CLASSIFICATION AND BIOGEOGRAPHY OF NEW WORLD GRASSES: CHLORIDOIDEAE

PAUL M. PETERSON,[1,3] J. TRAVIS COLUMBUS,[2] AND SUSAN J. PENNINGTON[1]

[1]*Department of Botany, National Museum of Natural History, Smithsonian Institution,*
Washington, D.C. 20013-7012, USA;
[2]*Rancho Santa Ana Botanic Garden, 1500 North College Avenue, Claremont, California 91711-3157, USA*
[3]*Corresponding author (peterson@si.edu)*

ABSTRACT

Subfamily Chloridoideae (Poaceae) in the New World includes 72 genera (61 native, 11 introduced), 678 species (607 native), and, including intraspecific taxa, 817 total taxa. The five largest genera are *Muhlenbergia* (147 species), *Eragrostis* (111), *Sporobolus* (76), *Bouteloua* (57), and *Chloris* (35). Three tribes are recognized in this study: Cynodonteae, Eragrostideae, and Zoysieae, with ten, three, and two subtribes, respectively. Cynodonteae, the largest tribe, comprise 58 genera and 451 species (67% of all New World chloridoids), including 25 genera (98 species, 22% of all New World Cynodonteae) with unknown affinities (incertae sedis). In Mexico, the USA, and Canada there are 477 native and introduced chloridoid species (70% of all New World species), whereas in Central America (including the Caribbean) and South America there are 196 and 304 species, respectively. Mexico is the center of diversity with 343 species (51%). There appear to be five biogeographical patterns exhibited by New World chloridoid species: (1) North America, centered in northern Mexico and the southwestern USA, (2) southern South America, centered in northern Argentina, Paraguay, Uruguay, and southern Brazil, (3) northwestern South America, centered in Ecuador and Peru, (4) amphitropical disjuncts, occurring in North America and southern South America, and (5) widespread species, occurring in North America, Central America, and South America. Subtribes Boutelouinae (*Bouteloua*) and Muhlenbergiinae are predominantly North American, whereas Eragrostidinae (*Eragrostis*) and Chloridinae are better represented in the southern South American center. Two subtribes of Cynodonteae, **Gouiniinae** and **Hilariinae**, are described as new, and two others, **Orcuttiinae** and **Traginae**, are newly treated at that rank.

Key words: biogeography, Chloridoideae, classification, Poaceae, taxonomy.

INTRODUCTION

The grass (Poaceae) subfamily Chloridoideae was first validly published in 1833 by Carl Traugott Beilschmied, a German botanist and pharmacist, who used an earlier description of sect. Chlorideae by Kunth (1815). That same year, Kunth (1833) published his *Agrostographia Synoptica* in which he recognized the following genera in the group (Chlorideae): *Chloris, Ctenium, Cynodon, Dactyloctenium, Eleusine, Eustachys, Gymnopogon, Harpochloa* Kunth, *Leptochloa, Microchloa, Pleuraphis, Schoenefeldia* Kunth, *Spartina, Triplasis,* and eight genera now treated as synonyms of *Bouteloua*. Clearly our modern understanding of Chloridoideae is much greater, and there now appear to be more than 1420 species in the subfamily worldwide. Later isonyms of the subfamily were published by Burmeister (1837) and Rouy (1913), and, as currently circumscribed, Chloridoideae include genera that were placed in Eragrostoideae (Pilger 1956) and Pappophoroideae (Burmeister 1837).

The core species in the subfamily share two structural synapomorphies: all exhibit Kranz or C_4 leaf anatomy (except *Eragrostis walteri* Pilg. from South Africa; Ellis 1984) and most have chloridoid bicellular microhairs (broad, short terminal cell the same thickness as the basal cell) present on leaf surfaces. Two main subtypes of C_4 photosynthesis, NAD-ME (nicotinamide adenine dinucleotide co-factor malic enzyme) and PCK (phosphoenolpyruvate carboxykinase), have been found and verified by biochemical assay to occur in Chloridoideae (Gutierrez et al. 1974; Brown 1977; Hattersley and Watson 1992). Ecologically, there appears to be some separation in habitat preference according to C_4 subtype (Ellis et al. 1980; Hattersley 1992). Taxa possessing the NAD-ME subtype seem to prefer habitats that are relatively hot and dry. In cross section, their leaf blades exhibit columns of colorless cells between the vascular bundles, which promote involution of the blade during drought stress, reducing transpirational water loss (P. M. Peterson pers. obs.). In comparison, PCK taxa seem to prefer more mesic habitats (e.g., in canyons, under canopy of forest margins, and along creeks), and their blades are usually flat and soft, with the chlorenchyma continuous between vascular bundles (Peterson 2000). The PCK subtype is thought to represent an apomorphy in grasses because this C_4 cycle appears to be a modification of the NAD-ME subtype (Hattersley and Watson 1992). In addition, the PCK subtype is known only to occur in grasses, whereas the NAD-ME subtype is also found in other monocot and dicot families (Hattersley and Watson 1992; Peterson and Herrera-Arrieta 2001).

Other character trends in chloridoids include a base chromosome number of $x = 10$ (a plesiomorphy), fruits (caryopses) with nonlinear hilums that are usually punctiform or small, embryos with elongated mesocotyl internodes, and two non-membranous (fleshy) lodicules (Soreng and Davis 1998; Grass Phylogeny Working Group [GPWG] 2001). However, most of these character trends are seen in the closely related subfamilies Aristidoideae, Arundinoideae,

Table 1. Classification of New World Chloridoideae and number of species per genus. * = endemic genus. i = all species in genus introduced.

Taxon	No. species
Tribe CYNODONTEAE (syn. Chlorideae)	
Subtribe BOUTELOUINAE	
Bouteloua Lag.*	57
Subtribe CHLORIDINAE	
Chloris Sw.	35
Cynodon Rich.	16
Enteropogon Nees	4
Eustachys Desv.	12
Microchloa R. Br.	2
Trichloris E. Fourn. ex Benth.*	2
Subtribe ELEUSININAE	
Eleusine Gaertn.	4
Subtribe **Gouiniinae**	
Gouinia E. Fourn. ex Benth. & Hook. f.*	10
Vaseyochloa Hitchc.*	1
Subtribe **Hilariinae**	
Hilaria Kunth*	7
Pleuraphis Torr.*	3
Subtribe MONANTHOCHLOINAE	
Distichlis Raf.	6
Monanthochloe Engelm.*	2
Reederochloa Soderstr. & H. F. Decker*	1
Subtribe MUHLENBERGIINAE	
Aegopogon Humb. & Bonpl. ex Willd.	4
Bealia Scribn.*	1
Blepharoneuron Nash*	2
Chaboissaea E. Fourn.*	4
Lycurus Kunth*	3
Muhlenbergia Schreb.	147
Pereilema J. Presl*	4
Redfieldia Vasey*	1
Schaffnerella Nash*	1
Schedonnardus Steud.*	1
Subtribe MUNROINAE	
Dasyochloa Willd. ex Rydb.*	1
Erioneuron Nash*	3
Munroa Torr.*	5
Subtribe **Orcuttiinae**	
Neostapfia Burtt Davy*	1
Orcuttia Vasey*	5
Tuctoria Reeder*	3
Subtribe **Traginae**	
Tragus Haller i	4
Willkommia Hack.	1
Incertae sedis	
Acrachne Wight & Arn. ex Chiov. i	1
Allolepis Soderstr. & H. F. Decker*	1
Blepharidachne Hack.*	4
Ctenium Panz.	10
Dactyloctenium Willd. i	5
Dinebra Jacq. i	1
Gymnopogon P. Beauv.	12
Jouvea E. Fourn.*	2
Leptochloa P. Beauv.	17

Table 1. Continued.

Taxon	No. species
Leptothrium Kunth	1
Lepturidium Hitchc. & Eckman*	1
Neesiochloa Pilg.*	1
Neobouteloua Gould*	2
Neyraudia Hook. f. i	1
Pappophorum Schreb.*	8
Rheochloa Filg., P. M. Peterson, & Y. Herrera*	1
Saugetia Hitchc. & Chase*	2
Scleropogon Phil.*	1
Sohnsia Airy Shaw*	1
Swallenia Soderstr. & H. F. Decker*	1
Trichoneura Andersson	3
Tridens Roem. & Schult.*	16
Triplasis P. Beauv.*	2
Tripogon Roem. & Schult.	2
Triraphis R. Br.	2
Tribe ERAGROSTIDEAE	
Subtribe COTTEINAE	
Cottea Kunth*	1
Enneapogon Desv. ex P. Beauv.	2
Subtribe ERAGROSTIDINAE	
Cladoraphis Franch. i	1
Eragrostis Wolf	111
Pogonarthria Stapf i	1
Steirachne Ekman*	2
Subtribe UNIOLINAE	
Fingerhuthia Nees ex Lehm. i	1
Tetrachne Nees i	1
Uniola L.*	5
Tribe ZOYSIEAE	
Subtribe SPOROBOLINAE	
Calamovilfa (A. Gray) Hack. ex Scribn. & Southw.*	5
Crypsis Aiton i	3
Spartina Schreb.	15
Sporobolus R. Br.	76
Subtribe ZOYSIINAE	
Zoysia Willd. i	3

Danthonioideae, and Panicoideae. A recent morphological and ecological description of the subfamily is given in GPWG (2001). Some salient features include: plants herbaceous, rarely woody, occurring in dry climates, sheaths usually nonauriculate, inflorescence paniculate, racemose, or spicate, spikelets bisexual or unisexual (plants monoecious or dioecious) with one to many fertile florets, usually laterally compressed, usually disarticulating above the glumes, palea well developed, lodicules usually two, fleshy, ovary glabrous, styles and stigmas two, caryopsis with pericarp often free or loose, hilum short, endosperm hard, without lipid, embryo with an epiblast (usually), scutellar cleft, and elongated mesocotyl internode.

In this paper, based on the latest phylogenetic evidence, we introduce a new tribal and subtribal classification for Chloridoideae, presenting the salient morphological features of the groups, and we examine the biogeography of the subfamily in the New World. In Cynodonteae, two subtribes,
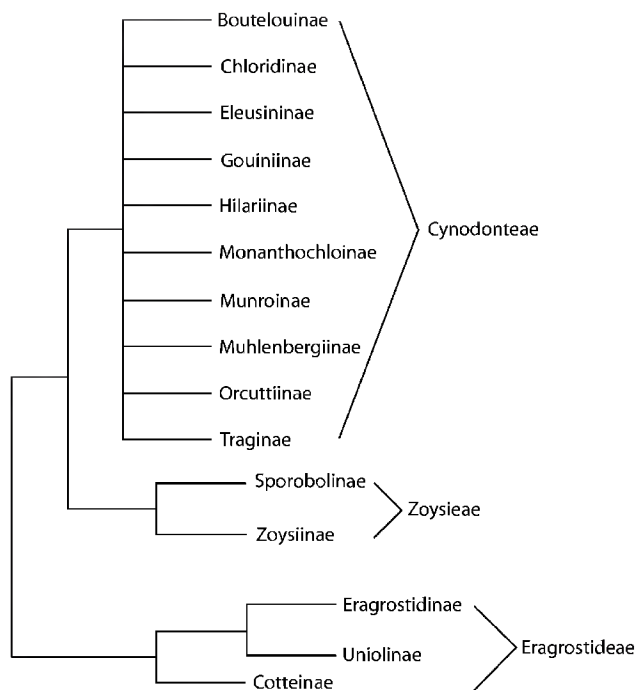
Fig. 1.—Evolutionary relationships of the tribes and subtribes of New World Chloridoideae (based on Columbus et al. 2007).

Table 2. Number of native and introduced species of New World Chloridoideae in each tribe and subtribe.

Tribe/subtribe	Native	Introduced	Total	% of total
Cynodonteae	422	29	451	66.5
Boutelouinae	57	0	57	8.4
Chloridinae	63	8	71	10.5
Eleusininae	1	3	4	0.6
Gouiniinae	11	0	11	1.6
Hilariinae	10	0	10	1.5
Monanthochloinae	9	0	9	1.3
Muhlenbergiinae	167	1	168	24.8
Munroinae	9	0	9	1.3
Orcuttinae	9	0	9	1.3
Traginae	1	4	5	0.7
Incertae sedis	85	13	98	14.5
Eragrostideae	95	30	125	18.4
Cotteinae	2	1	3	0.4
Eragrostidinae	88	27	115	17.0
Uniolinae	5	2	7	1.0
Zoysieae	90	12	102	15.0
Sporobolinae	90	9	99	14.6
Zoysiinae	0	3	3	0.4
Total	607	71	678	100

Gouiniinae and Hilariinae, are described as new, and two others, Orcuttiinae and Traginae, are newly treated at that rank.

METHODS

As part of the ongoing *Catalogue of New World Grasses* project (Soreng et al. 2000; Peterson et al. 2001*b*), the distributions of all accepted taxa (native and introduced) were recorded at the level of country with the Caribbean (West Indies) nations treated as a single unit. Although there is much regional variation within countries that these data do not capture, the broad-scale geographic patterns for the subfamily in the New World can be addressed. This paper represents a summary of distribution patterns of the native species, but all of the original data are available online at *mobot. mobot.org/W3T/Search/nwgc.html*. For each native species, its presence or absence in each country and the Caribbean was recorded even if its occurrence in a particular country likely represents a recent, human-mediated introduction. That is, no attempt was made in this study to assess the role of humans in expanding or reducing the ranges of the native New World species.

The morphological discussion was derived in part from an analysis of a DELTA data set (541 characters in the *Grass Genera of the World* compiled by Watson and Dallwitz 1999) using only the New World chloridoid genera (including naturalized introductions), and run on INTKEY (Dallwitz et al. 1998). INTKEY was used to combine data for all representative genera of each subtribe and tribe before searching for similarities and differences among the taxa.

CLASSIFICATION

Chloridoideae in the New World include 72 genera (61 native, 11 introduced) and 678 species (607 native). Intra-

specific taxa are recognized for 148 species, bringing the total number of taxa to 817 (excluding autonyms). Three tribes and 15 subtribes are recognized (Table 1). Tribe Cynodonteae contains ten subtribes (Boutelouinae, Chloridinae, Eleusininae, Gouiniinae, Hilariinae, Monanthochloinae, Muhlenbergiinae, Munroinae, Orcuttiinae, and Traginae). Eragrostideae contain three subtribes (Cotteinae, Eragrostidinae, and Uniolinae), and Zoysieae have two subtribes (Sporobolinae and Zoysiinae). In addition, the largest tribe, Cynodonteae, contains 25 genera (98 spp.) of uncertain alliance (incertae sedis). This realignment is new and is a synthesis of previous morphological and molecular work (Duvall et al. 1994; Peterson et al. 1995, 1997, 2001*a*; Van den Borre and Watson 1997, 2000; Columbus et al. 1998, 2000; Hilu and Alice 2000, 2001; Ortiz-Diaz and Culham 2000; Peterson 2000) with major emphasis on results reported in Columbus et al. (2007).

Figure 1 summarizes our present understanding of the evolutionary history of the tribes and subtribes within New World Chloridoideae. Cynodonteae and Zoysieae are sister, and sister to this clade are Eragrostideae. All three tribes are supported by DNA sequence data from the chloroplast (*mat*K, *trn*L–F region) and nuclear (ITS) genomes (Hilu and Alice 2000, 2001; Columbus et al. 2007). Relationships among the ten subtribes within Cynodonteae, as well as the 25 unplaced genera, are uncertain pending additional study. ITS sequences analyzed alone or in combination with *trn*L–F sequences place *Zoysia* (Zoysiinae) sister to the remaining members (Sporobolinae) of Zoysieae (Columbus et al. 2007). Eragrostideae comprise three main lineages and subtribes, with Eragrostidinae and Uniolinae sister, and Cotteinae sister to this clade.

A suprageneric summary of New World Chloridoideae (Table 2) shows that Cynodonteae include 451 species (67% of all New World chloridoids), only 29 introduced. Within Cynodonteae, Muhlenbergiinae contain 168 species (25%),

Table 3. Numbers of native species in the five largest chloridoid genera ocurring in the four most diverse countries of the New World.

	Mexico	USA	Brazil	Argentina	% of species in genus occurring in one or more of these countries
Muhlenbergia	107	68	3	13	92.5
Eragrostis	36	27	39	24	77.9
Sporobolus	29	28	29	14	90.3
Bouteloua	51	24	5	8	96.5
Chloris	10	15	11	13	75.8
Total	233	162	87	72	
Total native chloridoid species	319	259	150	146	
% of total native chloridoid species accounted for by these genera	73.0	62.5	58.0	49.3	

followed by the orphan (incertae sedis) genera with 98 species (15%), Chloridinae with 71 (11%), and Boutelouinae with 57 (8%). Eragrostideae are the next largest tribe with 125 species (18%), 30 introduced. One in four species in Eragrostideae is introduced, compared to only one in 15 in Cynodonteae. Eragrostidinae are the largest subtribe within Eragrostideae, containing 115 species (17%), 27 introduced. Finally, Zoysieae have 102 species (15%), 12 introduced. Sporobolinae are the largest subtribe within Zoysieae with 99 species (14.6%), nine introduced.

Muhlenbergia (147 spp.), *Eragrostis* (111), *Sporobolus* (76), *Bouteloua* (57), and *Chloris* (35) are the five largest genera of Chloridoideae in the New World, and collectively account for 65% (394 spp.) of all native New World chloridoids. Of all native chloridoid species in any given country, these five genera together compose 73% (233 spp.) in Mexico, 63% (162 spp.) in the USA, 58% (87 spp.) in Brazil, and 49% (72 spp.) in Argentina (Table 3). Mexico, the USA, Brazil, and Argentina collectively include, of all native species per genus, 93% of *Muhlenbergia*, 78% of *Eragrostis*, 90% of *Sporobolus*, 97% of *Bouteloua*, and 76% of *Chloris* (Table 3).

Eragrostideae

Tribe Eragrostideae has been treated by many authors (e.g., Pilger 1956; Gould and Shaw 1983; Clayton and Renvoize 1986; Watson and Dallwitz 1992; Peterson et al. 1995, 1997) in a broader sense than treated herein. We recognize two small subtribes, Cotteinae and Uniolinae, and one larger subtribe, Eragrostidinae. Trends in the tribe include spikelets with many florets, lemmas with 3–13 nerves, and many species adapted to xeric habitats.

Subtribe Cotteinae includes two genera, *Cottea* and *Enneapogon*, characterized by hairy culm nodes, hairy rachillas, lemmas 9–13-nerved and hairy, apices deeply cleft and 9–13-lobed, each lobe terminating in an awn, the awns often hairy, and microhairs on the abaxial epidermis of the leaf blade having long (60–180 μm) basal cells. With the realignment of *Pappophorum* in Cynodonteae (Columbus et al. 2007), *Cottea pappophoroides* Kunth and *Enneapogon desvauxii* P. Beauv., each an amphitropical disjunct, are the only native New World species currently assigned to the group, which has long been treated as tribe Pappophoreae. The origin of Cotteinae appears to be in Australia/Africa, where the majority of the species of *Enneapogon* occur today. In the *mat*K phylogeny (Hilu and Alice 2001), the Old World genus *Schmidtia* Steud. forms a strongly supported clade with *Cottea* and *Enneapogon*. Another Old World (Africa) genus in the group is *Kaokochloa* de Winter (Clayton and Renvoize 1986), but it has yet to be sampled for molecular phylogenetic study.

Subtribe Eragrostidinae as treated here includes four genera: *Cladoraphis cyperoides* (Thunb.) S. M. Phillips introduced from Africa, *Eragrostis* with 111 species (86 native) (Peterson 2003a), *Pogonarthria squarrosa* (Roem. & Schult.) Pilg. introduced from southern Africa, and *Steirachne* with two South American species. *Cladoraphis* and *Steirachne* are only provisionally placed in the subtribe because they were not sampled in the molecular phylogenetic studies of Hilu and Alice (2000, 2001) and Columbus et al. (2007), but they were included in tribe Eragrostideae by Clayton and Renvoize (1986). The subtribe is characterized by hairy or glabrous culm nodes, hairy or glabrous rachillas, lemmas (1) 3 (5)-nerved, glabrous or scabrous, apices entire and awnless, mucronate, or short awned (only in the last two genera), and microhairs on the abaxial epidermis of the leaf blade having short (15–75 μm) basal cells. Morphologically, the two species of *Steirachne* (*S. barbata* (Trin.) Renvoize and *S. diandra* Ekman) are hardly separable from *Eragrostis acutiflora* (Kunth) Nees, as all have acuminate to attenuate or subaristate, 3-nerved lemmas.

Subtribe Uniolinae includes three genera, *Fingerhuthia*, *Tetrachne*, and *Uniola*, characterized by glabrous culm nodes, spikelets that disarticulate below the glumes, glabrous rachillas, lemmas 3–10-nerved, hairy or glabrous, apices entire, awnless or mucronate, microhairs on the abaxial epidermis of the leaf blade having short (15–35 μm) basal cells, and abaxial sclerenchyma in the leaf blade continuous with columns of colorless cells. The subtribe is currently an odd assemblage in the New World because *Fingerhuthia africana* Lehm. and *Tetrachne dregei* Nees are both introduced and known only from cultivation. *Uniola* (5 spp.) is the only native representative, characterized by strongly laterally compressed spikelets with 6–20 florets and coriaceous, sharply keeled lemmas.

Zoysieae

Tribe Zoysieae was treated by Clayton and Richardson (1973) and Clayton and Renvoize (1986) as including 12 Old World genera characterized by spikelets with a single floret, spiciform inflorescences of numerous deciduous racemelets disposed along a central axis, lemmas usually rounded and rarely with apical awns, and glumes often modified and oddly shaped. With the addition of subtribe Sporobolinae, the tribe now contains the New World representatives *Calamovilfa* (5 spp., endemic to North America), *Spartina* (13 native spp.), and *Sporobolus* (76 total spp., 72 native) (Peterson et al. 2003). Trends in Zoysieae as here circumscribed include glabrous culm nodes, ligule a line of hairs or fringed membrane, bisexual spikelets that are laterally compressed (or terete, rarely dorsiventrally com-

pressed) and have a single floret, lower glumes nerveless or 1-nerved (sometimes absent in *Zoysia*), lemmas 1- or 3-nerved, awnless, ovaries glabrous, a base chromosome number of $x = 7$–10, and a preference for saline habitats.

Subtribe Zoysiinae in the New World includes a single introduced genus, *Zoysia*, represented by three species. *Zoysia* comprises about ten homogeneous species worldwide (Clayton and Renvoize 1986). They are primarily mat-forming perennials with cylindrical racemes, spikelets that usually disarticulate below the glumes, lower glumes absent or much reduced, upper glumes laterally compressed and coriaceous, and 1–3-nerved hyaline lemmas with entire or mucronate apices. In the New World, Zoysiinae are differentiated from Sporobolinae by having spikelets oriented adaxially along the axis (lemma facing away from the rachis), lemmas less firm than the glumes, paleas relatively short or very reduced when compared with the lemma, and pericarps fused (fruit a caryopsis).

Subtribe Sporobolinae shares most of the same character trends with the tribe, with the addition that the fruits have free pericarps (reluctantly so in *Spartina*). *Crypsis*, with three New World species, is the only introduced genus. A more complete synoptic description of the subtribe, excluding *Spartina*, appears in Peterson et al. (1995). In the New World, Sporobolinae are separated from Zoysiinae by having spikelets oriented abaxially along the axis (lemma facing the rachis), lemmas similar in texture to the glumes, paleas relatively long and about the same length as the lemma, and pericarps free (fruit an achene).

Cynodonteae

Tribe Cynodonteae is here broadly circumscribed, though less inclusive than by Campbell (1985) and Watson and Dallwitz (1992; as Chlorideae), who also did not recognize subtribes. We recognize ten subtribes covering 33 genera, and treat an additional 25 genera as incertae sedis. There are no definitive non-molecular characters that differentiate Cynodonteae from Eragrostideae and/or Zoysieae, as most of the structural variation present in the entire subfamily is exhibited in the tribe.

Subtribe Boutelouinae consists of a single genus, *Bouteloua*, with 57 species (Columbus et al. 1998, 2000; Columbus 1999) centered in the southwestern USA and Mexico, including the dominant range grass *B. gracilis* (Kunth) Lag. ex Griffiths (blue grama). The subtribe is characterized by an inflorescence of 1–many spicate primary branches distributed along the main axis, branch axes persistent or falling entire, spikelets bisexual, unisexual (plants monoecious or dioecious), or sterile, solitary, paired, or in triplets, sometimes secund, biseriate, glumes awned or awnless, lemmas 3-nerved, awned or unawned, a base chromosome number of $x = 10$, and a preference for xeric habitats.

Subtribe Chloridinae is represented by six genera: *Chloris* (35 spp.), *Cynodon* (16), *Enteropogon* (4), *Eustachys* (12), *Microchloa* (2), including *M. indica* (L. f.) P. Beauv. in South America and the wide-ranging *M. kunthii* Desv., and *Trichloris* (2). The subtribe is characterized by an inflorescence of 1–many spicate primary branches usually digitately or subdigitately arranged, branch axes persistent, spikelets bisexual, staminate, or sterile, solitary or paired, secund, bi-

seriate, glumes awned or awnless, lemmas 3-nerved, awned or unawned, subterranean cleistogenes occasionally present, and a base chromosome number of $x = 9$ or 10.

Subtribe Eleusininae contains a single genus, *Eleusine*, with three introduced species and a single native, *E. tristachya* (Lam.) Lam., from South America. In the New World, Eleusininae are characterized by an inflorescence of 1–many spicate primary branches usually digitately or subdigitately arranged, branch axes persistent, spikelets bisexual, solitary, secund, biseriate, glumes awnless, lemmas 3-nerved, unawned or mucronate, and a base chromosome number of $x = 9$.

Subtribe Gouiniinae contains two genera, *Gouinia*, with ten species, and the monotypic *Vaseyochloa* (*V. multinervosa* (Vasey) Hitchc.), restricted to southern Texas (Appendix 1). The subtribe is characterized by perennials, an inflorescence of 3–many spicate primary branches distributed along the main axis, branch axes persistent, spikelets bisexual, solitary, sometimes secund, biseriate, glumes awnless or awned (in *G. isabelensis* J. J. Ortíz), lemmas 3 or 5–9-nerved, awned or unawned, and a base chromosome number of $x = 10$.

Subtribe Hilariinae is represented by two North American genera: *Hilaria* with seven species and *Pleuraphis* with three (Appendix 1). The subtribe is characterized by the inflorescence a false spike of contracted primary branches, branch axes falling entire, spikelets bisexual or unisexual (plants monoecious), three per branch, the central (bisexual or carpellate) differing in form from the laterals (staminate), all glumes together forming a false involucre, lemmas 3-nerved, awned or unawned, a base chromosome number of $x = 9$, and a preference for xeric habitats.

Subtribe Monanthochloinae consists of three genera: *Distichlis*, with six species, *Monanthochloe*, with two, and the monotypic *Reederochloa* (*R. eludens* Soderst. & H. F. Decker), restricted to central Mexico. The subtribe is characterized by perennials, an inflorescence of spicate primary branches or a single raceme, usually contracted, branch axes persistent, spikelets unisexual (plants dioecious or monoecious), solitary, glumes unawned, lemmas 7–13-nerved, unawned, a base chromosome number of $x = 10$, and a preference for xeric and saline environments.

Subtribe Muhlenbergiinae consists of ten genera: *Aegopogon* (4 spp.), *Bealia* (1 sp., *B. mexicana* Scribn. in northern Mexico; Peterson 1989), *Blepharoneuron* (2 spp. in North America, *B. shepherdii* (Vasey) P. M. Peterson & Annable and *B. tricholepis* (Torr.) Nash, the latter an important range grass in the southwestern USA and northern Mexico; Peterson and Annable 1990, 2003), *Chaboissaea* (4 spp., three in central Mexico and *C. atacamensis* (Parodi) P. M. Peterson & Annable in Argentina and Bolivia; Peterson and Annable 1992; Peterson and Herrera-Arrieta 1995; Sykes et al. 1997), *Lycurus* (3 spp., including the amphitropical disjunct *L. setosus* (Nutt.) C. Reeder; Peterson and Morrone 1998), *Muhlenbergia* (147 spp. centered in northern Mexico and the southwestern USA, containing the important range grass *M. montana* (Nutt.) Hitchc. and the amphitropical disjuncts *M. arenicola* Buckley and *M. torreyi* (Kunth) Hitchc. ex Bush; Peterson and Ortíz-Diaz 1998; Peterson 2003*b*), *Pereilema* (4 spp.), *Redfieldia* (1 sp., *R. flexuosa* (Thurb. ex A. Gray) Vasey in the southwestern USA, of probable hybrid

origin; Duvall et al. 1994), *Schaffnerella* (1 sp., *S. gracilis* (Benth.) Nash in San Luis Potosí, Mexico; Columbus et al. 2002), and *Schedonnardus* (1 sp., *S. paniculatus* (Nutt.) Trel., an amphitropical disjunct with spicate primary inflorescence branches). Muhlenbergiinae are characterized by the inflorescence rebranched or of spicate primary branches, branch axes persistent or falling entire, spikelets bisexual, staminate, or sterile, solitary, rarely paired or in triplets, occasionally secund, glumes awned or unawned, lemmas 3-nerved, awned or unawned, cleistogenes occasionally present in the leaf sheaths, and a base chromosome number of $x = 8$–10. A phylogenetic study of Muhlenbergiinae based on nuclear and chloroplast DNA sequences is in progress (J. T. Columbus et al. unpubl. data). In preliminary analyses of these data, *Muhlenbergia* is paraphyletic, with all nine remaining genera nested within it (Peterson et al. 2001*a*; Columbus et al. 2007). All species in the subtribe are being targeted for sequencing and analysis before any taxonomic changes are proposed.

Subtribe Munroinae is represented by three genera: the monotypic *Dasyochloa* (*D. pulchella* (Kunth) Willd. ex Rydb.), occurring in the deserts of the southwestern USA and Mexico, *Erioneuron*, with three species and seven subspecies, including the amphitropical disjuncts *E. avenaceum* (Kunth) Tateoka and *E. pilosum* (Buckley) Nash, and *Munroa*, with five species. The subtribe is characterized by the inflorescence paniculate or unbranched, usually contracted, branch axes persistent or falling entire, spikelets bisexual, carpellate (plants gynomonoecious), or sterile, solitary, glumes awned or unawned, lemmas 3-nerved, awned, embryo waisted (with a horizontal constriction), a base chromosome number of $x = 7$ or 8, and a preference for xeric habitats.

Subtribe Orcuttiinae contains three North American genera: the monotypic *Neostapfia* (*N. colusana* (Burtt Davy) Burtt Davy), found only in central California, *Orcuttia* with five species ranging from northern California to Baja California, and *Tuctoria* with three species ranging from central California to Baja California Sur (Appendix 1). Orcuttiinae are characterized by annuals, absence of a ligule, the inflorescence a spike or raceme, usually contracted, spikelets bisexual or sterile, solitary, distichous or spirally arranged, glumes unawned, lemmas 7–17-nerved, awned or unawned, a base chromosome number of $x = 10$, and are restricted to vernal pools.

Subtribe Traginae includes two genera, *Tragus*, with four introduced species, and *Willkommia texana* Hitchc., a native amphitropically disjunct species apparently related to three other species in the genus, all from tropical southern Africa (Appendix 1). The subtribe is characterized by an inflorescence of spicate primary branches, a false spike when the branches contracted, branch axes persistent or falling entire, spikelets bisexual or sterile, solitary or paired, glumes awnless, lemmas 3-nerved, awned or unawned, and a base chromosome number of $x = 10$.

BIOGEOGRAPHY

Worldwide

Centers of modern chloridoid diversity in southern and north-central Africa, India/Pakistan, Australia, and south-

Table 4.   World centers of Chloridoideae diversity.

Region	Total grass species	Chloridoid species	%
Mexico (Soreng et al. 2000)	1172	343	29.3
USA (Soreng et al. 2000)	1395	321	23.0
Southern Africa (Gibbs Russell et al. 1990)	957	232	24.2
Tanzania (Cross 1980)	687	183	26.9
Australia (Bryan Simon pers. comm. 2003)	1330	270	20.3

western North America have been identified and discussed by Hartley and Slater (1960) and Cross (1980). Chloridoideae appear to be most diverse near the tropics of Cancer and Capricorn in hot, arid climates (Hartley and Slater 1960). However, aridity alone does not determine the distribution of the subfamily; other important factors include summer precipitation or no distinct rainy season, and mean temperatures of the coldest months above 10°C (Hartley and Slater 1960). A compilation of the numbers of chloridoids and the total number of grass species that occur in Australia, Mexico, southern Africa, Tanzania, and the USA is given in Table 4. Because climatic factors in Mexico seem to favor members of the subfamily it is not surprising that 29% (343) of all grass species from this country are chloridoid. This is the highest percentage known for any country worldwide. Tanzania is the next highest with nearly 27% of the grasses belonging to Chloridoideae. Southern Africa, the USA, and Australia round out the top five with 24%, 23%, and 20% of their grass flora represented by the subfamily, respectively.

New World

Our analysis was based on the presence or absence of chloridoid grasses in modern political units. The data do not allow fine-scale discrimination of habitat or description of specific ecological preferences. However, one can discern broad continental-scale patterns, which can help to elucidate or at least frame the questions about the biogeographical history of chloridoids in the New World. In Mexico, the USA, and Canada there are 477 native and introduced chloridoid species (70% of all New World species), whereas in Central America (including the Caribbean) and South America there are 196 and 304, respectively. As can be seen in Table 5, Mexico, the USA, Brazil, and Argentina are the only countries containing more than 20% of all native New World chloridoid species. Figure 2 shows the areas of high diversity. Except for the Caribbean region, these four countries also have the most endemics (Table 5). Of the five largest genera in the New World, over 90% of the species of *Muhlenbergia*, *Sporobolus*, and *Bouteloua*, and over 75% of *Eragrostis* and *Chloris* species occur in these countries combined (Table 3). However, the four countries account for 56% of the total land area of the New World. If one controls for country size, only Mexico (5% of total area) shows a significantly higher percentage of species and endemics than expected. Although Mexico and the USA have the greatest representation of chloridoid species in terms of numbers, the diversity is not evenly represented across the tribes and sub-

Table 5. Numbers of native and introduced chloridoid species in 23 New World countries and the Caribbean (West Indies) region (arranged from north to south).

Country or region	Native	(Endemic)	Intro-duced	Total	% of New World chloridoids (678)	% of native New World chloridoids (607)
Canada	36	(0)	5	41	6.0	5.9
USA	259	(62)	52	321	47.3	42.7
Mexico	319	(104)	24	343	50.6	52.6
Caribbean	77	(17)	15	92	13.6	12.7
Belize	29	(0)	9	38	5.6	4.8
Guatemala	87	(3)	9	96	14.2	14.3
El Salvador	45	(0)	11	56	8.3	7.4
Honduras	73	(0)	13	86	12.7	12.0
Nicaragua	45	(0)	10	55	8.1	7.4
Costa Rica	57	(2)	13	70	10.3	9.4
Panama	44	(1)	7	51	7.5	7.2
Colombia	55	(1)	5	60	8.8	9.1
Venezuela	70	(4)	15	85	12.5	11.5
Guyana	30	(0)	7	37	5.5	4.9
Suriname	20	(0)	4	24	3.5	3.3
French Guiana	21	(0)	6	27	4.0	3.5
Ecuador	66	(4)	14	80	11.8	10.9
Peru	83	(8)	11	94	13.9	13.7
Brazil	150	(28)	21	171	25.2	24.7
Bolivia	97	(3)	14	111	16.4	16.0
Chile	44	(3)	5	49	7.2	7.2
Paraguay	72	(3)	6	78	11.5	11.9
Argentina	146	(17)	18	164	24.2	24.1
Uruguay	66	(2)	9	75	11.1	10.9

Fig. 2.—Areas of high species diversity for New World Chloridoideae. Shown are the equator and tropics of Cancer and Capricorn.

tribes. For example, only 14 of the 63 native species in subtribe Chloridinae occur in Mexico; the same is true for approximately half of the native members of the Eragrostidinae and Sporobolinae subtribes. Therefore, the distribution patterns centered around these four countries were analyzed to determine if there is a South American center that is largely distinct from the North American center. An examination of the species in Peru and Ecuador was found to be useful in determining the extents of these two broad distribution patterns.

Taking these six countries as the primary regions for comparison, five basic distribution patterns of native New World chloridoid species were identified: (1) North America—species present in Mexico or the USA and absent from Argentina, Brazil, Ecuador, and Peru, (2) southern South America—species present in Argentina or Brazil and absent from Mexico, the USA, Ecuador, and Peru, (3) northwestern South America—characterized as a region of overlap between the first two patterns, (4) amphitropical disjuncts—species occurring in Mexico or the USA and Argentina or Brazil, and absent from Central America and the Caribbean, and (5) widespread species, occurring in more than a third (eight) of all New World countries and also present in North America, Central America, and South America. Of the 22 unplaced species that fit none of these five patterns, 17 are endemic to the Caribbean, three are endemic to Costa Rica and Panama, and two are shared among the three areas.

North American center.—Three hundred twenty-two (53%) native chloridoid species occur in Mexico or the USA and
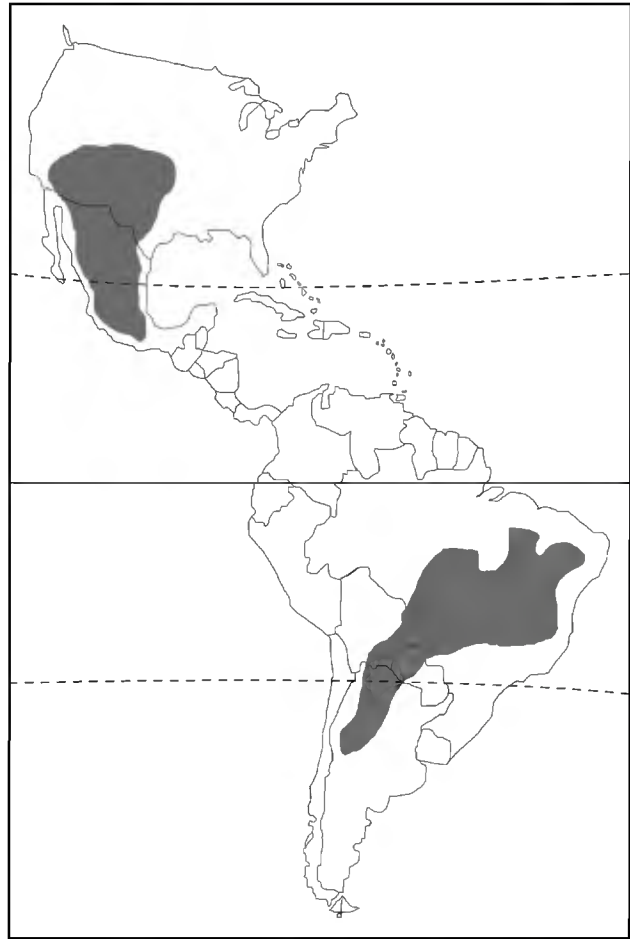
are absent from Argentina, Brazil, Ecuador, and Peru. None of these species occur in Bolivia, Chile, Paraguay, Uruguay, Guyana, Suriname, or French Guiana. This is not to say that those countries do not share species with Mexico or the USA, but rather that any species shared with North America also occur in Argentina, Brazil, Ecuador, or Peru. In other words, those seven countries do not have an independent relationship with the North American center.

This pattern accounts for more than 70% of the native chloridoid species in Mexico, the USA, or Canada. It is also the most dominant pattern in the Guatemalan flora, accounting for ca. 43% of its species. For that reason, the Guatemalan endemics have been included in the total. For the other Central American countries, although their chloridoid floras are, for the most part, dominated by widespread species, this is the most important secondary pattern, accounting for 20% to nearly 40% of their floras. However, the overwhelming majority of the species present in Central America do not extend as far north as the USA.

The modern climate in northern Mexico is hot, arid to semi-arid with summer rainfall, and has relatively warm winter minimum temperatures. The fault-block uplifting of the Mexican Plateau and further development of the Sierra Madre Occidental and Sierra Madre Oriental in the Eocene

(Ferrusquía-Villafranca 1993) created an environment well suited to the expansion of C_4 grasses.

Over 80% percent of the species in Boutelouinae (*Bouteloua*) and Muhlenbergiinae follow this pattern, and these two subtribes account for 56% or 179 of the native species in the North American center. All species of Hilariinae, Orcuttiinae, and four incertae sedis genera (*Allolepis*, *Sohnsia*, *Swallenia*, and *Triplasis*) also follow this pattern.

Southern South American center.—One hundred twenty-three (20%) native chloridoid species occur in Brazil or Argentina but do not occur in Mexico, the USA, Peru, and Ecuador.

The largest group, by far, consists of 105 species that are shared between Argentina or Brazil and Paraguay or Uruguay, or are endemic to one of the countries. There are 28 species endemic to Brazil, 17 to Argentina, three to Paraguay, and two to Uruguay. Of the remaining 55 species, only two occur in the Caribbean (*Eustachys paspaloides* (Vahl) Lanza & Mattei and *Leptochloa procera* Nees, the latter also the only species from the group occurring in Venezuela), and 5 and 19 occur in Chile and Bolivia, respectively. None of the species in the group occur in Central America or the remaining northern South American countries. *Eragrostis* (24 spp.) and *Sporobolus* (22) are the best-represented genera. Twenty-one species represent subtribe Chloridinae, and 25 species represent 11 of the incertae sedis genera, including the monotypic Brazilian endemics *Neesiochloa* and *Rheochloa*. Approximately half of the native South American species of *Eragrostis* occur in this region, as well as a third of the Chloridinae and *Sporobolus* species. However, the distribution pattern accounts for a third or less of all native New World species of *Eragrostis*, *Sporobolus*, and Chloridinae. Although it is uncertain if the region should be characterized as the center of diversity for New World *Eragrostis* and Chloridinae, it is definitely a center of speciation independent of the North American center.

This distribution pattern seems to be centered in the grass communities of the xerophytic open forest of the Gran Chaco west to the Monte and Prepuna regions (east of the Andes) and the western portion of the tall grass Pampa regions, where the four countries intersect. Zuloaga et al. (1999) characterized the Argentine portion of this region as having high biodiversity, Poaceae often the dominant family.

Unlike the North American center, Muhlenbergiinae and Boutelouinae are conspicuously underrepresented here. Only one member of Muhlenbergiinae, *Muhlenbergia breviaristata* (Hack.) Parodi, an Argentine endemic, and one Boutelouinae, *Bouteloua megapotamica* (Spreng.) Kuntze, have this particular distribution pattern. Morphologically, *M. breviaristata* is very similar to *M. dubia* E. Fourn., a species from the southwestern USA and Mexico. Both species have narrow, contracted inflorescences, greenish spikelets, and short-awned lemmas (awns 1–6 mm long).

The remaining 18 species in the southern South American center (i.e., those not shared between Argentina or Brazil and Paraguay or Uruguay, or endemic to one of the countries) have two patterns of distribution. Seven occur only in Argentina and Chile or Bolivia, including *Neobouteloua lophostachya* (Griseb.) Gould, two of the five species of *Munroa*, one *Chloris* species, one *Sporobolus* species, and one

member of Muhlenbergiinae, *Chaboissaea atacamensis*. Eleven occur in Brazil and some combination of Venezuela, Guyana, and Suriname, with three species extending into Central America. This is the distribution of the two *Steirachne* species, as well as three species of *Eragrostis*, two of *Sporobolus*, and one each of *Ctenium*, *Gymnopogon*, *Pappophorum*, and *Tridens*. These few species represent the only unique chloridoid element in the Guyana Shield region, which is otherwise inhabited by widespread chloridoid species. These species also contribute to the chloridoid component of the Caatinga grasslands.

Northwestern South American center.—Fifty-three (9%) native chloridoid species occur in Ecuador or Peru. Twenty-one of them do not occur in Mexico, the USA, Argentina, or Brazil. Eight and four species are endemic to Peru and Ecuador, respectively, but no species is distributed in both of these countries and nowhere else. However, four species occur only in Peru and Chile, and five are found elsewhere in northern South America and Bolivia. The Llanos grasslands and scattered open xerophytic forests in Ecuador and Peru that receive less than 100 cm of annual rainfall might well have provided suitable habitats for chloridoids moving down from the north. However, both the Puna vegetation of the Andean Cordillera and the Gran Chaco vegetation would have provided ready corridors for dispersal of chloridoids from the south as well. Although all four taxa in the *Bouteloua*/Muhlenbergiinae and *Eragrostis*/Chloridinae groups are present in this region, none predominates.

Five species—*Chloris submutica* Kunth, *Jouvea straminea* E. Fourn., *Muhlenbergia diversiglumis* Trin., *M. microsperma* (DC.) Kunth, and *Uniola pittieri* Hack.—occur in Ecuador (three also occur in Peru) and Mexico or the USA but do not extend into Argentina or Brazil. Because four of these five species also occur in Colombia and Venezuela, the group was broadened to include the five Colombian and Venezuelan endemics and one species, *Muhlenbergia inaequalis* Soderstr., limited to Colombia and Venezuela. None of the species occur in Chile, Paraguay, Uruguay, Guyana, Suriname, or French Guiana, but a few are present in Honduras, El Salvador and Costa Rica.

Thirteen species—*Aegopogon bryophilus* Döll, *Chloris halophila* Parodi, *C. pycnothrix* Trin., *Cynodon maritimus* Kunth, *Enteropogon mollis* (Nees) Clayton, *Eragrostis lurida* J. Presl, *E. nigricans* (Kunth) Steud., *E. pastoensis* (Kunth) Trin., *Gouinia paraguayensis* (Kuntze) Parodi, *Muhlenbergia angustata* (J. Presl) Kunth, *M. fastigiata* (J. Presl) Henrard, *M. ligularis* (Hack.) Hitchc., and *Munroa decumbens* Phil.—occur in Argentina or Brazil and Peru and/or Ecuador but do not occur in Mexico or the USA. Seven of the species are in Chloridinae or Eragrostidinae, suggesting an affinity with the southern South American center.

The northwestern South American center is primarily represented by a mixture of taxa with distributions extending northward or southward. It appears to be a region where the North American and southern South American patterns overlap or transition.

Amphitropical disjuncts and widespread species.—Eighty-seven species are shared by Mexico or the USA and Argentina or Brazil. Fifty-nine are best characterized as wide-

spread; they occur in more than a third of the New World countries and are present in North America, Central America, and South America. Despite representing only 10% of native New World Chloridoideae, widespread species account for over 50% of the floras of Belize, Honduras, Nicaragua, Costa Rica, Guyana, Suriname, and French Guiana. In contrast, these species account for less than 20% of the chloridoid floras of Canada, the USA, Mexico, and Argentina.

The remaining 28 species are amphitropical disjuncts, occurring in Canada, the USA, or Mexico and in South America, but absent from Central America and the Caribbean: *Bouteloua barbata* Lag., *B. gracilis*, *B. simplex* Lag., *Chloris canterae* Arechav., *Cottea pappophoroides*, *Eleusine tristachya*, *Enneapogon desvauxii*, *Eragrostis refracta* (Muhl. ex Elliott) Scribn., *E. scaligera* Salzm. ex Steud., *E. spicata* Vasey, *Erioneuron avenaceum*, *E. pilosum*, *Eustachys distichophylla* (Lag.) Nees, *E. retusa* (Lag.) Kunth, *Leptochloa chloridiformis* (Hack.) Parodi, *Lycurus setosus*, *Muhlenbergia arenicola*, *M. asperifolia* (Nees & Meyen ex Trin.) Parodi, *M. peruviana* (P. Beauv.) Steud. (also in Guatemala), *M. schreberi* J. F. Gmel., *M. torreyi*, *Pappophorum philippianum* Parodi, *P. vaginatum* Buckley, *Schedonnardus paniculatus*, *Scleropogon brevifolius* Phil., *Sporobolus cryptandrus* (Torr.) A. Gray, *Trichloris crinita* (Lag.) Parodi, and *Willkommia texana* (* indicates a recent introduction). Interestingly, all native species of Cotteinae, Eleusininae, and Traginae are amphitropical disjuncts, as are most of the southern South American species of Muhlenbergiinae and *Bouteloua*.

The Caribbean and unplaced species.—The Caribbean region is a possible migration route between North and South America. Its geological history is complex, however (Coney 1982). The Greater Antilles formed first, during the late Cretaceous, as a subduction zone developed along the border with the Florida-Bahama platform, while its western edge slipped past the Yucatán Peninsula along a transform fault. At this point, the Greater Antilles were much closer to continental North America than they are now. During the late Eocene/early Oligocene, the Lesser Antilles subduction zone was initiated and has remained more closely linked to Venezuela and South America, though the plate was perhaps 700 km west of its current position. As North and South America continued to close, they "pinched" the Caribbean plate, sweeping it eastward and fragmenting the Greater Antilles into their modern arrangement. As the South American continent overthrust the Caribbean plate, it probably initiated the "twist" in Panama, as it too was dragged eastward by the collision (Coney 1982). It is clear, then, that the Greater and Lesser Antilles have different geological histories and closer ties to North and South America, respectively (Raven and Axelrod 1974). However, because the Caribbean chloridoid flora is composed primarily of endemic (17) and widespread (55) species, it is difficult to address the relative importance of South versus North American contributions. A few points can be made nonetheless.

There are two species of *Bouteloua* endemic to the West Indies, *B. juncea* (Desv. ex P. Beauv.) Hitchc. and *B. vaneedenii* Pilg. *Muhlenbergia capillaris* (Lam.) Trin. is the only member of Muhlenbergiinae present in the Caribbean. There

are four *Eragrostis* species (*E. bahamensis* Hitchc., *E. berteroniana* (Schult.) Steud., *E. cubensis* Hitchc., and *E. urbaniana* Hitchc.) endemic to the Caribbean and three others (*E. elliottii* S. Watson, *E. excelsa* Griseb., and *E. glutinosa* (Sw.) Trin.) that occur only in the Caribbean, the USA, Mexico, Honduras, and Belize. It is interesting to note that all of the Caribbean endemics plus *E. elliottii* have only two stamens per floret and caryopses that generally lack a well-developed adaxial groove (*E. berteroniana* has flattened to shallowly grooved caryopses). L. H. Harvey (pers. comm. 1988) indicated that four of these five species (*E. berteroniana* excluded) and *E. glutinosa*, also without a well-developed adaxial groove on the caryopsis, were perhaps derived from a common ancestor.

Finally, for five unplaced species, namely the endemics of Costa Rica and Panama and the species uniquely shared among these countries and the Caribbean, a parallel is perhaps to be found in Gentry's (1982) identification of a unique Andean component of the Neotropical flora that is strongly represented in Costa Rica and Panama, which he cites as a secondary region of speciation for that group.

DISCUSSION

Chloridoideae in the New World exhibit two main distribution patterns, one centered in Mexico and the USA, and the other centered in Argentina and Brazil (Fig. 2). If one sets aside the species occurring in Peru and Ecuador, there are two large groups of species—246 in the North American center and 123 in the South American center—whose ranges do not overlap. The two patterns transition in northwestern South America, where only 21 species show no clear geographical connection with either of the major centers; otherwise it is possible to discern a group of 12 species with northern affinities and a group of 20 with southern affinities.

Appendix 2 summarizes the distributions of native New World chloridoid species under the following categories: (1) North America, including species extending into northern South America; (2) southern South America, including species extending into northern South America; (3) amphitropical disjuncts (28 spp.) and species (21) centered in Peru and Ecuador; (4) widespread (59 spp.); and (5) other (22 spp.).

The distribution of Chloridoideae in the New World accords with other studies that have identified a hybrid origin of the South American flora. The northern South American flora shows closer ties to North America, whereas the southern South American flora is usually more closely allied with Australian or African taxa (Humphries and Parenti 1986; Crisci et al. 1991), though the latter connections cannot yet be determined for the chloridoids.

Many chloridoid species are shared among the arid coastal plant communities of Venezuela, Ecuador, and Peru, e.g., *Bouteloua disticha* (Kunth) Benth., *Eragrostis bahiensis* Schrad. ex Schult., *E. hypnoides* (Lam.) Britton, Sterns & Poggenb., *E. maypurensis* (Kunth) Steud., *E. prolifera* (Sw.) Steud., *E. secundiflora* J. Presl, *Gouinia latifolia* (Griseb.) Vasey, *Gymnopogon foliosus* (Willd.) Nees, *Leptochloa scabra* Nees, *Leptothrium rigidum* Kunth, *Muhlenbergia microsperma*, *Sporobolus cubensis* Hitchc., *S. tenuissimus* (Mart. ex Schrank) Kuntze, *S. virginicus* (L.) Kunth, and *Trichloris pluriflora* E. Fourn. Also, Sarmiento (1975) point-

ed out the importance of the isolated dry valleys in the northern Andes as connecting the arid coastal plant communities of Venezuela with more southerly Andean communities.

The major taxonomic difference between the two main distribution patterns is the low representation of Muhlenbergiinae and *Bouteloua* in South America. As well, subtribes Hilariinae and Orcuttiinae are restricted to North America. Interestingly, at the generic level, over half (33) of the 60 native genera have species in both centers, and 36 genera are distributed on both continents. Of the 18 genera that are endemic to the North American center, 13 are represented by only one or two species. *Calamovilfa* (Zoysieae) is the only non-Cynodonteae genus restricted to North America. *Spartina* is another Zoysieae genus with predominantly North American species (62% of native New World species). Four genera, each with one or two species, are endemic to South America, as is the sole native New World species of *Triraphis*; all of these genera are incertae sedis within Cynodonteae. Two other incertae sedis genera, *Lepturidium* (1 sp.) and *Saugetia* (2 spp.), are endemic to the Caribbean. *Cynodon* (91%), *Munroa* (80%), *Eustachys* (75%), and *Distichlis* (67%) are genera present in North America but with the larger proportion of their species in South America.

Disjuncts between North and South America have long attracted the attention of botanists (e.g., Gray and Hooker 1880; Raven 1963; Thorne 1972). Raven (1963) mentioned several chloridoid genera and species as temperate or desert amphitropical disjuncts of the New World. Overall, disjuncts were described as isolated opportunistic species of open habitats that could quickly become established, forming a small, "dysharmonic sample" of either extratropical flora. There are too few disjuncts to argue for past long-term, continuous intercontinental contact, e.g., via an extended region of arid habitats along the Pacific Coast. Instead, these species represent successful colonizers that "hopped" the tropics either by a long-range dispersal mechanism, such as birds, or undertook a series of shorter steps along isolated amenable habitats in the Cordilleran system. The climatic perturbations of the Pleistocene were seen as presenting ample opportunities for species to migrate, though Raven (1963) mentioned the possibility of more recent human-mediated exchange. Subsequent research has only refined this basic premise. For example, newer paleoenvironmental data show that during the Pleistocene glaciation cycles, the tropical rain forest often became very fragmented, opening up larger avenues for possible interchange between the continents, and convergent evolution, as opposed to colonization, has been muted as an explanation for morphological similarities in some disjuncts (Solbrig 1972; Thorne 1986). However, the basic conclusion that these are isolated, opportunistic incidents has not been fundamentally challenged (Raven and Axelrod 1974; Gentry 1982; Cox 1990). Yet, although relatively few species are disjunct, over half of the native New World chloridoid genera are represented on both continents, and about half of these genera have species native to other continents. The monophyly of most grass genera has yet to be tested with molecular data, but the significant number of wide-ranging chloridoid genera suggests a long history of migration over long distances, including across oceans. Moreover, some researchers have characterized the Mexican dry area flora as having many taxa derived from South America (Rzedowski

1973; Gentry 1982). Raven (1963) indicated that a majority of desert species may have dispersed from south to north. However, at least within Muhlenbergiinae, migration has occurred predominantly from a center of diversity in southwestern North America (centered in northern Mexico) to northern Argentina-southwestern Bolivia (Peterson and Herrera-Arrieta 1995; Peterson and Columbus 1997; Sykes et al. 1997; Peterson and Morrone 1998; Peterson and Ortíz-Diaz 1998; Peterson 2000).

The evolutionary history of Poaceae based on fossils is poorly known. Assigning Poales macro- and microfossils to a particular family is difficult (Crepet and Feldman 1991). The oldest undoubted fossils of Poaceae are from the Wilcox Formation of western Tennessee, USA, and date to the Paleocene/Eocene boundary, about 56 million years ago (mya) (Crepet and Feldman 1991). However, it is not until the Miocene that fossil grasses become more common (MacFadden 2000). Molecular evidence suggests that the family originated in Gondwana more than 65 mya, after the separation of Africa, with subsequent opportunities for overland intercontinental migrations until the breakup of the Antarctic connection between South America and Australia ca. 35 mya (Bremer 2002). On a geological time scale, there has never been a true barrier between North America and Eurasia, with passages either available through Greenland or through the repeated appearance of the Bering land bridge (Raven and Axelrod 1974). North and South America only came into direct contact in the last 3–7 million years with the formation of the Panamanian Isthmus, although opportunities for biotic exchange via island hopping existed as far back as the late Cretaceous (Raven and Axelrod 1974).

The fossil history of chloridoids is even more obscure. Dugas and Retallack (1993) assigned grass fossils from Miocene paleosols in Kenya, Africa, to the subfamily based on silica body type. Perhaps more reliable is Thomasson et al.'s (1986) identification of Kranz anatomy in a fossil from the Miocene Ogallala formation in Kansas, USA. Because more than half of the genera of Chloridoideae reside in Africa and the larger tribes and subtribes, excluding Muhlenbergiinae, have centers of diversity there, Hartley and Slater (1960) concluded that the subfamily probably originated on the African continent (perhaps during the Oligocene) and spread to other parts of the world. Thus far, molecular phylogenetic studies (Hilu and Alice 2000, 2001; Columbus et al. 2007) have not revealed the continent of origin, although numerous intercontinental migrations are inferred.

Lacking direct fossil evidence, there are other data that may provide insight into the radiation of chloridoids in the New World. Paleontologists have long recognized that the development of high-crowned or constantly growing teeth in horses and other grazers was an evolutionary response to grazing on the silica-rich grasses (MacFadden 2000). Throughout the Northern Hemisphere during the Miocene, there was a great diversification of grazing (as opposed to browsing) species with these specially adapted teeth. The widely accepted explanation is that climate change resulted in an expansion of grasslands and opened up many new ecological niches for exploitation. In the 1990s, stable isotope analysis of fossil tooth enamel allowed the discrimination of grazers of plants undergoing C_3 vs. C_4 photosynthesis. In modern ecological systems, the plants consumed by grazers

are overwhelmingly C_4 grasses, whereas browsers are primarily C_3 plant eaters. However, when researchers tested the early Miocene grazer fossils, they found that these animals were apparently eating C_3 grasses, a rare occurrence in modern ecosystems. It wasn't until 7 mya that the isotope levels indicated a switch in dominance of the forage to C_4 grasses. This switch coincides with the "global carbon shift" in many plants from C_3 to C_4, as atmospheric levels of CO_2 dropped, and many climates became more arid with more pronounced seasonality. Therefore, although the chloridoids might indeed date to the Oligocene and already were dispersed around the globe, it is probably during the Pliocene that they underwent a major radiation and began to replace C_3 grasses (e.g., the stipoids of North America) as an important component of grassland communities. The same basic pattern holds true for South America. A grazing guild actually developed 10–15 million years earlier (i.e., during the Oligocene) in South America, which argues for a concomitant earlier expansion of grasslands. However, the timing of the C_3 to C_4 transition is the same. Therefore, it is likely that C_4 grasses also became more dominant 7 mya in South America. It remains unknown if the C_4 grasses that came to dominate were chloridoids, because the pathway exists in other subfamilies. However, if there was an already established chloridoid flora, this would also be a time of radiation, or it might have been a time of expansion of North American chloridoids southward.

By 7 mya, even if the Panamanian land bridge had not yet formed, it would have been relatively easy for plants to disperse between North and South America. This is probably the earliest date for a significant exchange of chloridoids, however, given the greater distance between the continents in the Paleogene and the almost complete lack, as late as the Miocene, of grass fossils or any plants associated with arid environments in Central American paleoenvironmental data (Graham 1987). Therefore, this time period merely represents an early favorable opportunity for chloridoid species to migrate, much like the periods of increased aridity during the Pleistocene glaciation cycles.

In conclusion, although broad phytogeographic patterns are revealed, the use of political boundaries for tallying and comparing New World chloridoid diversity does not address important regional patterns. For example, these data do not discern the chloridoid contribution to the Brazilian Caatinga grass flora and the various Argentine grassland communities, nor do they parse the complex Caribbean phytogeography. As well, the present dearth of molecular phylogenetic studies of Chloridoideae means that we are only beginning to understand the diversification of the subfamily. A small fraction of the species has been sampled, and few genera have been tested for monophyly. The continent of origin remains unknown for the subfamily, as do the frequency and directionality of past intercontinental migrations. Without more detailed studies of present-day distributions, and greater knowledge of the phylogeny, it is difficult to address phylogeographic questions, such as the exact nature or directionality of disjuncts (Thorne 1972; Wood 1972).

However, some broad patterns and possible explanations relating to New World Chloridoideae are as follows. Cynodonteae subtribes Muhlenbergiinae, Boutelouinae, Hilariinae, and Orcuttiinae are clearly centered in North America,

and may be derived from a Laurasian ancestor, given the distribution of *Muhlenbergia*. Because New World Chloridinae are more diverse in South America, they may have given rise to the North American representatives; the same can be said for Monanthochloinae and Munroinae. Eragrostideae and Zoysiinae are most likely West Gondwanan groups, though the timing and routes of migration to South and North America are unknown. Except for a few amphitropically disjunct species, Muhlenbergiinae and Boutelouinae have not penetrated southern South America. Although the chloridoid floras of North and South America are largely distinct at the species level, there has been interchange between the continents, perhaps predating formation of the Panamanian land bridge, but almost certainly throughout the Pleistocene. This may be reflected in the large number of genera shared by the continents.

LITERATURE CITED

BEILSCHMIED, C. T. 1833. *Flora* **16**: 52, 105.

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

BROWN, W. V. 1977. The Kranz syndrome and its subtypes in grass systematics. *Mem. Torrey Bot. Club* **23**: 1–97.

BURMEISTER, H. C. 1837. Handbuch der Naturgeschichte 205.

CAMPBELL, C. S. 1985. The subfamilies and tribes of Gramineae (Poaceae) in the southeastern United States. *J. Arnold Arbor.* **66**: 123–199.

CLAYTON, W. D., AND S. A. RENVOIZE. 1986. Genera graminum: grasses of the world. *Kew Bull., Addit. Ser.* **13**: 1–389.

———, AND F. R. RICHARDSON. 1973. Studies in the Gramineae XXXII, the tribe Zoysieae Miq. *Kew Bull.* **28**: 37–48.

COLUMBUS, J. T. 1999. An expanded circumscription of *Bouteloua* (Gramineae: Chloridoideae): new combinations and names. *Aliso* **18**: 61–65.

———, H. L. BELL, R. CERROS-TLATILPA, M. P. GRIFFITH, AND J. M. PORTER. 2002. *Schaffnerella* rediscovered! (Gramineae, Chloridoideae). *Aliso* **20**: 45–50.

———, R. CERROS-TLATILPA, M. S. KINNEY, M. E. SIQUEIROS-DELGADO, H. L. BELL, M. P. GRIFFITH, AND N. F. REFULIO-RODRIGUEZ. 2007. Phylogenetics of Chloridoideae (Gramineae): a preliminary study based on nuclear ribosomal internal transcribed spacer and chloroplast *trn*L–F sequences, pp. 565–579. *In* J. T. Columbus, E. A. Friar, J. M. Porter, L. M. Prince, and M. G. Simpson [eds.], Monocots: comparative biology and evolution—Poales. Rancho Santa Ana Botanic Garden, Claremont, California, USA.

———, M. S. KINNEY, R. PANT, AND M. E. SIQUEIROS DELGADO. 1998. Cladistic parsimony analysis of internal transcribed spacer region (nrDNA) sequences of *Bouteloua* and relatives (Gramineae: Chloridoideae). *Aliso* **17**: 99–130.

———, ———, M. E. SIQUEIROS DELGADO, AND J. M. PORTER. 2000. Phylogenetics of *Bouteloua* and relatives (Gramineae: Chloridoideae): cladistic parsimony analysis of internal transcribed spacer (nrDNA) and *trn*L–F (cpDNA) sequences, pp. 189–194. *In* S. W. L. Jacobs and J. Everett [eds.], Grasses: systematics

and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

CONEY, P. J. 1982. Plate tectonic constraints on the biogeography of Middle America and the Caribbean Region. *Ann. Missouri Bot. Gard.* **69**: 432–443.

COX, C. B. 1990. New geological theories and old biogeographical problems. *J. Biogeogr.* **17**: 117–130.

CREPET, W. L., AND G. D. FELDMAN. 1991. The earliest remains of grasses in the fossil record. *Amer. J. Bot.* **78**: 1010–1014.

CRISCI, J. V., M. M. CIGLIAN, J. J. MORRONE, AND S. ROIG-JUNENT. 1991. Historical biogeography of southern South America. *Syst. Zool.* **40**: 152–171.

CROSS, R. A. 1980. Distribution of sub-families of Gramineae in the Old World. *Kew Bull.* **35**: 279–289.

DALLWITZ, M. J., T. A. PAINE, AND E. J. ZURCHER. 1998. Intkey for Windows, vers. 5.11. *delta-intkey.com*

DUGAS, D. P., AND G. J. RETALLACK. 1993. Middle Miocene fossil grasses and wooded grasslands at Fort Ternan, Kenya. *J. Paleontol.* **67**: 113–128.

DUVALL, M. R., P. M. PETERSON, AND A. H. CHRISTENSEN. 1994. Alliances of *Muhlenbergia* (Poaceae) within New World Eragrostideae are identified by phylogenetic analysis of mapped restriction sites from plastid DNAs. *Amer. J. Bot.* **81**: 622–629.

ELLIS, R. P. 1984. *Eragrostis walteri*—a first record of non-Kranz leaf anatomy in the sub-family Chloridoideae (Poaceae). *S. African J. Bot.* **3**: 380–386.

———, J. C. VOGEL, AND A. FULS. 1980. Photosynthetic pathways and the geographical distribution of grasses in south west Africa/Namibia. *S. African J. Sci.* **76**: 307–314.

FERRUSQUÍA-VILLAFRANCA, I. 1993. Geology of Mexico: a synopsis, pp. 3–107. *In* T. P. Ramamoorthy, R. Bye, A. Lot, and J. Fa [eds.], Biological diversity of Mexico: origins and distribution. Oxford University Press, New York, USA.

GENTRY, A. H. 1982. Neotropical floristic diversity: phytogeographical connections between Central and South America, Pleistocene climatic fluctuations, or an accident of the Andean orogeny? *Ann. Missouri Bot. Gard.* **69**: 557–593.

GIBBS RUSSELL, G. E., L. WATSON, M. KOEKEMOER, L. SMOOK, N. P. BARKER, H. M. ANDERSON, AND M. J. DALLWITZ. 1990. Grasses of southern Africa. *Mem. Bot. Surv. South Africa* **58**: 1–437.

GOULD, F. W., AND R. B. SHAW. 1983. Grass systematics, 2nd ed. Texas A&M University Press, College Station, USA. 397 p.

GRAHAM, A. 1987. Miocene communities and paleoenvironments of southern Costa Rica. *Amer. J. Bot.* **74**: 1501–1518.

GRASS PHYLOGENY WORKING GROUP [GPWG]. 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Ann. Missouri Bot. Gard.* **88**: 373–457.

GRAY, A., AND J. D. HOOKER. 1880. The vegetation of the Rocky Mountain region and a comparison with that of other parts of the world. *Bull. U.S. Geol. Geogr. Surv. Territ.* **6**: 1–77.

GUTIERREZ, M., V. E. GRACEN, AND G. E. EDWARDS. 1974. Biochemical and cytological relationships in C_4 plants. *Planta* **119**: 279–300.

HARTLEY, W., AND C. SLATER. 1960. Studies on the origin, evolution, and distribution of the Gramineae. III. The tribes of the subfamily Eragrostoideae. *Austral. J. Bot.* **8**: 256–276.

HATTERSLEY, P. W. 1992. C_4 photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands, pp. 181–212. *In* G. P. Chapman [ed.], Desertified grasslands: their biology and management. Academic Press, London, UK.

———, AND L. WATSON. 1992. Diversification of photosynthesis, pp. 38–116. *In* G. P. Chapman [ed.], Grass evolution and domestication. Cambridge University Press, Cambridge, UK.

HILU, K. W., AND L. A. ALICE. 2000. Phylogenetic relationships in subfamily Chloridoideae (Poaceae) based on *mat*K sequences: a preliminary assessment, pp. 173–179. *In* S. W. L. Jacobs and J.

Everett [eds.], Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

———, AND ———. 2001. A phylogeny of Chloridoideae (Poaceae) based on *mat*K sequences. *Syst. Bot.* **26**: 386–405.

HUMPHRIES, C. J., AND L. R. PARENTI. 1986. Cladistic biogeography. Oxford Monographs on Biogeography No. 2, Clarendon Press, Oxford, UK. 98 p.

KUNTH, C. S. 1815. Considérations générales sur les graminées. *Mém. Mus. Hist. Nat.* **2**: 62–75.

———. 1833. Enumeratio plantarum . . . . Agrostographia synoptica . . . . J. G. Cottae, Stuttgart and Tübingen, Germany. 606 p.

MACFADDEN, B. J. 2000. Origin and evolution of the grazing guild in Cenozoic New World terrestrial mammals, pp. 223–244. *In* H. Sues [ed.], Evolution of herbivory in terrestrial vertebrates: perspectives from the fossil record. Cambridge University Press, Cambridge, UK.

ORTIZ-DIAZ, J.-J., AND A. CULHAM. 2000. Phylogenetic relationships of the genus *Sporobolus* (Poaceae: Eragrostideae) based on nuclear ribosomal DNA ITS sequences, pp. 184–188. *In* S. W. L. Jacobs and J. Everett [eds.], Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

PETERSON, P. M. 1989. A re-evaluation of *Bealia mexicana* (Poaceae: Eragrostideae). *Madroño* **36**: 260–265.

———. 2000. Systematics of the Muhlenbergiinae (Chloridoideae: Eragrostideae), pp. 195–212. *In* S. W. L. Jacobs and J. Everett [eds.], Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

———. 2003a. *Eragrostis*, pp. 65–105. *In* M. E. Barkworth, K. M. Capels, S. Long, and M. B. Piep [eds.], Magnoliophyta: Commelinidae (in part): Poaceae, Part 2, Flora of North America north of Mexico, Vol. 25. Oxford University Press, New York, USA.

———. 2003b. *Muhlenbergia*, pp. 145–201. *In* M. E. Barkworth, K. M. Capels, S. Long, and M. B. Piep [eds.], Magnoliophyta: Commelinidae (in part): Poaceae, Part 2, Flora of North America north of Mexico, Vol. 25. Oxford University Press, New York, USA.

———, AND C. R. ANNABLE. 1990. A revision of *Blepharoneuron* (Poaceae: Eragrostideae). *Syst. Bot.* **15**: 515–525.

———, AND ———. 1992. A revision of *Chaboissaea* (Poaceae: Eragrostideae). *Madroño* **39**: 8–30.

———, AND ———. 2003. *Blepharoneuron*, pp. 47, 48, 50. *In* M. E. Barkworth, K. M. Capels, S. Long, and M. B. Piep [eds.], Magnoliophyta: Commelinidae (in part): Poaceae, Part 2, Flora of North America north of Mexico, Vol. 25. Oxford University Press, New York, USA.

———, AND J. T. COLUMBUS. 1997. Allelic variation in the amphitropical disjunct *Scleropogon brevifolius* (Poaceae: Eragrostideae). *BioLlania, Ed. Espec.* **6**: 473–490.

———, AND Y. HERRERA-ARRIETA. 1995. Allozyme variation in the amphitropical disjunct *Chaboissaea* (Poaceae: Eragrostideae). *Madroño* **42**: 427–449.

———, AND ———. 2001. A leaf blade anatomical survey of *Muhlenbergia* (Poaceae: Muhlenbergiinae). *Sida* **19**: 469–506.

———, AND O. MORRONE. 1998. Allelic variation in the amphitropical disjunct *Lycurus setosus* (Poaceae: Muhlenbergiinae). *Madroño* **44**: 334–346.

———, AND J. J. ORTÍZ-DIAZ. 1998. Allelic variation in the amphitropical disjunct *Muhlenbergia torreyi* (Poaceae: Muhlenbergiinae). *Brittonia* **50**: 381–391.

———, J. T. COLUMBUS, R. CERROS T., AND M. S. KINNEY. 2001a. Phylogenetics of *Muhlenbergia* and relatives (Poaceae: Chloridoideae) based on internal transcribed spacer region sequences (nrDNA). Abstract. Botany 2001/American Society of Plant Taxonomists annual meeting, Albuquerque, New Mexico, USA. *www.botany2001.org/section12/abstracts/33.shtml*

———, S. L. HATCH, AND A. S. WEAKLEY. 2003. *Sporobolus*, pp. 115–139. *In* M. E. Barkworth, K. M. Capels, S. Long, and M. B.

Piep [eds.], Magnoliophyta: Commelinidae (in part): Poaceae, Part 2, Flora of North America north of Mexico, Vol. 25. Oxford University Press, New York, USA.

————, R. J. SORENG, G. DAVIDSE, T. S. FILGUEIRAS, F. O. ZULOAGA, AND E. J. JUDZIEWICZ. 2001b. Catalogue of New World grasses (Poaceae): II. Subfamily Chloridoideae. *Contr. U.S. Natl. Herb.* **41**: 1–255.

————, R. D. WEBSTER, AND J. VALDÉS-REYNA. 1995. Subtribal classification of the New World Eragrostideae (Poaceae: Chloridoideae). *Sida* **16**: 529–544.

————, ————, AND ————. 1997. Genera of New World Eragrostideae (Poaceae: Chloridoideae). *Smithsonian Contr. Bot.* **87**: 1–50.

PILGER, R. 1956. Gramineae II, pp. 1–168. *In* H. Melchior and E. Werdermann [eds.], Die natürlichen Pflanzenfamilien . . ., 2nd ed. Vol. 14d. Duncker & Humblot, Berlin, Germany.

RAVEN, P. H. 1963. Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* **38**: 151–177.

————, AND D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* **61**: 539–673.

ROUY, G. 1913. Flore de France, Graminées. *Ann. Soc. Sci. Nat. Charente-Infér.*: 1–351.

RZEDOWSKI, J. 1973. Geographical relationships of the flora of Mexican dry regions, pp. 61–72. *In* A. Graham [ed.], Vegetation and vegetational history of northern Latin America. Elsevier Scientific Publishing Company, Amsterdam, Netherlands.

SARMIENTO, G. 1975. The dry plant formations of South America and their floristic connections. *J. Biogeogr.* **2**: 233–251.

SOLBRIG, O. T. 1972. The floristic disjunctions between the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the United States. *Ann. Missouri Bot. Gard.* **59**: 218–223.

SORENG, R. J., AND J. I. DAVIS. 1998. Phylogenetics and character evolution in the grass family (Poaceae): simultaneous analysis of morphological and chloroplast DNA restriction site character sets. *Bot. Rev.* **64**: 1–85.

————, G. DAVIDSE, P. M. PETERSON, F. O. ZULOAGA, E. J. JUDZIEWICZ, AND T. S. FILGUEIRAS. 2000. Catalogue of New World grasses (Poaceae). *mobot.mobot.org/W3T/Search/nwgc.html*

SYKES, G. R., A. H. CHRISTENSEN, AND P. M. PETERSON. 1997. A chloroplast DNA analysis of *Chaboissaea* (Poaceae: Eragrostideae). *Syst. Bot.* **22**: 291–302.

THOMASSON, J. R., M. E. NELSON, AND R. J. ZAKRZEWSKI. 1986. A fossil grass (Gramineae: Chloridoideae) from the Miocene with Kranz anatomy. *Science* **233**: 876–878.

THORNE, R. F. 1972. Major disjunctions in the geographic ranges of seed plants. *Quart. Rev. Biol.* **47**: 365–411.

————. 1986. A historical sketch of the vegetation of the Mojave and Colorado deserts of the American Southwest. *Ann. Missouri Bot. Gard.* **73**: 642–651.

VAN DEN BORRE, A., AND L. WATSON. 1997. On the classification of the Chloridoideae (Poaceae). *Austral. Syst. Bot.* **10**: 491–531.

————, AND ————. 2000. On the classification of the Chloridoideae: results from morphological and leaf anatomical data analyses, pp. 180–183. *In* S. W. L. Jacobs and J. Everett [eds.], Grasses: systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.

WATSON, L., AND M. J. DALLWITZ. 1992. The grass genera of the world. CAB International, Wallingford, UK. 1038 p.

————, AND ————. 1999. Grass genera of the world: descriptions, illustrations, identification, and information retrieval; including synonyms, morphology, anatomy, physiology, phytochemistry, cytology, classification, pathogens, world and local distribution, and references. *delta-intkey.com/grass*

WOOD, C. E. 1972. Morphology and phytogeography: the classical approach to the study of disjunctions. *Ann. Missouri Bot. Gard.* **59**: 107–124.

ZULOAGA, F. O., O. MORRONE, AND D. RODRÍGUEZ. 1999. Análisis de la biodiversidad en plantas vasculares de la Argentina. *Kurtziana* **27**: 17–167.

Appendix 1. Nomenclatural novelties in tribe Cynodonteae (Poaceae, Chloridoideae).

Gouiniinae P. M. Peterson & Columbus, subtrib. nov.—

TYPE: *Gouinia* E. Fourn. ex Benth. & Hook. f., Gen. Pl. 3: 1178 (1883).

Ab Americana sub-tribu sub-familiae Chloridoidearum perennitate cum spiculis perfectis, inflorescentia paniculata cum ramis tri-vel pluri-spicatis, spiculis cum axibus persistentibus, spiculis solitaribus vel interdum secundis, biseriatis, glumis aristata vel anaristata, lemmatibus cum tribus, vel quinque usque ad novem nervis, aristatis vel anaristatis, chromosomatum numero basico decem distinguenda est.

The subtribe is characterized by perennials, an inflorescence of 3–many spicate primary branches distributed along the main axis, branch axes persistent, spikelets bisexual, solitary, sometimes secund, biseriate, glumes awnless or awned (in *G. isabelensis* J. J. Ortíz), lemmas 3 or 5–9-nerved, awned or unawned, and a base chromosome number of $x = 10$.

Included genera: *Gouinia* and *Vaseyochloa*.

Hilariinae P. M. Peterson & Columbus, subtrib. nov.—

TYPE: *Hilaria* Kunth, Nov. Gen. Sp. 1: 116–117, pl. 37 (1816).

A septentrionali Americana sub-tribu sub-familiae Chloridoidearum cum inflorescentia ut spica falsa axium contractarum distinguenda est, axis cum spicula disintegratur et omnine cadet, spiculis perfectis vel unisexuales, spiculae triplicantur per ramos, specula centralis perfectis vel carpellatis in formis differt ab lateralibus staminatis, glumae falsumque involucrum faciunt, lemmata tri-nervata, aristata vel anaristata sunt, chromosomatum numerus basicus per *x* novem est, praefert sicca loca.

The subtribe is characterized by the inflorescence a false spike of contracted primary branches, branch axes falling entire, spikelets bisexual or unisexual (plants monoecious), three per branch, the central (bisexual or carpellate) differing in form from the laterals (staminate), all glumes together forming a false involucre, lemmas 3-nerved, awned or unawned, a base chromosome number of $x = 9$, and a preference for xeric habitats.

Included genera: *Hilaria* and *Pleuraphis*.

Subtribe Orcuttiinae (Reeder) P. M. Peterson & Columbus, stat. nov.—TYPE: *Orcuttia* Vasey, Bull. Torrey Bot. Club 13: 219 (1886).

Basionym: Tribe Orcuttieae Reeder, *Madroño* **18**: 20 (1965).

Included genera: *Neostapfia*, *Orcuttia*, and *Tuctoria*.

Subtribe Traginae (Hitchc.) P. M. Peterson & Columbus, stat. nov.—TYPE: *Tragus* Haller, Hist. Stirp. Helv. 2: 203 (1768).

Basionym: Tribe Trageae Hitchc., *Contr. U.S. Natl. Herb.* **24**: 559 (1927).

Included genera: *Tragus* and *Willkommia*.

Appendix 2. Number of native New World chloridoid species according to genus and geographic category. North America—species present in Mexico or the USA and absent from Argentina and Brazil; includes 12 species extending into northern South America. Southern South America—species present in Argentina or Brazil and absent from Mexico and the USA; includes 20 species extending into northern South America. Amphitropical disjuncts and northwestern South America—species present in northwestern South America or in both Mexico or the USA and Argentina or Brazil, but absent from Central America and the Caribbean region. Widespread—species present in more than a third (eight) of all New World countries. Other—species with distribution patterns different from the preceding categories, namely 17 Caribbean endemics, three Costa Rican and Panamanian endemics, and two species shared among the three areas.

Tribe/subtribe	Genus	North America		Southern South America		Amphitropical disjuncts and northwestern South America		Widespread		Other		Total
		No.	%	No.	%	No.	%	No.	%	No.	%	
Cynodonteae												
Boutelouinae	*Bouteloua*	47	82.5	1	1.8	4	7.0	5	8.8	0	0	57
Chloridinae	*Chloris*	9	27.3	10	30.3	1	3.0	6	18.2	7	21.2	33
	Cynodon	0	0	10	90.9	0	0	1	9.1	0	0	11
	Enteropogon	2	66.7	1	33.3	0	0	0	0	0	0	3
	Eustachys	3	25	6	50	2	16.7	1	8.3	0	0	12
	Microchloa	0	0	1	50	0	0	1	50	0	0	2
	Trichloris	0	0	0	0	1	50	1	50	0	0	2
Eleusininae	*Eleusine*	0	0	0	0	1	100	0	0	0	0	1
Gouiniinae	*Gouinia*	3	30	4	40	0	0	2	20	1	10	10
	Vaseyochloa	1	100	0	0	0	0	0	0	0	0	1
Hilariinae	*Hilaria*	7	100	0	0	0	0	0	0	0	0	7
	Pleuraphis	3	100	0	0	0	0	0	0	0	0	3
Monanthochloinae	*Distichlis*	1	16.7	4	66.7	0	0	1	16.7	0	0	6
	Monanthochloe	1	50	1	50	0	0	0	0	0	0	2
	Reederochloa	1	100	0	0	0	0	0	0	0	0	1
Muhlenbergiinae	*Aegopogon*	2	50	1	25	0	0	1	25	0	0	4
	Bealia	1	100	0	0	0	0	0	0	0	0	1
	Blepharoneuron	2	100	0	0	0	0	0	0	0	0	2
	Chaboissaea	3	75	1	25	0	0	0	0	0	0	4
	Lycurus	1	33.3	0	0	1	33.3	1	33.3	0	0	3
	Muhlenbergia	127	87	4	2.7	9	6.2	5	3.4	1	0.7	146
	Pereilema	1	25	0	0	0	0	2	50	1	25	4
	Redfieldia	1	100	0	0	0	0	0	0	0	0	1
	Schaffnerella	1	100	0	0	0	0	0	0	0	0	1
	Schedonnardus	0	0	0	0	1	100	0	0	0	0	1
Munroinae	*Dasyochloa*	1	100	0	0	0	0	0	0	0	0	1
	Erioneuron	1	33.3	0	0	2	66.7	0	0	0	0	3
	Munroa	1	20	4	80	0	0	0	0	0	0	5
Orcuttiinae	*Neostapfia*	1	100	0	0	0	0	0	0	0	0	1
	Orcuttia	5	100	0	0	0	0	0	0	0	0	5
	Tuctoria	3	100	0	0	0	0	0	0	0	0	3
Traginae	*Willkommia*	0	0	0	0	1	100	0	0	0	0	1
Incertae sedis	*Allolepis*	1	100	0	0	0	0	0	0	0	0	1
	Blepharidachne	2	50	2	50	0	0	0	0	0	0	4
	Ctenium	4	40	5	50	0	0	0	0	1	10	10
	Gymnopogon	3	25	7	58.3	0	0	2	16.7	0	0	12
	Jouvea	2	100	0	0	0	0	0	0	0	0	2
	Leptochloa	3	23.1	2	15.4	1	7.7	5	38.5	2	15.4	13
	Leptothrium	0	0	0	0	1	100	0	0	0	0	1
	Lepturidium	0	0	0	0	0	0	0	0	1	100	1
	Neesiochloa	0	0	1	100	0	0	0	0	0	0	1
	Neobouteloua	0	0	2	100	0	0	0	0	0	0	2
	Pappophorum	1	12.5	4	50	2	25	1	12.5	0	0	8
	Rheochloa	0	0	1	100	0	0	0	0	0	0	1
	Saugetia	0	0	0	0	0	0	0	0	2	100	2
	Scleropogon	0	0	0	0	1	100	0	0	0	0	1
	Sohnsia	1	100	0	0	0	0	0	0	0	0	1
	Swallenia	1	100	0	0	0	0	0	0	0	0	1
	Trichoneura	1	33.3	0	0	2	66.7	0	0	0	0	3
	Tridens	11	68.8	5	31.3	0	0	0	0	0	0	16
	Triplasis	2	100	0	0	0	0	0	0	0	0	2
	Tripogon	0	0	1	50	0	0	1	50	0	0	2
	Triraphis	0	0	1	100	0	0	0	0	0	0	1

Appendix 2.   Continued.

Tribe/subtribe	Genus	North America		Southern South America		Amphitropical disjuncts and northwestern South America		Widespread		Other		Total
		No.	%	No.	%	No.	%	No.	%	No.	%	
Eragrostideae												
Cotteinae	*Cottea*	0	0	0	0	1	100	0	0	0	0	1
	Enneapogon	0	0	0	0	1	100	0	0	0	0	1
Eragrostidinae	*Eragrostis*	24	27.9	33	38.4	11	12.8	14	16.3	4	4.7	86
	Steirachne	0	0	2	100	0	0	0	0	0	0	2
Uniolinae	*Uniola*	2	40	0	0	2	40	0	0	1	20	5
Zoysieae												
Sporobolinae	*Calamovilfa*	5	100	0	0	0	0	0	0	0	0	5
	Spartina	8	61.5	3	23.1	0	0	2	15.4	0	0	13
	Sporobolus	34	47.2	26	36.1	4	5.6	7	9.7	1	1.4	72
Total		334	54.8	143	23.5	49	8.0	59	9.7	22	3.9	607