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Research Article

# Phylogeny, classification, and biogeography of *Afrotrichloris, Apochiton, Coelachyrum, Dinebra, Eleusine, Leptochloa, Schoenefeldia*, and a new genus, *Schoenefeldiella* (Poaceae: Chloridoideae: Cynodonteae: Eleusininae)

Paul M. Peterson[1]*, Konstantin Romaschenko[1,2], Yolanda Herrera Arrieta[3], and Maria S. Vorontsova[4]

[1]Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, USA
[2]M.G. Kholodny Institute of Botany, National Academy of Sciences, Kiev 01601, Ukraine
[3]Instituto Politécnico Nacional, CIIDIR Unidad-Durango-COFAA, C.P, Durango 34220, Mexico
[4]Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond Surrey TW9 3AE, UK
*Author for correspondence. E-mail: peterson@si.edu
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**Abstract** To investigate the evolutionary relationships among species of *Afrotrichloris, Apochiton, Coelachyrum, Dinebra, Eleusine, Leptochloa*, and *Schoenefeldia* of subtribe Eleusininae, a phylogeny based on DNA sequences from nine gene regions (ITS, *rps16-trnK, rps3, rps16, rpoC2, rpl32-trnL, ndhF, ndhA, ccsA*) is presented. Previous molecular phylogenies indicated that *Coelachyrum* was polyphyletic and *Schoenefeldia* was paraphyletic, with *Afrotrichloris* embedded within it. *Apochiton burttii* was embedded in the *Coelachyrum* clade paired with *C. longiglume*, *Coelachyrum poiflorum* was placed outside of *Coelachyrum* and sister to *Eleusine*, and *Schoenefeldia* is paraphyletic, with its two species forming a grade sister to *Afrotrichoris*. Our molecular phylogeny supports recognition of a new genus, *Schoenefeldiella*, and a new combination, *Schoenfeldiella transiens*. In addition, we provide generic emendations for *Coelachyrum*, which now includes five species including a new combination proposed here, *Coelachyrum burttii*, and *Eleusine*, which now includes 11 species.

**Key words:** Biogeography, *Coelachyrum*, grasses, ITS, molecular systematics, plastid DNA sequences, Poaceae, *Schoenefeldiella*, taxonomy.

## 1 Introduction

The tribe Cynodonteae currently includes 850 species in 94 genera and 21 subtribes, and it has received high support as a monophyletic lineage in recent molecular analyses (Peterson et al., 2014a, 2015a, 2016; Soreng et al., 2015, 2017). Within the subtribe Eleusininae (236 species in 27 genera), Peterson et al. (2015a) found *Coelachyrum* Hochst. & Nees to be polyphyletic because *C. lagopoides* (Burm.f.) Senaratna, *Apochiton burttii* C.E. Hubb., and *Coelachyrum poiflorum* Chiov. form a grade sister to *Eleusine* Gaertn., and *Schoenefeldia* Kunth is paraphyletic with respect to two samples of *Afrotrichloris martinii* Chiov.

*Coelachyrum* is a heterogeneous group of five annual or perennial semi-desert grasses that have been grouped together based on having paniculate inflorescences composed of loose to dense racemes, these often spaced (racemose) or clustered (digitate) on a central axis; 3-veined, broadly elliptic to ovate, rounded-on-the-back lemmas; and dorso-ventrally flattened caryopses with free pericarps that are highly ornamented and often rugulose (Phillips, 1974, 1995; Clayton et al., 2016; Cope, 2007). The genus was described by Hochstetter & Nees von Esenbeck based on *Coelachyrum brevifolium* Hochst. & Nees, the type species (Nees von Esenbeck & Schauer, 1842). Twelve years later, Steudel (1854) transferred this species into *Eleusine* along with 15 other species. Recently, *Coelachyrum yemenica* (Schweinf.) S.M. Phillips was transferred to *Disakisperma* Steud. based on the shared morphology and sequence similarity of five DNA markers (Snow et al., 2013). The most recent treatment of *Eleusine* includes 10 species, and eight of these were found in a strongly supported clade sister to *C. poiflorum* in a molecular DNA sequence study (Liu et al., 2011; Peterson et al., 2015a; Soreng et al., 2017).

*Apochiton* C.E. Hubb. is a monotypic genus known only from Tanzania and is characterized as having an annual habit, panicle branches often reduced to racemes; 3-veined, short-awned lemmas; awned palea keels; and trigonous caryopses with free pericarps (Hubbard, 1936, 1974a). The species has never been attributed to any other genus, and Hubbard

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(1936) mentions in his description that the unusual grain (free pericarp) is only known in a few species of *Eragrostis* Wolf, Sporoboleae [=Sporobolinae], *Sclerodactylon* Stapf, *Dinebra* Jacq., *Eleusine*, *Dactyloctenium* Willd., and *Coleachyrum*. However, *Afrotrichloris*, *Austrochloris* Lazarides, *Daknopholis* Clayton, *Tetrapogon* Desf., and the Unioliinae Clayton also have grains with a free pericarp (Clayton & Renvoize, 1986).

For most of the 20th century, *Dinebra* was represented by three species (Clayton & Renvoize, 1986; Watson & Dallwitz, 1992). Based on results of molecular DNA sequence studies, many species formerly placed in *Leptochloa* s.l. were transferred to an expanded *Dinebra* now with ±23 species, while *Leptochloa* s.s. was reduced to eight species with recognition of *Diplachne* P. Beauv. (2 spp.), *Disakisperma* (4 spp.), and *Trigonochloa* P.M. Peterson & N. Snow (2 spp.) (Peterson et al., 2012, 2014c, 2015a; Snow & Peterson, 2012; Snow et al., 2013, 2018, in prep.; Soreng et al., 2017).

*Schoenefeldia* includes two species, *S. gracilis* Kunth (the type) and *S. transiens* (Pilg.) Chiov., both characterized by having solitary, paired, or digitate racemes and spikelets with long-awned lemmas with the awns braided along the culm (Hubbard, 1974b; Cope, 2007). *Schoenefeldia transiens* can be separated from *S. gracilis* in having two-flowered spikelets, with the upper floret sterile and awned, perennial habit, and flat leaf blades 5–35 cm long.

*Afrotrichloris* Chiov. also includes two species: *A. martinii* and *A. hyaloptera* Clayton. *Afrotrichloris hyaloptera* can be separated from *A. martinii* by the presence of shorter lateral lemma lobes with a longer central awn and longer inflorescence spikes (Clayton, 1967). Clayton (1967) indicated that *Afrotrichloris* bears some similarity to *Trichloris* E. Fourn. ex Benth., although the two species traditionally placed in *Trichloris* now reside within *Leptochloa* P. Beauv. s.s. (Peterson et al., 2012, 2015a). Clayton also mentioned that *A. hyaloptera* is not unlike *Enteropogon* Nees and that *Afrotrichloris* probably represents different lines of divergence from a common *Chloris* Sw. stock.

Using plastid (*rps16-trnK, rps3, rps16, rpoC2, rpl32-trnL, ndhF, ndhA, ccsA*) and nuclear ITS DNA sequence markers, we present a new phylogenetic analysis of 85 species in 24 genera of Eleusininae, emphasizing those species surrounding *Coelachyrum, Apochiton, Schoenefeldia*, and *Afrotrichloris*, along with *Dinebra, Leptochloa*, and *Eleusine*. We expand the number of species sampled to include all five accepted species of *Coelachyrum* and both species of *Afrotrichloris* (Clayton et al., 2016; Snow et al., 2013). In addition, we discuss the morphological and anatomical characteristics supporting relationships, discuss biogeography, and propose changes to the classification of studied taxa.

## 2 Material and Methods

### 2.1 Taxon sampling

Our sampling consists of 141 samples, representing 85 species of grasses, of which 84 are included in the Cynodonteae and one is included in the Zoysieae. In addition, we include all six species that have been attributed to *Coelachyrum* and two species of *Afrotrichloris* (Clayton et al., 2006). Outside of the Cynodonteae, *Sporobolus indicus* (L.) R. Br. was chosen as the out group. A complete list of taxa, voucher information, and GenBank numbers can be found in Appendix S1. All collections gathered by PMP after 1998 were collected in silica, but the majority of samples used in this study were obtained from herbarium specimens.

### 2.2 DNA extraction, amplification, and sequencing

All procedures were performed in the Laboratory of Analytical Biology (LAB) at the Smithsonian Institution. DNA isolation, amplification, and sequencing of the *rpl32-trnL* spacer and the *ndhA* intron (small single-copy region); the *rps16-trnK* spacer and the *rps16* intron (large single-copy region); *ndhF, ccsA, rpoC2*, and *rps3* (encoding region); and ITS were accomplished following the procedures outlined in Peterson et al. (2010a, 2010b, 2012, 2014c). We specifically targeted plastid regions that proved to be most informative in our previous studies on chloridoid grasses (Peterson et al., 2010a, 2010b, 2011, 2012, 2014a, 2014b, 2014c, 2015a, 2015b, 2016; Liu et al., 2011).

### 2.3 Phylogenetic analyses

We used Geneious 5.3.4 (Drummond et al., 2011) for contig assembly of bidirectional sequences of *rpl32-trnL*, *ndhA, ndhF, rps3, rps16*, *rps16-trnK, rpoC2, ccsA*, and ITS regions, and Muscle (Edgar, 2004) to align consensus sequences and adjust the final alignment. We identified models of molecular evolution for the cpDNA and nrDNA regions using jModeltest (Posada, 2008) and applied maximum likelihood (ML) and Bayesian searches to infer overall phylogeny. The combined data sets were partitioned in accordance with the number of markers used. Nucleotide substitution models selected according to Akaike's information criterion, as implemented in jModelTest v.0.1.1, were specified for each partition (Table 1). The ML analysis was conducted using GARLI 0.951 (Zwickl, 2006). The ML bootstrap analysis was performed with 1000 replicates, with 10 random additional sequences per replicate. The output file containing trees of ML found for each bootstrap data set was then read into PAUP, where the majority rule consensus tree was constructed. Bootstrap (BS) values of 90%–100% were interpreted as strong support, 70%–89% as moderate support, and 50%–69% as weak support.

Bayesian posterior probabilities (PP) were estimated using a parallel version of MrBayes v3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003), where the run of eight Markov chain Monte Carlo iterations was split between an equal number of processors. Bayesian analysis was initiated with random starting trees and was initially run for four million generations, sampling once per 100 generations. The analysis was run until the value of the standard deviation of split sequences decreased below 0.01 and the potential scale reduction factor was close to or equal to 1.0. The fraction of the sampled values discarded as burn-in was set at 0.25. PP of 0.95–1.00 were considered to indicate strong support.

In the phylogram (Fig. 1), the native distribution of each species is indicated by color as follows: North America (red), South America (tan), Africa (dark green), Australia + Pacific (dark purple), and Eurasia (light purple).

**Table 1** Characteristics of the nine regions, *rps3*, *rps16-trnK*, *rps16* intron, *rpoC2*, *rpL32-trnL*, *ndhF*, *ndhA* intron, *ccsA*, and ITS, and parameters used in Bayesian analyses indicated by the Akaike information criterion (AIC)

| | *rps3* | *rps16-trnK* | *rps16 intron* | *rpoC2* | *rpL32-trnL* | *ndhF* | *ndhA intron* | *ccsA* | Combined plastid data | *ITS* | Overall |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Total aligned characteristics | 612 | 1079 | 898 | 808 | 884 | 765 | 1150 | 954 | 6949 | 746 | 7695 |
| Number of sequences | 77 | 101 | 92 | 77 | 120 | 73 | 80 | 70 | 690 | 135 | 825 |
| Number of new sequences | 47 (61%) | 5 (5%) | 3 (3%) | 43 (56%) | 10 (8%) | 30 (41%) | 3 (4%) | 13 (19%) | 154 (22%) | 15 (11%) | 167 (20%) |
| Likelihood score (-lnL) | 1804.51 | 4012.8 | 3463.46 | 3041.68 | 4562.75 | 3779.90 | 4493.11 | 3048.45 | | 11973.22 | |
| Number of substitution types | 6 | 6 | 6 | 6 | 6 | 6 | 6 | 6 | – | 6 | – |
| Model for among-site rate variation | gamma | gamma | gamma | gamma | gamma | gamma | gamma | gamma | – | gamma | – |
| Substitution rates | 1.67364 | 1.37867 | 1.17620 | 3.50734 | 0.97820 | 2.18640 | 1.38202 | 1.48282 | – | 1.26970 | – |
| | 3.41539 | 2.83812 | 1.13839 | 5.16054 | 1.93638 | 3.03867 | 3.41070 | 3.95747 | | 3.24444 | |
| | 0.48663 | 0.47934 | 0.25602 | 0.30343 | 0.36141 | 0.52675 | 0.70511 | 0.59455 | | 1.92507 | |
| | 0.76892 | 1.70272 | 1.00798 | 2.04551 | 1.03125 | 1.65272 | 2.76200 | 1.27255 | | 0.95472 | |
| | 4.82223 | 2.86646 | 1.92645 | 10.40906 | 1.52720 | 3.94143 | 3.61463 | 3.97891 | | 4.87150 | |
| | 1.00000 | 1.00000 | 1.00000 | 1.00000 | 1.00000 | 1.00000 | 1.00000 | 1.00000 | | 1.00000 | |
| Characteristic state frequencies | 0.43286 | 0.30958 | 0.39282 | 0.39745 | 0.37470 | 0.32680 | 0.36119 | 0.30032 | – | 0.23398 | – |
| | 0.15127 | 0.14992 | 0.10761 | 0.14583 | 0.13243 | 0.12869 | 0.13661 | 0.15882 | | 0.20819 | |
| | 0.16885 | 0.14703 | 0.16687 | 0.23401 | 0.12790 | 0.17034 | 0.14784 | 0.16227 | | 0.25067 | |
| | 0.24701 | 0.39348 | 0.33271 | 0.22272 | 0.36497 | 0.37417 | 0.35436 | 0.37860 | | 0.30716 | |
| Proportion of invariable sites | 0.68799 | 0.10426 | 0.33335 | 0.00000 | 0.18741 | 0.29544 | 0.34523 | 0.54699 | – | 0.23903 | – |
| Substitution model | TVM+G | TVM+G | GTR+I+G | TIM3+I+G | GTR+G | TPM3uf+G | TVM+I+G | TPM3uf+G | – | GTR+I+G | – |
| Gamma shape parameter (α) | 0.792707 | 1.05499 | 0.97074 | 0.57086 | 0.99039 | 0.78355 | 0.95969 | 0.96672 | – | 0.97093 | – |

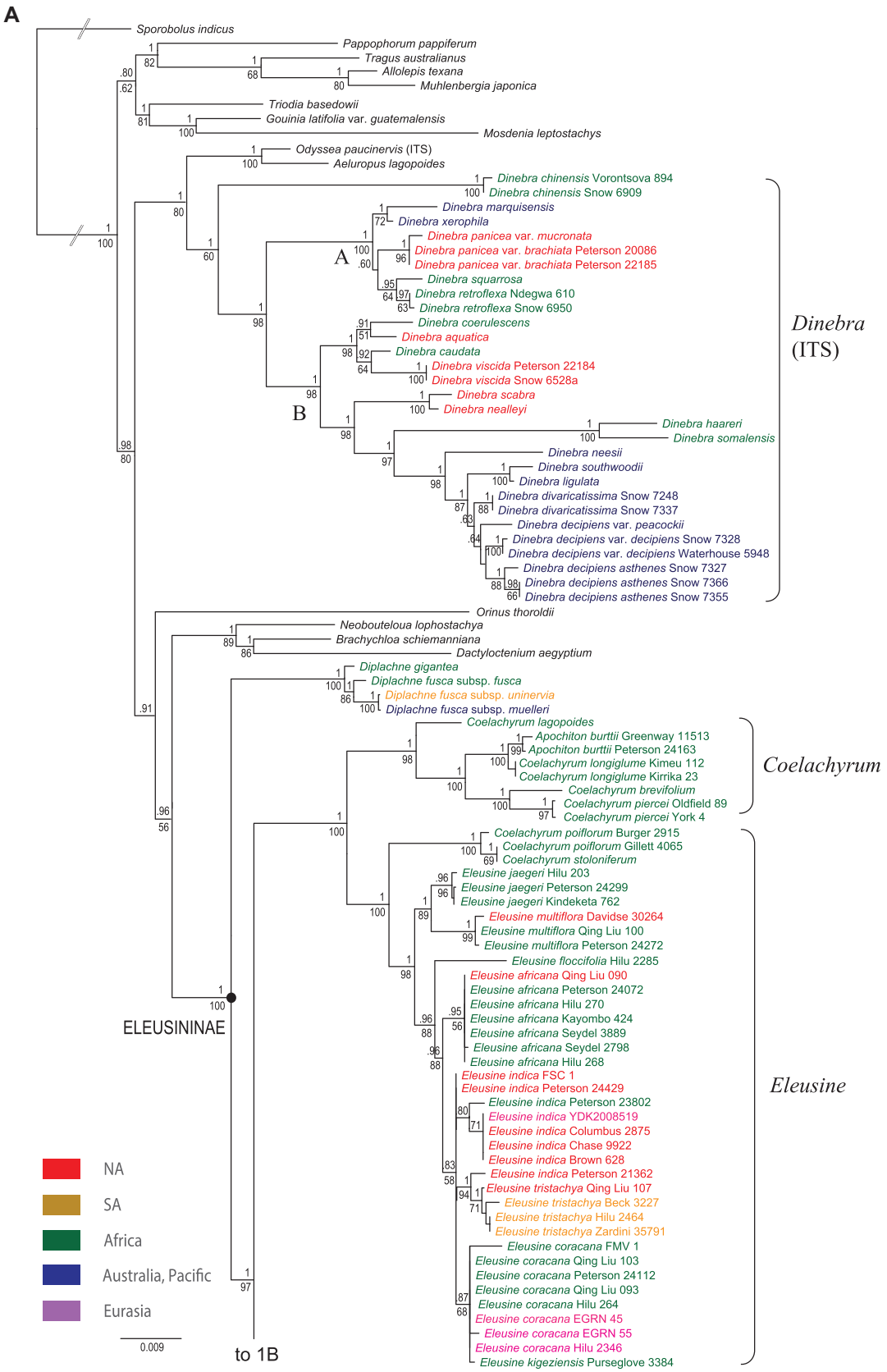



**Fig. 1. A and B** Maximum-likelihood tree inferred from combined plastid (*rps16-trnK*, *rps3*, *rps16*, *rpoC2*, *rpl32-trnL*, *ndhF*, *ndhA*, *ccsA*) and ITS sequences. Numbers above branches show posterior probabilities; numbers below branches show bootstrap values; color indicates where the sample was collected, usually indicative of native status; and vertical bars indicate our classification. Scale bar = 0.9% substitutions/site.

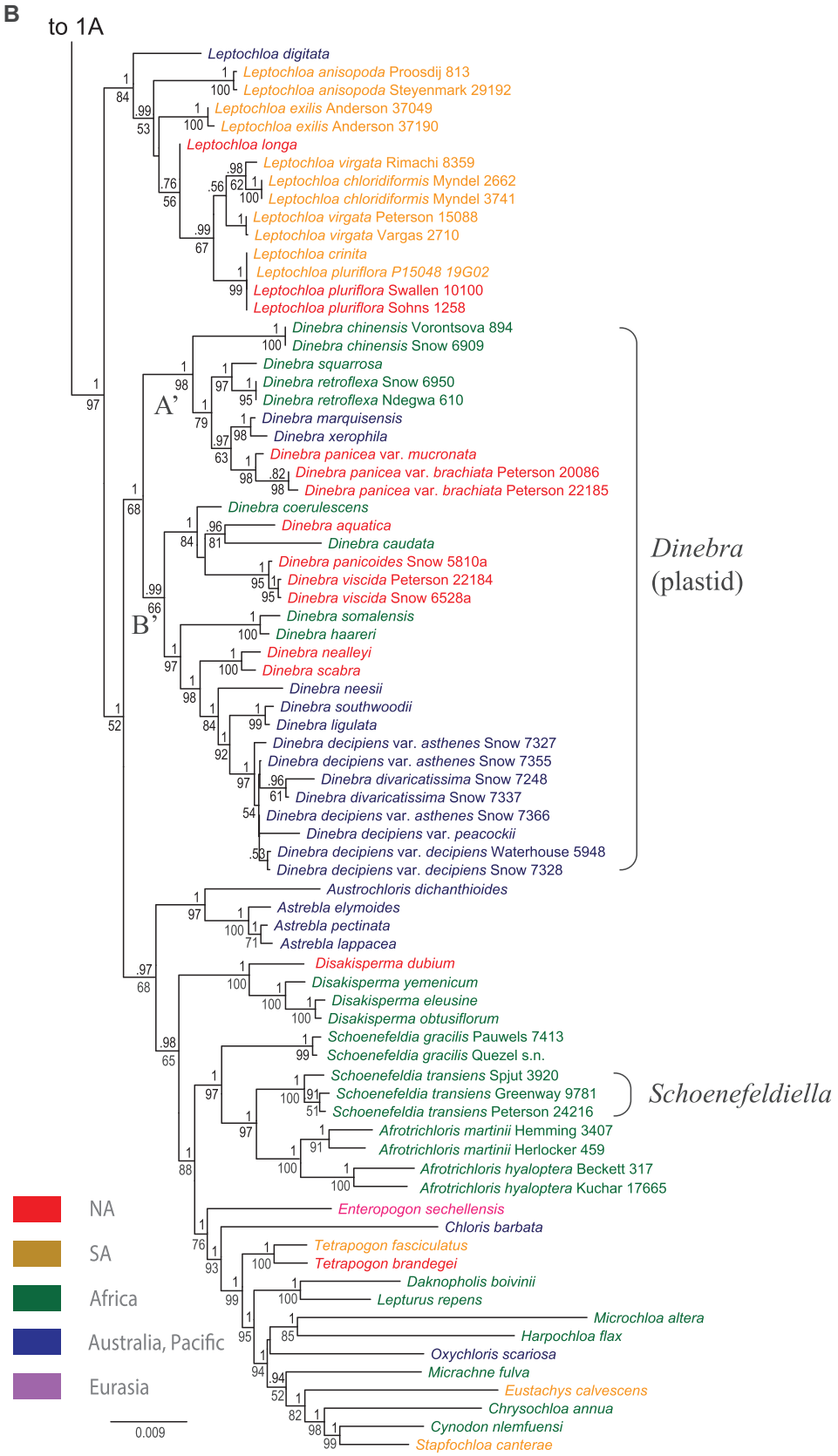



**Fig. 1.** Continued

### 2.4 Assessment of incongruence and data combining strategy

The resulting plastid and ITS topologies were inspected for conflicting nodes (see Fig. 1) with ≥ 80% bootstrap support (BS) and/or PP ≥0.95. If no supported conflict was found, plastid and ITS sequences were combined. Where conflicting topologies were found, the data sets for inconsistently placed taxa were duplicated in the matrix. One set of the taxon was represented by the corresponding plastid sequences only and the other taxon set by only ITS sequences. The remaining positions for the truncated data sets were then coded as missing data. We use this "taxon duplication" approach (Pirie et al., 2008; Pelser et al., 2010; Peterson et al., 2015b, 2016) to resolve our phylogenetic tree minimizing the diffusing effects of taxa with strongly supported incongruence between the plastid and ITS data, and to represent their alternative placements in relation to the remaining phylogenetic groups among which relationships are congruent (see Fig. 1). The combination of data is advantageous because it can provide better backbone support for nodes through the use of plastid data and improve resolution for terminal nodes within the main phylogenetic groups using ITS sequences.

## 3 Results

### 3.1 Phylogenetic analyses

Twenty percent (167/823) of the sequences used in our study are newly reported here (Appendix S1). The characteristics of the nine regions are presented in Table 1. Forty-seven sequences of *rps3* (61%), 43 for *rpoC2* (56%), and 30 for *ndhF* (41%), 13 for *ccsA* (19%), 15 for ITS (11%), 10 for *rpl32-trnL* (8%), 5 for *rps16-trnK* (5%), 3 for *ndhA* (4%), and 3 for *rps16* (3%) are newly reported. Sequence alignment length for *ndhA* is 1150 bp, that for *rps16-trnK* is 1079 bp, that for *ccsA* is 954 bp, that for *rps16* is 898, that for *rpl32-trnK* is 884 bp, that for *rpoC2* is 808 bp, that for *ndhF* is 765 bp, that for ITS is 746 bp, and that for *rps3* is 612 bp. Four hundred and forty-six sequences or 35% (446/1269) were missing.

### 3.2 Incongruence between ITS and combined plastid phylograms

The ITS signal places the *Dinebra* clade as sister to *Aeluropus lagopoides—Odyssea paucinervis* (PP = 1, BS = 80 in the Aeluropodinae) outside the Eleusininae, whereas the combined plastid signal places the *Dinebra* clade within Eleusininae (PP = 1, BS = 68). The topology among the species of *Dinebra* in the ITS- and plastid-derived trees is also different (Figs. 1A and 1B).

In the ITS-derived tree, *Dinebra chinensis* (L.) P.M. Peterson & N. Snow are sister to all remaining species in the genus that forms two clades (labeled A and B on Fig. 1A). Clade A (PP = 1, BS = 100) contains two varieties of *D. panicea* (Retz.) P.M. Peterson & N. Snow (PP = 1, BS = 96) that are sister to *D. squarrosa* (Pilg.) P.M. Peterson & N. Snow—*D. retroflexa* (Vahl.) Panz. (PP= 0.95, BS = 64), and these are sister to *D. marquisensis* (F. Br.) P.M. Peterson & N. Snow—*D. xerophila* (P.M. Peterson & Judz.) P.M. Peterson & N. Snow. Clade B contains an Australian clade with a monophyletic *D. decipiens* (R. Br.) P.M. Peterson & N. Snow, with three varieties sister to *D. divaricatissima* (S.T. Blake) P.M. Peterson & N. Snow. Sister to *D. decipiens—D. divaricatissima* is *D. ligulata* (Lazarides) P.M. Peterson & N. Snow—*D. southwoodii* (N. Snow & B.K. Simon) P.M. Peterson & N. Snow (PP = 1, BS = 100). The basal member of the Australian clade is *D. neesii* (PP = 1, BS = 87), and sister to the Australian clade *D. haareri* (Stapf & C.E. Hubb.) P.M. Peterson & N. Snow—*D. somalensis* (Stapf) P.M. Peterson & N. Snow (PP = 1, BS = 98). Sister to *D. haareri—D. somalensis* + the Australian clade is *D. nealleyi* (Vasey) P.M. Peterson & N. Snow—*D. scabra* (Nees) P.M. Peterson & N. Snow (PP = 1, BS = 97). Sister to *D. nealleyi—D. scabra* + *D. haareri—D. somalensis* + the Australian clade is *D. aquatica* (Scribn. & Merr.) P.M. Peterson & N. Snow—*D. coerulescens* (Steud.) P.M. Peterson & N. Snow + *D. caudata* (K. Schum.) P.M. Peterson & N. Snow—*D. viscida* (Scribn.) P.M. Peterson & N. Snow (PP = 1, BS = 98).

In the plastid-derived tree, there are also two clades (labeled A' and B' in Fig. 1B). In clade A', the two varieties of *D. panicea* (PP = 1, BS = 98) are sister to *D. marquisensis—D. xerophila* (PP = 1, BS = 98). Sister to *D. panicea* + *D. marquisensis—D. xerophila* is *D. retroflexa—D. squarrosa* (PP = 1, BS = 97), and all of these are sister to *D. chinensis* (PP = 1, BS = 79). In clade B', the monophyletic Australian clade includes *D. divaricatissima* embedded with the three varieties of *D. decipiens* and this is sister to *D. nealleyi—D. scabra* (PP = 1, BS = 84). *Dinebra haareri—D. somalensis* (PP = 1, BS = 100) is sister (PP = 1, BS = 98) to *D. nealleyi—D. scabra* + the Australian clade, and all of these form a clade (PP = 0.99, BS = 66) with *D. panicoides* (J. Presl) P.M. Peterson & N. Snow—*D. viscida* + *D. aquatica—D. caudata* sister to *D. coerulescens* (PP = 1, BS = 84).

### 3.3 Phylogenetic tree of Eleusininae

The ML tree from the combined plastid and ITS regions is well resolved, with strong support (PP = 1, BS ≥ 98) for the Eleusininae and the following genera: *Afrotrichloris, Astrebla* F. Muell., *Ceolachyrum* s.s., *Diplachne, Disakisperma*, and *Eleusine* (Figs. 1A and 1B).

*Diplachne* is sister to all remaining genera in the Eleusininae (PP = 1, BS = 97). *Coelachyrum* is polyphyletic because *C. poiflorum* is sister to all species of *Eleusine* (PP = 1, BS = 98). *Apochiton burttii* C.E. Hubb. is embedded within *Coelachyrum* and sister to *C. longiglume* Napper, and this pair is sister to *C. brevifolium* Hochst. & Nees + *C. piercei* (Benth.) Bor (PP = 1, BS = 100). *Coelachyrum lagopoides* (type) is sister to the rest of the *Coelachyrum* s.s. clade. *Eleusine* is monophyletic with *E. jaegeri* Pilg.+ *E. multiflora* Hochst. ex A. Rich. sister to remaining species in the genus. *Eleusine floccifolia* (Forssk.) Spreng. is sister (PP = 0.96, BS = 88) to *E. africana* Kenn.-O'Byrne + *E. indica* (L.) Gaertn. + *E. tristachya* (Lam.) Lam. + *E coracana* (L.) Gaertn. + E. *kigeziensis* S.M. Phillips. Seven accessions of *E. africana* form a clade (PP = 0.95, BS = 56) and these are sister to a polytoma that includes *E. indica* (polyphyletic), *E. tristachya* (PP = 1, BS = 71), and *E. coracana* + *E. kegeziensis* (PP = 87, BS = 68).

The *Leptochloa* clade is moderately supported (PP = 1, BS = 84), with *L. crinita* (Lag.) P.M. Peterson & N. Snow and *L. pluriflora* (E. Fourn.) P.M. Peterson & N. Snow forming a clade showing little variation sister to a clade containing *L. chloridiformis* Parodi–*L. virgata* (L.) P. Beauv. (PP = 0.56), where a single individual of *L. virgata* (*Rimachi 8359*) is sister

to two accessions of *L. chloridiformis*, rendering *L. virgata* polyphyletic. *L. longa* Griseb. is sister to the *L. crinita–L. pluriflora* + *L. chloridiformis–L. virgata* clade. *Leptochloa digitata* (R. Br.) Domin is the first split, followed by two accessions of *L. anisopoda* (Scribn. ex B.L. Rob.) P.M. Peterson, and *L. exilis* (Renvoize) P.M. Peterson.

*Austrochloris* Lazarides + *Astreba* F. Muell. (PP = 1, BS = 97) are sister to the remaining Eleusininae genera (PP = 0.98, BS = 65; Fig. 1B). The next split includes the *Disakisperma* clade (PP = 1, BS =100) sister to remaining Eleusininae. *Schoenefeldia* appears polyphyletic, with its two species in a grade sister to a monophyletic *Afrotrichloris* (PP = 1, BS = 100). *Schoenefeldia gracilis* is basal and sister to *S. transiens* + *Afrotrichloris*.

# 4 Discussion

## 4.1 Phylogeny

We found strong support for the following lineages recognized as genera: *Afrotrichloris, Astrebla, Coelachyrum, Dinebra, Diplachne, Disakisperma, Eleusine*, and *Leptochloa*. However, our *Coelachyrum* clade is paraphyletic because it includes *Apochiton burttii* in a subclade with *C. longiglume*. These two species share morphological synapomorphies of an annual habit, a paniculate inflorescence, and pedicelled spikelets, whereas the other three species of *Coelachyrum* are perennial and have a raceme inflorescence (the branches inserted digitally or along the main axis), and nearly sessile spikelets. Therefore, we create the new combination for *Apochiton* below and emend *Coelachyrum* to include short-awned lemmas and paleas, and trigonous caryopses.

Chiovenda (1915) was the first to recognize the affinities of *C. poiflorum* by placing it in *Eleusine*. However, he mentions two other species, *Eleusine somalensis* Hack. and *E. yemensis* (Schweinf) Chiov., that, based on our earlier molecular studies, are placed in *Dinebra* and *Disakisperma*, respectively (Peterson et al., 2012; Snow et al., 2013). *Coelachyrum poiflorum* [≡ *Eleusine poiflora* (Chiov.) Chiov.] has hairy florets, villous lemmas villous with spreading hairs on the midvein and flanks below, and villous palea keels (Phillips, 1995). The only distinguishing characteristic separating *C. poiflorum* from other species of *Eleusine* is hairy florets. Therefore, it seems best to align *C. poiflorum* within *Eleusine*, splitting at the same hierarchical level as *Coelachyrum* in our tree (Fig. 1A), rather than erect a new genus.

Our new phylogeny of *Eleusine* is topologically similar to that found in Liu et al. (2011) in their investigation of low-copy nuclear genes. However, we found a moderately supported *E. jaegeri* + *E. multiflora* clade (PP = 1, BS = 89), whereas Liu et al. (2011) found a strongly supported *E. jaegeri* + *E. floccifolia* clade (BS = 90–100, PP = 1) for both nuclear trees derived from *EF-1a* and *Pepc4* markers. We did not include *E. intermedia* (Chiov.) S.M. Phillips in our current study, and this may have affected our topology.

We verify for the first time using molecular data that *Leptochloa longa* aligns within *Leptochloa* and the number of species within the genus increases to eight. However, the exact placement of *L. longa* within the *Leptochloa* clade is tentative because we were only able to sequence the *rps3* marker for this species, although morphologically, *L. longa* fits easily into the genus. The overall topology among the species of *Leptochloa* in our phylogeny is similar to that found in Peterson et al. (2015a). There are still three species that have historically been placed in *Leptochloa*: *L. malayana* (C.E. Hubb.) Jansen ex Veldkamp, *L. monticola* Chase, and *L. tectoneticola* (Backer) Jansen ex Veldkamp, that have not been included in a molecular DNA phylogeny and need further study.

The unresolved placement of the *Dinebra* clade (inside or outside of the Eleusininae) has been documented previously in Peterson et al. (2012, 2015a, 2016). Incongruence between the plastid and nuclear DNA signal is common, especially within the Poaceae, and more study of *Dinebra* is necessary to untangle its evolutionary history, although it appears to be another case of hybridization and subsequent genomic introgression (Peterson et al., 2016). In addition, there are four species currently placed in *Dinebra*, *D. perrieri* (A. Camus) Bosser., *D. polycarpha* S.M. Phillips, *D. simoniana* (N. Snow) P.M. Peterson & N. Snow, and *D. srilankensis* (N. Snow) P.M. Peterson & N. Snow, that have not been included in a molecular DNA phylogeny and require further study.

The inclusion of *Afrotrichloris hyaloptera* in our current study as a strongly supported sister to *A. martinii* provides evidence for retaining *Afrotrichloris* as a separate genus characterized by having a racemose inflorescence, 3- to 5-veined upper glumes shorter than the lemma, and deeply cleft lemma apices that can be awned (Watson & Dallwitz, 1992; Phillips, 1995; Clayton et al., 2016). *Afrotrichloris* shares many morphological features with *Schoenefeldia*, including racemose inflorescences, long-awned lemmas, and caryopses with free pericarps. However, in our phylogeny, *Schoenefeldia* is paraphyletic, with the two species of *Schoenefeldia* in a grade sister to *Afrotrichoris*. We are left with two options to interpret the taxonomy of these four species: (A) recognize all four species in *Schoenefeldia* or (B) erect a new genus for *S. transiens* because it does not pair with the type, *S. gracilis*. We chose B and describe a new genus, *Schoenefeldiella* below.

## 4.2 Biogeography

The Eleusininae (crown age of 25.85 Ma), a diverse assemblage now consisting of 28 genera with addition of *Schoenefeldiella*, may have originated in Africa because it shares a common ancestor with subtribe Dactylocteniinae P.M. Peterson, Romasch. & Y. Herrera, also of African origins (Peterson et al., 2015a, 2016; Gallaher et al., 2022). Both species of *Afrotrichloris* (African), five species of *Coelachyrum* (primarily African, spreading to Asia), 10 of the 11 species of *Eleusine* Gaertn. (primarily African, Asian, and Australasian; only *E. tristachya* radiated to South America), and a single species each of *Schoenefeldia* and *Schoenefeldiella* occur in Africa (Liu et al., 2011; Clayton et al., 2016). *Dinebra* (±23 species, African, Australasian, and North American) also seems to have African origins as shown in our analyses. *Dinebra chinensis* (native to east Africa, Asia, Malaysia, Papua New Guinea, Philippines, and Japan) is depicted as the basal split in our ITS-derived clade and in the plastid-derived A' clade, whereas in the plastid-derived B' clade, the first bifurcation *D. coerulescens* (African) is sister to the remaining species and the second bifurcation *D. haareri* + *D. somalensis* (African) is sister to the remaining species in the genus. The origins of *Leptochloa* are more difficult to speculate about because the basal species *L. digitata* is endemic to

Australia and shares a common ancestor with the remaining species of *Leptochloa*, many of which are widespread in the western hemisphere (4 spp.) or restricted to South America and/or the Caribbean (2 spp.), and Panama and Trinidad (1 spp.) (Snow et al., in prep). As mentioned previously, there are still three species only tentatively placed in *Leptochloa*; two of these, *L. malayana* and *L. tectoneticola* from tropical Asia, Indo-China, and Malaysia, were initially placed in *Diplachne* (Veldkamp, 1971; Clayton et al., 2016).

## 5 Taxonomy

**5.1 *Coelachyrum*** Hochst. & Nees, Linnaea 16(2): 221. 1842. **gen. emend.** Type: *Coelachyrum brevifolium* Hochst. & Nees

Description: Annuals or perennials, tufted, sometimes stoloniferous. Culms 7–90 cm long, geniculately ascending or decumbent, usually rooting at the lower nodes. Leaf sheaths glabrous; ligules membranous, sometimes with a ciliate fringe, apex usually truncate; and blades linear or lanceolate, occasionally rounded or cordate near base, flat. Inflorescence a panicle with pedicelled spikelets (*C. burttii* & *C. longiglume*) or composed of racemes; these either digitately inserted or racemosely inserted along a main axis with nearly sessile spikelets. Spikelets 3- to 14-flowered, ovate, elliptic, or oblong, laterally compressed; disarticulation below the glumes, the spikelet falling as a unit; glumes shorter than the spikelet, 1–3 (–7)-veined, membranous, persistent, apex obtuse to acute, sometimes mucronate, and occasionally short-awned (*C. burttii*); lemmas 3-veined, membranous, glabrous, asperulous, or hairy, apex truncate, obtuse or acute to mucronate, occasionally short-awned (*C. burttii*); paleas shorter than the lemma, two-keeled, the keels ciliate or glabrous, occasionally the keels extending into awns (*C. burttii*); stamens 3. Caryopses ellipsoid, ovoid, oblong, or reniform, concavo–convex flattened or trigonous (*C. burttii*), the surface granular or rugose, pericarp free.

Distribution: Five species comprise *Coelachyrum*, which are found in west and east tropical Africa and tropical Asia in Arabia, Pakistan, and India (Phillips, 1995; Cope, 2007).

**5.2 *Coelachyrum burttii*** (C.E. Hubb.) P.M. Peterson, **comb. nov.** ≡ *Apochiton burttii* C.E. Hubb., Hooker's Icon. Pl. 34: t. 3319. 1936. Type: Tanzania, Tanganyika Territory, Kondoa Irangi District near Sambala, 19 May 1929, *B.D. Burtt 2602* (holotype: K000366648 [image!]; isotype: US-1646885!).

**5.3 *Eleusine*** Gaertn., Fruct. Sem. Pl. 1:7. 1788. **gen. emend.** Type: *Eleusine coracana* (L.) Gaertn. (≡ *Cynosurus coracanus* L.)

Description: Tufted annuals or perennials, sometimes rhizomatous or stoloniferous. Culms 10–200 cm tall, erect, geniculately ascending or decumbent; internodes flattened and elliptical in cross section. Leaf sheaths usually shorter than the internodes, keeled; ligules membranous, apex truncate, ciliate; blades smooth, occasionally with scattered papillose-based hairs, mostly flat. Inflorescence with digitate, subdigitate, or with a main axis of racemes, the spikelets biseriate on one side of the triangular rachis, sessile. Spikelets 6- to 18-flowered, ovate, laterally compressed; disarticulation above the glumes and between the florets; glumes shorter than the spikelets, usually 1-veined, but occasionally 2- to 7-veined, ovate, membranous, apex acute to obtuse, occasionally mucronate; lemmas 3-veined, membranous, the veins usually glabrous or occasionally with shaggy hairs below (*E. poiflora*), margins glabrous or sometimes hairy, apex acute, obtuse or truncate, occasionally mucronate; paleas shorter than the lemmas, 2-veined, the veins glabrous or occasionally with hairs (*E. poiflora*); stamens 3. Caryopses mostly trigonous, but occasionally dorsally or laterally compressed or concavo-convex, the surface granular, striate or rugose, hilum punctiform, and pericarp free.

Distribution: With the inclusion of *Eleusine poiflora* (≡ *Coelachyrum poiflorum* Chiov. = *Coelachyrum stoloniferum* C.E. Hubb.), there are now 11 species of *Eleusine,* of which nine are found in Africa; of these nine, *E. indica* is a pantropical weed and *E. poiflora* extends into Somalia, Djibouti, Saudi Arabia, Yemen, and Oman; *E. tristachya* is native to South America; and *E. coracana* (finger millet) is known only from cultivation (Phillips, 1972, 1995; Peterson et al., 2001, 2015a; Cope, 2007).

**5.4 *Schoenefeldiella*** P.M. Peterson, **gen. nov.** – Type: *Schoenefeldiella transiens* (Pilg.) P.M. Peterson [≡ *Schoenefeldia transiens* (Pilg.) Chiov.]

Diagnosis: *Schoenefeldiella* differs from *Schoenefeldia* in having 2-flowed spikelets with the upper floret sterile and awned, perennial habit, and flat leaf blades 5–35 cm long.

Description: Plants perennial, tufted. Culms 70–120 cm tall, erect, or geniculately ascending. Leaf blades 5–35 cm long, 1–5 mm wide, flat, scaberulous, or smooth below, glabrous, or loosely pilose. Inflorescence with 2–4 racemes digitately inserted; racemes 10–20 cm long, straight or flexuous, one-sided and two-rowed with sessile spikelets, rachis 0.5–0.8 mm wide; and disarticulation below the spikelets. Spikelets 3.5–5 mm long, 2-flowered, laterally compressed, the lower floret perfect, the upper floret reduced (vestigial) and sterile; glumes 2–5 mm long, 1-veined; lower glume 1.5–3 mm long, awned, the awn 1–2.5 mm long; upper glumes 3.5–5 mm long, unawned; perfect lemmas 3–4 mm long, 3-veined, membranous, awned, margins ciliate, the awns 25–45 mm long usually twisting and closely appressed to the raceme, apically inserted between a minutely bifid apex; sterile lemmas 0.4–1 mm long, awned, the awn 10–25 mm long; callus pilose, obtuse; paleas hyaline, 2-veined; stamens 3, anthers 0.5–1 mm long. Caryopses ellipsoid, laterally compressed, hilum punctiform, and pericarp free.

Distribution: *Schoenefeldiella transiens* is found in Eastern Africa from Ethiopia, South Sudan, Somalia, Uganda, Kenya, Tanzania, Zimbabwe, Mozambique, and South Africa (Hubbard, 1974b; Phillips, 1974, 1995; Russell et al., 1990; Cope, 1995, 1999; Mashau & Götze, 2014)

***Schoenefeldiella transiens*** (Pilg.) P.M. Peterson, **comb. nov.** ≡ *Chloris transiens* Pilg., Bot. Jahrb. Syst. 51: 418. 1914 ≡ *Schoenefeldia transiens* (Pilg.) Chiov., Res. Sci. Somal. Ital. 1: 186. 1916 – Lectotype (designated by C.E. Hubbard in Fl. Trop. E. Afr., Gramineae 2: 309. 1974): TANZANIA. Pare District, Kwa Sengiwa-Maji ya juu, steppe below Kilimanjaro, 900 m, 14 Dec 1901, *C. Uhlig 882* (B10 0002186 [image!]; isolectotype: EA00000056 [image!]).

Etymology: The name is derived from *Schoenefeldia* because both genera share many morphological features.

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## Supplementary Material

The following supplementary material is available online for this article at http://onlinelibrary.wiley.com/doi/10.1111/jse.12803/suppinfo:

**Appendix S1.** Taxon voucher (collector, number, and where the specimen is housed), country of origin, and GenBank accession for DNA sequences of rps3, rps16-trnK, rps16 intron, rpoC2, rpl32-trnL, ndhF, ndhA intron, ccsA, and ITS regions (bold indicates new accession); a dash (—) indicates missing data; and an asterisk (*) indicates sequences not generated in our lab.