SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 44

The Genera of Bambusoideae (Poaceae) of the American Continent: Keys and Comments

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SMITHSONIAN INSTITUTION PRESS
City of Washington
1980

ABSTRACT

Calderón, Cleofé E., and Thomas R. Soderstrom. The Genera of Bambusoideae (Poaceae) of the American Continent: Keys and Comments. *Smithsonian Contributions to Botany,* number 44, 27 pages, 1980.—The history of the grass subfamily Bambusoideae is reviewed and nomenclatural problems of subfamilial and tribal level are explored. Characters are presented to distinguish the subfamily from all other grasses and differentiating features of the two major groups of bamboos—herbaceous and woody—are included. Keys are given for the tribes and genera of herbaceous American bamboos and genera of woody American bamboos, the latter based principally on vegetative characters. A conspectus of the subfamily also appears, with a list of all 37 genera recognized in the American continent, each with nomenclatural and taxonomic notes. Comments on the morphology of the bamboo plant and the systematic value of some characters, especially vegetative, are given in the introduction.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year.* SERIES COVER DESIGN: Leaf clearing from the Katsura tree *Cercidiphyllum japonicum* Siebold and Zuccarini.

Library of Congress Cataloging in Publication Data
Calderón, Cleofé E.
The genera of Bambusoideae (Poaceae) of the American Continent.
(Smithsonian contributions to botany ; no. 44)
Bibliography: p.
1. Bamboo—America—Classification. 2. Grasses—America—Classification. 3. Botany—America—Classification. I. Soderstrom, Thomas R., joint author. II. Title. III. Series: Smithsonian Institution. Smithsonian contributions to botany ; no. 44.
QK1.S2747 no. 44 [QK495.G74] 581'.08s [584'.93] 79-14750

Contents

Dedicated to Professor C.G.D. Nees von Esenbeck
(1776–1858), father of the Bambusoideae

Bambuseae, quidquid dicant alii, propriam
subfamiliam s. ordinem graminum efformant,
cum vicinis omnino connexam.

Ruprecht, 1839

The Genera of Bambusoideae (Poaceae) of the American Continent: Keys and Comments

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Introduction

Bamboos are a unique group of arborescent grasses that occur throughout the world, although they are generally associated with Eastern cultures, where they play such a significant role in the everyday life of the people. The New World shares equally in the bounty of bamboos, but they are less known. The rich forests of the New World provided man with all his needs and bamboo was only one of many useful plants at his disposal. While bamboo is used by man wherever he comes into contact with it, only in a few places of the New World has he used it to any great extent, such as the lowlands of Colombia and Ecuador, where the native Guaduas are used in construction.

Many bamboos, though, are herbaceous in nature and, looking like palm seedlings or ferns, inhabit the dark rain forests. Many of these are diploids, unlike the larger tetraploid and hexaploid bamboos. The arborescent and the herbaceous genera, however, are similar in basic morphological and anatomical features and their alliance has been demonstrated by many corroborative studies. We consider all of the genera to comprise a single subfamily, Bambusoideae.

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The concept of the subfamily Bambusoideae, with woody and herbaceous members, has evolved over a long period of time as part of the developing classification of the grass family. While the concept of the subfamily, as we espouse it today, was first presented by Nees von Esenbeck in the early part of the last century, few followed his ideas and only now, with additional data to support it, do most agrostologists accept the concept.

Unlike most grasses, the woody bambusoid species (bamboos) and herbaceous bambusoid (which we call herbaceous bamboos) have biological peculiarities that have hampered their study. Most bamboos, for example, are large and complex plants that remain in a vegetative state for many years, flowering only occasionally. Collectors generally shy away from bamboos because of their size and complexity and usually because they are rarely in flower. Herbaceous bamboos, on the other hand, flower continuously or at least for several months during the year, but their flowers are generally hidden under leaves or are inconspicuous, causing the plants to look sterile.

Nevertheless, there are many more collections of herbaceous bamboos than of bamboos themselves, and most collections of bamboos are incomplete. Our earlier field experience was directed especially toward the herbaceous bamboos, on which a greater number of studies had already been made than on

the bamboos. As a result we can now assign all the genera of herbaceous to tribes, while the state of knowledge does not allow this for all the bamboos. It was McClure's opinion also, as evidenced in his final paper, published posthumously (1973), that the American genera of bamboos were still too imperfectly known to be placed in tribes.

Arborescent forms occur in a variety of unrelated monocotyledonous families, for example the Palmae, Pandanaceae, Strelitziaceae, and Agavaceae. This growth form is also known in some members of otherwise herbaceous families: *Aloe* of Liliaceae, *Puya* of Bromeliaceae, and some genera of Araceae. In the same category the bamboos are one of the remarkable examples of arborescent forms in a predominantly herbaceous family, the Poaceae. All of these arborescent monocotyledons exhibit fundamental differences in construction, both from dicotyledonous trees and among themselves. Bamboos represent one of the few groups of arborescent monocotyledons that compete with dicotyledonous trees in size and branching habit. Some species of *Bambusa* in South America may reach over 30 m in height and 20 cm in diameter. Examples of this and even greater size are known in Asiatic members, such as *Dendrocalamus giganteus,* the largest of all. Bamboos, like the majority of arborescent monocotyledons, lack vascular cambia. Some essential features of the growth-form and growth-limiting characteristics in some arborescent monocotyledons have been described by Tomlinson (1964). In the example that he gave, branching is in general considered limited, in some cases absent, or more commonly the production of lateral branches occurs only in the inflorescence. It has been said that the absence of a vascular cambium from the aerial axis restricts branching in monocotyledons, while dicotyledonous trees with vascular cambia are typically much branched. The bamboos are probably the exception to this rule, and they present us with many questions still unsolved.

Very little is known about branching in bamboos from a morphological and physiological point of view. The production of lateral vegetative branches does not correspond exactly with any of the cases cited by Tomlinson. In the aerial axis of a bamboo, lateral branches are produced from axillary buds, usually one at each node, although multiple buds are produced at the node in *Chusquea.*

A bamboo culm does not usually produce branches at the lower nodes but only at some distance above the ground, in the manner of a dicotyledonous tree. The number of branches at a node in the middle of the plant ("midculm node") may be one or (some species of *Merostachys*) as many as 150 or more. In many cases the original number of branches is augmented in successive years by rebranching from buds at the base of the branches. The adult pattern of this set of branches presents very useful diagnostic characters of generic validity. For descriptive purposes we refer to this aggregation of branches as a "branch complement."

The underground axis of a bamboo also branches and produces a strong rhizome system. There are basically two types, sympodial and monopodial. McClure (1966) refers to these as pachymorph and leptomorph, respectively.

For practical descriptive purposes we use the term "bud complement" for the set of buds at the midculm node, which represents an early stage of the bud development and is typical for the genus. We avoid reference, however, to the number of initial buds since it can be known only from developmental studies, which are still lacking.

Bamboos possess a basic pattern of construction that consists of a strongly segmented axis with solid or hollow internodes and with a particular system of ramification. The axis passes through different stages during its development. There are basically two phases, each recognized by a combination of morphological features. A detailed analysis of the growth habit of bamboos is outside the scope of this paper, mainly because complete developmental studies are largely lacking. For this reason we are not going to describe the morphological and physiological changes of a bamboo seedling, the very early stages of the juvenile phase, or the many intricate phenomena that occur with the onset of flowering.

We will refer very briefly to some features of the two major phases of growth form. These are different stages of the vegetative state of a bamboo plant and occur in the majority of known genera. As Tomlinson (1964) pointed out, bamboos constitute a peculiar and distinctive group with regard to their growth form and do not conform to any of the arborescent types that he defined.

Stem elongation plays a significant role in the development of the plant form and consequently in the dimorphism of leaves. During the first phase they produce from the rhizome long shoots with

a strong apical dominance, fast internode elongation, and almost full suppression of lateral appendages. The new stem produces only one leaf at each node, in the form of a sheathing organ that envelops it completely. This new stem, which is at full diameter as it emerges from the soil, grows quickly and in many species reaches full height within a relatively short time. When the new shoot has completed most of its growth, the second phase of the vegetative cycle begins with the development of the lateral members, branches and foliage, at the same time that the soft tissues of the stem harden. This phase may extend over a period of several years during which the branching and rebranching occur along with a moderate increase in height.

In the majority of grasses, including herbaceous bamboos, the development of the plant does not follow this pattern, which is associated with the arborescent habit. In general, grasses produce short shoots with a balance between apical dominance, moderate stem elongation, and a simultaneous production of lateral appendages, one leaf at a node in alternate fashion but very few or no lateral branches.

Culm leaves and bud complements are the outstanding morphological structures of the first phase of the bamboo growth form, while branches and foliage leaves are characteristic of the second. These structures offer numerous characters of great systematic importance, which merit special comment.

The extreme dimorphism in bamboo leaves has given rise to much confusion in leaf terminology. There are two basic types: "culm leaves" and "foliage leaves." Culm leaves cover the new growing culm and since their function is to protect the growing shoot, the greater part of the leaf is sheath; often, in fact, the blade is hardly developed. Because the blade is the less developed part of the culm leaf, it has generally been disregarded and the whole structure called merely "sheath" in the literature. Kurz (1876), in his perceptive account of the growth form of bamboos, drew particular attention to the useful characters in this structure to distinguish species.

Types of culm leaves are characteristic of genera, while differences in foliage leaves or in the culm leaf itself serve to distinguish species. This structure, which is of paramount importance in identifying bamboos, is often overlooked by collectors.

As opposed to culm leaves, foliage leaves exhibit a greater development in the blade or lamina, the sheath becoming more or less proportionate to the size of the blade or to the number of leaves in a branch. The blade in most Bambusoideae is broad, more or less lanceolate, with the base constricted and jointed to the sheath by a little stalk, which often bears a pulvinus. This stalk is like the petiole of dicotyledonous leaves and is often similar in appearance; for descriptive purposes we use the term "petiole" without any interpretive connotation.

Foliage leaves are produced laterally on the branches in most cases and are replaced periodically. The number of leaves on a branch varies within genera and species. Sometimes the leaves overlap closely, forming a distinct and recognizable set of leaves in the distal part of a branch. In our descriptions we refer to this group of leaves as a "leaf complement."

At this point we wish to stress the significance of the occurrence of two growth forms in bamboos, a phenomenon that does not occur elsewhere in the grasses. Moreover, the specialized leaves that cover the new shoot and later the numerous vegetative branches produced from almost every node are features unique among the grasses and rare in monocotyledons. Characters from these structures have proved to be of great systematic value at the generic and specific levels. Unfortunately these are the very structures that are usually not collected.

Flowers are of equal systematic importance in bamboos as they are in other grasses and flowering plants, but because they are so seldom available we must generally resort to distinguishing bamboos by vegetative characters, of which, fortunately, there are many.

After a limited period of vegetative growth the reproductive phase starts with the production of inflorescences. In most bamboos this takes place at intervals from few to many years, at which times it is generally gregarious. In some others the frequency of flowering in a population is almost yearly, as in species of *Swallenochloa* and *Myriocladus,* both genera that inhabit high mountains. It is interesting to note that many bamboos cease vegetative growth for a long period prior to the flowering and often lose all foliage at the peak of this process, which may last for a few years or more. In many cases the development of inflorescences is not limited to the distal parts of the branches or culm, but to every part of the plant where meristematic tissue

allows it, from the base of the plant up. Thus, the complexity of bamboo inflorescences increases, making the traditional terms used in descriptions of grasses, such as spike, raceme, and panicle, inappropriate.

Generally in bamboos and, to a lesser extent, in herbaceous bamboos, inflorescences are complex systems of ramification throughout which bracts and prophylla are well developed. The basic units of this system are partial inflorescences, in themselves clusters of spikelets. In some bamboos the production of partial inflorescences starts at the base of the spikelet by the activity of buds in the axils of the glumes, as in the "pseudospikelets" of *Bambusa* (McClure, 1966, 1973). Along very general lines the inflorescences of bamboos can be divided into two major groups. In one the production of inflorescences is restricted, limited to a single group of spikelets. In the other case it is unrestricted, with unlimited production of inflorescences brought about by rebranching from buds at the base of any one of the partial inflorescences. The complexity of an inflorescence is increased by the different basic types of partial inflorescences themselves. These may be of either limited (determinate) or unlimited (indeterminate) growth.

The use of a very simplified terminology is highly desirable until detailed morphological analyses are carried out. For general descriptive words, such as "bract," "partial inflorescences," or the concept of "complex inflorescences," we refer to Troll (1964). In his more modern typological terminology the term "synflorescence" could be applied to the bamboo flowering system, but this would require an elaborate morphological analysis. More details on this subject are given in a previous paper (Calderón & Soderstrom, 1973), and for general meanings of different bamboo structures we refer the reader to the glossaries in two of McClure's publications (1966, 1973).

In the following keys to bamboos we have given particular emphasis to the vegetative characters that are generally available, and for the herbaceous genera we have used both floral and vegetative characters since these are commonly present. In the keys to bamboos we have added floral characters as supplementary information. Following the keys we have listed the genera of Bambusoideae and for each genus we have given the author, type-species, type-locality, and a few notes on distribution and ecology.

Because the concept Bambusoideae as we understand it today has taken almost two centuries to develop, we have followed its history and tried to clarify its development and present this in the following chapter. Confusion has reigned not only in the systematics of this unusual group of grasses but in its nomenclature as well, and only by understanding its history could we identify those responsible for conceptualizing the subfamily and the major divisions within it.

ACKNOWLEDGMENTS.—We are grateful to Dr. Rupert Barneby of the New York Botanical Garden and to Dr. Dan Nicolson of the Smithsonian Institution for advice on nomenclatural problems and for their careful review of the manuscript. We owe a continuous debt of gratitude to Dr. José Cuatrecasas of the Smithsonian for his illuminating discussions of morphology, advice on nomenclature, and ever-ready help in all botanical problems, big and small.

History of the Bambusoideae

In 1763 Adanson, in his treatment of Gramineae for the families of flowering plants, divided the family into several natural groups on the basis of a combination of characters, both floral and vegetative. His major groups are maintained to this day, the Poae and Panica being two of the most important, presently called tribes Poeae and Paniceae.

The beautifully executed and printed grass flora of New Holland (Australia) by Robert Brown in 1810 presented early ideas on relationships within the family. Brown remarked that, while grasses were connected in a reticulate fashion, he was nonetheless able to recognize three groups, delimited chiefly by modifications in the fruiting (spikelet) structure. The group of genera that contained *Poa* was characteristic of temperate regions and the other, which contained *Panicum,* was characteristic of hot and tropical regions. He was familiar with both groups, the former in his native England and the latter in the warm regions of Australia. Brown also listed a third group that contained a mixture of genera, which he admitted was scarcely natural. In 1814 he contributed a treatise on the botany of Terra Australis (Australia) for the report of the voyage during 1801–1803 of the *Investigator,* of which Matthew Flinders was commander and Brown, him-

self, the naturalist. In this account, Brown clarified his earlier remarks on grasses and divided the family into two tribes, which he called the Paniceae and Poaceae. He gave a very good explanation of the spikelets in each group and how they differ. Many later authors have interpreted these tribes of Brown to represent what many regard today as the subfamilies Panicoideae and Pooideae. While Adanson first named these two groups and characterized them, Brown elaborated upon them.

The genius of Charles Kunth is apparent early in the career of this German botanist who, at the age of 27, published a highly significant paper on grasses (1815) while he was at Paris. "Having had the occasion to examine a large number of species of grasses, living [plants] as well as [specimens] in the rich herbaria of this capital [Paris]," he was convinced that the genera could be ordered into many natural groups. He presented a list of 10 such groups, among them the familiar Paniceae (as "Gramina Panicea"). His tenth, the bamboos (as "Gramina Bambusacea"), to our knowledge marks the first appearance of this group in a system of grasses. Kunth's 10 groups were repeated in a later treatment of the grass family in his *Synopsis Plantarum* of 1822.

During the same year there appeared in Sweden the *Aphorismi* of Agardh, in which nine groups of grasses were listed, one of them bamboos. It is likely that Agardh's division of the family was modeled on the ideas presented by Kunth in 1815, since the groups are almost identical.

Kunth (1815, 1822b) and Agardh (1822) were thus evidently the first authors to regard bamboos as a separate category of grasses. They included the few genera known at the time.

In 1827 Link listed the plants in cultivation in the botanical garden in Berlin, of which he was curator. Then, as now, one of the widely cultivated bamboos was *Bambusa glaucescens,* an oriental species with small foliage and slender branches, which adapts easily to indoor culture. Link called the bamboo *Ludolfia* and placed it in the Triglossae, one of two sections that he erected for the bamboos. His other section was called Bracteiflorae and in this he included *Nastus* and *Bambusa arundinacea,* the type of the genus, which is commonly called the "thorny bamboo of India." Link's sections were admirably based on characters from the inflorescence and spikelet, but faulty observations regarding stamen number caused him to include species of the same genus in each of his sections.

It was not until 1829 and 1835 that the bamboos were to receive a much more detailed treatment by the gifted Christian Nees von Esenbeck, a close friend of Goethe and a renowned botanist interested in all branches of natural history, philosophy, and social ethics. His 1829 treatment of the grasses of Brazil is a masterpiece. Bamboos constitute his tenth group, which he further divided into two parts, including in one of them the herbaceous genus *Streptochaeta.*

The 1835 work of Nees dealt solely with the bamboos of Brazil, a group that must have intrigued him during his earlier study of the grasses of that country. He now divided the bamboos into three groups: Bambuseae (including *Bambusa*); Arundinariae (including *Arundinaria);* and a third, without a name, that contained *Streptochaeta.* However, the latter was listed as Streptochaeteae the following year (1836) in his enumeration of grass genera in Lindley's *Natural History of Botany.*

In the above system Nees gave the genus *Bambusa* a detailed treatment and divided it into two subgenera, *Bambusa* and *Guadua.* The former contained species native to the Old World and the latter species native to the New World. Many authors have since regarded them as independent genera, but Hackel (1903) and McClure (1973) are among those who have followed Nees.

In our opinion Nees' 1835 paper was not only the first taxonomic monograph to be offered for bamboos but also one that embodied the most natural system, as we interpret it today, *Bambusa* and *Arundinaria* being among our woody bambusoid grasses (bamboos) and *Streptochaeta* an herbaceous bambusoid (Calderón & Soderstrom, 1973). Further, *Bambusa* belongs to those bamboos that have sympodial (pachymorph) rhizomes and pseudospikelets, and *Arundinaria* belongs to those that have monopodial (leptomorph) rhizomes and spikelets of the usual grass type. It is significant that Nees recognized the relationship of an herbaceous grass like *Streptochaeta* to the woody bamboos and accorded the genus equal rank. This paper is a testament to the perceptive mind of one of the greatest agrostologists of all times, yet it went unheeded and unnoticed for over a century after its publication.

Few authors after Nees accepted his placement of

herbaceous and woody members together. Most, in fact, followed the lead of the Russian botanist, Franz Ruprecht, who, in 1839, published a large monograph on the bamboos. In his lengthy introduction, Ruprecht remarked that, whatever others might say, bamboos form a natural subfamily or order of grasses wholly connected to the other members. Ruprecht placed the 67 species of woody bamboos in two groups, following the system of Nees.

Ruprecht's contribution was not to the system of classification of bamboos but rather to the extensive worldwide treatment that he gave them. He devoted several pages to the morphology of the plant, discussed geographical distribution, and gave descriptions and keys to all the species. In its restriction to woody bamboos, this monograph had a greater influence on later workers than did that of Nees.

The excellent monograph of Colonel Munro (1868) followed that of Ruprecht in its exclusive treatment of woody genera. Distinguished both as soldier and botanist, Munro was an outstanding agrostologist, who was often consulted by his colleague, George Bentham, on grass problems. Munro formulated three groups to accommodate his bamboo genera. The first two were those of Nees, but he added a new one, the Bacciferae, to contain the genus *Melocanna* and others from Asia. He divided the first group (which he called Triglossae out of personal preference) into three parts, the Arundinariae, Arthrostylideae, and Chusqueae, the latter two containing the New World genera with which he dealt.

Munro's system rested upon the foundation laid by Nees half a century earlier for the genera of Brazil but expanded to cover bamboos of the world. His system was thus more complete and introduced a whole new group, the Bacciferae, of eight genera, all Asiatic. All the groups and subgroups that Munro recognized have remained in systems to this day, albeit at different rank or with different name. Like Nees, Munro had a keen perception of natural relationships in bamboos.

In 1881 George Bentham published his classic paper, "Notes on Gramineae." His friend, William Munro, had recently died and Bentham lauded the colonel upon whom he had depended for ideas regarding natural relationships in the grass family. In this paper, Bentham listed four groups of bamboos, adopting the concepts of Nees and Munro, with slight modifications in name and rank.

The treatment of grasses that appeared in 1887 in *Die Natürlichen Pflanzenfamilien* by the Austrian agrostologist, Eduard Hackel, has had a tremendous influence up to the present time. The major divisions of grasses that he enumerated were followed by most subsequent investigators. He divided the bamboos into four groups, which were exactly the same as those of Bentham. Hackel's expertise in grasses such as *Andropogon* and *Festuca* did not extend to the bamboos, especially not to the herbaceous ones, which he dispersed among several distantly related groups.

The most recent treatment of grasses in *Die Natürlichen Pflanzenfamilien* was prepared by Robert Pilger (1954), who omitted the woody genera of Bambusoideae. He did, however, assemble the majority of herbaceous monoecious bambusoid genera in one subfamily, which he called Olyroideae, and established another just for the herbaceous bamboo, *Anomochloa*. In this context it is interesting to note that Pilger recognized nine subfamilies, three of which are based on genera that we regard as bambusoid.

At the time of Hackel's paper, Franchet (1887) described three new herbaceous genera of grasses from tropical West Africa: *Atractocarpa, Guaduella,* and *Puelia,* all of which he stated to be bambusoid. The superficial similarity in spikelets of one of the genera to those of the American bamboo, *Guadua,* in fact prompted its diminutive name.

The most complete monograph on Indian bamboos was published in 1896 by James S. Gamble, who was director of the Imperial Forest School at Dehra Dun, India, in the latter part of the past century. Although the monograph is a highly valuable treatise, it did not contribute anything new to the system of classification since Gamble employed the same four groups as Bentham.

In 1913 Edmond-Gustave Camus published a monograph on bamboos, which was little more than a compilation of the literature to that time, although it did present a slightly modified system. His major groups were those already recognized by Munro except for the inclusion of Franchet's herbaceous genera and some alterations in group names and rank.

Aimée Camus, like her father, Edmond-Gustave, worked at Paris and published many new genera and species of grasses, especially from the French colonies of the time. Her classification of bamboos (1935) differed little from her father's except for

the rearrangement of some existing tribes and the addition of two new subdivisions to accommodate recently described genera of Madagascan bamboos.

Both the Camusian systems incorporated woody genera. Interestingly, the only herbaceous ones were, however, those of their compatriot, Adrien Franchet.

The characters used in systems of classification up through the time of A. Camus were for the most part floral, little importance being attached to vegetative structures. Probably for this reason Nees included *Streptochaeta* with the bamboos; the hermaphrodite spikelet, three lodicules, six stamens, and three stigmas were similar enough to those of bamboos to justify inclusion with them. A few other authors (Meisner, 1843; Steudel, 1855; Doell, 1880) followed Nees and placed that genus, along with *Streptogyna* (from tropical America, Africa, and Asia), next to bamboos. Trinius (1820), however, aligned *Streptogyna* with *Bromus,* and it remained with that genus through recent systems, an indication of his strong influence.

Other herbaceous broad-leaved forest grasses like *Leptaspis, Olyra, Pariana,* and *Pharus,* although closely resembling the above genera, were seldom associated with them. Grisebach (1864) did recognize the relationship of *Pariana* to bamboos, but most other authors misinterpreted its spikelike inflorescence as evidence of a close affinity to members of the Hordeae. The unisexual spikelets and monoecious condition, common to all of these genera but not features of any woody bamboo, probably account for the fact that these grasses were all placed elsewhere in most systems.

While Kunth, in his 1815 paper, regarded *Olyra* as representing a distinct group of grasses related to the bamboos, he was soon thereafter influenced by his contemporary, Carl Trinius, who treated the genus with *Panicum* in his monograph on that and allied genera (1826). Superficially the anthecia of *Panicum* and *Olyra* are indeed remarkably similar and many astute botanists since the time of Trinius have accepted without question the opinion of this influential Russian agrostologist. In fact, this disposition was endorsed by Hackel (1887) and adhered to by his many disciples to the present. Some other authors felt that the monoecious condition of these genera was an indication of a natural alliance between *Olyra, Zea,* and *Zizania,* the latter two genera belonging to widely unrelated groups by our present understanding. While not linked in early systems with bamboos, some of these monoecious genera were placed together since early times: *Pharus* and *Leptaspis,* for example, had been associated with *Olyra* by Kunth (1815), Agardh (1822), and Link (1827).

It is well to recall the early words of Adanson (1763), who remarked that botanists were prejudiced in favor of divisions based on floral characters. He considered this a pitfall and, in establishing his natural groups of grasses, felt that all parts of the plant should be considered together. But his advice was not heeded until 1931, when Avdulov brought together data from many lines of investigation that had been developing in the grasses since the end of the nineteenth century.

Study of the anatomy of the grass leaf has shown that there are great structural differences between major groups, and anatomical characters are now used widely in grass systematics. Of the numerous anatomical papers that we have previously cited (Calderón & Soderstrom, 1973:36), that of Brandis (1907) is of particular interest here. In his well-documented paper, Brandis referred to the similarities of the structure between the leaves of bamboos and those of several herbaceous grasses such as *Olyra, Diandrolyra,* and *Pharus.* A short time later, on the basis of leaf anatomy, Krause (1909) divided the family into three major groups, of which one was the Bambusoideae. The findings of Brandis were corroborated by Michaud-Page (1947) and Metcalfe (1956), who pointed out that leaves of *Streptochaeta,* as well as some other herbaceous genera, had the same anatomical structure as those of bamboos.

The embryo, endosperm, and seedling have also provided characters of systematic value. Van Tieghem (1897) studied the embryo and seedling and was the first to point out their value in distinguishing major groups of genera. His work has been added to by the embryo studies of Yakovlev (1950), Kinges (1961), and Reeder (1962). In the latter study, the author pointed out similarities between embryos of the "olyroid" genera and bamboos. Characters of the endosperm have provided the basis of a system of classification developed by Hayek (1925).

The detailed morphological and anatomical studies that became fashionable toward the end of the last century, and have continued since, were

directed as well to the grass inflorescence and spikelet. The unusual spikelet of *Streptochaeta* has intrigued most serious agrostologists since the genus was described by Nees in 1829 and placed by him with the bamboos. Čelakovský (1889) published detailed morphological studies of the spikelet and interpreted the flower as the most primitive of any grass, an idea that has persisted to the present. The classic paper on the morphology of the grass flower by Goebel's student Schuster (1909) corroborated the opinion of Čelakovský. In his phylogenetic scheme for the family, Schuster regarded *Streptochaeta* as the type closest to the hypothetical ancestor of the family. Several other investigators, such as Arber (1929) and Michaud-Page (1951), have tackled this well-studied genus and published still further scholarly accounts.

The appearance of significant papers by Avdulov and Prat in 1931 marks this year as a milestone in the development of a modern system of classification for the grasses. Nikolai Pavlovič Avdulov was a cytologist at the Institute of Applied Botany and New Cultures in Leningrad, of which N. I. Vavilov was director. Henri Prat was a French anatomist, who had recently completed his thesis on a study of grass leaf epidermis.

Avdulov, working under the cytologist G. A. Levitskii, made a survey of the karyotype of all the grasses he was able to obtain. He studied the chromosome number, size, and form, in addition to the seedling and leaf anatomy. Combining his extensive data with those of others, he was able to develop an original system of classification.

Prat (1931) showed that the grass leaf epidermis also provided numerous characters of systematic value. He expanded upon the data presented in that paper and in 1936 offered a new system, incorporating his own data with those of Avdulov and others. While Avdulov had presented little data on bamboos—due to lack of study material—Prat recognized the bambusoid as a major division of the family.

Avdulov had set a precedent for evolutionary considerations in the grasses and made them the basis of a new phylogenetic scheme. His colleague, Roman Yulievič Roshevits, an agrostologist at the Botanic Garden in Leningrad, aided Avdulov in identifying the grasses that the latter used in his studies. In 1937 Roshevits published a large treatise on grasses of the world.

In his classification Roshevits followed Avdulov with some modifications and presented ideas on evolution in the family derived mainly from Schuster's phylogenetic interpretation of *Streptochaeta* and other bamboo genera. In 1946 he presented another scheme in which his subfamily Bambusoideae contained six tribes, five consisting of herbaceous and one of woody genera. Hubbard's system (1934), in which many new tribes were described, had appeared between the two papers of Roshevits and in the second the author adopts Hubbard's new tribal names. In the 1946 scheme of Bambusoideae, Roshevits did not give a description of the subfamily nor his reasons for the tribal arrangement, stating that he would do so in a later paper.

Jacques-Félix (1955) published a paper on primitive African grasses, which he brought together in his bambusoid series. The author stressed the leaf anatomy common to all the genera, which he allocated to four tribes that included both woody and herbaceous genera. This paper established the modern concept of the Bambusoideae, based on a combination of natural relationships.

A few years later Parodi (1961) formalized the nomenclatural status of the subfamily Bambusoideae and in his diagnosis added further substantiating characters from embryo structure, chromosome type and number, geographical distribution, and ecology. In this particular paper Parodi dealt only with the genera of grasses from Argentina so that his subfamily Bambusoideae circumscribed only the tribes with Argentinian representatives. In agreement with this concept, we are following Parodi's system, extending it to cover, in the present paper, the whole of the American continent.

A few systems of Bambusoideae have, however, confined themselves to the woody genera. Stebbins & Crampton (1961), in their system of grasses for temperate North America, felt that the commingling of herbaceous and woody members would result in a heterogeneous subfamily. They therefore recognized only *Arundinaria* as bambusoid and relegated to the Oryzoideae the herbaceous genera *Olyra* and *Pharus*. Grosser & Liese (1973) presented a classification of the woody bamboos, based on characters from culm anatomy of a number of Asiatic genera they studied.

The most eminent bamboo specialists of recent

times have been Richard E. Holttum, of England, and Floyd A. McClure, of the United States, both of whom have made significant contributions to our knowledge of woody bamboos. Perhaps because both had such extensive experience with bamboos in the field, the former in Singapore and Malaysia and the latter in China and tropical America, they stressed the value of vegetative characters in this group, whose members flower so seldom, without devaluating those of the inflorescence, some of which are unique in the grass family.

Holttum (1956) commented upon some morphological characters that previous authors had used in their systems of classification and divided the bamboos into four groups, using characters from the gynoecium He did not attach formal names to the groups nor did he bring herbaceous genera into his discussion.

McClure (1961) limited his detailed description of the subfamily Bambusoideae to his own group of expertise, the woody bamboos. He did, however, later agree with the concept of Bambusoideae offered by Parodi in 1961, to which he refers in a revision of bamboos of Santa Catarina, Brazil (McClure & Smith, 1967).

N. N. Tsvelev, of the Komarov Botanical Institute, has published a number of papers on evolution in the grass family. Of particular interest to us is his system of classification proposed in 1968, in which he divided the family into two subfamilies, the Bambusoideae and Pooideae, each further divided into a number of tribes. Tsvelev recognized the unique set of characters shared by genera of the Bambusoideae, which collectively form a group of equivalent rank to that formed by all other members of the family. In his revision of the grasses of the Soviet Union, Tsvelev (1976) employed this new system.

We recognize the Bambusoideae as a subfamily of the Poaceae, with a set of characters that binds together a large number of herbaceous and woody genera. To most agrostologists today the Bambusoideae is one of six or seven subfamilies of grasses; to Tsvelev it is one of two.

Nomenclature

In 1812 Palisot de Beauvois described 69 new genera and 640 new species of grasses and proposed many new binomials and new names. He divided the grasses into families, tribes, cohorts, and sections, and while all of these appeared in his "Tabula Methodica," none of them is given formal description. Trinius, a short time later (1820), in his *Fundamenta Agrostographiae,* continued to use the old Linnean system, and his genera of grasses are to be found under such categories as "Triandria Monogynia" and "Monoecia Hexandria Monogynia."

As the number of described genera of grasses increased, especially during the first half of the last century, the idea of tribes was developed in order to bring together genera with similar characters. Robert Brown, in fact, used the term "tribe" for the Poaceae and Paniceae, which he characterized in 1814. In the following year Kunth stated that "there is not at all a natural distribution of genera into tribes as has been done with success in other plant families. However, the possibility of this distribution should not be denied, which is the principal object of this memoir." Kunth listed 10 tribes, for which he used such Latin group names as *"Gramina Panicea"* and *"Gramina Stipacea."* In a later paper (1822b), he repeated his 10 groups of 1815, but called each a "Sectio" and gave new endings, for example, "Sectio 1. Paniceae and Sectio 2. Stipaceae." Link (1827) offered a more elaborate system than his predecessors and divided the grasses into sections, but these were not comparable to those of Kunth, for his sectional category was superior to those of family, division, and suborder, terms that he used interchangeably. Thus the Paniceae was a suborder of a section and the Stipaceae a division of his section called "Paniculatae Uniflorae."

It would serve no purpose to review other systems of the time except to point out two items that are already obvious: (1) agrostologists recognized that the genera of grasses could be grouped together on similar characters and (2) there was no agreement on names for these groups. For example, in the case of the well-known genus *Panicum,* Adanson established a section called "Panica." Another section was his "Poae," which included several genera he felt related to *Poa.* Robert Brown recognized the Paniceae, calling it a "tribe," characterized it further, and added more genera. Kunth recognized the same group, as one of his sections, but called it "Gramina Panicea" in 1815 and later just "Paniceae" (1822b). To Link, the Paniceae was a suborder of a section.

Regardless of what authors called the group of genera that included *Panicum*, they agreed that it was one of the natural divisions of grasses. Today we call a group of related genera a "tribe" and for this group we use the tribe Paniceae.

The first author to recognize and establish that *Panicum* and allies represented a natural group was Adanson. By present definition we regard this group as tribe Paniceae, of which the authorship must be credited to Adanson. Article 19 of the *International Code of Botanical Nomenclature (ICBN)*, note 2, states that when an improper termination has been published, it should be changed to accord with the present rules. We thus change "Panica" to "Paniceae," but still give Adanson credit for establishing the tribe.

In the subfamily of special concern to us, the Bambusoideae, there is little agreement in the literature regarding authors of tribes such as Olyreae and Bambuseae, or even of the subfamily itself. For example, Butzin (1973) credited Munro (1868) as author of the subfamily, while McClure, in his various publications, gave credit to others. In our opinion credit should go to Nees von Esenbeck (1835), who first recognized the bamboos and allies as constituting a major natural division of the family.

In order to decide who was responsible for each category, we have followed the development of the concept of the bamboos as a subfamily of grasses. In tracing the ideas from one author to another, we have attempted to follow the development of the concept of natural groups of bambusoid genera (which we call "tribes") and the aggregation of smaller groups into a large one (which we call "subfamily").

In presenting the history of the Bambusoideae above, we referred to these aggregates of genera as "groups," to avoid using the actual terms of the authors, since there was no uniformity in these terms. For the tribe Bambuseae, we thus give credit to Kunth who, in 1815, recognized the bamboos as a natural group. Nees von Esenbeck, in 1835, went further and established a larger group —subdivided into three parts, two containing woody genera and one an herbaceous genus—similar to the system we recognize today at the subfamily level. We thus give credit to Nees for the recognition of the bamboos as a subfamily of grasses.

Later authors recognized even further groups of genera of bamboos. Munro's monograph of 1868 covered the Bambusoideae in the sense of our subfamily, even though he called it a tribe and named it "Bambusaceae." Munro divided his Bambusaceae into sections and subsections, two of which, Arthrostylidiae and Chusqueae, were recognized as natural groups for the first time. Today these groups are regarded as tribes and we give credit to him as their author.

Article 35 of the *ICBN* states that "a new name published on or after 1 Jan 1953 without a clear indication of the rank of the taxon concerned is not validly published. For such names published before 1 Jan 1953 the choice made by the first author who assigned a definite rank is to be followed."

As we have pointed out, there was no uniformity in the names of rank applied to grass taxa in the older literature. Since different names were used interchangeably for the same intended rank, they cannot be accepted in a literal sense. For example, *Bambusa* and allied genera constituted a section in the systems of Kunth (1822b) and Link (1827). Several years later, however, Link (1833) made them a family "Bambusaceae," which he listed as a subdivision of the section. On the other hand, Meisner (1843) called this group a subtribe.

We must look to the first author who recognized the taxon, whatever rank name he gave it, and assign the rank name that applies to the group by our present understanding. We have followed this way of thinking in our interpretation of the nomenclature of bambusoid taxa prior to 1 January 1953, when guidelines were lacking. Since that date the rules for valid publication, as set forth in the *ICBN*, must be followed.

Sometimes the selection of the authorship of a subfamily was based solely on the use of the first correct spelling by modern rules, an interpretation with which we do not agree. For this reason, McClure (1966) cited Rehder (1945) as author of the subfamily Bambusoideae of the "Gramineae" and Ascherson & Graebner (1902) as authors of the subfamily Bambusoideae of the "Gramina." It was not until late in the last century that the term "subfamily" was in fact used as a category for a major subdivision of the grass family. Nees von Esenbeck's concept of the bamboos as constituting a major natural division of the grass family thus

preceded both the term we use for that group today and the rules that govern its correct Latin spelling.

Characterization of the Bambusoideae versus Other Grasses

BAMBUSOIDEAE.—Perennial herbaceous or woody and arborescent, but without secondary thickening, rhizomatous; culms when woody branched at the nodes, the branches in some species with thorns or spines; leaf blades usually flat, broad, lanceolate or linear-lanceolate, articulate with the sheath by a petiole that twists and moves the blade in different positions; blades with tessellate venation strongly or weakly manifest superficially; flowering not seasonal, in some cases (bamboo) in cycles of long intervals of several years or almost continuous through several months of the year; inflorescences of different types, usually composed of complex systems of partial inflorescences with a limited or unlimited and continuing ramification and production of new partial inflorescences of restricted or unrestricted type (pseudospikelets), usually with very well-developed bracts (subtending leaves and prophylla); spikelets or pseudospikelets 1- to many-flowered, without glumes or with 2 to several "transitional glumes;" lemma (3-)5- to many-nerved, not awned or only seldom so, and the awn then not geniculate; palea 2- to many-nerved, keeled or rounded dorsally, exceptionally bifid; lodicules generally 3 (rarely 0 to 6 or many), usually large and with hairs of different types and well-developed vascularization; stamens 3 to 6 or many (rarely 2), sometimes partially fused or monadelphous; stigmas 2 or 3 (rarely 1); fruit of variable type, dry (caryopsis or achene) or fleshy (drupe or berry-like), sometimes very large and many times the size of the original gynoecium; hilum linear, almost as long as the fruit; embryo several times smaller than the fruit.

Seedling: Coleoptile short and not elevated from the caryopsis by an internode, first two to several leaves bladeless or with a reduced blade, the first expanded blade broad, ovate or lanceolate, horizontal in position.

Leaf Anatomy: Leaf blade (lamina) with a very conspicuous midrib containing a complex vascular system of several bundles in two rows, strongly developed sclerenchyma and ground tissue; mesophyll with cells arranged in horizontal layers parallel to the epidermis, not radiate; chlorenchyma composed of arm cells and translucent fusoid cells at each side of the vascular bundle and in between layers of arm cells; bundle sheaths always double and well developed, the outer sheath with very few chloroplasts; transverse veinlets connecting the longitudinal vascular bundles present.

Leaf Epidermis: With short cells in pairs or sometimes in rows over the veins; silica bodies usually cross-shaped, saddle-shaped, of olyroid type, or of intermediate forms; microhairs nearly always present, bicellular with both cells of about the same length and with rounded apex, microhairs of 3 or 4 cells sometimes occurring; papillae common and abundant on the long cells and overarching the stomata; long cells with thick sinuous walls; stomata usually with low dome-shaped or sometimes triangular subsidiary cells.

Physiology: C_3 pathway of CO_2 fixation.

Cytology: Chromosomes small, $x=12$, with most bamboos tetraploid ($2n=48$) or hexaploid ($2n=72$), and herbaceous bamboos diploid or polyploid, with n numbers of 7, 9, 10, 11, and 12 reported.

Ecology and Geographical Distribution: Plants growing in association with trees or shrubs, usually in warm temperate woodlands, tropical rain forest or, if herbaceous, in the shaded understory of warm forests, also along streams or, if in rather open areas, always in shade of taller vegetation; usually dependent on humidity, shade, and warm temperatures in the environment; abundant in the tropics and subtropics of the world, only some woody members reaching temperate-cold areas of both hemispheres.

GRASSES (excluding Bambusoideae). – Perennial or annual herbs, sometimes tall and robust but neither with lignified culms nor complex ramification at nodes of the culm, nor thorns, nor spines; cespitose, stoloniferous or rhizomatous, but then not with strong complex systems; nodes with only one bud or none; plants without a special growth pattern, i.e., not producing differentiated elongated new culms, the leaves all alike and produced progressively as the plant grows; leaf blades usually linear and if lanceolate petiolate, not deciduous; outer ligule never present; flowering seasonal, with one flowering period each year, either in spring or summer, according to the group; inflorescence spiciform, racemiform, or paniculiform, usually lacking bracts and prophylla and not forming complex sys-

tems of ramification; pseudospikelets not formed; spikelets 1- to many-flowered, usually with 2 glumes; lemma awnless or with an awn, this sometimes geniculate; palea usually 2-nerved and 2-keeled; lodicules usually 2, relatively small; stamens usually 3; stigmas 2. Fruit a caryopsis, exceptionally of a different type, but then not fleshy; hilum punctiform, ovate or linear, short or long; embryo small or large.

Seedling: Of different types according to the group, but not bambusoid.

Leaf Anatomy and Epidermis: Of different types but not bambusoid.

Physiology: C_3 and C_4 pathways of CO_2 fixation according to the group.

Cytology: Chromosomes small or large, $x=7$, 9, 10, and sometimes 12.

Ecology and Geographical Distribution: Forming dense covers in open, sunny places, being the main component of prairies, steppes, savannas, and mountain slopes; common elements of the herbaceous vegetation from dry or arid zones to humid ones, from cold, temperate to warm, tropical, reaching the extreme limits of vegetation in the mountains or near the poles of both hemispheres; relatively few species adapted to the dark conditions of the woodlands or tropical forests.

Characterization of Woody versus Herbaceous Bamboos

Woody Bamboos.—Plants with a woody, strongly segmented cauline axis, often arborescent and with a prominently developed rhizome system; plants with a special growth pattern, producing at the initial period unbranched, elongated new shoots covered by overlapping modified leaves ("culm leaves"), and at the nodes one to multiple buds arranged in different patterns, leading when developed to complex systems of ramification; leaves dimorphic, those covering the new culm ("culm leaves") with a greater development in the sheath, the blade usually smaller and of variable shape and orientation, caducous or persistent, the petiole sometimes lacking, auricles and oral setae often greatly developed; foliage leaves usually with a lanceolate blade, articulate to the persistent sheath by a petiole and deciduous, and often with tessellate venation strongly or weakly manifest, outer ligule commonly developed, auricles and oral setae usually well developed; flowering in cycles of several-year intervals, the individual usually monocarpic; inflorescences of different types in complex systems of ramification, with production of partial inflorescences either limited (one) or unlimited as the result of continuous ramification and production of several partial inflorescences of restricted or unrestricted type (pseudospikelets); partial inflorescences composed of 1 to many spikelets arranged in racemiform or paniculiform fashion; spikelets or pseudospikelets 1- to many-flowered, the flowers all hermaphrodite; fruit a caryopsis, achene, or fleshy. Plants common in tropical or subtropical lowlands, some reaching the temperate or cold regions and altitudes up to 4500 m, usually associated with woody plants.

Herbaceous Bamboos.—Herbaceous, very small and delicate to robust plants, but without lignified culms and with rhizomes only weakly to moderately developed, never so strongly as in the bamboos; plants without a special pattern of development, not producing tall, unbranched new shoots; nodes with only one bud, not developing vegetative branches or if exceptionally so, then the branch solitary; culms never armed; leaves not dimorphic, with only foliage leaves formed; blades lanceolate or exceptionally linear, not deciduous or exceptionally so, and rarely with manifest tessellate venation; outer ligule generally lacking; auricles lacking or weakly developed; oral setae lacking except in the tribe Parianeae; flowering almost continuous or for several months of the year, not in cycles of several years; inflorescences of different types, sometimes in complex systems resulting from the continuous ramification and production of new partial inflorescences; pseudospikelets not produced; spikelets 1-flowered, hermaphrodite or unisexual (the plants then monoecious) or many-flowered, the flowers then hermaphrodite or rarely polygamous, the female distal to the male; fruit a caryopsis, rarely an achene. Plants common in forests of the tropics and subtropics, not reaching the temperate or cold regions or generally elevations greater than 1000 m, inhabiting the shade of forest or in more open places such as savannas, campos, or stream banks, sheltering under taller vegetation.

Key to the Tribes of American Herbaceous Bamboos

1. Spikelets hermaphrodite 2
   Spikelets unisexual and 1-flowered, dimorphic; plants monoecious 4
2. Spikelets many-flowered; leaves lacking a petiole between sheath and blade, ribbon-like as in the majority of grasses; outer ligule developed ..... STREPTOGYNEAE
   Spikelets 1-flowered; leaves with a petiole between sheath and blade; outer ligule not developed; blade with strong tessellate venation 3
3. Leaves mostly basal, the sheaths strongly compressed-keeled, overlapping, and forming a fan-shaped fascicle; petioles up to 25 cm long; inflorescence of cymoid type, with large bracts developed; spikelets 2 or 3 in the axil of each bract; lodicules 0; a ring of hairs present around the base of the flower; stamens 4; stigma 1 (Bahia only)..... ANOMOCHLOEAE
   Leaves distributed evenly along the culm, the sheaths rounded, not overlapping; petioles no longer than 1 cm when developed; inflorescence spicate, without large bracts developed; spikelets solitary at each node of the axis, without subtending bracts; lodicules 3, long and large; a ring of hairs lacking around the base of the flower; stamens 6; stigmas 3 ..... STREPTOCHAETEAE
4. Veins of blades not parallel to but diverging from midvein; culms forming compressed fascicles, leaves long-petiolate, all in one plane in a fanlike arrangement; inflorescence paniculate, disarticulating and falling in sections of several branches; lemma of female spikelet papery or slightly indurated; stamens 6; stigmas 3 ..... PHAREAE
   Veins of blades parallel to the midvein as normal in Poaceae; plants otherwise; leaves short-petiolate; lemma of female spikelet leathery to indurate 5
5. Rhizomes of monopodial type, spreading, the culms not forming very dense clumps; inflorescences terminal and solitary, usually not rebranching or producing secondary partial inflorescences; lateral inflorescences from nodes at axils of leaves not produced; inflorescence spiciform, disarticulating and falling in segments; stamens 2 to many; stigmas 2; oral setae of leaves usually well developed ..... PARIANEAE
   Rhizomes of sympodial type; culms appressed, forming dense, small or large clumps; inflorescences terminal and lateral, rebranching at base and producing 2 to several partial inflorescences of higher order in succession, exceptionally only 1; partial inflorescences paniculate or racemiform; stamens 3 (rarely 2); oral setae lacking ..... OLYREAE

Key to the Genera of American Herbaceous Bamboos

1. Spikelets hermaphrodite 2
   Spikelets unisexual; plants monoecious 4
2. Spikelets many flowered; leaves without a petiole between sheath and blade, ribbon-like as in the majority of grasses; outer ligule produced ..... ***Streptogyna***
   Spikelets 1-flowered; leaves petiolate; outer ligule not developed 3
3. Petiole of leaves up to 25 cm long; blade with a cordate base; spikelets in the axils of very large bracts; lodicules 0; stamens 4; stigma 1 ..... ***Anomochloa***
   Petiole less than 1 cm long; blades lanceolate; inflorescence without large bracts; lodicules very long, 3; stamens 6; stigmas 3 ..... ***Streptochaeta***
4. Veins of blade not parallel to the midvein but diverging from it; culms forming compressed fascicles, the leaves all displayed in one plane in a fanlike arrangement; leaves long-petiolate; inflorescence paniculate, disarticulating and falling in sections of several branches ..... ***Pharus***
   Veins of blade parallel to the midvein; plants otherwise; leaves short-petiolate 5
5. Inflorescence spiciform, disarticulating and falling in segments; oral setae usually well developed (Parianeae) 6
   Inflorescence paniculate or racemiform; oral setae lacking (Olyreae) 7
6. Inflorescence consisting of several segments, disarticulating from each other and falling separately at maturity; inflorescences produced only at the apex of the main culms or on short bladeless culms; male spikelets with numerous stamens; stigmas plumose; sheaths with one or more scarlike marks toward the summit (Amazonia) ..... ***Pariana***
   Inflorescence completely covered by several bracts and only 1 terminal segment disarticulating at maturity; inflorescences produced as in *Pariana* in addition to subterranean (cleistogamous) ones; male spikelets with 2 stamens, their filaments fused; stigmas not

plumose; sheaths with no scarlike marks (Bahia and northern Espírito Santo) ..... ***Eremitis***

7. Inflorescences usually produced on specialized culms (bladeless or with few blades), at the base of the main one, the inflorescence rarely developing at the apex of the main culm ..8
   Inflorescences always produced on main, leafy culms 11
8. Spikelets of both sexes mixed in each inflorescence 9
   Female and male spikelets separated into 2 digitate racemose branches (endemic to Cuba) 10
9. Specialized culms decumbent, shorter or longer than the main axis, bearing very reduced blades and several partial inflorescences; anthecium appressed-pilose (Bahia and Amazonia to the West Indies) ..... ***Piresia***
   Specialized culms erect, much shorter than the main axis, bearing only 1 fully developed blade at its apex and a single inflorescence; anthecium glabrous (São Paulo to Bahia) ..... ***Diandrolyra***
10. Lemma of female spikelet obtuse or subacute, awnless; plants delicate, small, erect or spreading, 5–15 cm tall ..... ***Mniochloa***
    Lemma of female spikelet acuminate, awned; plants firm, erect, 50–100 cm tall ..... ***Ekmanochloa***
11. Inflorescence consisting of several partial inflorescences, each containing 2 to 4 clusters of 1 large female and several smaller male spikelets, the clusters falling as a unit; filaments of stamens fused into a tube (northeastern Amazonia and French Guiana) .... ***Froesiochloa***
    Inflorescences of different types, never disarticulating and falling partially 12
12. Basal internode of culms thickened, cormlike; pedicel of male spikelets longer than the female spikelet (Amazonas; Surinam) ..... ***Rehia***
    Basal internode of culms not thickened; pedicel of male spikelet shorter than the female spikelet 13
13. Female spikelets disarticulating below the glumes; glumes with a cushion-shaped, pulviniform base; pedicel of female spikelet not thickened at the summit; delicate plants with weak, decumbent, or trailing culms ..... ***Raddiella***
    Female spikelets disarticulating above the glumes; glumes without a cushion-shaped base; pedicel of female spikelet thickened at the summit; plants otherwise 14
14. Sexes separated in different inflorescences; glumes of the female spikelet with cartilaginous undulating margins; apex of blades asymmetrically apiculate 15
    Sexes mixed in the same inflorescence; glumes without cartilaginous margins; apex of blades not asymmetrically apiculate 16
15. Leaves many, crowded and distally imbricate, forming a definite leaf complement; partial inflorescences all lateral, the male predominant, these small and paniculiform, 2 or more developing at each node of the leaf complement; female inflorescences small and racenose, few developing mostly at the middle nodes of the culm (Venezuela, Guianas, northern Brazil, and Bahia) ..... ***Strephium***
    Leaves few, evenly spaced along the culm; partial inflorescences lateral and terminal, the female predominant, these racemose, several developing acropetally at each node; male inflorescences few, large and open paniculiform, developing at the summit of culm (eastern Brazil: Pernambuco to Rio de Janeiro) ..... ***Raddia***
16. Internode of rachilla between the glumes and anthecium elongated; partial inflorescences produced at the summit of the culm and from several nodes below 17
    Internode of rachilla between the glumes and anthecium not elongated 18
17. Anthecium laterally compressed, triangular in outline, zygomorphic (gibbous) ..... ***Lithachne***
    Anthecium dorsally compressed, fusiform, actinomorphic ..... ***Cryptochloa***
18. Inflorescence dense and contracted, borne singly at the summit of the culm; lemma of male spikelet similar in texture to glumes, 7- to 9-nerved; stigmas with short appressed processes, not plumose and curling at maturity; culms with only 1 to 3 blades developed (Panama) ..... ***Maclurolyra***
    Inflorescence composed of several partial inflorescences produced at the summit of the culm and from 1 to few nodes below; lemma of male spikelet unlike that of female glumes, thin and papery, 3-nerved; stigmas with long processes, plumose, not curling at maturity; culms with most of the blades developed 19
19. Inflorescence open, paniculate or digitate; female lemma many-nerved; female anthecium not mottled at maturity (Mexico to northern Argentina and West Indies) ..... ***Olyra***
    Inflorescence small, condensed; female lemma 5-nerved; female anthecium mottled at maturity (southeastern Brazil) ..... ***Reitzia***

Key to the Genera of American Bamboos

1. Rhizomes monopodial (leptomorph); midculm branch complement basally appressed, composed of 3 axes, the central one slightly dominant, all later rebranched; inflorescence solitary, restricted, of limited branching; stamens 3; stigmas 3 (temperate regions of the Northern Hemisphere; 1 species native to continental United States) ..... ***Arundinaria***

   Rhizomes sympodial (pachymorph) (subtropical and tropical regions of both hemispheres)..2

2. Culms in the vegetative state usually not branched 3

   Culms in the vegetative state usually branched 4

3. Culms highly modified, juncoid in both vegetative and flowering stages, with a few bladeless leaves developed only in the basal part; the greater part of each culm consisting of a single elongated internode, thin-walled and with pith septa at close intervals; large, paniculiform inflorescence; stamens 3; stigmas 2 (Serra dos Orgãos, state of Rio de Janeiro, Brazil) ..... ***Glaziophyton***

   Culms leafy, of a coarse grasslike appearance, with unusually large leaves up to 2 m long, the sheath and blade not strongly differentiated; internodes with more or less thick walls and without septa; inflorescence terminal to the culm, open or contracted; spikelets with 1 fertile floret, 4 transitional glumes (plants of very high elevations) ..... ***Neurolepis***

4. Branch complement at midculm nodes consisting of 1 branch; inflorescence single, restricted, of limited branching 5

   Branch complement at midculm nodes consisting of few to numerous branches 6

5. Culm characterized by 1 or 2 usually elongated internodes separated by several short ones; culm leaves very thick and leathery with sessile or subsessile blade; sheath persistent, the blade deciduous; inflorescence long and narrow; spikelets usually 2-flowered (isolated tepuis in Venezuela) ..... ***Myriocladus***

   Culms without elongated internodes, these evenly spaced and separated from each other by 1 node; culm leaves herbaceous, not leathery, with a petiole between the blade and sheath, tardily deciduous; inflorescence open, racemose or paniculiform; spikelets many-flowered ..... ***Aulonemia***

6. Branches of the branch complement slender, all equal or subequal 7

   Branches of the branch complement of two sizes, a dominant larger branch and subsidiary ones, several times smaller 11

7. Branches arising at different and symmetrical levels, in a fan-shaped arrangement and leaving a triangular, unsegmented space between them; culms normally hollow, thin- to thick-walled 8

   Branches arising all at the same level in a more or less horizontal line 9

8. Culm leaf petiolate; base of blade much narrower than upper edge of the sheath; blade reflexed, caducous; spikelets usually 1- or 2-flowered, shortly pedicellate and secund along the unbranched axis; fruit an achene ..... ***Merostachys***

   Culm leaf without a petiole, falling entire; blade erect, appressed, sessile, at the base as wide as the upper edge of the sheath, the edges of both in a continuous line; spikelets many-flowered, solitary and sessile, alternate along the rachis; fruit a caryopsis ..... ***Rhipidocladum***

9. Plants characteristic of the vegetation above treeline at very high altitudes in the tropics known as "páramo"; rather small, erect bamboos with stiff culms, very short internodes and very thick leaves; inflorescences contracted, dense, usually narrow; spikelets with 1 fertile floret and 4 transitional glumes (Costa Rica to northern Peru) ..... ***Swallenochloa***

   Plants of low to high elevations but never of "páramo"; habit of plants otherwise; inflorescences usually loose, open; transitional glumes 2 10

10. Midculm branch complement of 3 subequal axes with a common prominent or rounded, tapered base extended downward; culms very thick-walled with a small lumen; inflorescence paniculiform with numerous spikelets, lacking subtending bracts; transitional glumes not widely separated from the first anthecium (Mexico to Honduras) ..... ***Otatea***

    Midculm branch complement usually of 5 branches without a common rounded base; culms hollow or solid; inflorescence racemose, consisting of 1 to few spikelets, usually subtended by a large bract; transitional glumes widely separated from the first anthecium (central and southern Brazil) ..... ***Apoclada***

11. Plants with spines or thorns; culms hollow, sometimes robust; culm leaf deciduous, without a petiole; blade erect, sessile, more or less triangular; inflorescence unrestricted, of un-

limited branching; pseudospikelets many-flowered; stamens 6; stigmas typically 3 ..... ***Bambusa*** subg. ***Guadua***

Plants without spines 12

12. Culms solid 13

Culms hollow, with thin walls or, if the walls thick, with a small central lumen 14

13. Culms in cross section with air canals in a ring near the epidermis; young stages of bud complement with 3 subequal buds; branches developing intravaginally, i.e., the branches growing upward emerging from the summit of the sheath; culm leaf-blade reflexed, caducous; inflorescence unrestricted, of unlimited branching; pseudospikelets 1-flowered; transitional glumes 0; stamens 3; stigmas 2 ..... ***Atractantha***

Culms in cross section without manifest air canals; young stages of bud complement with more than 3, usually several buds, the central one several times larger than the lateral; each bud within a separate prophyllum; branches developing extravaginally, i.e., the branches emerging through the base of the sheath; culm leaf-blade erect, persistent; inflorescence restricted, single, of limited branching; transitional glumes 4; spikelets with 1 fertile floret and 4 transitional glumes ..... ***Chusquea***

14. Plants with a midculm branch complement of 3 subequal branches, the central one slightly dominant; culm leaves and foliage leaves with dense, long oral setae; inflorescence condensed, capitate; spikelets 1- or 2-flowered; transitional glumes 2 (state of Rio de Janeiro to Bahia, eastern Brazil) ..... ***Athroostachys***

Plants with a midculm branch complement of more than 3 branches, the central one very much larger and dominant over the secondary ones 15

15. Nodal region delimited by 2 ridges, the upper one more prominent than the lower, forming a narrow crest on the opposite side of the branch complement; nodes with a girdle; secondary branches crowded at the base and sides of the main branch; blade of culm leaf petiolate, reflexed; inflorescence loose, open, racemiform or paniculiform; spikelets many-flowered (southern and eastern Brazil) ..... ***Colanthelia***

Nodal region without a prominent crest and without a girdle; branch complement with many secondary branches verticillate at the base of the central, dominant axis; inflorescence otherwise 16

16. Blade of culm leaf sessile, erect, without a petiole, the base as wide as the upper edge of the sheath; oral setae short; plants climbing or hanging from trees, usually with thin culms and a very small lumen, sometimes hollow but the walls then thick; inflorescence restricted, of limited branching, spicate-racemose; spikelets sessile, many-flowered; transitional glumes 2 or 3; stamens 3; stigmas 2 ..... ***Arthrostylidium***

Blade of culm leaf petiolate, strongly reflexed, several times narrower than the top of the sheath; oral setae exceptionally long and stiff; plants cespitose, the culms erect below and arching over vegetation, the larger ones with very thin walls; inflorescence unrestricted, of unlimited branching; pseudospikelets 1-flowered; transitional glumes 0; stamens 6; stigmas 2 ..... ***Elytrostachys***

Conspectus of the Grass Subfamily Bambusoideae in the Western Hemisphere

Subfamily Bambusoideae Nees, 1835

Tribe Anomochloeae: *Anomochloa*
Tribe Arthrostylidieae: *Arthrostylidium, Rhipidocladum*
Tribe Arundinarieae: *Arundinaria*
Tribe Bambuseae: *Bambusa* subg. *Guadua*
Tribe Chusqueeae: *Chusquea, Neurolepis, Swallenochloa*
Tribe Olyreae: *Cryptochloa, Diandrolyra, Ekmanochloa, Froesiochloa, Lithachne, Maclurolyra, Mniochloa, Olyra, Piresia, Raddia, Raddiella, Rehia, Reitzia, Strephium*
Tribe Parianeae: *Eremitis, Pariana*
Tribe Phareae: *Pharus*
Tribe Streptochaeteae: *Streptochaeta*
Tribe Streptogyneae: *Streptogyna*

Genera Not Yet Assigned to Tribes

Apoclada
Athroostachys
Atractantha
Aulonemia
Colanthelia
Elytrostachys
Glaziophyton
Merostachys
Myriocladus
Otatea

Tribes of American Herbaceous Bamboos

Tribe ANOMOCHLOEAE C. E. Hubbard (in Hutchinson, 1934:219).—This is a monotypic tribe based on the genus *Anomochloa,* which was described in 1851 by Alphonse Brongniart, the director of the Muséum d'Histoire Naturelle in Paris,

on the basis of plants cultivated in the Jardin des Plantes. The plants had been grown from seeds sent to France in the early 1840s by M. Pinel, a Frenchman in Brazil. The bizarre grass, which looks more like a member of the Maranthaceae than Poaceae (hence its specific name, *A. marantoidea*), was cultivated in the great European conservatories during the 1850s. By the early part of the following decade it had disappeared from cultivation and remained unknown from the wild until 1976, when the senior author discovered a colony of plants growing in an undisturbed, densely shaded forest in Bahia, Brazil.

TRIBE OLYREAE KUNTH (1815:75).—The Olyreae is one of the oldest recognized tribes of grasses and is the largest of the herbaceous bambusoids, with 14 described genera. The tribe is endemic to tropical America, except for one species, *Olyra latifolia* L., that occurs also in tropical Africa and Madagascar, where it is apparently introduced. *Olyra,* with about 22 species, is widespread and extends from Mexico and the West Indies to northern Argentina. Some genera are quite restricted, such as *Ekmanochloa* and *Mniochloa,* found only in Cuba, and *Maclurolyra,* known only from Panama. While most species grow in shaded forests, their habitats are diverse. Species of *Raddia,* a genus of eastern Brazil, often occur in scrub forests associated with bromeliads and cacti and experience long periods of dryness. On the other hand, *Froesiochloa* inhabits the continuously wet rain forests of French Guiana and the neighboring states of Amapá and Pará, Brazil.

TRIBE PARIANEAE (HACKEL) HUBBARD (in Hutchinson, 1934:219-220).—Hackel (1887:88) had recognized the distinctiveness of *Pariana* and established a subtribe Parianeae for it, but he included this in a distantly related group, the Hordeae.

This is an American tribe of two described genera, *Pariana* and *Eremitis.* The larger of the two is *Pariana* with about 30 species in tropical lowland rain forest, primarily of the Amazonian basin, but extending north to Costa Rica and south to Peru, Bolivia, and Ecuador, the distribution following the natural outline of the basin. *Pariana,* like *Hevea,* is a rather good indicator plant of the Amazonian hylaea. The other genus, *Eremitis,* has been known from the single described species, *E. parviflora,* from Bahia. In recent years we have found a number of further species of this genus, all from rain forests in Bahia and northern Espírito Santo.

TRIBE PHAREAE STAPF (in Thiselton-Dyer, 1898:319).—When Stapf established the tribe Phareae in *Flora Capensis,* he included in it only *Olyra,* since that genus occurs in South Africa and *Pharus* does not. That he considered *Pharus* to be a member of the tribe, although obvious from the name, is confirmed by Brandis (1907:87), who states that Stapf "has kindly informed me that three other genera [besides *Olyra*] . . . in his opinion belong to the same tribe." From the list following that statement in Brandis, the three genera are *Diandrolyra, Leptaspis,* and *Pharus.*

The tribe contains two genera. *Pharus* embraces about eight species that inhabit shaded tropical forests of the New World from central Mexico (San Luís Potosí) and the West Indies to Argentina (as far south as Corrientes and Tucumán). The other genus, *Leptaspis,* was originally described by Robert Brown on the basis of a species from Australia. There are about six species in the genus, one occurring in tropical Africa and the others in southern India and Ceylon, Southeast Asia, Indonesia, Australia, and the Philippines.

TRIBE STREPTOCHAETEAE NEES (in Lindley, 1836:378).—Nees (1835) regarded *Streptochaeta* as forming one of the three divisions of his bambusoid group. In his monograph he did not give a name to this division, which included only the genus *Streptochaeta.* The formal name Streptochaeteae appeared for the first time in Lindley (1836:378) in a list of grass genera prepared by Nees and dated 12 December 1835.

This is a monotypic American tribe consisting of *Streptochaeta,* the first herbaceous genus to be associated with the bamboos by Nees (1835) and the subject of various morphological studies (Čelakovský, 1889; Schuster, 1909; Arber, 1929). Of the two described species one, *S. spicata,* is widespread, ranging from southern Mexico through Central America, Trinidad, and in South America as far south as Misiones, Argentina.

The more restricted species is *S. sodiroana,* which inhabits forests from Belize (British Honduras) through Costa Rica and Panama, into the lowlands of Ecuador. A third, undescribed species has been found in a single locality in Espírito Santo, eastern Brazil.

All species occur in shaded tropical forests, usually on hilly terrain.

Tribe STREPTOGYNEAE C. E. Hubbard ex Calderón & Soderstrom

Gramina perennia; foliorum ligula externa evoluta; racemi erecti, elongati, lineares, rigidi, secundi; spiculae subteretes, multiflorae; lemmata fertilia convoluta et maturitate teretia, indurata; lodiculae 3, lanceolato-acutae; stamina 2; stylus singularis, longissimus; stigmata 2 vel 3, longissima, persistentia, demum spiraliter torta et firma; caryopsis linearis; hilum angustissime lineare, caryopsi aequilongum; embryo ca. 1/10 partem caryopseos aequans.

Pilger (1954:311) placed *Streptogyna* in a new subtribe of the Festuceae but did not give a Latin description. Hubbard (1956:1) elevated the subtribe to tribe Streptogyneae but did not add a Latin description, which we are herein doing in order to validate the name.

Streptogyna is a monotypic genus with two species, one (*S. americana* C. E. Hubbard) occurring in the New World and the other (*S. crinita* P. de Beauv.) in the Old World. The American species inhabits primary forests, where it forms rare patches and ranges from southern Mexico (Chiapas) through Central America to Trinidad, northern South America, and eastern Brazil (Bahia to northern Espírito Santo). The Old World species is found in forests in tropical West Africa, from Congo to Sudan, and again in southern India and Ceylon.

Tribes of American Bamboos

Tribe ARTHROSTYLIDIEAE (Munro) E.-G. Camus (1913:16). – Munro (1868:13) first used the name Arthrostylidiae for a subsection of the section Triglossae and included *Arthrostylidium* and a couple of other genera. E.-G. Camus, in 1913, elevated this subsection to the rank of tribe.

The tribe includes at least *Arthrostylidium* and *Rhipidocladum,* a genus recently segregated from it by McClure (1973).

Tribe ARUNDINARIEAE Nees (1835:466).—Nees von Esenbeck established the Arundinariae as one of his three major groups of bamboos and included in it *Arundinaria* and three other genera.

In our present limited knowledge of the tribe, the only genus of the Western Hemisphere is *Arundinaria,* restricting the tribe therefore to North America.

Tribe BAMBUSEAE Kunth (1815:75).—This was one of the original tribes of Kunth, in which he included all of the bamboo genera known to him.

In the New World the tribe includes only the species that belong to the subgenus *Guadua* of *Bambusa.*

Tribe CHUSQUEEAE (Munro) E.-G. Camus (1913:16). – Munro (1868:13) named Chusqueeae as one of his subsections of the section Triglossae and included in it the genera *Chusquea* and *Neurolepis* (as *Platonia*). E.-G. Camus elevated this subsection to the rank of tribe in 1913.

As presently understood, the tribe is endemic to the New World and contains the genera *Chusquea, Neurolepis,* and *Swallenochloa.* It is the most widely distributed tribe of Bambusoideae in the New World.

Genera of American Bambusoideae

Anomochloa Brongniart, 1851:368–370

Type-species: *A. marantoidea* Brongniart, 1851: 368-372, 1 plate.

Type-locality: Bahia, Brazil.

Comments: Same as those on tribe.

Apoclada McClure, in McClure & Smith, 1967:57

Type-species: *A. simplex* McClure & L. B. Smith, 1967:59–60.

Type-locality: Santa Catarina (Campos Novos), Brazil.

Comments: Four described species from southern Brazil, two of which are known from the cerrados of Mato Grosso, Goiás, and Minas Gerais, and two from mountainous regions of Santa Catarina.

Arthrostylidium Ruprecht, 1839:27

Type-species: *A. cubense* Ruprecht, 1839:28. Of the species enumerated by Ruprecht in his original description of the genus, Hitchcock (1927b:307) designated the above as the type of the genus.

Type-locality: Province of La Habana (Ramón de la Sagra), Cuba.

Comments: A widespread genus of about 20 species of clambering or climbing bamboos that range from the Caribbean Islands and Mexico to Venezuela and northern Brazil.

Arundinaria Michaux, 1803, I:73

TYPE-SPECIES: *A. macrosperma* Michaux = *A. gigantea* (Walter) Muhlenberg, 1813:14, based on *Arundo gigantea* Walter, 1788:81.

TYPE-LOCALITY: Eastern United States (probably South Carolina).

COMMENTS: A large genus of bamboos of temperate and cold regions of the Northern Hemisphere. Only one species, *A. gigantea* (Walter) Muhlenberg, is represented in the New World, where it grows in marshes and wet sandy banks of streams and rivers in eastern and southern United States.

Athroostachys Bentham, in Bentham & Hooker, 1883:1208

TYPE-SPECIES: *A. capitata* (Hooker) Bentham, based on *Merostachys? capitata* Hooker, 1840, plates 273–274.

TYPE-LOCALITY: Rio de Janeiro, Brazil.

COMMENTS: A monotypic genus, the single clambering species occurring in forests of the Serra do Mar of eastern Brazil, from Bahia south to Rio de Janeiro.

Atractantha McClure, 1973:42–48

TYPE-SPECIES: *A. radiata* McClure, 1973:50–53.

TYPE-LOCALITY: Bahia, Brazil.

COMMENTS: A genus of 9 or 10 species of climbing bamboos of humid tropical forests and low-tree coastal forests on sandy soils of Bahia in eastern Brazil, one species extending into northern Espírito Santo.

Aulonemia Goudot, 1846:75

TYPE-SPECIES: *A. queko* Goudot, 1846:76.

TYPE-LOCALITY: Quindío, Colombia.

COMMENTS: A genus of over 20 species, many occurring in high-altitude forests from Mexico and Central America through the Andes to Bolivia and Peru, eastward to the Guianas, and southward to the Serra do Mar of eastern Brazil.

Bambusa Schreber, 1789:236, nom. cons. subgenus *Guadua* (Kunth) Nees, 1835:465, based on *Guadua* Kunth, 1822a:150–151

TYPE-SPECIES OF THE SUBGENUS: *Guadua angustifolia* Kunth, 1822b:253, based on *Bambusa guadua* Humboldt & Bonpland, 1808:63, pl. 20 (for an explanation of this lectotype and synonymy, see McClure, 1957:203).

TYPE-LOCALITY: Probably Quindío, Colombia.

COMMENTS: This is a large genus with representatives in the tropics of Asia and America. All of the New World species, of which there are about 30, belong to the subgenus *Guadua*. These are erect and usually robust, clump-forming bamboos that grow along rivers, mixed with tall trees in dense, humid forests, or occasionally in drier areas, where the plants occupy locally wet and more protected sites.

Chusquea Kunth, 1822a:151

TYPE-SPECIES: *C. scandens* Kunth, 1822b:254, based on *Nastus chusque* H.B.K., 1816:201.

TYPE-LOCALITY: Bogotá, Colombia.

COMMENTS: The largest genus of American bamboos, with over 90 species that occur in every country from Mexico to Chile and Argentina and on many of the islands of the Caribbean. Some species reach the southernmost latitude of any Bambusoideae in the continent in the Andes, between Argentina and Chile at ca. 47° S latitude. The majority are typical of cool forests at high elevations, but a few occur in forests on slopes at low elevations of eastern Brazil.

Colanthelia McClure & E. W. Smith, in McClure, 1973:77–79

TYPE-SPECIES: *C. cingulata* (McClure & L. B. Smith) McClure, based on *Aulonemia cingulata* McClure & L. B. Smith, 1967:50.

TYPE-LOCALITY: Santa Catarina (Sombrio, Garapuvu), Brazil.

COMMENTS: Seven species described from forests at low to medium altitudes of southeastern Brazil northwest to Minas Gerais.

Cryptochloa Swallen, in Woodson & Schery, 1942: 317–318

TYPE-SPECIES: *C. variana* Swallen, in Woodson & Schery, 1942:318–320, 1 figure.

TYPE-LOCALITY: Coclé (Valle de Antón), Panama.

COMMENTS: About 15 species of shaded, mesophytic forests, extending from southern Mexico to the Pacific lowlands of northern South America, through Amazonia, and to eastern Brazil.

Diandrolyra Stapf, 1906:204

TYPE-SPECIES: *D. bicolor* Stapf, 1906:204–205.

TYPE-LOCALITY: "Native country unknown" (raised at Kew from fruits communicated by Messrs. Sander & Son).

COMMENTS: About 6 species of humid rain forests of southeastern Brazil, from Bahia to São Paulo.

Ekmanochloa Hitchcock, 1936:374–375

TYPE-SPECIES: *E. subaphylla* Hitchcock, 1936: 375–377, fig. 343.

TYPE-LOCALITY: Province of Oriente (Sierra de Nipe), Cuba.

COMMENTS: Two species known only from the province of Oriente, Cuba, on limestone hills and pinelands.

Elytrostachys McClure, 1942:173

TYPE-SPECIES: *E. typica* McClure, 1942:174–175, fig. 4.

TYPE-LOCALITY: Distrito Federal, Venezuela.

COMMENTS: Two species of wet lowland and midaltitude forests, recorded from Honduras to Venezuela.

Eremitis Doell, in C.F.P. von Martius, 1877:338

TYPE-SPECIES: *E. parviflora* (Trinius) Calderón & Soderstrom, based on *Pariana parviflora* Trinius, 1834:17. Doell (in Martius 1877:338–339, pl. 48) described the species as *Eremitis monothalamia,* but this name is illegitimate since Trinius' earlier diagnosis constitutes valid publication. Presumably Trinius had examined the same specimen—Riedel 1591—in the Leningrad herbarium as had Doell, although he does not cite it as Doell did.

TYPE-LOCALITY: Bahia (Castelnovo [Castelo Novo]), Brazil.

COMMENTS: About 7 species known only from Bahia and northern Espírito Santo in eastern Brazil, inhabiting forests and forest margins, sometimes in disturbed places.

Froesiochloa G. A. Black, 1950:29–30

TYPE-SPECIES: *F. boutelouoides* G. A. Black, 1950:30–31, pl. (estampa) 1.

TYPE-LOCALITY: Territory of Amapá (Igarapé Nataia, a tributary of the rio Oiapoque), Brazil.

COMMENTS: Two or 3 species from wet, densely shaded primary forests of French Guiana and northern Pará and Amapá in Brazil.

Glaziophyton Franchet, 1889:277

TYPE-SPECIES: *G. mirabile* Franchet, 1889:277-278, fig. A.

TYPE-LOCALITY: Vicinity of Rio de Janeiro, Brazil.

COMMENTS: A monotypic genus known only from the mountaintops of the Serra dos Orgãos near Rio de Janeiro.

Lithachne Palisot de Beauvois, 1812:135

TYPE-SPECIES: *L. pauciflora* (Swartz) Palisot de Beauvois, 1812:135, pl. 24: fig. 11, based on *Olyra pauciflora* Swartz, 1788:21.

TYPE-LOCALITY: Jamaica.

COMMENTS: Four species of which one is widespread, ranging from Mexico (San Luís Potosí) and the West Indies to northern Argentina. Of the others, one is endemic to Cuba, one to Honduras, and one to eastern Brazil near the boundary of the states of Rio de Janeiro and Minas Gerais.

Maclurolyra Calderón & Soderstrom, 1973:6–12

TYPE-SPECIES: *M. tecta* Calderón & Soderstrom, 1973:6–12, figs. 4–7.

TYPE-LOCALITY: Province of Colón (Santa Rita), Panama.

COMMENTS: One species known only from rain forests of Panama.

Merostachys Sprengel, 1825:132

TYPE-SPECIES: *M. speciosa* Sprengel, 1825:132.

TYPE-LOCALITY: None given for type, but Brazil according to Kunth, 1829:139.

COMMENTS: A genus of 40 or more forest species, especially common in Bahia, Brazil, but ranging as far north as Guatemala and as far south as northeastern Argentina.

Mniochloa Chase, 1908:185–186

TYPE-SPECIES: *M. pulchella* (Grisebach) Chase, 1908:186, pl. 4, based on *Digitaria pulchella* Grisebach, 1866:231.

TYPE-LOCALITY: El Yunque de Baracoa, Cuba.

COMMENTS: Two species endemic to Cuba, one on shady limestone rocks in the eastern part of the country, and the other on shady banks and ravines in the western part.

Myriocladus Swallen, in Steyermark, 1951:34

TYPE-SPECIES: *M. virgatus* Swallen, 1951:34–35, fig. 4.

TYPE-LOCALITY: Cerro Duida (Territorio Federal Amazonas), Venezuela.

COMMENTS: About 20 described species endemic to the sandstone tabletop mountains of Venezuela in mesophytic habitats at elevations of 1000 to 2500 meters.

Neurolepis Meisner, 1843, vol. 1:426, vol. 2:325

TYPE-SPECIES: *N. elata* (Kunth) Pilger, in Engler & Prantl, 1906:21.

TYPE-LOCALITY: Loja, Quito, Ecuador.

COMMENTS: About 10 species in the Andes of northern South America at high elevations

(2900–4500 m), from Venezuela and Colombia to Peru, some species occurring in the paramos.

Olyra L., 1759:1261

TYPE-SPECIES: *O. latifolia* L., 1759:1261.

TYPE-LOCALITY: Jamaica.

COMMENTS: A genus of about 22 species widespread throughout tropical and subtropical America, from Mexico and the West Indies to northern Argentina, in shaded forests. One species, *O. latifolia* L., which is especially weedy and polymorphic and inhabits forest margins and disturbed sites, has spread from the New World to Africa and Madagascar.

Otatea (McClure & Smith) Calderón & Soderstrom, based on *Yushania* K. H. Keng, 1957:357, subgenus *Otatea* McClure & E. W. Smith, in McClure, 1973:116

TYPE-SPECIES: *Otatea aztecorum* (McClure & Smith) Calderón & Soderstrom, based on *Yushania aztecorum* McClure & E. W. Smith, in McClure, 1973:116–119, fig. 47.

TYPE-LOCALITY: Rosario (state of Sinaloa), Mexico.

COMMENTS: Two described species of erect bamboos that inhabit seasonally dry chaparral, edges of canyon walls, and limestone cliffs in central and southern Mexico, locally to Nicaragua and El Salvador. McClure originally established *Otatea* as a distinct genus and prepared the text and illustrations of it for inclusion in his revision of the New World genera of bamboos. According to his dated and unpublished manuscripts and notes, which we have seen, it was less than two months before his death (15 April 1970) that he decided, with some hesitation, to make *Otatea* a subgenus of the Old World bamboo, *Yushania*. With new perspectives on generic concepts of the Bambusoideae of the Western Hemisphere, we feel that McClure's original concept of *Otatea* as a genus was correct and are so recognizing it in this treatment. In addition to the type-species, a second was listed by McClure, based on *Arundinaria acuminata* Munro (1868:25), which now becomes *Otatea acuminata* (Munro) Calderón & Soderstrom.

Pariana Fusée-Aublet, 1775, vol. 2:876–877

[Regarding the name Fusée-Aublet, see Bernardi, 1976.]

TYPE-SPECIES: *P. campestris* Fusée-Aublet, 1775, vol. 2:877–879, vol. 4, pl. 337.

TYPE-LOCALITY: Loyola, French Guiana.

COMMENTS: About 30 species of the rain forests of northern South America, especially abundant in the Amazon basin, whose southern and eastern boundaries mark the limits of the genus. Only a couple of species reach Central America, where they are of rare occurrence in Panama and Costa Rica.

Pharus P. Browne, 1756:344, pl. 38: fig. 3

TYPE-SPECIES: *P. latifolius* L., 1759:1269. [In the second edition (1789) of P. Browne, the plates are re-engraved and reversed and carry the Linnean binomials, according to Stafleu & Cowan (1976:372).]

TYPE-LOCALITY: Jamaica.

COMMENTS: A genus of about 8 species of densely shaded tropical and subtropical forests, from southern Mexico and the West Indies to northern Argentina.

Piresia Swallen, 1964:152

TYPE-SPECIES: *P. goeldii* Swallen, 1964:153.

TYPE-LOCALITY: Pará (Maguary-assú, Bragança Railroad), Brazil.

COMMENTS: Two described species from the rain forest of the Amazonian basin, reaching north to Surinam, Venezuela, and Trinidad and west to Peru. Several undescribed species, endemic to rain forests of Bahia and Pernambuco in eastern Brazil, exhibit a disjunct distribution for the genus.

Raddia A. Bertoloni, 1819:410–411

TYPE-SPECIES: *R. brasiliensis* A. Bertoloni, 1819: 411.

TYPE-LOCALITY: Province of Rio de Janeiro, Brazil.

COMMENTS: About 9 species found only in eastern Brazil, from Pernambuco to Rio de Janeiro, in wet and seasonally dry forests.

Raddiella Swallen, in Maguire et al., 1948:89

TYPE-SPECIES: *R. esenbeckii* (Steudel) Calderón & Soderstrom, based on *Panicum esenbeckii* Steudel, 1854:90. [The type-species, cited by Swallen as *R. nana* (Doell) Swallen, nom. illeg., was based on *Olyra nana* Doell (in Martius, 1877:329), based in turn on the same specimen as *P. esenbeckii,* which provides the earlier and, therefore, valid epithet.]

TYPE-LOCALITY: Province of Rio Negro (Ega), Brazil.

COMMENTS: Eight to 10 described species that occur in wet depressions of savannas in the protection of vegetation, on wet rocky slopes, and on cliffs near waterfalls, from Trinidad and Panama to Mato Grosso, Brazil. The plants are among the smallest and most delicate of the subfamily. So diminutive are some of the species that grow among mosses on wet cliff faces that they may easily be confused with other grasses of dwarf stature, as was the case with *R. molliculma* (Swallen) Calderón & Soderstrom, originally described as *Panicum molliculmum* Swallen, in R. E. Schultes, 1953: 57–58.

Rehia Fijten, 1975:416

[As pointed out by Fijten (1975:416), *Bulbulus* is not admissible under Article 20 of the *ICBN*, as it is a technical term, nor under Article 64, as it is an orthographic variant and thus later homonym of *Bulbilis* Rafinesque, 1819.]

TYPE-SPECIES: *R. nervata* (Swallen) Fijten, based on *Bulbulus nervatus* Swallen, 1964:154.

TYPE-LOCALITY: Maranhão (Caxias to Barra do Corda), Brazil.

COMMENTS: A monotypic genus known only from primary rain forests of the eastern Amazon basin and the Guianas.

Reitzia Swallen, 1956:7–8

TYPE-SPECIES: R. smithii Swallen, 1956:8–9, 1 plate.

TYPE-LOCALITY: Santa Catarina (Azambuja), Brazil.

COMMENTS: One species from subtropical forests of Santa Catarina and São Paulo in southern Brazil.

Rhipidocladum McClure, 1973:101–104

TYPE-SPECIES: *R. harmonicum* (Parodi) McClure, 1973:104, fig. 42, based on *Arthrostylidium harmonicum* Parodi, 1944:478, fig. 1.

TYPE-LOCALITY: Alturas de Pintobamba, Peru.

COMMENTS: About 10 species in forests at low to moderate elevations, from Mexico to Brazil and northwestern Argentina.

Strephium Schrader ex C.G.D. Nees von Esenbeck, 1829:298

TYPE-SPECIES: *S. distichophyllum* Schrader ex C.G.D. Nees von Esenbeck, 1829:298–299.

TYPE-LOCALITY: Bahia (Felisberto), Brazil.

COMMENTS: Four or 5 species of small, delicate, fernlike plants that occupy extremely wet spots along streams in dark forests, exhibiting a disjunct distribution between the rain forests of Bahia in eastern Brazil and the Guianas (including Amapá and northern Pará, Brazil), Trinidad, and Venezuela.

Streptochaeta Schrader ex C.G.D. Nees von Esenbeck, 1829:536–537

TYPE-SPECIES: *S. spicata* Schrader ex C.G.D. Nees von Esenbeck, 1829:537–538.

TYPE-LOCALITY: Bahia (Felisberto), Brazil.

COMMENTS: Same as those on tribe.

Streptogyna Palisot de Beauvois, 1812:80

TYPE-SPECIES: *S. crinita* Palisot de Beauvois, 1812:80, pl. 16: fig. 8 (Atlas).

TYPE-LOCALITY: Old World. The specimen that the author described has 2 stigmas. He mentioned other specimens he had seen from the New World that have 3 stigmas and, while he did not describe these as distinct, he mentioned a *S. guyanensis* in the index but not in the text. Since the Old World species has 2 stigmas and the New World species has 3 stigmas, the name *Streptogyna* applies to the Old World species.

COMMENTS: Same as those on tribe.

Swallenochloa McClure, 1973:106–112

TYPE-SPECIES: *S. subtessellata* (Hitchcock) McClure, 1973:108, fig. 44, based on *Chusquea subtessellata* Hitchcock, 1927a:81.

TYPE-LOCALITY: Cerro de la Muerte, Costa Rica.

COMMENTS: The genus contains about 9 species, which are mostly small, clump-forming bamboos with stiff, erect culms, characteristic of the vegetation above treeline in the biome known as paramo. One species occurs in Costa Rica and the others in Venezuela and Colombia to Peru.

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