-y-Pérez JL, Mejía-Saules MT, Sosa V. 2008. A taxonomic revision of *Luziola* (Poaceae: Oryzeae). *Systematic Botany* 33(4): 702–718.

Matthei O. 1975. Der *Briza*-Komplex in SüdAmerika: *Briza, Calotheca, Chascolytrum, Poidium* (Gramineae). Eine Revision. (The *Briza*-Complex: *Briza, Calotheca, Chascolytrum*, and *Poidium* (Gramineae) in South-America. A Revision). *Willdenowia. Beiheft* 8: 1–168.

Matzke NJ. 2012. Founder-event speciation in BioGeoBEARS package dramatically improves likelihoods and alters parameter inference in Dispersal-Extinction-Cladogenesis (DEC) analyses. *Frontiers of Biogeography* 4(suppl. 1): 210.

Matzke NJ. 2013a. Probabilistic historical biogeography: New models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Frontiers of Biogeography* 5: 242–248.

Matzke NJ. 2013b. BioGeoBEARS: BioGeography with Bayesian (and Likelihood) Evolutionary Analysis in R Scripts. R package, version 0.2 1 [online]. Available from http://CRAN.R-project.org/package=BioGeoBEARS [accessed 2 November 2021].

Matzke NJ. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63: 951–970.

McAllister CA, McKain MR, Li M, Bookout B, Kellogg EA. 2018. Specimen-based analysis of morphology and the environment in ecologically dominant grasses: The power of the herbarium. *Philosophical Transactions of the Royal Society B* 374: 20170403.

McLoughlin S. 2001. The breakup history of Gondwana and its impact on pre-Cenozoic floristic provincialism. *Australian Journal of Botany* 49: 271–300.

Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: 2010 Gateway Computing Environments Workshop, GCE 2010. 14 Nov. 2010, New Orleans, LA, 1–8.

Minaya M, Hackel J, Namaganda M, Brochmann C, Vorontsova MS, Besnard G, Catalán P, Catalan P. 2017. Contrasting dispersal histories of broad- and fine-leaved temperate Loliinae grasses: Range expansion, founder events, and the roles of distance and barriers. *Journal of Biogeography* 44: 1980–1993.

Morrone O, Aliscioni SS, Veldkamp JF, Pensiero JF, Zuloaga FO, Kellogg EA. 2013. Revision of the Old World species of *Setaria* (Poaceae: Panicoideae: Paniceae). *Systematic Botany Monographs* 96: 1–154.

Morrone O, Aagesen L, Scataglini 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.

Nagahama N, Norrmann GA. 2012. Review of the Genus *Andropogon* (Poaceae: Andropogoneae) in America Based on Cytogenetic. *Studies. Journal of Botany* 2012: 1–9.

Naz N, Rafique T, Hameed M, Ashraf M, Batool R, Fatima S. 2014. Morpho-anatomical and physiological attributes for salt tolerance in sewan grass (*Lasiurus scindicus* Henr.) from Cholistan Desert, Pakistan. *Acta Physiologiae Plantarum* 36: 2959–2974.

Nicola MV, Lizarazu MA, Scataglini MA. 2015. Phylogenetic analysis and taxonomic position of section *Verrucosa* of *Panicum* and its relationship with taxa of the *Sacciolepis–Trichanthecium* clade

(Poaceae: Panicoideae: Paniceae). *Plant Systematics and Evolution* 301: 2247–2260.

Nobis M, Gudkova PD, Nowak A. 2019. *Neotrinia* gen. nov. and *Pennatherum* sect. nov. in *Achnatherum* (Poaceae: Stipeae). *Turczaninowia* 22: 37–41.

Oliveira ILC, Matos AO, Silva C, Carvalho MLS, Tyrrell CD, Clark LG, Oliveira RP. 2020a. Delving deeper into the phylogenetics of the herbaceous bamboos (Poaceae, Bambusoideae, Olyreae): Evaluation of generic boundaries within the *Parodiolyra*/*Raddiella*. clade uncovers a new genus. *Botanical Journal of the Linnean Society* 192: 61–81.

Oliveira RP, Silva C, Welker CAD, Da Dórea MC, Oliveira ILC, Vieira JPS, Leite KRB, Clark LG. 2020b. Reinterpreting the phylogenetic position, systematics, and distribution of the *Raddia-Sucrea* lineage (Poaceae, Olyrinae), with a new monotypic and endangered herbaceous bamboo genus from Brazil. *Botanical Journal of the Linnean Society* 192: 34–60.

Orr AR, Sundberg MD. 2007. Inflorescence development in the teosinte *Zea luxurians* (Poaceae) and implication for the origin of maize inflorescences. *Maydica* 52: 31–47.

Orton LM, Barberá P, Nissenbaum MP, Peterson PM, Quintanar A, Soreng RJ, Duvall MR. 2021. A 313 plastome phylogenomic analysis of Pooideae: Exploring relationships among the largest subfamily of grasses. *Molecular Phylogenetics and Evolution* 159: 1–14.

Osborne CP, Salomaa A, Kluyver TA, Visser V, Kellogg EA, Morrone O, Vorontsova MS, Clayton WD, Simpson DA. 2014. A global database of C_4 photosynthesis in grasses. *New Phytologist* 204: 441–446.

Palmer J, Lazarides M, McCusker A, Weiller CM. 2005. Eragrostis. In: Mallet K ed. *Flora of Australia, vol. 44B, Poaceae, 3*. Melbourne: Commonwealth Scientific and Resesearch Organiation (CSIRO). 346–409.

Parodi LR, Calderon CE. 1961. Estudio histotaxonomico del genero *Lygeum* (Gramineae). *Revista Argentina de Agronomía* 28: 81–99.

Peichoto MC, Moreno EMS, Welker CAD, Solís Neffa VG, Scataglini MA. 2022. Delimitation of the genus *Schizachyrium* (Poaceae, Andropogoneae) based on molecular and morphological data. *Journal of Systematics and Evolution* 60(2): 319—330. https://doi.org/10.1111/jse.12807

Persson NL, Rydin C. 2016. Phylogenetic relationships of the '*Briza* complex' to other members of the subfamily Pooideae (Poaceae). *Plant Ecology and Evolution* 149: 216–227.

Peterson PM, Columbus T, Pennington S. 2007. Classification and Biogeography of New World Grasses: Chloridoideae. *Aliso* 23: 580–594.

Peterson PM, Romaschenko K, Barker NP, Linder HP. 2011. *Centropodieae* and *Ellisochloa*, a new tribe and genus in Chloridoideae (Poaceae). *Taxon* 60: 1113–1122.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2022a. A phylogeny of the Triraphideae including *Habrochloa and Nematopoa* (Poaceae, Chloridoideae). *PhytoKeys* 194: 123–133.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2014a. A molecular phylogeny and classification of the Cteniinae, Farragininae, Gouiniinae, Gymnopogoninae, Perotidinae, and Trichoneurinae (Poaceae: Chloridoideae: Cynodonteae). *Taxon* 63: 275–286.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015a. Phylogeny and subgeneric classification of *Bouteloua* with a new species, *B. herrera-arrietae* (Poaceae: Chloridoideae: Cynodonteae: Boutelouinae). *Wiley Online Library* 53: 351–366.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2015b. A molecular phylogeny and classification of the Eleusininae with a new genus, *Micrachne* (Poaceae: Chloridoideae: Cynodonteae). *Taxon* 64: 445–467.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2016. A molecular phylogeny and classification of the Cynodonteae (Poaceae: Chloridoideae) with four new genera: *Orthacanthus*, *Triplasiella*, *Tripogonella*, and *Zaqiqah*; three new subtribes: Dactylocteniinae, Orininae, and Zaqiqahinae; and a subgeneric classification of Distichlis. *Taxon* 65: 1263–1287.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2017a. Four new subtribes: Allolepiinae, Jouveinae, Kaliniinae, and Sohnsiinae in the Cynodonteae (Poaceae: Chloridoideae). *Phytoneuron* 2017–44: 1–9.

Peterson PM, Romaschenko K, Herrera Arrieta Y. 2020a. A phylogeny of the Hubbardochloinae including *Tetrachaete* (Cynodonteae: Chloridoideae: Poaceae). *Phytoneuron* 2020–81: 1–13.

Peterson PM, Romaschenko K, Herrera Arrieta Y, Saarela JM. 2014b. A molecular phylogeny and new subgeneric classification of *Sporobolus* (Poaceae: Chloridoideae: Sporobolinae). *Taxon* 63: 1212–1243.

Peterson PM, Romaschenko K, Herrera Arrieta Y, Saarela J. 2017b. A molecular phylogeny of the subtribe Sporobolinae and a classification of the subfamily Chloridoideae (Poaceae). *Diversity and Phylogeny in the Monocotyledons: Contributions from Monocots V* 118: 125–146.

Peterson PM, Romaschenko K, Herrera Arrieta Y, Vorontsova MS. 2022b. [2021]. Phylogeny, classification, and biogeography of *Afrotrichloris, Apochiton, Coelachyrum, Dinebra, Eleusine, Leptochloa, Schoenefeldia,* and a new genus, *Schoenefeldiella* (Poaceae: Chloridoideae: Cynodonteae: Eleusininae). *Journal of Systematics and Evolution* 60: 630–639.

Peterson PM, Soreng RJ, Romaschenko K, Barberá P, Quintanar A, Aedo C, Saarela JM. 2022c. Phylogeny and biogeography of *Calamagrostis* (Poaceae: Pooideae: Poeae: Agrostidinae), description of a new genus, *Condilorachia* (Calothecinae), and expansion of *Greeneochloa* and *Pentapogon* (Echinopogoninae). *Journal of Systematics and Evolution* 60: 570–590.

Peterson PM, Romaschenko K, Johnson G. 2010a. A classification of the Chloridoideae (Poaceae) based on multi-gene phylogenetic trees. *Molecular Phylogenetics and Evolution* 55: 580–598.

Peterson PM, Romaschenko K, Johnson G. 2010b. A phylogeny and classification of the Muhlenbergiinae (Poaceae: Chloridoideae: Cynodonteae) based on plastid and nuclear DNA sequences. *American Journal of Botany* 97: 1532–1554.

Peterson PM, Romaschenko K, Soreng RJ, Reyna JV. 2019a. A key to the North American genera of Stipeae (Poaceae, Pooideae) with descriptions and taxonomic names for species of *Eriocoma, Neotrinia, Oloptum*, and five new genera: *Barkworthia, ×Eriosella, Pseudoeriocoma, Ptilagrostiella*, and *Thorneochloa*. *PhytoKeys* 126: 89–125.

Peterson PM, Romaschenko K, Snow N, Johnson G. 2012. A molecular phylogeny and classification of *Leptochloa* (Poaceae: Chloridoideae: Chlorideae) *sensu lato* and related genera. *Annals of Botany* 109: 1317–1329.

Peterson PM, Roquet C, Romaschenko K, Herrera Arrieta Y, Susanna A. 2022d. [2021]. A biogeographical analysis of *Muhlenbergia* (Poaceae: Chloridoideae: Cynodonteae: Muhlenbergiinae). *Journal of Systematics and Evolution* 60: 621–629.

Peterson PM, Soreng RJ, Romaschenko K, Barberá P, Quintanar A, Aedo C. 2019b. New combinations and new names in American *Cinnagrostis, Peyritschia*, and *Deschampsia*, and three new genera: *Greeneochloa, Laegaardia*, and *Paramochloa* (Poeae, Poaceae). *Phytoneuron* 39: 1–23.

Peterson PM, Sánchez Vega I, Romaschenko K, Giraldo-Cañas D, Refulio Rodriguez NF. 2018. Revision of *Muhlenbergia* (Poaceae, Chloridoideae, Cynodonteae, Muhlenbergiinae) in Peru: Classification, phylogeny, and a new species, *M. romaschenkoi*. *PhytoKeys* 114: 123–206.

Peterson PM, Sylvester SP, Romaschenko K, Soreng RJ, Barberá P, Quintanar A, Aedo C. 2020b. A phylogeny of species near *Agrostis* supporting the recognition of two new genera, *Agrostula* and *Alpagrostis* (Poaceae, Pooideae, Agrostidinae) from Europe. *PhytoKeys* 167: 57–82.

Philipson WR. 1935. A grass with spiral Phyllotaxis: *Micraira subulifolia*. *Bulletin of Miscellaneous Information (Royal Botanic Gardens, Kew)* 1935(5): 324–326.

Phillips SM. 1982. A numerical analysis of the Eragrostideae (Gramineae). *Kew Bulletin* 37: 133–162.

Pimentel M, Sahuquillo E, Torrecilla Z, Popp M, Catalán P, Brochmann C. 2013. Hybridization and long-distance colonization at different time scales: Towards resolution of long-term controversies in the sweet vernal grasses (*Anthoxanthum*). *Annals of Botany* 112: 1015–1030.

Pirie MD, Humphreys AM, Galley C, Barker NP, Verboom GA, Orlovich D, Draffin SJ, Lloyd K, Baeza CM, Negritto M, Ruiz E, Sanchez JHC, Reimer E, Linder HP. 2008. A novel supermatrix approach improves resolution of phylogenetic relationships in a comprehensive sample of danthonioid grasses. *Molecular Phylogenetics and Evolution* 48: 1106–1119.

Pleines T, Blattner FR. 2008. Phylogeographic implications of an AFLP phylogeny of the American diploid *Hordeum* species (Poaceae: Triticeae). *Taxon* 57: 875–881.

Poinar G. 2011. Silica bodies in the Early Cretaceous *Programinis laminatus* (Angiospermae: Poales). *Palaeodiversity* 4: 1–6.

Poinar G, Alderman S, Wunderlich J. 2015. One hundred million year old ergot: Psychotropic compounds in the Cretaceous? *Paleodiversity* 8: 13–19.

Poinar GO. 2003. Early Cretaceous grass-like monocots in Burmese amber. *Australian Systematic Botany* 497–504.

Pourmoshir Z, Amirahmadi A, Naderi R. 2019. An overview of the phylogenetic relationships of *Bromus pumilio* (Poaceae) and allies based on nrDNA ITS and trnL-F sequences. *Iranian Journal of Botany* 25: 1–10.

POWO. 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew [online]. Available from http://www.plantsoftheworldonline.org/ [accessed January 2022].

Prasad V, Strömberg CAE, Alimohammadian H, Sahni A. 2005. Paleontology: Dinosaur coprolites and the early evolution of grasses and grazers. *Science* 310: 1177–1180.

Prasad V, Strömberg CAE, Leaché AD, Samant B, Patnaik R, Tang L, Mohabey DM, Ge S, Sahni A. 2011. Late Cretaceous origin of the rice tribe provides evidence for early diversification in Poaceae. *Nature communications* 2(1): 1–9.

Preston JC, Christensen A, Malcomber ST, Kellogg EA. 2009. MADS-box gene expression and implications for developmental origins of the grass spikelet. *American Journal of Botany* 96: 1419–1429.

Probatova. 2003. The genus *Arctopoa* (Griseb.) Probat. (Poaceae): Taxonomy, chromosome numbers, biogeography, and differentiation. *Komarov Memorial Lectures* 49: 89–130.

Punina EO, Nosov NN, Myakoshina YA, Gnutikov AA, Shmakov AI, Olonova MV, Rodionov AVV. 2016. New octoploid *Catabrosa* (Poaceae) species from Altai. *Kew Bulletin* 71: 1–8.

Rambaut A. 2018. FigTree, version 1.4.4 [online]. Available from http://tree.bio.ed.ac.uk/software-/figtree/ [accessed 2 November 2021].

Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.

Rao X, Dixon RA. 2016. The differences between NAD-ME and NADP-ME subtypes of C4 photosynthesis: More than decarboxylating enzymes. *Frontiers in Plant Science* 7: 1–9.

Ree RH, Moore BR, Webb CO, Donoghue MJ. 2005. A likelihood framework for inferring the evolution of geographic range on phylogenetic trees. *Evolution* 59: 2299–2311.

Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4–14.

Reeder JR. 1957. The embryo in grass systematics. *American Journal of Botany* 44: 756–768.

Reeder JR. 1962. The Bambusoid embryo: A reappraisal. *American Journal of Botany* 49: 639.

Reinheimer R, Kellogg EA. 2009. Evolution of AGL6-like MADS box genes in grasses (Poaceae): Ovule expression Is ancient and palea expression is new. *Plant Cell* 21: 2591–2605.

Renvoize SA. 1985. A Survey of Leaf-Blade Anatomy in Grasses. VII Pommereulleae, Orcuttieae & Pappophoreae. *Kew Bulletin* 40: 737–744.

Ripley B, Visser V, Christin PA, Archibald S, Martin T, Osborne C. 2015. Fire ecology of C_3 and C_4 grasses depends on evolutionary history and frequency of burning but not photosynthetic type. *Ecology* 96: 2679–2691.

Rodionov AV, Gnutikov AA, Nosov NN, Machs EM, Mikhaylova YV, Shneyer VS, Punina EO. 2020. Intragenomic polymorphism of the ITS 1 region of 35s rRNA gene in the group of grasses with two-chromosome species: Different genome composition in closely related *Zingeria* species. *Plants* 9: 1–11.

Rodionov AV, Kotsinyan AR, Gnutikov AA, Dobroradova MA, Machs EM. 2013. Variability of the ITS1-5.8S rDNA-ITS2 sequence during the divergence of sweet-grass species (*Glyceria* R. Br.). *Russian Journal of Genetics: Applied Research* 3: 83–90.

Romaschenko K, Garcia-Jacas N, Peterson PM, Soreng RJ, Futorna O, Susanna A. 2008. Molecular phylogenetic analysis of the American Stipeae (Poaceae) resolves *Jarava sensu lato* polyphyletic: Evidence for a new genus, *Pappostipa*. *Journal of the Botanical Research Institute of Texas* 2: 165–192.

Romaschenko K, Garcia-Jacas N, Peterson PM, Soreng RJ, Vilatersana R, Susanna A. 2014. Miocene-Pliocene speciation, introgression, and migration of *Patis* and *Ptilagrostis* (Poaceae: Stipeae). *Molecular Phylogenetics and Evolution* 70: 244–259.

Romaschenko K, Peterson PM, Soreng RJ, Futorna O, Susanna A. 2011. Phylogenetics of *Piptatherum s.l.* (Poaceae: Stipeae): Evidence for a new genus, *Piptatheropsis*, and resurrection of *Patis*. *Taxon* 60: 1703–1716.

Romaschenko K, Peterson PM, Soreng RJ, Garcia-Jacas N, Futorna O, Susanna A. 2012. Systematics and evolution of the needle grasses (Poaceae: Pooideae: Stipeae) based on analysis of multiple chloroplast loci, ITS, and lemma micromorphology. *Taxon* 61: 18–44.

Romero-Zarco C. 2011. *Helictochloa* Romero Zarco (Poaceae), a new genus of oat grass. *Candollea* 66: 87–103.

Romero-Zarco C, Sáez, Goñalons L. 2018. Notas taxonómicas sobre el género *Avellinia* Parl. (Poaceae: Poeae: Aveninae). *Acta Botanica Malacitana* 43: 167–169.

Ruiz-Sanchez E, Sosa V, Ortiz-Rodriguez AE, Davidse G. 2019. Historical biogeography of the herbaceous bamboo tribe Olyreae (Bambusoideae: Poaceae). *Folia Geobotanica* 54: 177–189.

Ruiz-Sanchez E, Tyrrell CD, Londoño X, Oliveira RP, Clark LG. 2021. Diversity, distribution, and classification of neotropical woody bamboos (Poaceae: Bambusoideae) in the 21st century. *Botanical Sciences* 99: 198–228.

Saarela JM, Bull RD, Paradis MJ, Ebata SN, Peterson PM, Soreng RJ, Paszko B. 2017. Molecular phylogenetics of cool-season grasses in the subtribes Agrostidinae, Anthoxanthinae, Aveninae, Brizinae, Calothecinae, Koeleriinae and Phalaridinae (Poaceae, Pooideae, Poeae, Poeae chloroplast group 1). *PhytoKeys* 87: 1–139.

Saarela J, Peterson P, Keane R, Cayouette J, Graham S. 2007. Molecular phylogenetics of *Bromus* (Poaceae: Pooideae) based on chloroplast and nuclear DNA sequence data. *Aliso* 23: 450–467.

Saarela JM, Burke SV, Wysocki WP, Barrett MD, Clark LG, Craine JM, Peterson PM, Soreng RJ, Vorontsova MS, Duvall MR. 2018. A 250 plastome phylogeny of the grass family (Poaceae): Topological support under different data partitions. *PeerJ* 2018: e4299.

Saarela JM, Peterson PM, Soreng RJ, Chapman RE. 2003. A taxonomic revision of the Eastern North American and Eastern Asian disjunct genus *Brachyelytrum* (Poaceae): Evidence from morphology, phytogeography and AFLPs. *Systematic Botany* 28: 674–692.

Saarela JM, Wysocki WP, Barrett cf, Soreng RJ, Davis JI, Clark LG, Kelchner SA, Pires JC, Edger PP, Mayfield DR, Duvall MR. 2015. Plastid phylogenomics of the cool-season grass subfamily: Clarification of relationships among early-diverging tribes. *AoB PLANTS* 7: 1–27.

Sage RF. 2004. The evolution of C_4 photosynthesis. *New Phytologist* 161: 341–370.

Sage RF, Christin PA, Edwards EJ. 2011. The C_4 plant lineages of planet Earth. *Journal of Experimental Botany* 62: 3155–3169.

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. *Molecular Phylogenetics and Evolution* 56: 355–369.

Saltonstall K, Peterson PM, Soreng RJ. 2004. Recognition of *Phragmites australis* subsp. *americanus* (Poaceae: Arundinoideae) in North America: Evidence from morphological and genetic analyses. *SIDA, Contributions to Botany* 21: 683–692.

Sánchez-Ken JG. 2019. Panic or erect veldt grass *Ehrharta erecta* var. *erecta* (Ehrharteae, Oryzoideae, Poaceae): New records of an introduced genus in México in the states of Michoacán and Baja California. *Phytotaxa* 402: 45–51.

Sánchez-Ken JG, Clark LG. 2010. Phylogeny and a new tribal classification of the Panicoideae s.l. (Poaceae) based on plastid and nuclear sequence data and structural data. *American Journal of Botany* 97: 1732–1748.

Sánchez-Ken JG, Clark LG, Kellogg EA, Kay EE. 2007. Reinstatement and emendation of subfamily Micrairoideae (Poaceae). *Systematic Botany* 32: 71–80.

Sancho R, Cantalapiedra CP, López-Alvarez D, Gordon SP, Vogel JP, Catalán P, Contreras-Moreira B. 2018. Comparative plastome genomics and phylogenomics of *Brachypodium*: flowering time signatures, introgression, and recombination in recently diverged ecotypes. *New Phytologist* 218: 1631–1644.

Scataglini MA, Lizarazu MA, Zuloaga FO. 2014. A peculiar amphitropical genus of Paniceae (Poaceae, Panicoideae). *Systematic Botany* 39: 1108–1119.

Schafer JL, Mack MC. 2018. Nutrient limitation of plant productivity in scrubby flatwoods: does fire shift nitrogen versus phosphorus limitation? *Plant Ecology* 219: 1063–1079.

Schneider J, Winterfeld G, Röser M. 2012. Polyphyly of the grass tribe Hainardieae (Poaceae: Pooideae): Identification of its different lineages based on molecular phylogenetics, including morphological and cytogenetic characteristics. *Organisms Diversity and Evolution* 12: 113–132.

Schubert M, Grønvold L, Sandve SR, Hvidsten TR, Fjellheim S. 2019a. Evolution of cold acclimation and its role in niche transition in the temperate grass subfamily Pooideae. Plant Reviews *Plant Physiology* 180: 404–419.

Schubert M, Humphreys AM, Lindberg CL, Preston JC, Fjellheim S. 2020. To coldly go where no grass has gone before: A multidisciplinary review of cold adaptation in Poaceae. In: *Annual Plant Reviews online.*Wiley.523–562.

Schubert M, Marcussen T, Meseguer AS, Fjellheim S. 2019b. The grass subfamily Pooideae: Cretaceous–Palaeocene origin and climate-driven Cenozoic diversification. *Global Ecology and Biogeography* 28: 1168–1182.

Sclovich SE, Giussani LM, Cialdella AM, Sede SM. 2015. Phylogenetic analysis of *Jarava* (Poaceae, Pooideae, Stipeae) and related genera: testing the value of the awn indumentum in the circumscription of *Jarava*. *Plant Systematics and Evolution* 301: 1625–1641.

Scoppola A, Cancellieri L. 2019. Comparative morphometry as a diagnostic tool applied to species delimitation in the genus *Gastridium* P. Beauv. (Poaceae). *Wiley Online Library* 37: 1–20.

Sede SM, Zuloaga FO, Morrone O. 2009. Phylogenetic studies in the Paniceae (Poaceae-Panicoideae): *Ocellochloa*, a new genus from the New World. *Systematic Botany* 34: 684–692.

Silva C, Snak C, Schnadelbach AS, van den Berg C, Oliveira RP. 2015. Phylogenetic relationships of *Echinolaena* and *Ichnanthus* within Panicoideae (Poaceae) reveal two new genera of tropical grasses. *Molecular Phylogenetics and Evolution* 93: 212–233.

Silva C, Snak C, Davidse G, Van Den Berg C, Oliveira RP. 2020. Assessing the molecular diversity of *Hildaea* (Poaceae, Panicoideae): Reaching a compromise between the splitter and the lumper. *Botanical Journal of the Linnean Society* 192: 121–147.

Silva C, Besnard G, Piot A, Razanatsoa J, Oliveira RP, Vorontsova MS. 2017. Museomics resolve the systematics of an endangered grass lineage endemic to north-western Madagascar. *Annals of Botany* 119: 339–351.

Simon B, Weiller C, Kodela P. 2009. Dichelachne. In: Wlson A ed. *Flora of Australia 44A (Poaceae)*. Melbourne: CSIRO Publishing. 214–221.

Simon BK. 2005. *Sporobolus*. In: Mallet K ed. Flora of Australia, vol. 44B, Poaceae 3. Melbourne: Commonwealth Scientific and Research Organization (CSIRO) Publishing. 324–326.

Simon BK, Jacobs SWL. 1999. Revision of the genus *Sporobolus* (Poaceae, Chloridoideae) in Australia. *Australian Systematic Botany* 12: 375–448.

Simpson KJ, Ripley BS, Christin PA, Belcher CM, Lehmann CER, Thomas GH, Osborne CP. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.

Smith O, Nicholson WV, Kistler L, Mace E, Clapham A, Rose P, Stevens C, Ware R, Samavedam S, Barker G, Jordan D, Fuller DQ, Allaby RG. 2019. A domestication history of dynamic adaptation and genomic deterioration in *Sorghum*. *Nature Plants* 5: 369–379.

Snow N, Peterson PM. 2012. Systematics of *Trigonochloa* (Poaceae, Chloridoideae, Chlorideae). *PhytoKeys* 13: 25–38.

Snow N, Peterson PM, Romaschenko K, Simon BK. 2018. Monograph of *Diplachne* (Poaceae, Chloridoideae, Cynodonteae). *PhytoKeys* 1–102.

Soderstrom TR, Judziewicz EJ. 1987. Systematics of the Amphi-Atlantic Bambusoid Genus *Streptogyna* (Poaceae). *Annals of the Missouri Botanical Garden* 74: 871–888.

Soderstrom TR, Judziewicz EJ, Clark LG. 1988. Distribution patterns of Neotropical bamboos. In: Vanzolini P, Heyer R eds. *Proceedings of a Workshop on Neotropical Distribution Patterns*. 121–157.

Soreng RJ, Davis JI. 2000. Phylogenetic structure in Poaceae subfamily Pooideae as inferred frommolecular and morphological characters: Misclassification versus reticulation. In: Jacobs SWL, Everett J eds. *Grasses: Systematics and Evolution*. Melbourne: CSIRO. 61–74.

Soreng RJ, Gillespie LJ, Boudko EA, Cabi E. 2022a. Biogeography, timing, and life-history traits in the PPAM clade: Coleanthinae (syn. Puccinelliinae), Poinae, Alopecurinae superclade, Miliinae, and Avenulinae and Phleinae (Poaceae, Pooideae, Poeae). *Journal of Systematics and Evolution* 60: 591–620.

Soreng RJ, Gillespie LJ. 2007. *Nicoraepoa* (Poaceae, Poeae), a new South American genus based on *Poa* subg. Andinae, and emendation of *Poa* sect. *Parodiochloa* of the sub-Antarctic Islands. *Annals of the Missouri Botanical Garden* 94: 821–849.

Soreng RJ, Gillespie LJ, Jacobs JD. 2009. *Saxipoa* and *Sylvipoa* – two new genera and a new classification for Australian *Poa* (Poaceae: Poinae). *Australian Systematic Botany* 22: 401–412. https://doi.org/10.1071/SB09003

Soreng RJ, Gillespie LJ, Koba H, Boudko E, Bull RD. 2015a. Molecular and morphological evidence for a new grass genus, *Dupontiopsis* (Poaceae tribe Poeae subtribe Poinae s.l.), endemic to alpine Japan, and implications for the reticulate origin of *Dupontia* and *Arctophila* within Poinae s.l. *Journal of Systematics and Evolution* 53: 138–162.

Soreng RJ, Olonova MV, Probatova NS, Gillespie LJ. 2020. Breeding systems and phylogeny in *Poa*, with special attention to Northeast Asia: The problem of *Poa shumushuensis* Ohwi and sect. *Nivicolae* (Poaceae). *Journal of Systematics and Evolution* 58(6): 1031–1058. https://doi.org/10.1111/jse.12647

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Teisher JK, Clark LG, Barberá P, Gillespie LJ, Zuloaga FO. 2017. A worldwide phylogenetic classification of the Poaceae (Gramineae) II: An update and a comparison of two 2015 classifications. *Journal of Systematics and Evolution* 55: 259–290.

Soreng RJ, Peterson PM, Romaschenko K, Davidse G, Zuloaga FO, Judziewicz EJ, Filgueiras TS, Davis JI, Morrone O. 2015b. A worldwide phylogenetic classification of the Poaceae (Gramineae). *Journal of Systematics and Evolution* 53: 117–137.

Soreng RJ, Peterson PM, Zuloaga FO, Romaschenko K, Clark LG, Teisher JK, Gillespie LJ, Barberá P, Welker CAD, Kellogg EA, Li D-Z, Davidse G. 2022b. A worldwide phylogenetic classification of the Poaceae (Gramineae) III: An update. *Journal of Systematics and Evolution* 60: 476–521.

Stapleton CMA. 2021. We need to talk about *Fargesia*: new combinations and a new genus in the temperate Sino-Himalayan bamboos (Poaceae: Bambusoideae). *Journal of the American Bamboo Society* 31: 1–16.

Stewart A, Joachimiak A, NW E. 2011. Phleum. In: Kole C ed. *Wild crop relatives: Genomic and breeding resources—Millets and grasses*. Heidelberg, Dordrechte, London, New York: Springer International Publishing. 257–274.

Stinca A, Mei G. 2019. *Ehrharta erecta* Lam. (Poaceae, Ehrhartoideae): Distribution in Italy and taxonomy of one of the most invasive plant species in the world. *BioInvasions Records* 8: 742–752.

Strömberg CAE. 2005. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proceedings of the National Academy of Sciences of the United States of America* 102: 11980–11984.

Strömberg CAE. 2011. Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* 39: 517–544.

Sundberg MD, LaFargue C, Orr AR. 1995. Inflorescence development in the "standard exotic″ maize, Argentine popcorn (Poaceae). *American Journal of Botany* 82: 68–74.

Sundberg MD, Orr AR. 1996. Early inflorescence and floral development in *Zea mays* land race Chapalote (Poaceae). *American Journal of Botany* 83: 1255–1265.

Sungkaew S, Stapleton CMA, Salamin N, Hodkinson TR. 2009. Non-monophyly of the woody bamboos (Bambuseae; Poaceae): A multi-gene region phylogenetic analysis of Bambusoideae s.s. *Journal of Plant Research* 122: 95–108.

Sylvester SP, Soreng RJ, Bravo-Pedraza WJ, Cuta-Alarcon LE, Giraldo-Cañas D, Aguilar-Cano J, Peterson PM. 2019. Páramo *Calamagrostis* s.l. (Poaceae):An updated list and key to the species known or likely to occur in páramos of NW South America and southern Central America including two new species, one new variety, and five new records for Colombia. *PhytoKeys* 122: 29–78.

Syme AE, Murphy DJ, Holmes GD, Gardner S, Fowler R, Cantrill DJ. 2012. An expanded phylogenetic analysis of *Austrostipa* (Poaceae: Stipeae) to test infrageneric relationships. *Australian Systematic Botany* 25: 1–10.

Tang L, Zou X, Achoundong G, Potgieter C, Second G, Zhang D, Ge S. 2010. Phylogeny and biogeography of the rice tribe (Oryzeae): Evidence from combined analysis of 20 chloroplast fragments. *Molecular Phylogenetics and Evolution* 54: 266–277.

Teerawatananon A, Jacobs SWL, Hodkinson TR. 2011. Phylogenetics of Panicoideae (Poaceae) based on chloroplast and nuclear DNA sequences. *Telopea* 13: 115–142.

Teisher JK, McKain MR, Schaal BA, Kellogg EA. 2017. Polyphyly of Arundinoideae (Poaceae) and evolution of the twisted geniculate lemma awn. *Annals of Botany* 120: 725–738.

Teisher JK, McKain MR, Schaal BA, Kellogg EA. 2019. Plastome phylogenetics of tribe Eriachneae and evolution of C_4 photosynthesis in subfamily Micrairoideae (Poaceae). *Systematic Botany* 44: 32–40.

Thomasson JR. 1985. Miocene Fossil Grasses: Possible Adaptation in Reproductive Bracts (Lemma and Palea). *Annals of the Missouri Botanical Garden* 72: 843.

Thompson EJ. 2019. A re-evaluation of the taxonomic status of the Australian species of *Arthraxon* Beauv. and *Thelepogon* Roth (Poaceae: Panicoideae: Andropogoneae). *Austrobaileya* 10: 480–505.

Thompson EJ, Fabillo MM. 2021. The impact of multiple molecular and morphological data sets on the phylogenetic reconstruction of subtribe Neurachninae (Poaceae: Panicoideae: Paniceae). *Australian Systematic Botany* 34(3): 227–251.

Tkach N, Schneider J, Döring E, Wölk A, Hochbach A, Nissen J, Winterfeld G, Meyer S, Gabriel J, Hoffmann MH, Röser M. 2020. Phylogenetic lineages and the role of hybridization as driving force of evolution in grass supertribe Poodae. *Taxon* 69: 234–277.

Tong YH, Zheng XR, Zhang YY, Qin QM, Ni JB, Vu TC, Xia NH. 2020. Khoonmengia honbaensis, a new genus and species of temperate bamboo (Poaceae, Bambusoideae) from central-southern Vietnam. *PhytoKeys* 138: 163.

Triplett JK, Clark LG. 2021. Hybridization in the temperate bamboos (Poaceae: Bambusoideae: Arundinarieae): A phylogenetic study using AFLPs and cpDNA sequence data. *Systematic Botany* 46: 48–69.

Tutin TG. 1980. CXCIII Gramineae (Poaceae). In: Tutin TG, Heywood VH, Burges NA, Valentine DH, Walters SM, Webb DA eds. *Fl. Eur.* Cambridge: Cambridge University Press. 118–267

Tyrrell CD, Londoño X, Prieto RO, Attigala L, McDonald K, Clark LG. 2018. Molecular phylogeny and cryptic morphology reveal a new genus of West Indian woody bamboo (Poaceae: Bambusoideae: Bambuseae) hidden by convergent character evolution. *Taxon* 67: 916–930.

Tzvelev NN. 2013. Notes on some genera of the family Poaceae. *Novosti Sist. Vyssh. Rast.* 44: 26–48.

Tzvelev NN, Probatova NS. 2019. *Zlaki Rossii/Grasses of Russia*. Moscow: KMK Scientific Press.

Udvardy MDF. 1975. A Classification of the Biogeographical Provinces of the World. Occasional Paper 18. Morges: International Union for Conservation of Nature and Natural Resources.

Van Slageren M. 1994. *Wild wheats: A monograph of* Aegilops *L. and* Amblyopyrum *(Jaub.\& Spach) Eig (Poaceae)*. Wageningen: Agricultural University Wageningen.

Vasquez SI, Welker CAD, Solís Neffa VG, Peichoto MC. 2022. Morphometric analysis of the Saccharum complex (Poaceae, Andropogoneae). *Plant Systematics and Evolution* 308: 10.

Veldkamp JF. 2002. Revision of *Eragrostis* (Gramineae, Chloridoideae) in Malesia. *Blumea: Journal of Plant Taxonomy and Plant Geography* 47: 157–204.

Veldkamp JF. 2012. *Koordersiochloa* Merr. (Gramineae), the correct name for *Streblochaete* Hochst. ex Pilg. *Reinwardtia* 13: 299–304.

Veldkamp JF. 2015. An attempt to unravel the synonymy of *Avenella flexuosa* (L.) Drejer (Gramineae). *Plant Diversity and Evolution* 131: 239–262.

Veldkamp JF. 2018. *Schmidiella* Veldk., gen. nov., an enigmatic new genus of Gramineae from Laos. *Adansonia* 40: 55–58.

Veldkamp JF, de Koning R, Sosef MSM. 1986. Generic delimitation of *Rottboellia* and related genera (Gramineae). *Blumea* 31: 281–307.

Vicentini A, Barber JC, Aliscioni SS, Giussani LM, Kellogg EA. 2008. The age of the grasses and clusters of origins of C4 photosynthesis. *Global Change Biology* 14: 2963–2977.

Vorontsova MS, Besnard G, Razanatsoa J, Hackel J. 2020. The endemic 'sugar canes' of Madagascar (Poaceae, Saccharinae: *Lasiorhachis*) are close relatives of *Sorghum*. *Botanical Journal of the Linnean Society* 192: 148–164.

Voshell SM, Hilu KW. 2014. Canary Grasses (*Phalaris*, Poaceae): biogeography, molecular dating, and the role of floret structure in dispersal. *Wiley Online Library* 23: 212–224.

Voshell SM, Baldini RM, Hilu KW. 2015. Infrageneric treatment of *Phalaris* (Canary grasses, Poaceae) based on molecular phylogenetics and floret structure. *Australian Systematic Botany* 28: 355–367.

Waterhouse AM, Procter JB, Martin DMA, Clamp M, Barton GJ. 2009. Jalview Version 2-A multiple sequence alignment editor and analysis workbench. *Bioinformatics* 25: 1189–1191.

Watson L, Dallwitz MJ. 1992. *The grass genera of the world*. Wallingford, Oxfordshire: CAB international.

Weaver JE. 1954. *North American Prairie*. Lincoln: Johnsen Publishing.

Weaver JE. 1968. *Prairie plants and their environment: A fifty-year study in the Midwest*. Lincoln: University of Nebraska Press.

Webster RD, Kirkbride JH, Reyna JV. 1989. New World genera of the Paniceae (Poaceae: Panicoideae). *Sida* 13: 393–417.

Weiller CM, Kodela PG, Thompson IR. 2009. *Echinopogon*. In: Wilson A ed. *Flora of Australia*. 44a, (*Poaceae* 2). Melbourne: ABRS/CSIRO Publishing. 222–228.

Welker CAD, Prado J, Kellogg EA, Gandhi KN. 2021. Clarifying the type of the polyphyletic genus Schizachyrium (Poaceae: Andropogoneae). *Kew Bulletin* 76: 327–331.

Welker CAD, McKain MR, Vorontsova MS, Peichoto MC, Kellogg EA. 2019. Plastome phylogenomics of sugarcane and relatives confirms the segregation of the genus *Tripidium* (Poaceae: Andropogoneae). *Taxon* 68: 246–267.

Welker CAD, Souza-Chies TT, Longhi-Wagner HM, Peichoto MC, McKain MR, Kellogg EA. 2015. Phylogenetic analysis of *Saccharum* s.l. (Poaceae; Andropogoneae), with emphasis on the circumscription of the South American species. *American Journal of Botany* 102: 248–263.

Welker CAD, Souza-Chies TT, Longhi-Wagner HM, Peichoto MC, McKain MR, Kellogg EA. 2016. Multilocus phylogeny and phylogenomics of *Eriochrysis* P. Beauv. (Poaceae-Andropogoneae): Taxonomic implications and evidence of interspecific hybridization. *Molecular Phylogenetics and Evolution* 99: 155–167.

Welker CAD, McKain MR, Estep MC, Pasquet RS, Chipabika G, Pallangyo B, Kellogg EA. 2020. Phylogenomics enables biogeographic analysis and a new subtribal classification of Andropogoneae (Poaceae—Panicoideae). *Journal of Systematics and Evolution* 58: 1003–1030.

Weller CM, Lazarides M. 2005. *Enneapogon*. In: Mallett K ed. *Flora of Australia 44B (Poaceae 3)*. Melbourne: CSIRO Publishing: 188–202.

Wharton DA, Selvanesan L, Marshall CJ. 2010. Ice-active proteins from New Zealand snow tussocks, *Chionochloa macra* and C. rigida. *Cryo-Letters* 31: 239–248.

Whipple IG, Barkworth ME, Bushman BS. 2007. Molecular insights into the taxonomy of *Glyceria* (Poaceae: Meliceae) in North America. *American Journal of Botany* 94: 551–557.

Winterfeld G, Schneider J, Perner K, Röser M. 2014. Polyploidy and hybridization as main factors of speciation: Complex reticulate evolution within the grass genus *Helictochloa*. *Cytogenetic and Genome Research* 142: 204–225.

Wölk A, Röser M. 2017. Hybridization and long-distance colonization in oat-like grasses of South and East Asia, including an amended circumscription of *Helictotrichon* and the description of the new genus *Tzveleviochloa* (Poaceae). *Taxon* 66: 20–43.

Wu Y, You HL, Li XQ. 2018. Dinosaur-associated Poaceae epidermis and phytoliths from the Early Cretaceous of China. *National Science Review* 5: 721–727.

Wysocki WP, Clark LG, Attigala L, Ruiz-Sanchez E, Duvall MR. 2015. Evolution of the bamboos (Bambusoideae; Poaceae): A full plastome phylogenomic analysis Genome evolution and evolutionary systems biology. *BMC Evolutionary Biology* 15: 50.

Ye XY, Ma PF, Yang GQ, Guo C, Zhang YX, Chen YM, Guo ZH, Li DZ. 2019. Rapid diversification of alpine bamboos associated with the uplift of the Hengduan Mountains. *Journal of Biogeography* 46: 2678–2689.

Zeng CX, Zhang YX, Triplett JK, Yang JB, Li DZ. 2010. Large multilocus plastid phylogeny of the tribe Arundinarieae (Poaceae: Bambusoideae) reveals ten major lineages and low rate of molecular divergence. *Molecular Phylogenetics and Evolution* 56(2): 821–839.

Zhang XZ, Zeng CX, Ma PF, Haevermans T, Zhang YX, Zhang LN, Guo ZH, Li DZ. 2016. Multi-locus plastid phylogenetic biogeography supports the Asian hypothesis of the temperate woody bamboos (Poaceae: Bambusoideae). *Molecular Phylogenetics and Evolution* 96: 118–129.

Zhang YX, Guo C, Li DZ. 2020. A new subtribal classification of Arundinarieae (Poaceae, Bambusoideae) with the description of a new genus. *Plant Diversity* 42: 127–134.

Zhang YX, Ma PF, Li DZ. 2018. A new genus of temperate woody bamboos (Poaceae, Bambusoideae, Arundinarieae) from a limestone montane area of China. *PhytoKeys* 109: 67–76.

Zhang YX, Zeng CX, Li DZ. 2012. Complex evolution in Arundinarieae (Poaceae: Bambusoideae): Incongruence between plastid and nuclear GBSSI gene phylogenies. *Molecular Phylogenetics and Evolution* 63: 777–797.

Zhao H, Yang JR, Xu H, Zhang J. 2010. Pseudogenization of the umami taste receptor gene Tas1r1 in the giant panda coincided with its dietary switch to bamboo. *Molecular Biology and Evolution* 27: 2669–2673.

Zhong J, Robbett M, Poire A, Preston JC. 2018. Successive evolutionary steps drove Pooideae grasses from tropical to temperate regions. *New Phytologist* 217: 925–938.

Zhou MY, Liu JX, Ma PF, Yang JB, Li DZ. 2022. Plastid phylogenomics shed lights on intergeneric relationships and spatio-temporal evolutionary history of Melocanninae (Poaceae: Bambusoideae). *Journal of Systematics and Evolution* 60: 640–652.

Zhou MY, Zhang YX, Haevermans H, Li DZ. 2017. Towards a complete generic-level plastid phylogeny of the paleotropical woody bamboos (Poaceae: Bambusoideae). *Taxon* 66: 539–553.

Zuloaga FO, Aliscioni SS, Scataglini MA. 2020. *Cnidochloa*: A new genus of grasses from Brazil (Poaceae: Panicoideae: Paniceae). *Annals of the Missouri Botanical Garden* 105: 183–194.

Zuloaga FO, Salomón L, Scataglini MA. 2015. Phylogeny of sections Clavelligerae and Pectinatae of *Panicum* (Poaceae, Panicoideae, Paniceae): Establishment of the new subtribe Dichantheliinae and the genus *Adenochloa*. *Plant Systematics and Evolution* 301: 1693–1711.

Zuloaga FO, Salariato DL, Scataglini A. 2018. Molecular phylogeny of *Panicum s. str*. (Poaceae, Panicoideae, Paniceae) and insights into its biogeography and evolution. *PLoS ONE* 13: e0191529.

Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12857/suppinfo:

Table S1. GenBank accession numbers for taxa sampled in this study.

Table S2. A list of genera sampled, those not sampled, and comments about clades.

Table S3. Clade constraints for the temporal calibration of the phylogeny.

Table S4. Geographic distributions. The presence or absence of the genus on each of six biogeographical realms.

Table S5. Likelihoods and other parameters from model selection in BioGeoBEARS.

Table S6. Age estimates and posterior probabilities for stem and crown of select nodes from this study (in bold) and other recent studies.

Table S7. Ancestral area estimates for the stem and crown of select nodes from this study (in bold) were inferred using the DEC + J biogeographical model and the results from some other studies that performed biogeographical reconstruction.