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CLASSIFICATION AND BIOGEOGRAPHY OF NEW WORLD GRASSES: ANOMOCHLOOIDEAE, PHAROIDEAE, EHRHARTOIDEAE, AND BAMBUSOIDEAE

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ABSTRACT

Molecular data support Anomochlooideae and Pharoideae as the two most basal extant clades within Poaceae. Anomochlooideae are endemic to the New World and have two tribes and two genera including the widespread Streptochaeteae (3–4 spp.) and the critically endangered Anomochloae (1 sp.) of coastal Bahia, Brazil. Pharoideae are pantropical with one tribe, three genera, and 14 species; all eight species of *Pharus* occur only in the New World. Bambusoideae and Ehrhartoideae are sister groups and together form a clade sister to Pooideae, although support for this set of relationships is low. Ehrhartoideae are a worldwide subfamily represented in the New World by three tribes (Ehrharteae [as several introduced species], Oryzeae, and Streptogyneae), eight genera, and 33 species. Bambusoideae, also worldwide, include two tribes, Bambuseae (woody bamboos) and Olyreae (herbaceous bamboos). The native New World members of Bambuseae (21 genera, 359 spp.) are divided into four subtribes (Arundinariinae, Arthrostylidiinae, Chusqueinae, Guaduinae), including the genera *Chusquea* (136 spp.), *Merostachys* (46 spp.), *Aulonemia* (34 spp.), *Arthrostylidium* (32 spp.), and *Guadua* (25 spp.). Together they are most diverse in the central and northern Andes and southeastern Brazil (from Santa Catarina to Bahia), with secondary centers of diversity in tropical Mexico, the West Indies, Costa Rica, and the Guayana Highlands of South America, and all (especially *Chusquea*) have a number of undescribed species especially in the Andes, Guayana Highlands, and mountainous southeastern Brazil. Olyreae (21 genera, 116–120 spp.) are almost exclusively American and are dominated by *Olyra* (23 spp.) and *Pariana* (several to 38 spp.), with one monotypic genus endemic to New Guinea (for which a new subtribe, **Buergersiochloinae**, is proposed) and with one species (*Olyra latifolia*) occurring in Africa as well as tropical America.

Key words: Anomochlooideae, bamboos, Bambusoideae, biogeography, classification, Ehrhartoideae, New World, Pharoideae, Poaceae, taxonomy.

INTRODUCTION

The four grass (Poaceae) subfamilies dealt with in this paper once were all classified as members of a broadly circumscribed bamboo subfamily, which was considered to be the most primitive within the family, but their true relationships are more complex and not yet entirely resolved. Until recently, Bambusoideae were regarded as a heterogeneous collection of broad-leaved forest grasses (Soderstrom and Calderón 1974) with fusoid cells in their leaf blade mesophyll, pseudopetiolate blades, three lodicules per flower, and often bracteate synflorescences that often (but not always) produce pseudospikelets (McClure 1966, 1973; Calderón and Soderstrom 1980; Soderstrom 1981a; Soderstrom and Ellis 1987; see summary in Clark et al. 1995). The number of tribes included within the subfamily has ranged from five in the “core” Bambusoideae (Soderstrom and Ellis 1987) to 14 (Clayton and Renvoize 1986; Watson and Dallwitz 1992 onwards; who included Ehrhartoideae, various pooid tribes, and even Centothecae within Bambusoideae). Now, however, molecular data combined with traditional morphological evidence have shown that a monophyletic Bambusoideae should be restricted to include only the woody bamboos (Bambuseae) and the herbaceous bamboos (Olyreae, including *Buergersiochloa*, *Eremitis*, and *Pariana* [Clark et al.

1995; Soreng and Davis 1995, 1998; Zhang 1996; Hilu and Alice 1999; Grass Phylogeny Working Group 2000, 2001; Zhang and Clark 2000; Kellogg 2001]), and should exclude Anomochloae, Oryzeae, Phareae, Streptochaeteae, and Streptogyneae, as well as Brachyelytreae, Diarrheneae, Phaenospermatideae (three clearly pooid tribes), and Centothecae. It should be noted that, based on morphological evidence, the tropical African genera *Guaduella* Franch. and *Puelia* Franch., once also included in Bambusoideae, are now placed in their own subfamily, Puelioideae (Clark et al. 2000). Likewise, Ehrhartoideae accommodates the rices and their allies (Ehrharteae, Oryzeae, and provisionally Streptogyneae; Grass Phylogeny Working Group [GPWG] 2001).

The first branch at the base of the grass family is Anomochlooideae, consisting of the tribes Anomochloae and Streptochaeteae; the next diverging branch is Pharoideae; and the third diverging branch is the Paleotropical Puelioideae (Clark et al. 2000; GPWG 2001). These first three serial branches at the base of Poaceae have been given the informal name of “basal grasses” (Clark et al. 1995; Judziewicz et al. 1999) or “the early-diverging lineages” (GPWG 2001). Above these branches, the family diversified extensively, apparently into two major lineages, informally called the BEP and PACCAD clades. The BEP clade is not strongly

supported, nor are the relationships among the three constituent lineages, Bambusoideae, Ehrhartoideae, and Pooideae (GPWG 2001). The PACCAD clade is strongly supported, although relationships among its subclades also remain poorly resolved.

Elucidation of the broad cladistic structure of the grass family has allowed a much improved understanding of character evolution and biogeography within the family (GPWG 2001). For example, the caryopsis and highly specialized embryo are synapomorphic for Poaceae, whereas the presence of fusoid cells in the leaf blades is plesiomorphic. Biogeographically, the sister groups (Ecdeiocoleaceae, Joinvilleaceae; Michelangeli et al. 2003) and the three early diverging lineages (Anomochloideae, Pharoideae, Puelioideae) of Poaceae are all Gondwanan, clearly implying a Southern Hemisphere origin of the family. In this paper, we review and summarize the classification (Table 1) and biogeography of Anomochloideae, Bambusoideae, Ehrhartoideae, and Pharoideae based upon recent data and phylogenetic studies.

The New World Grasses project (Judziewicz et al. 2000) treated Anomochloideae, Bambusoideae, Ehrhartoideae, and Pharoideae, including distribution data and nomenclature for all accepted taxa. This paper is a summary of the classification and biogeography for these four subfamilies in the New World; the original data are available online at <http://mobot.mobot.org/W3T/Search/nwgc.html>. Additionally, this paper serves as an update of papers and a book that we have published together and with others over the years (Soderstrom et al. 1988; Clark 1995; Judziewicz et al. 1999) that dealt, wholly or in part, with the classification and biogeography of New World bamboos (Calderón and Soderstrom 1980; Clayton and Renvoize 1986; Soderstrom and Ellis 1987; Soderstrom et al. 1988). The focus of this paper is primarily on Bambusoideae, the group with which we are most familiar and where more work needs to be done. We have not included distribution maps; these can be found for all bamboos and basal grasses in Judziewicz et al. (1999). Judziewicz et al. (2000) included a considerable number of Old World woody bamboos (Bambusoideae: Bambuseae: most of Arundinariinae, and all of Bambusinae J. Presl, Melocanninae Benth., Shibataeinae (Nakai) Soderstr. & R. P. Ellis; Soderstrom and Ellis 1987). Except for five species, these taxa are not treated in this paper because we now consider them not to be truly naturalized in the New World, merely long-persisting relicts of cultivation that may have spread slightly from long-established planted clumps or recent horticultural introductions.

DISCUSSION

Anomochloideae

This subfamily is the earliest diverging lineage in Poaceae (Clark et al. 1995; Zhang et al. 1995; Clark and Judziewicz 1996; Judziewicz et al. 1999; GPWG 2001), a position supported by both morphological and molecular data. It includes two monogeneric tribes, Anomochloae and Streptocheateae. The tribes have rather anomalous and disparate morphological and anatomical characters, but are united by the following features: lack of ligules, exceptionally long microhairs with an unusual morphology, a distinctive leaf blade midrib structure, and five-nerved coleoptiles (Judziewicz and Soderstrom 1989).

The presence of a pulvinus at the summit of the pseudopetiole is a possible synapomorphy for the subfamily (GPWG 2001). Members of the subfamily pose the most difficult challenge to interpreting a grass synflorescence in standard agrostological terms, as conventional spikelets with glumes, lemmas, and paleas appear to be lacking. On a molecular level, the subfamily, as presently conceived, may or may not be monophyletic; the apparent monophyly could be due to long-branch attraction and thus Anomochloae and Streptocheateae might serially diverge from the branch leading to the remainder of the grass family (Soreng and Davis 1998; Hilu and Alice 1999).

Streptocheateae (Soderstrom 1981a; Judziewicz and Soderstrom 1989) include just the genus *Streptocheata*, with three species, a variety, and perhaps a fourth species (from eastern Brazil) as yet undescribed (L. G. Clark pers. obs.). Anomochloae include only a single species, *Anomochloa marantoidea* Brongn., which grows on steep, rocky hillsides in the wet lowland forests (120–200 m elevation) of Bahia, Brazil. First described from greenhouse plants cultivated in Paris, France, in the 1840s (Brongniart 1851), it survived there in cultivation until at least 1866, but then was not seen again until 1976, when Cleofé E. Calderón and Talmon S. dos Santos relocated a colony in Atlantic Brazil (Judziewicz and Soderstrom 1989). Since 1986, the species has been in cultivation at the Iowa State University greenhouse, but as of 2001 the three known wild populations have declined dramatically (L. G. Clark pers. obs.).

Anomochloa and *Streptocheata* are strictly Neotropical lowland rain forest genera; the center of diversity appears to be Atlantic Brazil, where *Anomochloa* and two or three taxa of *Streptocheata* occur. Even though *Streptocheata* is externally dispersed by mammals (Judziewicz and Soderstrom 1989), the dispersal units are large and unwieldy and would not likely have been carried across more than a few miles of the then-narrower Atlantic Ocean by early Tertiary Period birds. *Anomochloa* appears to be dispersed by ants (Davidse 1987) and thus is even less vagile than *Streptocheata*.

Pharoideae

This subfamily is clearly the second most basal group in Poaceae (Clark et al. 1995; Clark and Judziewicz 1996; Judziewicz et al. 1999; GPWG 2001). Pharoideae are pantropical with one tribe, three genera, and 14 species; all eight species of *Pharus* occur exclusively in the New World. Phareae have fossil spikelets (of *Pharus*) dating to 15–20 million years ago on the island of Hispaniola (Poinar and Columbus 1992), as well as fossil leaf casts (perhaps *Leptaspis* R. Br.) from Africa dating to 12 million years ago (C. Kabuye and B. Jacobs pers. comm.; casts of fossil leaves at WIS). The Old World genera are *Leptaspis* and *Scrotochloa* Judz. The tropical African genus *Suddia* Renvoize (Judziewicz 1987; Clark and Judziewicz 1996) has been placed in Phareae (Clayton and Renvoize 1986; Watson and Dallwitz 1992 onwards); however, the leaf anatomy is not pharoid and the genus probably belongs in Ehrhartoideae (Judziewicz 1987). Phareae are very distinctive because of their inverted, obliquely veined leaf blades with long pseudopetioles, in combination with monoecious sexuality and spikelets with six stamens and three styles. On a molecular level, it is fairly

Table 1. Classification of New World Anomochlooideae, Pharoideae, Ehrhartoideae, and Bambusoideae. Numbers in parentheses following each genus represent the total number of species in the New World. I = all species in the genus are introduced. Taxa above the rank of genus are arranged in phylogenetic order.

Subfamily ANOMOCHLOOIDEAE Potztl

Streptochoetoideae (Nakai) Butzin

Tribe ANOMOCHLOEAE C. E. Hubb.
ANOMOCHLOA Brongn. (1)

Tribe STREPTOCHAETAEAE C. E. Hubb.
STREPTOCHAETA Nees (3–4)

Subfamily PHAROIDEAE L. G. Clark & Judz.

Tribe PHAREAE Stapf
PHARUS P. Browne (8)

Subfamily EHRHARTOIDEAE Link

Oryzoideae Burmeist.

Tribe EHRHARTEAE Nevski
EHRHARTA Thunb. (2) I

Tribe ORYZEAE Dumort.

Zizanieae Hitch.

Subtribe LUZIOLINAE Terrell & H. Rob.
LUZIOLA Juss. (10)
ZIZANOPSIS Döll & Asch. (5)

Subtribe ORYZINAE (rchb.) Griseb.
LEERSIA Sw. (6)
ORYZA L. (4)
RHYNCHORYZA Baill. (1)

Subtribe ZIZANIINAE Benth.
ZIZANIA L. (4)

Tribe STREPTOGYNEAE C. E. Calderón & Soderstr.
STREPTOGYNA P. Beauv. (1)

Subfamily BAMBUSOIDEAE Luerss.

Tribe BAMBUSEAE Dumort.

Subtribe ARUNDINARIINAE Lindl.
ARUNDINARIA Michx. (3)
PSEUDOSASA Nakai (1) I

Subtribe SHIBATAEINAE (Nakai) Soderstr. & R. P. Ellis
PHYLLOSTACHYS Siebold & Zucc. (1) I

Subtribe BAMBUSINAE J. Presl
BAMBUSA Schreb. (3) I

Subtribe CHUSQUEINAE Soderstr. & R. P. Ellis
CHUSQUEA Kunth (136)
NEUROLEPIS Meisn. (21)

Subtribe ARTHROSTYLIDIINAE Soderstr. & R. P. Ellis
ACTINOCCLADUM Soderstr. (1)
ALVIMIA Soderstr. & Longoño (3)
ARTHROSTYLIDIUM Rupr. (32)
ATHROSTACHYS Benth. (1)
ATRACTANTHA McClure (5)
AULONEMIA Goudot (34)
COLANTHELIA McClure & E. W. Sm. (7)
ELYTOSTACHYS McClure (2)
FILGUEIRASIA Guala (2)
GLAZIOPHYTON Franch. (1)
MEROSTACHYS Spreng. (46)
MYRIOCLADUS Swallen (12)
RHIPIDOCLADUM McClure (17)

Subtribe GUADUINAE Soderstr. & R. P. Ellis
APOCLADA McClure (1)
EREMOCAULON Soderstr. & Londoño (5)
GUADUA Kunth (25)

Table 1. Continued.

OLMECA Soderstr. (2)
OTATEA (McClure & E. W. Sm.) C. E. Calderón & Soderstr. (3)

Tribe OLYREAE Spenn.

Buergersiochloae S. T. Blake
Parianeae C. E. Hubb

Subtribe PARIANINAE Hack.
EREMITIS Döll (1–5)
PARIANA Aubl. (few–38)

Subtribe OLYRINAE Kromb.

AGNESIA Zuloaga & Judz. (1)
ARBERELLA Soderstr. & C. E. Calderón (7)
CRYPTOCHLOA Swallen (8)
DIANDROLYRA Stapf (3)
EKMANOCHLOA Swallen (2)
FORESIOCHLOA G. A. Black (1)
LITHACHNE P. Beauv. (3)
MACLUROLYRA C. E. Calderón & Soderstr. (1)
MNOCHLOA Chase (1)
OLYRA L. (23)
PARODIOLYRA Soderstr. & Zuloaga (4)
PIRESIA Swallen (4)
PIRESIELLA Judz., Zuloaga & Morrone (1)
RADDIA Bertol. (5)
RADDIELLA Swallen (7)
REHIA Fijten (1)
REITZIA Swallen (1)
SUCREA Soderstr. (3)

certain that the subfamily is a natural one and that it is the second most basal to the rest of the grasses, although only *Pharus* has been sampled.

The two Old World genera are united by the probable synapomorphy of inflated, spherical female florets, whereas the New World *Pharus* has narrow, cylindrical female florets. All species in the tribe have small, epizoochorous female spikelets that are well adapted to long-distance dispersal by birds (Judziewicz 1987). This is evidenced by herbarium specimens that have feathers adhering to the inflorescences, and, more important, by the presence of populations on oceanic islands that are hundreds (Swan Islands in the Caribbean) or even thousands (Fiji) of kilometers from continental land masses (Judziewicz 1987). Given tens of millions of years, members of the tribe could have easily crossed the Atlantic from Africa to South America or vice versa. Most species of *Pharus* are widespread, although there are two, *P. ecuadoricus* Judz. in Ecuador and *P. vittatus* Lem. in Mesoamerica and Colombia, that are more geographically restricted.

Ehrhartoideae

Ehrhartoideae (long known as Oryzoideae) and Bambusoideae may be sister groups and together form a clade sister to Pooideae. However, branch support is not very strong and the alternative topology has Pooideae sister to the PACCAD clade with Anomochlooideae, Pharoideae, Puelioideae, Bambusoideae, and Ehrhartoideae serially diverging in that order (Soreng and Davis 1998; GPWG 2001). Ehrhartoideae

are a worldwide subfamily, represented in the New World by three tribes, eight genera, and 33 species.

Streptogyneae are a monogeneric pantropical tribe that, because of the presence of fusoid cells in the leaf blade mesophyll, had long been placed in Bambusoideae (Calderón and Soderstrom 1980; Clayton and Renvoize 1986; Soderstrom and Ellis 1987; Soderstrom et al. 1987; Soderstrom and Judziewicz 1988). One animal-dispersed species with epizoochorous spikelets, *Streptogyna americana* C. E. Hubb., is widespread in the American tropics, and a second species occurs in the tropics of Africa and Sri Lanka (Soderstrom and Judziewicz 1988). Recent molecular evidence now indicates that the tribe is probably the sister group to the Ehrharteae–Oryzeae clade (Clark et al. 1995; GPWG 2001), although the Old World *S. crinita* P. Beauv. has not been sampled.

Ehrharteae are a small Old World tribe of four genera and 44 species (Watson and Dallwitz 1992 onwards); several South African species of *Ehrharta* have been introduced into California and they are barely naturalized in a few locations. Molecular evidence indicates that the tribe is the sister group to Oryzeae (Clark et al. 1995; GPWG 2001); however, the African Phyllorachideae C. E. Hubb. have not been sampled, and if they prove to be a basal member of the ehrhartoid clade, that might possibly imply an Old World, even African, origin for the subfamily.

Oryzeae are a worldwide, mainly aquatic or subaquatic tribe with about 12 genera and 73 species (Clayton and Renvoize 1986; Watson and Dallwitz 1992 onwards) and are most diverse in the Old World tropics. Six genera occur in the New World, within three subtribes. The American subtribe Luzioliinae is monoecious and the pericarp is free, so that the caryopsis is modified and could be considered cistoid (Sendulsky et al. 1987). The subtribe includes *Luziola* (10 spp.) and *Zizaniopsis* (5 spp.), which are widely distributed in the tropics and subtropics. Oryzinae are a worldwide subtribe with hermaphroditic spikelets dominated by two widespread genera, *Oryza* (rices) and *Leersia* (cutgrasses), each with about 20 species, although only four and six species, respectively, are found in the New World. Two *Oryza* species are introduced and naturalized. A third, monotypic genus in Oryzinae is *Rhynchoriza*, found in swamps in austral South America. Zizaniinae are a monogeneric, monoecious subtribe with typical graminoid caryopses. *Zizania* (wild rice) is native to eastern Asia (1 spp.) and North America (3 spp.).

The phylogeny and biogeography of Ehrhartoideae in the New World have only now begun to be studied on a molecular level (Lu et al. 2000; Ge et al. 2002), and we do not offer any new interpretations in this paper.

Bambusoideae

Bambusoideae include two tribes (Soderstrom and Ellis 1987; Judziewicz et al. 1999; Zhang and Clark 2000), the woody bamboos (Bambuseae) and the herbaceous bamboos (Olyreae). Anatomically, the foliage leaves exhibit fusoid cells and the synapomorphy of well-developed, asymmetrically invaginated arm cells in cross section (Zhang and Clark 2000); a few taxa may lack fusoid cells or occasionally arm cells are only weakly developed. Papillae are characteristi-

cally present on one or sometimes both surfaces, sometimes only in association with the stomatal apparatus. The subfamily is generally associated with forest habitats and is the only major clade of grasses to diversify there (GPWG 2001).

Support for the monophyly of both Olyreae and Bambuseae is strong (Zhang and Clark 2000; L. G. Clark et al. unpubl. data). No unambiguous morphological synapomorphies diagnose Olyreae, but this clade is strongly supported by molecular data (Zhang and Clark 2000). Bambuseae, in contrast, are well supported by morphological data alone or morphological and molecular data combined, but are paraphyletic to Olyreae in analyses of molecular data alone (Zhang and Clark 2000; L. G. Clark et al. unpubl. data). The presence of culm leaves and gregarious flowering cycles support the monophyly of Bambuseae.

We treat the native American Bambuseae first, concluding with a paragraph on the five naturalized Asiatic species at the end of the Bambuseae section. Following that is a discussion of Olyreae, including comments on *Buergersiochloa*, because even though the genus is strictly Palearctic, it is thus far apparently sister to the rest of the tribe. Discussion of biogeography is presented where relevant.

Bambuseae.—On a worldwide scale, Bambuseae include eight or nine subtribes (McClure 1973; Soderstrom and Ellis 1987; Dransfield and Widjaja 1995). Watson and Dallwitz (1992 onwards) give 63 genera and 825 species for the tribe; if the number of new genera, generic segregates, and unpublished species are added, the figure would approach 80 genera and nearly 1200 species about equally distributed between the Old and New World, with somewhat greater species diversity in the Old World. Six subtribes are found in the Old World, while four subtribes are native to the New World; Arundinariinae are the only subtribe native to both hemispheres. In the New World, there are also three species that represent two introduced and naturalized Old World subtribes, as well as one Asiatic species of Arundinariinae that has become naturalized. The subtribal classification is being reevaluated using multiple data sets including molecular and morphological data, but some conclusions are discussed below.

The woody bamboos are characterized by the perennial habit, woody culms, differentiation of culm and branch leaves, complex vegetative branching, and cyclical, gregarious flowering (Zhang and Clark 2000; L. G. Clark et al. unpubl. data). Recent analyses suggest that sympodial, pachymorph rhizomes and determinate spikelets are plesiomorphic within the tribe. Leptomorph rhizomes appear to have arisen at least twice and pseudospikelets evolved three or possibly four times (Zhang and Clark 2000; Clark et al. 2007). In all analyses with sufficient sampling, Arundinariinae + Shibataeinae are supported, usually strongly, as monophyletic (e.g., Clark et al. 1995; Zhang and Clark 2000; Ní Chonghaile 2002; Clark et al. 2007), although relatively little resolution within the clade is recovered; this clade is typically referred to as the North Temperate bamboo clade (Zhang and Clark 2000). Of the remaining subtribes, support for the monophyly of Chusqueinae, Guaduinae, and Melocanninae is relatively strong, but the others as currently defined may not be monophyletic (Ní Chonghaile 2002; Clark et al. 2007).

The position of Paleotropical taxa at the base of Bambuseae and Olyreae, plus the sister relationship of Bambusoideae and Ehrhartoideae, imply a Paleotropical origin for the woody bamboos (and possibly for Bambusoideae). The North Temperate clade appears to have been derived from within the tropical bamboos, and the two Neotropical lineages appear to be the result of two independent radiations of woody bamboos in the New World. These can be treated as working hypotheses, but it is clear that much greater sampling among the woody bamboos, Olyreae, and potential outgroups such as *Streptogyne crinita* and other ehrhartoids is needed before any firm conclusions can be drawn.

Arundinariinae.—Arundinariinae and Shibataeinae form the well-supported North Temperate bamboo clade, which includes about 500 described species, or nearly half of the known global diversity of woody bamboos. The presence of leptomorph rhizomes may be considered a defining character in the evolution of the North Temperate bamboo clade, with a subsequent reversal to pachymorph rhizomes in the Asian *Thamnocalamus* group (Clark 1997a; Guo et al. 2002; Guo and Li 2004). Much more careful morphological and anatomical study, integrated with molecular data, is needed before generic boundaries can be adequately defined and the monophyly of both Arundinariinae and Shibataeinae tested.

As presently circumscribed, Arundinariinae (including the *Thamnocalamus* group) comprise 14–24 genera (depending on which authority is consulted) and 338 species. Members of the subtribe are mostly found in temperate eastern Asia, although a few species such as *Arundinaria alpina* K. Schum., *A. densifolia* Munro, and *Thamnocalamus tessellatus* (Munro) Soderstr. & R. P. Ellis, occur at relatively high elevations in tropical areas of Africa and Asia (Soderstrom and Ellis 1982, 1987). *Arundinaria* is the only genus of the subtribe represented in the Americas; three species are native to the southeastern USA (J. Triplett et al. in press). It is uncertain whether the genus includes any Asiatic taxa, but *A. gigantea* is the type species so its generic placement is secure.

The North Temperate bamboo clade clearly exhibits a Laurasian pattern of distribution (Raven and Axelrod 1974; Wen 1999; Guo and Ricklefs 2000). Assuming only one species in North America, diversification of the clade in Asia has been significant and is probably associated with the complex mountain systems in eastern Asia (Wen 1999) where Tertiary climatic effects were less severe (Guo and Ricklefs 2000). It is also possible that greater woody bamboo diversity once existed in North America, but for a variety of reasons was reduced by extinction. A project is underway to reconstruct a more robust phylogeny of the clade in order to examine these hypotheses, and to provide a basis for a more stable generic classification.

Chusqueinae.—Chusqueinae, including the Neurolepidinae of Soderstrom and Ellis (1987) and Soderstrom et al. (1988), are a clearly monophyletic group that is endemic to the New World. The subtribe appears as the sister group to the remainder of the tropical Bambuseae plus the North Temperate clade (Clark et al. 2007). Two genera, *Chusquea* (136 described spp.) and *Neurolepis* (21 spp.), are included within Chusqueinae. The genera are vegetatively dissimilar, but do share the presence of papillae on the subsidiary cells

of the stomates, and single-flowered spikelets with four glumes and no rachilla extension, a spikelet morphology unknown in other American bamboos. Molecular data also support a sister group relationship between the genera (Clark et al. 1995; Kelchner and Clark 1997; Zhang and Clark 2000), although recent results (Clark et al. 2007) suggest that *Neurolepis* may be paraphyletic to *Chusquea*. Within *Chusquea*, divergence between the primarily Brazilian subgen. *Rettbergia* (Raddi) L. G. Clark and the rest of the genus is strongly supported (Kelchner and Clark 1997; Clark et al. 2007), but the relationship between the two other subgenera, subgen. *Chusquea* and *Swallenochloa* McClure, remains unclear.

The aggregate range of Chusqueinae is from Mexico to Argentina and Chile, with species in southern, non-Andean Venezuela, the Guayana Highlands, and Brazil, and a few species in the Caribbean and Juan Fernández Islands. The distribution range of *Neurolepis* is included within that of *Chusquea*, with the exceptions of its occurrence in Trinidad and in southeastern Venezuela. Throughout their ranges, both genera primarily inhabit lush, misty montane forests and humid but windswept, high altitude grasslands (subpáramos and páramos), although some species of *Chusquea* can be found in tropical forests at lower altitudes and temperate forests at higher austral latitudes.

Chusquea is the largest genus in Bambusoideae (Clark 1989, 1990a, b, 1992, 1996b, 2003) and is distinguished by solid culms and the synapomorphies of multiple, dimorphic buds per node and a base chromosome number of $x = 10$. The genus has 15 species in southern South America, and single disjunct species each in the West Indies (*C. abietifolia* Griseb.), the Juan Fernández Islands in the South Pacific Ocean (*C. fernandeziana* Phil.), and southern Venezuela and the Guayana Highlands (*C. linearis* N. E. Br.). The principal centers of diversity are the central and northern Andes from Colombia to Peru (at least 75 spp.), central and southern Brazil (56 spp.), and Mexico, and Central America (35 spp.) (Clark 1995, 1997b). There are many more—at least 60—undescribed species in the genus, mainly in the Andes and eastern Brazil. *Chusquea* has the widest altitudinal (sea level to over 4000 m) and latitudinal (24°N to 47°S) range of any bamboo genus. Species are characteristic of montane forests, including cloud and elfin forests, but a number also grow in humid subpáramos, páramos, and campos. A few species (e.g., *C. simpliciflora* Munro) are found in lowland tropical forests, while other species at higher latitudes (both north and south) grow in more temperate forests, such as the southern beech forests of Chile and the pine-oak forests of Mexico.

Neurolepis aristata (Munro) Hitchc. has the distinction of growing at altitudes up to 4300 m in Ecuador, the highest known elevation for any bamboo. In general, *Neurolepis* is a high-elevation Andean genus although it occurs north to Costa Rica and east to the Venezuelan tepuis and the mountains of Trinidad, where the lowest altitudes recorded for the genus are about 800 m for *N. virgata* (Griseb.) Pilg. (Clark 1996a). *Neurolepis* is most remarkable for the incredible leaf sizes attained in some species. In *N. aperta* (Munro) Pilg., leaf blades can reach 3–4 m in length, the largest leaves known in the grass family (Davidse and Clark 1996). At the other end of the scale, species such as *N. nana* L. G. Clark

have very short internodes and leaves only 10–40 cm long and look very much like small, coarse páramo grasses. The aerial culms in *Neurolepis* are unbranched, giving some of the taller species such as *N. fimbriatigulata* L. G. Clark a reedlike appearance.

The position of *Neurolepis* as sister or paraphyletic to *Chusquea* is interesting from a biogeographic viewpoint, because *Neurolepis* is exclusively found in western and northern South America, with one otherwise Venezuelan species also occurring on the border of Costa Rica and Panama (almost certainly the result of long-distance dispersal). In contrast, *Chusquea* is much more widespread, with one major lineage, subgen. *Rettbergia*, that is almost exclusively Brazilian (one species in Colombia) and the other major lineage, the *Chusquea* clade (including both subgen. *Chusquea* and *Swallenochloa*), which is distributed throughout the range of the genus. One hypothesis (Kelchner and Clark 1997) assumed an early radiation of Chusqueinae in eastern South America, with subsequent diversification in the Andean region and eastern South America, but recent work (Clark et al. 2007) may indicate initial diversification in western South America, with subsequent radiation (including long-distance dispersal events) into eastern South America and continuing diversification in the Andes. Additional sampling of both *Neurolepis* and the *Chusquea* clade should help in distinguishing between these ideas.

Arthrotyliidiinae.—Arthrotyliidiinae (Soderstrom and Ellis 1987) include 13 genera and ca. 163 species. A very characteristic feature of the subtribe, which enables one to identify it even when vegetative, is the presence of a narrow, green marginal stripe on the blade undersurface, contrasting with the whitened-waxy cast of the remainder of the blade (Judziewicz et al. 1999). Anatomically, the subtribe is united by the presence of intercostal sclerenchyma fibers in the leaf blades. Analyses of *ndhF* sequence data support a sister relationship between the subtribe and Guaduinae (Guala et al. 2000; Zhang and Clark 2000), but a more recent study based on morphology and *rpl16* intron sequence data indicate that Guaduinae may be derived from within Arthrotyliidiinae (Clark et al. 2007). Much greater sampling within both subtribes will be required to establish robust phylogenetic relationships within the Arthrotyliidiinae + Guaduinae clade.

Arthrotyliidioids are usually small- to medium-sized woody bamboos from short-necked, pachymorph rhizomes. The culms are hollow and relatively thin-walled, or uncommonly, solid. In many genera, the species are erect at first but quickly become arching, scandent, or even vining. An unusual feature in several genera and species is the presence of a very long basal internode, followed by several very short ones (as in *Arthrotylidium schomburgkii* (Benn.) Munro, *Glaziophyton mirabile* Franch., and all species of *Myriocladus*), or alternating very long and very short internodes (as in *Aulonemia queko* Goudot and related species, and *Rhipidocladum* sect. *Didymogonyx* L. G. Clark & Londoño). A single bud is borne at each of the midculm nodes, which develops into a branch complement with one dominant branch and several smaller laterals (*Alvimia*, *Arthrotylidium*, *Aulonemia*, *Colantheria*, *Elytrostachys*, others), three or several subequal branches (*Athroostachys*, *Atractan-*

tha), or a fan-shaped cluster of several or many smaller subequal branches (*Actinocladum*, *Merostachys*, *Rhipidocladum*). The synflorescence is usually racemose or paniculate, with a straight or (in some species of *Arthrotylidium* and *Rhipidocladum*) zigzag synflorescence axis. True spikelets are produced in all genera save four (all species of *Alvimia*, all species of *Atractantha* save *A. amazonica* Judz., both species of *Elytrostachys*, and the single species of *Glaziophyton*), which have pseudospikelets. The fruit is fleshy and olive-like in *Alvimia*, but other members of the subtribe have a basic caryopsis.

The subtribe as a whole ranges from southern Mexico and the Caribbean Islands to southern Brazil, Paraguay, and northwestern Argentina. No members of the subtribe are known to be native to Uruguay or Chile. In order of importance, the richest centers of diversity are: (1) coastal Atlantic Brazil from Bahia to Santa Catarina, (2) the northern Andes from Ecuador to northwestern Venezuela, (3) the Guayana Highlands, (4) Mesoamerica from Chiapas, Mexico, to Costa Rica, and (5) Cuba and Hispaniola. The largest genera include *Merostachys* (46 spp.), mainly southern Brazilian, *Aulonemia* (34 spp.), widespread but mostly in mountainous areas, *Arthrotylidium* (32 spp.), also widespread but most diverse in the West Indies and Guayana Highlands, the mainly Andean, Mesoamerican, and Guayanian *Rhipidocladum* (17 spp.), and *Myriocladus* (12 spp.), nearly endemic to Guayana. *Alvimia* (3 spp.) is endemic to a small region of coastal Bahia, Brazil (Soderstrom and Londoño 1988; Soderstrom et al. 1988); the monotypic *Glaziophyton* is restricted to the mountains near Rio de Janeiro, Brazil (Burman and Soderstrom 1990); and the recently described *Filgueirasta* (2 spp.) is known from eastern Brazil (Guala 2003). Knowledge of phylogenetic relationships within the subtribe or the Arthrotyliidiinae + Guaduinae clade is insufficient at present to allow for any detailed biogeographic analyses.

The Atlantic (Bahian) Brazilian *Atractantha* (5 spp.) is an easily recognizable genus distinguished by its pungent, needlelike florets, often arrayed in fan-shaped clusters or dense heads (Judziewicz 1992). The only non-Bahian species, *A. amazonica*, has needlelike florets similar to those of the Bahian species, but this may only represent an evolutionary convergence and the genus may be polyphyletic. The Bahian *Alvimia* (Soderstrom and Londoño 1988), with fleshy fruits and pseudospikelets, may be the sister genus to *Atractantha*. Based on synflorescence structure and the presence of pseudospikelets, the poorly known *Elytrostachys* may be distantly related to the eastern Brazilian genera *Alvimia* (Soderstrom and Londoño 1988) and *Atractantha*, but its affinities within the arthrotyliidioid alliance are not well established (Clark et al. 1995).

Arthrotylidium has long been a catch-all for unusual arthrotyliidioid species not easily placed anywhere else in the subtribe. A major center of diversity is the West Indies, mainly Cuba and Hispaniola. A second center of diversity (8 spp.) is the Guayana Highlands of northern South America (Judziewicz and Clark 1993; Judziewicz 2004). Here, many intriguing populations are known only from sterile or fragmentary specimens collected in remote, seldom-visited areas. Venezuela and Central America are also rich in members of the genus, especially in lower montane areas. Ar-

throstylidiids grow in a variety of forested habitats from sea level to montane elfin forests.

Rhipidocladum grows from northeastern Mexico and Trinidad to northwestern Argentina and central Brazil. There is no real center of diversity for the genus, which has nine species in the Andes, eight species in Mexico and Central America, at least five species in the Guayana Highlands, and several species in Amazonian and Planaltine Brazil. There are three sections within the genus (Clark and Londoño 1990), with sect. *Rhipidocladum* containing only the Andean type species *R. harmonicum* (Parodi) McClure. *Rhipidocladum* has been considered to be closely related to *Arthrostylidium* and *Merostachys* (Soderstrom and Ellis 1987). However, the homologies of the vegetative structures, such as the fan-shaped meristem, may have been misinterpreted, and its true phylogenetic relationships within the arthrostylidioid alliance are unclear (Clark and Londoño 1991). *Rhipidocladum ampliflorum* (McClure) McClure appears intermediate to the genus *Arthrostylidium*.

Merostachys grows from southern Mexico (Chiapas) and Belize to Bolivia, Paraguay, northeastern Argentina, and southern Brazil, and is found in forests and forest margins from sea level to 2300 m. The genus is by far most diverse in central and southern Brazil, where 41 species occur (Sedulsky 1997). Five species, including several that are undescribed, grow in southern Mexico and Central America; two species each are found in the Guayana Highlands and Colombia; and one species occurs in Peru. The genus is closely related to *Rhipidocladum*; both share a roughly similar fan-shaped mid-culm bud complement.

Aulonemia species occur in wet, usually montane forests and páramos from southern Mexico through Central and northern South America to Bolivia and southern Brazil. The Andean and Central American species commonly grow at montane elevations, but Brazilian species are found from near sea level to, more commonly, montane elevations up to 2000 m. Centers of diversity include: (1) the Andes from Venezuela to Bolivia (15 spp.), (2) southern Atlantic Brazil (11 spp.), (3) the Guayana Highlands (at least 8 spp.), and (4) Central America (up to 5 spp.). The Mexican *A. clarkiae* Davidse & R. W. Pohl and *A. fulgor* Soderstr. have foliage leaf blades with papillae present on the upper surface, but no intercostal sclerenchyma, and may be misplaced in *Aulonemia* (L. G. Clark and X. Londoño pers. obs.).

Myriocladus, a relative of *Aulonemia*, grows on remote, uninhabited sandstone tepui summits and slopes of the Guayana Highlands in southern Venezuela, and barely extends into adjacent Brazil and Guyana (Judziewicz 1998, 2004).

The culms of *Glaziophyton*, alone among grasses, are chambered with pithy partitions at short intervals. The genus is a rare endemic of mountains near Rio de Janeiro, Brazil (Burman and Soderstrom 1990). There is chloroplast DNA evidence that the single species *G. mirabile*, has affinities among the arthrostylidioids (Zhang et al. 1995; Zhang 1996).

Guaduinae.—Guaduinae are closely related to and perhaps derived from within Arthrostylidiinae, as noted previously (Guala et al. 2000; Zhang and Clark 2000; Clark et al. 2007). However, Guaduinae are supported as monophyletic by molecular data (Guala et al. 2000; Clark et al. 2007) and by the presence of papillae surrounding the usually numerous ad-

axial stomates. The subtribe is endemic to the New World, and molecular evidence suggests that the Guaduinae + Arthrostylidiinae clade is part of a trichotomy with the Old World woody bamboos and the North Temperate clade (Clark et al. 2007). The subtribe consists of five genera and 35 described species distributed from northwestern Mexico through Central America to Argentina and Uruguay, though not represented in the West Indies or Chile. Guaduoids are generally low-elevation bamboos, but some members have been found at elevations up to 1500 m (or possibly 2200 m, but these may be cultivated populations). In order of importance, the richest centers of diversity are: (1) Mexico and Central America, from Sonora to Panama, (2) the Amazon basin, (3) the Brazilian Planalto Central (associated with gallery forests), and (4) lowland coastal Bahia, Brazil. The highest endemism is found in Mexico and in the coastal forests of southern Bahia, each region having four endemic species.

Anatomically, Guaduinae do not appear to be closely related to either Bambusinae or Arthrostylidiinae (Soderstrom and Ellis 1987). The guaduoids have stomates on both foliage leaf blade surfaces; what makes them distinctive is the great density of stomata present on the upper leaf surface and that these stomata usually have papillae associated with them.

The largest and most economically important genus in the subtribe is the thorny *Guadua* (25 spp.; Londoño and Clark 2002), which boasts the tallest of the native New World grasses in *G. chacoensis* (Rojas) Londoño & P. M. Peterson and *G. angustifolia* Kunth. *Guadua* ranges from northern Mexico to northern Argentina and Uruguay; *G. angustifolia* has been cultivated in Cuba, Puerto Rico, and Trinidad (Young and Judd 1992). Species range in elevation from 0 to 2200 m, but are much more abundant and diverse below 1500 m.

Other genera in the subtribe include the tropical Brazilian *Eremocaulon* (5 spp., now including *Criciuma* Soderstr. & Londoño; Soderstrom and Londoño 1987; Clark and Londoño 2002), the Mexican fleshy-fruited *Olmecca* (2 spp.; Soderstrom 1981b), and *Otatea* (2 spp.), with Mexican and Mesoamerican (and one Colombian) populations. *Otateas* grow in seasonally dry, tropical deciduous, subdeciduous, or oak forests, often on limestone-derived soils. The genus is distinguished by its branch complements with three subequal branches per node. The now-monotypic Brazilian *Apoclada* is the only guaduoid genus that lacks fusoid cells in the leaf blade mesophyll (Guala 1995, 2003; Guala et al. 2000).

Introduced and Naturalized Old World Bamboos in the New World.—The Asian subtribe Bambusinae is represented in the New World by the widespread Asian species *Bambusa multiplex* (Lour.) Schult. & Schult. f. (warm temperate USA, Mexico, Mesoamerica, South America), *B. tuldoidea* Munro, and the very robust, clump-forming *B. vulgaris* J. C. Wendl. (throughout tropical America). The Japanese ornamental bamboo *Pseudosasa japonica* (Steud.) Nakai (Arundinariinae) and the common, weedier *Phyllostachys aurea* Rivière & C. Rivière (Shibataeinae) are also frequent in warm temperate and subtropical America. A large number of other Old World Bambuseae (at least 29 genera and 200 spp.) have been introduced into New World botanical gardens and plan-

tations, and while often long persisting, have not spread from cultivation, and thus they are not treated in this paper. For lists of these taxa, we refer the reader to Judziewicz et al. (2000) and to the 2006 Bamboo Species Source List at the American Bamboo Society website: <http://www.americanbamboo.org/>.

Olyreae.—These are the “herbaceous bamboos.” Members of *Olyreae* are small- to medium-sized, non-lignified, clump-forming, stoloniferous, or occasionally scandent plants (*Olyra latifolia* L.) (Calderón and Soderstrom 1980), with restricted vegetative branching and unisexual spikelets. There are 21 genera and ca. 116–120 species in the tribe, which is endemic to the New World with two exceptions: *Buergersiochloa* is a rare monotypic endemic of New Guinea, while *O. latifolia* is a widespread American species that has presumably been introduced into Africa, where it is also widespread, and Sri Lanka. Thus, the tribe has a most unusual distribution pattern—tropical America and New Guinea.

Members of *Olyreae* are generally herbaceous perennials. A few species appear to be monocarpic (several *Olyra* spp.), and *O. filiformis* Trin. may be an annual. In physical stature, the genera range from almost mosslike plants only a few centimeters tall (*Mniochloa pulchella* (Griseb.) Chase and *Raddiella minima* Judz. & Zuloaga) to reedlike plants several meters tall (*O. taquara* Swallen). Leaves are produced in complements, which are often crowded towards the culm tips, particularly in the more diminutive genera. Synflorescences range from spicate (best developed in *Parianinae*) to more typically paniculate from the middle and upper nodes of leafy shoots (Calderón and Soderstrom 1973). In some genera, synflorescences may be borne on a culm with small, rudimentary leaf blades or none, these being different from the regular foliage leaves. In a few genera or species, the synflorescence on these “leafless” shoots may be partially (*Cryptochloa decumbens* Soderstr., *Piresia* spp.) to completely (*Eremitis*) buried in leaf litter or soil. Olyroid grasses are all monoecious; the spikelets are dimorphic, unisexual, usually with large female spikelets and small, quickly deciduous male spikelets mixed in the same synflorescence, or less commonly in separate synflorescences. Each spikelet is one-flowered. The glumes are deciduous or persistent, and usually exceed the enclosed floret. The floret is usually ellipsoid to fusoid and indurate, and the lemma is larger than the palea and usually tightly encloses the palea by its inrolled margins.

It is striking that *Olyreae* are most diverse at latitudes between 10° and 15°N (Costa Rica, Panama) and 10° and 15°S (Atlantic Brazil, western Amazonia) (Soderstrom et al. 1988), in rain forest habitats with high amounts of precipitation (over 3000 mm per year). At such latitudes are found many narrowly endemic species and some endemic genera (such as *Maclurolyra*). Other areas of generic diversity are Amazonia, in the widest sense, where *Agnesia*, *Froesiochloa*, and *Rehia* occur (also narrowly endemic species of *Olyra*, *Pariana*, and *Raddiella*), Cuba (with three endemic genera, *Ekmanochloa*, *Mniochloa*, and *Piresiella*), and Atlantic Brazil (with *Diandrolyra*, *Eremitis*, and *Sucrea*) (Mori et al. 1983; Soderstrom et al. 1988). Many olyroid species have specialized dispersal modes, such as the bird-dispersed “pseudoberries” (caryopses surrounded by a darkened, indurated protective lemma; Davidse 1987; Soderstrom and

Zuloaga 1989) of *Olyra latifolia*, the most widespread species and the only taxon, save *Buergersiochloa*, within the tribe to occur in the Old World, where it is presumed to have been introduced.

Parianinae.—*Parianinae* are the sister taxon to the remainder of *Olyreae* (minus *Buergersiochloa*) and are distinguished by spicate inflorescences in which whorls of male spikelets surround and conceal a single female spikelet at each node. The subtribe is sometimes recognized at the tribal level (Clayton and Renvoize 1986) as *Parianeae*. The leaves often have fimbriae present at the summit of their sheaths, a character never found in *Olyrinae*. The stamen number is frequently six or multiples of six. The subtribe has two genera and anywhere from several to over 40 species, depending on species delimitation, and ranges from Costa Rica and Trinidad to Amazonian Bolivia and Atlantic Brazil (Bahia). Members grow in shaded, wet, lowland forests, often in the periodically flooded *várzea*, or rarely in lower montane forests up to 1500 m in elevation.

Parianinae are the most taxonomically problematic group of American bamboos because specific limits are extremely difficult to define (Hollowell 1987, 1997; Judziewicz 1991). *Pariana* has anywhere from several to 38 species and grows throughout the range of the subtribe. Species are noteworthy for their cylindrical synflorescences with numerous (up to 36 or more) showy yellow or white stamens per male spikelet. It is generally agreed that these facilitate insect pollination (Soderstrom and Calderón 1971) by phorid flies and gall midges. *Eremitis* (1–5 spp.), endemic to the Atlantic coastal forests of Brazil, is one of the strangest herbaceous bamboos (Hollowell 1987). In addition to producing “normal” aerial synflorescences, as in its close relative *Pariana*, species of *Eremitis* also produce scaly, cleistogamous subterranean synflorescences from the tips of whiplike “stolons” that bury themselves in the leaf litter or soil. What pollination mechanism operates in these buried flowers, and what (if any) the dispersal mechanism might be, remain unknown.

Olyrinae.—*Olyrinae* have 18 genera and about 87 species in the New World ranging from Mexico and the West Indies to Argentina and southern Brazil. Genera within the subtribe are often poorly differentiated. In general, the subtribe differs from *Parianinae* by its open-paniculate to somewhat spicate synflorescences, and by the lack of fimbriae on the leaf sheath summits.

Ekmanochloa consists of two species, both endemic to rocky hills and pinelands in ultramafic (serpentine) areas of lowland Oriente in eastern Cuba (Zuloaga et al. 1993). It could possibly be the basal member of the subtribe, as it differs from most *Olyreae* in its exceptionally small, narrow, deciduous leaf blades and prominently long-awned female lemmas, the latter character shared among *Olyrinae* only by the distantly related *Agnesia*. Anatomically, the absence of leaf blade fusoid cells is also noteworthy. *Ekmanochloa* also shows some affinities with the monotypic genus *Buergersiochloa* of New Guinea (Fijten 1975), the basal member of tribe *Olyreae*. Both taxa have long-awned female florets, compound epidermal papillae on the leaf blades, and dimorphic culms.

Olyra is the most diverse olyroid genus and may be polyphyletic, even with the recent removal of a few species to

Agnesia and four species to *Parodiolyra* (Soderstrom and Zuloaga 1989; Zuloaga et al. 1993; Zuloaga and Davidse 1999). Within the genus there is great diversity in chromosome number, synflorescence structure and female floret morphology, texture, and indument. It seems inevitable that *Olyra* will be split into additional segregates when detailed molecular studies of Olyreae are performed.

Parodiolyra shows affinities with *Diandrolyra* and *Raddiella esenbeckii* (Steud.) C. E. Calderón & Sodestr. (Zuloaga and Judziewicz 1991) in the female spikelets borne on filiform peduncles that fall entire, with the bases of the glumes seemingly fused to the peduncle summit. The flowering culm of *Diandrolyra*, with its single, twisted, umbrella-like leaf “protecting” the hidden synflorescence (Soderstrom and Zuloaga 1985) is reminiscent of the Panamanian endemic *Maclurolyra* (Calderón and Soderstrom 1973). The cartilaginous female spikelet falls entire (Davidse 1987), as in species of *Parodiolyra*, while the stamen number is reduced from three to two, as in several other genera and species of olyroids. Vegetative variation is hard to assess in this genus.

Raddia species grow from Venezuela, Tobago, and French Guiana to Atlantic Brazil in forest understories at elevations of 0–500 (–1000) m. After flowering, the drying margins and bases of the female glumes contract and twist, ejecting the mature floret (with enclosed fruit) up to a meter from the parent plant in a dispersal mode known as ballistochory (Sendulsky 1993). Species of *Sucrea*, especially *S. maculata* Sodestr., have female spikelet glume morphologies similar to that of *Raddia*, and molecular data support their close relationship (Clark et al. 1995; Zhang 1996).

Lithachne has tooth-shaped female florets that are unique in the grass family (Soderstrom 1980). The downward-folding movement of the leaf blades at evening is unique in olyroid bamboos that exhibit sleep movements; in all other genera they fold upwards. *Cryptochloa* and several other olyroid genera also have female florets borne on a rachis internode, but they differ from *Lithachne* in their symmetrical female florets with the rachis internode containing oils and serving as an elaiosome for ant dispersal (Davidse 1987).

Buergersiochloinae.—Within Olyreae, *Buergersiochloa bambusoides* Pilg. is a rare grass from the northern coastal rain forests of the Indonesian island of New Guinea (Fijten 1975) and Papua New Guinea. *Buergersiochloa* is functionally unisexual, but lacks the characteristic olyroid silica bodies of Parianinae and Olyrinae (Zhang and Clark 2000; Clark et al. 2007). The genus is monotypic and shares with Parianinae the presence of fimbriae at the summit of leaf sheath, and with *Ekmanochloa* (Olyrinae) the presence of a long-awned female lemma. Its panicoid or saddle-shaped silica bodies, however, are atypical of both Olyrinae and Parianinae, and fusoid cells are absent (Watson and Dallwitz 1992 onwards). Other undoubted members of Olyrinae (species of *Ekmanochloa*, *Mniochloa*, *Parodiolyra*, and *Raddiella*) may also lack fusoid cells (Judziewicz et al. 1999), but all of these herbaceous genera are physically small in stature (at most ca. 30 cm tall), while *Buergersiochloa* is a robust plant up to 1 m tall. Molecular evidence indicates *Buergersiochloa* is sister to Olyrinae + Parianinae (Zhang

and Clark 2000), and so we here recognize it as a third subtribe of Olyreae:

Subtribe **Buergersiochloinae** (S. T. Blake) L. G. Clark & Judz., stat. nov.—TYPE: *Buergersiochloa* Pilg.

Basionym: Tribe Buergersiochloae S. T. Blake, *Blumea*, *Suppl.* 3: 62 (1946).

Future Inventory Needs

In terms of future exploration and inventory needs for New World Anomochlooideae, Bambusoideae, Ehrhartoideae, and Pharoideae, Bambusoideae will probably yield the greatest number of new species. The following geographic areas may be singled out as requiring more extensive fieldwork.

The Guayana Highlands of Venezuela will surely yield more species and perhaps another genus or two of bambusoid grasses. The area is remote, rugged, still essentially roadless, and currently closed to foreign scientists (Judziewicz 2004). While treating Bambusoideae for the Flora of the Venezuelan Guayana project, one of us (EJJ) had the opportunity to examine several distinctive, undescribed sterile woody bamboos in the Arthrotyliidiinae + Guaduinae clade. Until flowering material of these species is collected, their generic disposition will remain problematical.

Eastern Brazil from Bahia south to Santa Catarina will also yield new bamboo species, and perhaps new genera or generic realignments (e.g., Clark and Londoño 2002). Novelty may be expected in Arthrotyliidiinae, Guaduinae, Olyreae, and *Chusquea* of Chusqueinae.

The Andean cordillera from Venezuela to Bolivia is extremely rich in species of *Chusquea*, many yet to be described and/or discovered (Clark 2001). A few new species of Arthrotyliidiinae—principally in the genera *Arthrotylidium*, *Aulonemia*, and *Rhipidocladum*—may also be expected from low to moderate elevations in the Andes.

Amazonia is still poorly explored botanically. This vast area is not rich in numbers of woody bamboo genera and species, but new species of *Guadua* can probably be expected from this basin. Based on the number of species and even genera known only from one or two collections (Zuloaga and Judziewicz 1993), new herbaceous bamboo species (Olyreae) will probably be found throughout Amazonia.

The mountains of Mesoamerica from Oaxaca, Mexico, through Panama will probably also yield a few new species of woody bamboos. A few herbaceous bamboos perhaps also remain to be found. However, the pace of the description of novel olyroids (mainly from Costa Rica and Panama) has slackened since the 1970s and 1980s (Calderón and Soderstrom 1973; Davidse et al. 1994).

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LITERATURE CITED

- BRONGNIART, A. 1851. Description d'un nouveau genre de Graminées du Brésil. *Ann. Sci. Nat., Bot.* **16**: 368–372.
- BURMAN, A. G., AND T. R. SODERSTROM. 1990. In search of the world's oddest bamboo, *Glaziophyton mirabile*. *Bot. Gard. Conservation News* **1**: 27–31.
- CALDERÓN, C. E., AND T. R. SODERSTROM. 1973. Morphological and anatomical considerations of the grass subfamily Bambusoideae based on the new genus *Maclurolyra*. *Smithsonian Contr. Bot.* **11**: 1–55.
- , AND ———. 1980. The genera of Bambusoideae (Poaceae) of the American continent: keys and comments. *Smithsonian Contr. Bot.* **44**: 1–27.
- CLARK, L. G. 1989. Systematics of *Chusquea* section *Swallenochloa*, section *Verticillatae*, section *Serpentes*, and section *Longifoliae* (Poaceae–Bambusoideae). *Syst. Bot. Monogr.* **27**: 1–127.
- . 1990a. *Chusquea* section *Longiprophyllae* (Poaceae: Bambusoideae): a new Andean section and new species. *Syst. Bot.* **15**: 617–634.
- . 1990b. Diversity and biogeography of Neotropical bamboos (Poaceae: Bambusoideae). *Acta Bot. Bras.* **4**: 125–132.
- . 1992. *Chusquea* section *Swallenochloa* (Poaceae: Bambusoideae) and allies in Brazil. *Brittonia* **44**: 387–422.
- . 1995. Diversity and distribution of the Andean woody bamboos (Poaceae: Bambuseae), pp. 501–512. In S. P. Churchill, H. Balslev, J. L. Luteyn, and E. Forero [eds.], Biodiversity and conservation of Neotropical montane forests. New York Botanical Garden, Bronx, New York, USA.
- . 1996a. Six new species of *Neurolepis* (Poaceae: Bambusoideae: Bambuseae) from Ecuador and Peru. *Novon* **6**: 335–350.
- . 1996b. Four new species of *Chusquea* (Poaceae: Bambusoideae) from Brazil and Ecuador. *Brittonia* **48**: 250–262.
- . 1997a. Bamboos: the centerpiece of the grass family, pp. 237–248. In G. P. Chapman [ed.], The bamboos. Academic Press, London, UK.
- . 1997b. Diversity, biogeography and evolution of *Chusquea*, pp. 33–44. In G. P. Chapman [ed.], The bamboos. Academic Press, London, UK.
- . 2001. Diversification and endemism in Andean woody bamboos (Poaceae: Bambusoideae). *Bamboo Science and Culture: The Journal of the American Bamboo Society* **15**: 14–19.
- . 2003. A new species of *Chusquea* section *Swallenochloa* (Poaceae: Bambusoideae). *Bamboo Science and Culture: The Journal of the American Bamboo Society* **17**: 55–58.
- , S. DRANSFIELD, J. TRIPLETT, AND J. G. SÁNCHEZ-KEN. 2007. Phylogenetic relationships among the one-flowered, determinate genera of Bambuseae (Poaceae: Bambusoideae), pp. 315–332. 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.
- , AND E. J. JUDZIEWICZ. 1996. The grass subfamilies Anomochlooideae and Pharoideae. *Taxon* **45**: 641–645.
- , M. KOBAYASHI, S. MATHEWS, R. E. SPANGLER, AND E. A. KELLOGG. 2000. The Puelioideae, a new subfamily of Poaceae. *Syst. Bot.* **25**: 181–187.
- , AND X. LONDOÑO. 1990. Three new Andean species of *Aulonemia* (Poaceae: Bambusoideae). *Ann. Missouri Bot. Gard.* **77**: 353–358.
- , AND ———. 1991. A new species and new sections of *Rhipidocladum* (Poaceae: Bambusoideae). *Amer. J. Bot.* **78**: 1260–1279.
- , AND ———. 2002. A revision of the Brazilian bamboo genus *Eremocaulon* (Poaceae: Bambusoideae: Guaduinae). *Syst. Bot.* **27**: 703–721.
- , W. ZHANG, AND J. F. WENDEL. 1995. A phylogeny of the grass family (Poaceae) based on *ndhF* sequence data. *Syst. Bot.* **20**: 436–460.
- CLAYTON, D. K., AND S. A. RENVOIZE. 1986. Genera graminum: grasses of the world. *Kew Bull., Addit. Ser.* **13**: 1–389.
- DAVIDSE, G. 1987. Fruit dispersal in the Poaceae, pp. 143–155. In T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth [eds.], Grass systematics and evolution. Smithsonian Institution Press, Washington, D.C., USA.
- , AND L. G. CLARK. 1996. Two new species of *Neurolepis* (Poaceae: Bambusoideae) from Colombia. *Novon* **6**: 150–156.
- , M. SOUSA S., AND A. O. CHATER. 1994. Bambusoideae, pp. 193–221. In G. Davidse, M. Sousa S., and A. O. Chater [eds.], Flora Mesoamerica, Vol. 6, Alismataceae a Cyperaceae. Universidad Nacional Autónoma de México, Mexico City, D.F., Mexico.
- DRANSFIELD, S., AND E. WIDJAJA (editors). 1995. Plant resources of South-East Asia. No. 7, Bamboos. Backhuys Publishers, Leiden, The Netherlands. 189 p.
- FITJEN, F. 1975. A taxonomic revision of *Buergeriostochloa* Pilg. (Gramineae). *Blumea* **22**: 415–418.
- GE, S., A. LI, B.-R. LU, S.-Z. ZHANG, AND D.-Y. HONG. 2002. A phylogeny of the rice tribe Oryzaceae (Poaceae) based on *matK* sequence data. *Amer. J. Bot.* **89**: 1967–1972.
- GOU, Z.-H., Y.-Y. CHEN, AND D.-Z. LI. 2002. Phylogenetic studies on the *Thamnocalamus* group and its allies (Gramineae: Bambusoideae) based on ITS sequence data. *Molec. Phylogen. Evol.* **22**: 20–30.
- , AND D.-Z. LI. 2004. Phylogenetics of the *Thamnocalamus* group and its allies (Gramineae: Bambusoideae): inference from the sequences of GBSSI gene and ITS spacer. *Molec. Phylogen. Evol.* **30**: 1–12.
- GRASS PHYLOGENY WORKING GROUP [GPWG]. 2000. A phylogeny of the grass family (Poaceae), as inferred from eight character sets, pp. 3–7. In S. W. L. Jacobs and J. Everett [eds.], Grass systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.
- . 2001. Phylogeny and subfamilial classification of the grasses (Poaceae). *Ann. Missouri Bot. Gard.* **88**: 373–457.
- GUALA, G. F., II. 1995. A cladistic analysis and revision of the genus *Apoclada* (Poaceae: Bambusoideae: Bambusoideae). *Syst. Bot.* **20**: 207–223.
- . 2003. A new bamboo genus from the cerrados of Brazil. *Bamboo Science and Culture: The Journal of the American Bamboo Society* **17**: 1–3.
- , D. BOGLER, J. SADLE, AND J. FRANCISCO-ORTEGA. 2000. Molecular evidence for polyphyly in the genus *Apoclada*. *Bamboo Science and Culture: The Journal of the American Bamboo Society* **14**: 15–20.
- GUO, Q., AND R. E. RICKLEFS. 2000. Species richness in plant genera disjunct between temperate eastern Asia and North America. *Bot. J. Linn. Soc.* **134**: 401–423.
- HILU, K. W., AND L. A. ALICE. 1999. Evolutionary implications of *matK* indels in Poaceae. *Amer. J. Bot.* **86**: 1735–1741.
- HOLLOWELL, V. C. 1987. Systematics of the subtribe Parianinae (Poaceae: Bambusoideae: Olyreae). Ph.D. dissertation, University of South Carolina, Columbia, USA. 452 p.
- . 1997. Systematic relationships of *Pariana* and associated Neotropical taxa, pp. 45–60. In G. P. Chapman [ed.], The bamboos. Academic Press, London, UK.
- JUDZIEWICZ, E. J. 1987. Taxonomy and morphology of the tribe Phareae. Ph.D. dissertation, University of Wisconsin, Madison, USA. 529 p.
- . 1991 [as 1990]. Family 187, Poaceae, pp. 1–727. In A. R. A. Görts-van Rijn [ed.], Flora of the Guianas, Series A: Phanerogams. Koeltz Scientific Publications, Königstein, Germany.

- . 1992. A revision of *Atractantha* (Poaceae: Bambuseae). *Ann. Missouri Bot. Gard.* **79**: 160–183.
- . 1998. A revision of *Myriocladus* (Poaceae: Bambusoideae: Bambuseae). *Brittonia* **50**: 430–446.
- . 2004. [Various genera of Bambusoideae], Poaceae, pp. 1–297. In P. E. Berry, K. Yatskiyevych, B. K. Holst [eds.], Flora of the Venezuelan Guayana, Vol. 8, Poaceae–Rubiaceae. Timber Press, Portland, Oregon, USA.
- , AND L. G. CLARK. 1993. A revision of the South American species of *Arthrostylidium* (Poaceae: Bambuseae). *Syst. Bot.* **18**: 80–99.
- , ———, X. LONDOÑO, AND M. J. STERN. 1999. American bamboos. Smithsonian Institution Press, Washington, D.C., USA. 392 p.
- , AND T. R. SODERSTROM. 1989. A taxonomic-anatomical-morphological study of the Anomochloae and Streptochoeteae (Poaceae). *Smithsonian Contr. Bot.* **68**: 1–52.
- , R. J. SORENG, G. DAVIDSE, P. M. PETERSON, T. S. FILGUEIRAS, AND F. O. ZULOAGA. 2000. Catalogue of New World grasses (Poaceae): I. Subfamilies Anomochlooideae, Bambusoideae, Ehrhartoideae, and Pharoideae. *Contr. U.S. Natl. Herb.* **39**: 1–128.
- KELCHNER, S. A., AND L. G. CLARK. 1997. Molecular evolution and phylogenetic utility of the chloroplast *rpl16* intron in *Chusquea* and the Bambusoideae (Poaceae). *Molec. Phylogen. Evol.* **8**: 385–397.
- KELLOGG, E. A. 2001. Evolutionary history of grasses. *Pl. Physiol. (Lancaster)* **125**: 1198–1205.
- LONDOÑO, X., AND L. G. CLARK. 2002. Three new taxa of *Guadua* (Poaceae: Bambusoideae) from South America. *Novon* **12**: 64–76.
- LU, B.-R., M. E. B. NAREDO, A. B. JULIANO, AND M. T. JACKSON. 2000. Preliminary studies on taxonomy and biosystematics of the AA genome *Oryza* species (Poaceae), pp. 51–58. In S. W. L. Jacobs and J. Everett [eds.], Grass systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.
- MCCLURE, F. A. 1966. The bamboos: a fresh perspective. Harvard University Press, Cambridge, Massachusetts, USA. [Reprinted as “The bamboos” in 1993 by the Smithsonian Institution Press, Washington, D.C., USA. 345 p.]
- . 1973. Genera of bamboos native to the New World. *Smithsonian Contr. Bot.* **9**: 1–148.
- MICHELANGELI, F. A., J. I DAVIS, AND D. WM. STEVENSON. 2003. Phylogenetic relationships among Poaceae and related families as inferred from morphology, inversions in the plastid genome, and sequence data from the mitochondrial and plastid genomes. *Amer. J. Bot.* **90**: 93–106.
- MORI, S. A., B. BOOM, A. M. DE CARVALHO, AND T. S. DOS SANTOS. 1983. Southern Bahian moist forests. *Bot. Rev. (Lancaster)* **49**: 155–232.
- NÍ CHONGHAILE, G. 2002. Systematics of the woody bamboos (tribe Bambuseae). Ph.D. thesis, University of Dublin, Trinity College, Ireland.
- POINAR, G. O., JR., AND J. T. COLUMBUS. 1992. Adhesive grass spikelet with mammalian hair in Dominican amber: first fossil evidence of epizoochory. *Experientia (Basel)* **48**: 906–908.
- RAVEN, P. H., AND D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. *Ann. Missouri Bot. Gard.* **61**: 539–673.
- SENDULSKY, T. 1993. First report of ballistochory in the Poaceae. *Ann. Missouri Bot. Gard.* **80**: 518–521.
- . 1997. Twelve new species of *Merostachys* (Poaceae: Bambusoideae: Bambuseae) from Brazil. *Novon* **7**: 285–307.
- , T. S. FILGUEIRAS, AND A. G. BURMAN. 1987. Fruits, embryos, and seedlings of the Gramineae, pp. 31–36. In T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth [eds.], Grass systematics and evolution. Smithsonian Institution Press, Washington, D.C., USA.
- SODERSTROM, T. R. 1980. A new species of *Lithachne* (Poaceae: Bambusoideae) with remarks on its sleep movements. *Brittonia* **32**: 495–501.
- . 1981a. Some evolutionary trends in the Bambusoideae. *Ann. Missouri Bot. Gard.* **68**: 15–47.
- . 1981b. *Olmeca*, a new genus of bamboos with fleshy fruits. *Amer. J. Bot.* **68**: 1361–1374.
- , AND C. E. CALDERÓN. 1971. Insect pollination in tropical rain forest grasses. *Biotropica* **3**: 1–16.
- , AND ———. 1974. Primitive forest grasses and the evolution of the Bambusoideae. *Biotropica* **6**: 141–153.
- , AND R. P. ELLIS. 1982. Taxonomic status of the endemic South African bamboo, *Thamnocalamus tessellates*. *Bothalia* **14**: 53–67.
- , AND ———. 1987. The position of bamboo genera and allies in a system of grass classification, pp. 225–238. In T. R. Soderstrom, K. W. Hilu, C. S. Campbell, and M. E. Barkworth [eds.], Grass systematics and evolution. Smithsonian Institution Press, Washington, D.C., USA.
- , ———, AND E. J. JUDZIEWICZ. 1987. The Phareae and Streptogyneae of Sri Lanka: a morphological-anatomical study. *Smithsonian Contr. Bot.* **65**: 1–26.
- , AND E. J. JUDZIEWICZ. 1988. Systematics of the amphiatlantic bamboo genus *Streptogyne* (Poaceae: Bambusoideae). *Ann. Missouri Bot. Gard.* **74**: 871–888.
- , ———, AND L. G. CLARK. 1988. Distribution patterns in Neotropical bamboos, pp. 121–157. In P. E. Vanzolini and W. R. Heyer [eds.], Proceedings of the Neotropical biotic distribution pattern workshop, held in Rio de Janeiro, 12–16 Jan 1987. Academia Brasileira de Ciências, Rio de Janeiro, Brazil.
- , AND X. LONDOÑO. 1987. Two new genera of Brazilian bamboos related to *Guadua* (Poaceae: Bambusoideae: Bambuseae). *Amer. J. Bot.* **74**: 27–39.
- , AND ———. 1988. A morphological study of *Alvimia*, a new Brazilian bamboo genus with fleshy fruits. *Amer. J. Bot.* **75**: 819–839.
- , AND F. O. ZULOAGA. 1985. *Diandrolyra tatianae* (Poaceae: Olyreae), a new herbaceous bamboo from Brazil. *Brittonia* **37**: 1–5.
- , AND ———. 1989. A revision of the genus *Olyra* and the new segregate genus *Parodiolyra* (Poaceae: Bambusoideae: Olyreae). *Smithsonian Contr. Bot.* **69**: 1–79.
- SOORENG, R. J., AND J. I DAVIS. 1995. Phylogenetic structure of the Poaceae; results from morphology, molecules, and total evidence. *Amer. J. Bot.* **82**: 163. Abstract.
- , AND ———. 1998. Phylogenetics and character evolution in the grass family (Poaceae): simultaneous analysis of morphological and chloroplast DNA restriction site character sets. *Bot. Rev. (Lancaster)* **64**: 1–85.
- TRIPLETT, J., A. WEAKLEY, AND L. G. CLARK. In press. *Arundinaria appalachiana* (Poaceae: Bambusoideae), a new species of woody bamboo from the Southern Appalachian Mountains. *Sida* **22**.
- WATSON, L., AND M. J. DALLWITZ. 1992 onwards. 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. <http://delta-intkey.com> (Jun 2005).
- WEN, J. 1999. Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Ann. Rev. Ecol. Syst.* **30**: 421–455.
- YOUNG, S. M., AND W. S. JUDD. 1992. Systematics of the *Guadua angustifolia* complex (Poaceae: Bambusoideae). *Ann. Missouri Bot. Gard.* **79**: 737–769.
- ZHANG, W. 1996. Phylogeny and classification of the bamboos (Poaceae: Bambusoideae) based on molecular and morphological data. Ph.D. dissertation, Iowa State University, Ames, USA. 161 p.
- , AND L. G. CLARK. 2000. Phylogeny and classification of the Bambusoideae (Poaceae), pp. 35–42. In S. W. L. Jacobs and J.

- Everett [eds.], Grass systematics and evolution. CSIRO Publishing, Collingwood, Victoria, Australia.
- , ———, AND J. F. WENDEL. 1995. *ndhF* sequence data and the phylogeny of the subfamily Bambusoideae (Poaceae). *Amer. J. Bot.* **82**: 173. Abstract.
- ZULOAGA, F. O., AND G. DAVIDSE. 1999. A new species and a new combination in the genus *Parodiolyra* (Poaceae: Bambusoideae: Olyreae). *Novon* **9**: 587–591.
- , AND E. J. JUDZIEWICZ. 1991. A revision of *Raddiella* (Poaceae: Olyreae). *Ann. Missouri Bot. Gard.* **78**: 928–941.
- , AND ———. 1993. *Agnesia*, a new genus of Amazonian herbaceous bamboos (Poaceae: Bambusoideae: Olyreae). *Novon* **3**: 306–309.
- , O. MORRONE, AND E. J. JUDZIEWICZ. 1993. Endemic herbaceous bamboo genera of Cuba. *Ann. Missouri Bot. Gard.* **80**: 846–861.