Genera of Bamboos
Native to the New World
(Gramineae: Bambusoideae)

F. A. McClure
(EDITED BY THOMAS R. SODERSTROM)
ABSTRACT

McClure, F. A. (edited by Thomas R. Soderstrom). Genera of Bamboos Native to the New World (Gramineae: Bambusoideae). Smithsonian Contributions to Botany, number 9, 148 pages, 49 figures, 1973.—Seventeen genera of bamboos native to the New World are classified, compared, and illustrated, including four new genera and four new species. The introduction of several taxonomic characters based on hitherto neglected morphological features, both vegetative and reproductive, is undertaken with the objective of improving traditional perspectives. Two reforms are urged as essential to the elevation of the level of refinement at which future taxonomic treatments of bamboos may be executed. These are (1) the general adoption of improved collecting methods correlated with more extensive and sustained field observations, and (2) the fostering, through interdisciplinary collaboration, of progressive development and integration of diversified studies of documented materials drawn from a common source for each individual taxon.
Preface

On 15 April 1970, Dr. Floyd A. McClure passed away in his bamboo garden while removing a plant to give to a young friend. McClure had devoted his entire career to the bamboos, which he described as a "symbol of uprightness, chivalry, and devotion." His first book, *The Bamboos: A Fresh Perspective*, and the present work represent as rich a heritage as any man could hope to leave to the botanical world. Of all his numerous publications, these two books represent the synthesis of a lifetime study by one of the most productive minds in the botanical sciences, a mind which, to our good fortune, had matured to its full potential.

McClure, not only as a botanist but as a man, inspired and encouraged all those with whom he came in contact. My first acquaintance with him was here at the Smithsonian Institution in August 1961, since which time I had cherished his friendship and advice. In 1967, he persuaded me to extend my interest in the anatomy of the monocotyledons to include the vascular architecture of the bamboo culm. Utilizing the optical shuttle system and the data analyzer projector, this study confirmed the growing consensus that the structure of the bamboo culm, like that of maize, does not represent a typical monocotyledon stem as had been previously accepted.

A little over a year before McClure's death, Dr. Thomas R. Soderstrom, Smithsonian agrostologist, joined him in his bamboo studies; thus we are assured that McClure's life work will be carried on. Daily sessions between the two continued to the very day of his death. Soderstrom, following McClure's wishes, has undertaken the difficult and demanding task of seeing to fruition this present and final work of a great man and botanist.

McClure's original intention had been to revise the bamboos for *Die Natürlichen Pflanzenfamilien*; but when he realized that this would be too large a task, he decided to publish first the genera of the New World as represented in this book. Although the bulk of the manuscript was in near-readiness at the time of his death, significant portions of the work remained undone. It thus fell to Soderstrom to conduct an intensive program of organizing the material. Every effort was made to complete the book just as McClure would have, drawing upon his copious notes whenever possible to finish the uncompleted portions. Fortunately, Mrs. McClure, who had worked closely with her husband throughout his career and was completely knowledgable of the details of McClure's manuscript-preparation methods, was able to provide much needed help. Mr. Elmer Smith, a botanical illustrator at Harvard University, returned to the Smithsonian on two occasions for extended periods to complete all the figures. He had worked closely with McClure over the years, and the two had developed a personal rapport that transcended the usual scientist-artist relationship.

I want to congratulate Dr. Soderstrom for accepting the commitment to complete this monumental work, which, in its final form, I am sure would have pleased Dr. McClure. I also wish to stress that he has had to put aside his own research for extended periods to carry out this task.
I would also like to thank the National Science Foundation for its continued support of this work after Dr. McClure's death and Dr. Eric Holttum, who painstakingly reviewed the manuscript before submission to the Smithsonian Institution Press. Mr. H. K. Airy Shaw kindly reviewed the Latin descriptions, making a number of useful suggestions, and Dr. Alicia Lourteig compared parts of the text that appear in French with the original herbarium notes in Paris. Dr. Cleofé E. Calderón gave assistance and the benefit of her expertise in the final stages of manuscript preparation.

McClure was always concerned with the precise usage of words, and he developed over the years a glossary of bamboo terms which first appeared in his earlier book. Since publication of that glossary he modified some of the terms and wrote definitions for several new ones. Because of the practicality of having all terms appear in one reference, the decision was made to include in this volume the entire glossary, even though some of these terms are not used in connection with bamboos of the New World.

The archival materials and bamboo library of Dr. McClure are now incorporated into the Hitchcock-Chase Grass library in the Department of Botany, Smithsonian Institution. These materials will continue to be curated, updated, and utilized. Without the extensive holdings of bamboo specimens, literature, card files, and cross-references that Dr. McClure had accumulated over a lifetime, a book of this magnitude could never have been completed.

Edward S. Ayensu
Chairman

Department of Botany
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Washington, D.C.
21 September 1971
Foreword

My first acquaintance with Dr. McClure came through his articles on plants cultivated at Canton, which I read in Singapore, where I was also making myself acquainted with plants grown by Chinese people. We first met in Java in 1929, about which time I began to try to take some interest in bamboos, provoked by the fact that nearly all the bamboo plants in the Botanic Gardens at Singapore had lost their labels, and the consideration that bamboos were plants of importance which should not be neglected. This led me to examine native Malayan bamboos when I had the opportunity of botanical travel. In this rather casual study I was helped and stimulated by McClure's successive papers on his Chinese bamboos, from which I learned much. Our paths met again after World War II, in Singapore, London, and Washington, where I had the privilege of his hospitality on two occasions. I have enjoyed reading the text of this book, which brings many happy memories into my conscious thought, and am honored to be asked to write this Foreword, in which I wish to try to assess the significance of this, his last contribution to recorded knowledge of the plants to which he devoted so much of his life.

Most early descriptions of bamboos were based on flowering specimens by herbarium botanists who had never seen the living plants. Inevitably such descriptions omitted vegetative characters without which field botanists and cultivators could not name their plants, many of which flower only at long intervals. Inevitably, also, the herbarium botanists, familiar with the plants of north temperate regions, compared bamboo spikelets and flowers with those of the grasses with which they were familiar, and tried to fit bamboos into the grass pattern, not realizing that the reverse process leads to a better understanding of the whole.

Effective vegetative description, and its correlation with floral description, of the great bamboos of Southeast Asia was begun by Kurz, and was continued by Gamble in his comprehensive monograph of Indian bamboos (1896). Gamble, however, did not extend his thinking on the comparative morphology of the inflorescence beyond that of Munro and Bentham, and little further critical thought had been given to the subject when in 1924 McClure began his studies of the bamboos of southern China (related to those of India but in many cases distinct). Between 1924 and 1940 he established a plantation of six hundred bamboo plants, collected during numerous travels, so that he could watch their growth and flowering. In so doing he studied vegetative branching at culm nodes (which Japanese botanists had found important in describing their own bamboos) and also made detailed observations on the development of inflorescences. For the first time he correlated vegetative branching with that of the inflorescence, and established clearly a basic distinction between the two types of inflorescence, referred to in the present book as iterautant (indeterminate) and semelauant (determinate). Iterautant branching matches exactly the vegetative branching at culm nodes and its precise description involves a more careful observation of the sheathing organs at the bases of spikelet-like structures.
than had previously been undertaken. This is one of the keys to the under-
standing of bamboo classification. Japanese botanists also studied the branching
of bamboo rhizomes, a subject of great practical importance to growers; McClure
did the same for the bamboos of China, concerning which no such records had
been made.

Thus when McClure went to tropical America in 1942 he had acquired
an understanding of bamboos as living plants wider and more detailed than
that of any of his predecessors, and enriched by his own original thought. For
the first time he applied to American bamboos the same kind of comprehensive
observation and thought, and this has resulted in a synthesis, presented in this
book, of unique significance. He examined many native bamboos over a wide
range in the American tropics and sub-tropics, collecting specimens with all the
kind of detailed observation he had found to be necessary; he also examined
type-specimens and other material of all previously described species, attempting
to correlate specimens which often failed to show all the characters he believed
to be significant. He made a new bamboo garden, in which once more he could
study growing plants. The work is not completed; the imperfections of earlier-
collected specimens leave gaps in our knowledge. Although clear distinctions
between species in most genera remain to be established, the present work is a
firm foundation on which further work can be based, and an indispensible guide
to further thought and action. The excellent illustrations, designed to show
clearly a wealth of significant detail, are a very important complement to the text.

My own knowledge of bamboos as living plants is confined to the species
of Malaya and New Guinea, and some from India seen in cultivation. The
tropical American species dealt with in the present book are in the main very
different from those of the Malayan region, and prompt some thoughts, which
I hope may be of interest, though I have not an adequate knowledge of Japa-
nese bamboos. These are also important to the following statement concerning
the evolutionary significance of bamboos as members of the family Gramineae.

It seems to me possible that the development of woody culms, which is a
distinctive feature of bamboos, may have originated more than once in the
family; that is, the bamboos as we know them may not be monophyletic in this
respect. It seems likely that the Gramineae had developed a reduced and
specialized type of inflorescence before woody forms appeared (the very spec-
ialized woody nature of bamboos is unique and cannot be a relic of any
proto-monocotyledonous stock). The large bamboos of the genera Bambusa,
Dendrocalamus, and Gigantochloa (which I believe are closely allied, though
separated by Munro on fruit-characters for which he had little evidence, but
which were repeatedly copied by later authors), as well as Schizostachyum and
its allies, all have six stamens and a well-developed pericarp. They also all
have a caespitose habit with pachymorph rhizome-elements, and inflorescences
of the iterauctant type that matches exactly vegetative branching, with a
prophyllum at the base of every branch. Thus these bamboos, predominant in
Southeast Asia, in addition to the maximum development of woody habit, also
show a combination of primitive characters. Of this great group of “primitive”
 bamboos, only Bambusa migrated to the Americas from Asia, presumably at a
time when the land-bridge to North America from Asia experienced a mild
climate.

The other well-known genus shared by America and Asia is Arundinaria.
One may also postulate for it a similar migration (even as restricted by McClure)
since it is much more diversified in Asia than America. This genus has been
variously interpreted, both in America and Asia, by different authors. Japanese
botanists have recognized that some of their bamboos, originally included in
Arundinaria, differed in many ways, and have attempted to recognize new genera.
But the type-species of Arundinaria is North American, and so the species of
Asia must be judged by that type. In the present book McClure deals exhaust-
ively with A. gigantea, and indicates what he regards as the essential characters
of the genus, from which he excludes many American species formerly included
in it. Unfortunately he does not indicate which species of the Old World he
regards as congeneric with the American type. I believe that students of Japanese
bamboos would find the treatment of Arundinaria in the present work valuable
in a reassessment of their own species of the segregate genera.

Arundinaria has a semelauctant inflorescence in which the spikelets are
grass-like and the branches of the inflorescence lack prophylla at their bases.
In the Bambusa group of genera there is a prophyllum as first foliar organ on
every branch, leafy or flowering, right up to the prophylla called paleae which
enclose the true floral elements. In most grasses there are no prophylla (and no
bracts) at any branch of the inflorescence, but the paleae persist. There is, thus,
a gap between the prophylla of vegetative branches and the paleae, so that the
homology of vegetative prophylla and paleae was long unrecognized. The
semelauctant bamboos sometimes show intermediate stages, with prophylla
present at the base of inflorescence branches (Figures 3b, 19e). The presence
of such intermediate stages may be significant as indicating possible evolutionary
lines of transition from the Bambusa to the grass types of inflorescence. It seems
to me likely that the transition has occurred on several lines. The bamboos of
Japan might provide interesting evidence, if considered from this standpoint.
In any case, precise observation of bracts and prophylla in relation to flowering
branches of semelauctant bamboos may indicate significant diagnostic characters
for recognition of species.

Arundinaria has leptomorph rhizomes from which new culms arise as
axillary structures; that is, the growth of the rhizomes is monopodial. I have
produced evidence (Holttum, 1955) that sympodial branching of the stem pre-
dominates in all families of monocotyledons, and monopodial branching is
certainly the exception in Gramineae. The latter occurs in some genera of
Paniceae, but I believe it is rare in other divisions of the family. In some other
families (e.g., Palms) it has developed separately in distinct groups of genera,
and it may have done the same among woody Gramineae. Possibly therefore the
occurrence of leptomorph rhizomes in Arundinaria is less important as evidence
of relationship to other genera than some other characters.

In this book McClure describes a new species of bamboo which he includes
in the genus Yushania, previously known only from Taiwan. This looks like a
third migrant (or could both have evolved from a common northern ancestor
no longer extant?). Other genera of American bamboos, now more clearly dis-
tinguished than formerly, may be found to give indications of relationships
with Asia.

One group of species, however, appears to be quite exclusive to the New
World, and surely originated there, namely those here included in Chusquea and
its immediate allies Neurolepis and Swallenochloa. Munro (1868:13, 52) re-
marked on the resemblance between Chusquea and some panicoid grasses, and
also to the fact that in essentials of spikelet structure they are not far apart.
It is greatly to be regretted that McClure was not able to complete a survey of the bamboo genera of the Old World, of which he had such a wide and intimate knowledge. He accumulated, however, an immense amount of the reference material necessary for such a survey, which, together with his manuscript notes, is available as a basis for further study by his students. I hope such study will result in published works, so that more of the fruits of McClure's labors may become available to botanists, foresters, and others in Southeast Asia, and may be put to practical as well as scientific use. I believe that the peculiar and very remarkable properties of the bamboos of tropical Asia could find new uses in modern technology, but they have not yet received the attention they deserve. McClure's bamboo plantation at Canton could yet be of great service in providing more information about these plants.

A new study of bamboo anatomy, especially nodal anatomy, is certainly a key to understanding the branch patterns which McClure and others have shown to be distinctive characters. Plant anatomists have been too content to describe only internodal structure (which is, of course, important). Nodal anatomy is extremely complex, and doubtless difficult to understand, but on it depends the dynamics of growth of bamboos and of some other monocotyledons. Because there is not secondary growth of concentric woody tissue in bamboos, the primary structure of the node has to be far more precise than in dicotyledons, and intercalary growth at the base of each culm internode needs a far more complex organization. When this is better understood, respect for bamboos as highly specialized organisms may well be greatly enhanced. The question has also to be asked: How is the control of all this complexity organized?

R. E. HOLTUM

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November 1971
Acknowledgments

The laboratory studies and field work that serve as the basis for the following treatise cover a period dating back to 1943. In that year I initiated, under the auspices of the Smithsonian Institution, a project for the U. S. National Research Council: a survey of bamboo species of a special category occurring in Mexico, Central American countries, Colombia, Venezuela, and Brazil (McClure: 1944). Opportunities to continue the collection and field study of bamboos of the Western Hemisphere were afforded during my incumbency (1944–1954) as Field Service Consultant on Bamboo with the Office of Foreign Agricultural Relations of the U. S. Department of Agriculture. More recently, as Consultant on Tropical Forestry to the Maria Moors Cabot Foundation of Harvard University (1956–1959) I was given the opportunity to visit European herbaria to study types and critical specimens of Western Hemisphere bamboo genera, and to advance the organization of pertinent data from the literature and from personal experience. Since 1955, the Department of Botany of the Smithsonian Institution, as administrator of grants-in-aid from the U. S. National Science Foundation, has fostered the progress of my bamboo studies directed toward the revision of the descriptions of the bamboo genera of the world, for the second edition of Engler and Prantl’s *Die Natürlichen Pflanzenfamilien*.

Facilities for the study of the Gramineae (including the Bambusoideae) now available at the United States National Herbarium were greatly enriched by the fruits of the many mutually related activities pursued by Dr. Agnes Chase during the course of her long and distinguished career as agrostologist. Among these fruits are innumerable notes and photographs illuminating types and critical specimens of graminaceous plants that she investigated in the principal herbaria of Europe and America. In many cases these notes and photographs are accompanied by duplicate specimens or fragments from type-collections—specimens presented as tokens of appreciation for expert curatorial services (identifications, annotations, etc.) freely, but often at great personal sacrifice, bestowed upon taxonomically critical materials in extant (but in many cases neglected) classical collections. The acquisition of specimens representative of the grass (and bamboo) flora of the world was greatly augmented by a system of exchanges supported by long sets of duplicates by Dr. Chase on numerous wide-ranging field trips carried out in the United States and other New World countries. Fruitful discussions with Thomas R. Soderstrom, Associate Curator, Division of Grasses, and David B. Lellinger, Associate Curator, Division of Ferns, Department of Botany, Smithsonian Institution, are gratefully acknowledged.

The skills of several artists went into the preparation of the line drawings—some based on my own original sketches, others made specifically for the present work: Elmer W. Smith, Mrs. Gesina Berendina Threlkeld, Mrs. Martha Niepold, and Florence Mekeel (Mrs. H. J. Lambeth).

Essential to the fulfillment of the objectives of this study has been the opportunity to examine the types and critical specimens of the genera under consideration. In this connection, it is a pleasure to acknowledge the courtesies
extended by the responsible officials of the following botanical institutions: The Herbarium of the Field Museum of Natural History, Chicago; the Herbarium of the New York Botanical Garden; the Herbarium of the Arnold Arboretum, Cambridge; The Herbarium of the Museum National d'Histoire Naturelle, Paris; The Herbarium of the Royal Botanic Gardens, Kew; The Herbarium of the British Museum (Natural History), London; the Herbarium of the Botanische Museum, Berlin-Dahlem; The Herbarium of the University of Pisa; The Makino Herbarium, and the Herbarium of the Botanical Institute, Tokyo; and the United States National Herbarium (Smithsonian Institution), Washington, D. C.

F. A. McClure

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Washington, D. C.
1 March 1970

To Conrad Chapman, who from the beginning has manifested a sustained and sustaining interest in the objectives and the fruition of my bamboos studies.
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FRONTISPICE: A trumpeter from Otavalo, Ecuador, sounds the dinner call, using a bocina made from a single, 5-foot internode of a bamboo called, locally, Tunda. (See Aulonemia queko.)
Genera of Bamboos
Native to the New World
(Grainaeae: Bambusoideae)

F. A. McClure
(EDITED BY THOMAS R. SODERSTROM)

True knowledge can only be acquired piecemeal,
by the patient interrogation of nature.

Sir Edmund Whittaker

Introduction

It is now more than three quarters of a century since the preliminary publication of Hackel's treatment of the bamboo genera of the world, prepared as part of the first edition of Engler and Prantl's Die Natürlichen Pflanzenfamilien (1887). The fact that several supplements were published shortly after is eloquent of Hackel's feeling that his work on this group was incomplete and of an essentially tentative nature. It is sobering to reflect that, although the number of bamboo species known to science has more than doubled in the meantime, the nature of the material collected has changed but little. The problem of achieving an adequate perspective on the taxonomy of the group, however, has become immensely more complicated, rather than simplified, by much that has been done in this interval. Specimens collected continue to be fragmentary, field notes are still brief or lacking, and the published descriptions of entities have continued to omit reference to features of fundamental taxonomic importance, especially those relating to the nature of the branching habit of all axes of the plant. Published supplementary studies in the fields of anatomy and cytology have not, in general, improved the situation as they might have, had the workers in these fields collaborated more closely with the taxonomist.

The present treatment is neither monographic nor definitive in its intent or scope. It is offered as representing a preliminary step forward in the taxonomic conquest of the bamboos of the New World. The dominant objective of the studies on which this treatise is based has been to facilitate the recognition of the generic affiliation of each bamboo native to the Western Hemisphere that requires identification. To this end—and within the limits imposed by available materials—an effort has been made to bring into sharper focus the image (dependable features) and the apparent present boundaries of each genus. It has been possible to improve the concept and the circumscription of some genera by including generally neglected morphological features. The elimination

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of traditionally included features that do not hold good has improved the concept and the circumscription of some genera, and has suggested a revised taxonomic disposition of others. The diverse patterns of branching habit in the vegetative apparatus and in the inflorescence have been given particular attention, both here and in a broad survey published earlier (McClure, 1966b). The exploitation of the taxonomic potential of these patterns is limited to those entities in the available specimens of which this feature is represented.

The incompleteness and disparities (notably the incongruent representations of morphological and ontogenetic aspects of the plant) that characterize the available specimens, field notes, and descriptions of most recorded bamboo species exert serious restrictions upon the development of uniformly satisfactory circumscriptions of the genera. I have been able to improve and clarify the image of representative species of some of the genera through field studies. Available plants of the type-species and/or one or more representative species of fourteen genera of bamboos of the New World and the Old World, respectively, have been maintained under cultivation for a number of years for progressive collection and observation of their successive stages of development, on a comparative basis.

Owing to the incomplete and fragmentary representation of some genera in the existing herbarium material and the fact that living material of some of the genera has not been accessible to me, the drafting of generic descriptions that are uniform in their coverage of every detail is still an impossibility. In comparison with previous treatments, however, the coverage of taxonomically significant features has been greatly extended as far as gross morphology is concerned. Attention has thus been directed to structures and to dynamic aspects of the bamboo plant that have hitherto been largely or completely neglected. It is hoped that those who collect bamboo specimens for identification or for description and naming and those who address themselves to the description and classification of the bamboos will in the future find useful leads here, and that the taxonomic conquest of the bamboos will have received a perceptible impetus. Where feasible, the diversities are then given informal status as either subgenera or sections. However, it is possible that more comprehensive morphological studies, supplemented by correlated studies in other disciplines and deepened by the use of the electron scanning microscope of both vegetative and reproductive structures, may force the revision of the generic lines proposed here.

The proposed consolidation of currently recognized genera that apparently are not set off from each other by clearly disjunct patterns of morphological feature combinations is prompted by the desire to facilitate identifications to genus. Uncertainties often arise as a result of feature combinations that constitute intergradations between two or more such genera, especially where these intergradations have either been ignored or given separate generic rank. An effort has been made to eliminate these uncertainties by allowing the intergradations to fall within a single genus with an expanded circumscription. They then yoke together the recognizable extremes under one generic name. Where feasible, the diversities are then given informal status as either subgenera or sections. However, it is possible that more comprehensive morphological studies, supplemented by correlated studies in other disciplines and deepened by the use of the electron scanning microscope of both vegetative and reproductive structures, may force the revision of the generic lines proposed here.
It appears that some groups of closely related bamboos flout the intellectual concepts of morphological homogeneity and morphological disjunctions, at either the "species level" or the "genus level"—or both. Of course, the terms "genus level" and "species level" lack a sound semantic basis, since the component elements of both genera and species are, in fact, determined primarily on the basis of circumscription (fences) that reflect morphological similarities and disjunctions rather than levels of evolutionary advancement. As every perceptive taxonomist recognizes, the concepts "relatively advanced" and "relatively primitive" are properly focused upon the individual features or structures of an organism, rather than upon the organism as a whole or a group of organisms. Carlquist (1961:7) states the point very simply in these words: "One must remember that only characteristics, not plants, or species, are primitive or advanced." This is because features commonly evolve independently—as though possessing their own individual phylogeny—rather than simultaneously with other characters, as though linked with them, genotypically. Proposed phylogenetic arrangements of taxa, or groups of taxa, can be given meaning only by a projection of the relative incidence of supposedly "advanced" and supposedly "primitive" features in their component elements.

The temporal and morphological divergencies that, in most bamboos, isolate the vegetative state from the sexually reproductive state, combine to give rise to a physical isolation between the specimens, descriptions, and names that, in many cases, independently represent these two states of a given species. As a result of the practical difficulties involved in bringing adequate representation of the essential morphological features of the vegetative state of a bamboo into authentic association with the morphological features of its reproductive state, a dichotomy similar to that which has produced the mycological category "Fungi Imperfecti" has developed in the taxonomy of the bamboos. In comparison with the fungi, however, most bamboos confront both the collector and the taxonomist with formidable obstacles to the resolution of these difficulties. These obstacles are imposed by a very protracted vegetative state, and morphological gradations that appear in acropetal sequence within each component axis of the plant. These and other gradations appear also in temporal sequence among the component parts of the relatively massive body of the plant as it develops toward sexual maturity.

Another stumbling block has its origin in the radical changes in appearance and composition that often take place in the inflorescences during their development, especially in those genera where they are of the iterauctant (indeterminate) type (McClure, 1966b:93 et seq.). The generic affinities suggested by the morphological features of the vegetative apparatus of a given species may be, and often are, quite different from those suggested by the morphological features of the reproductive apparatus of the same species. Therefore, the full integration of the vegetative features with the reproductive features of each species is the only rational approach to the achievement of a realistic circumscription of the genera. This calls for drastic improvements in collecting methods and in taxonomic studies as well. The morphology and the ontogeny of the whole plant must eventually be assembled and brought under consideration. Until this has been accomplished the taxonomist cannot function effectively (or respectably) in collaboration with specialists in integrating the results of studies on paramorphological aspects of the bamboos for the progressive clarification of their taxonomy. A realistic approach to the solution of the "genus problem" requires the building up, maintenance, and sustained competent comprehensive interdisciplinary study of living collections embracing both the vegetative and the reproductive states of critical species of each genus.

In the first sentence of Chapter I of his illuminating review entitled *Comparative Plant Anatomy* (1961), Carlquist reminds us that "comparative anatomical studies of angiosperms have achieved a remarkable record within the past century, and one may safely say that few systematic studies would fail to benefit from incorporation of anatomical data." And again, on page 120, "certainly no generic monograph can be said to be complete without studies on leaf anatomy." This "guide to taxonomic and evolutionary application of anatomical data in angiosperms" serves the useful purpose of emphasizing the impressive number and diversity of the anatomical features that have been brought into focus by studies of angiosperms other than the bamboos. The sparsity of references to bam-
boos incorporated by Carlquist in his book emphasizes the retarded state of our current knowledge of the anatomy of this group of plants. It is regrettable, however, that so few of the published anatomical studies of the bamboos are sufficiently comprehensive or well documented to afford a reliable basis for conclusions as to their taxonomic significance for the differentiation of genera. It remains to be seen whether really comprehensive studies on their anatomy will be significant for the taxonomy of the bamboos as they have been shown to be in some other groups of the Gramineae.

In circumscription of genera, the taxonomic usefulness of features still to be revealed by paramorphological studies of the bamboos remains to be effectively explored. For the time being, at least, the illumination that is potential in such distinguished exploratory studies as those carried out by Shibata (1900), Brandis (1907), Ohki (1932), Takenouchi (1931a,b), Freier (1941), Metcalfe (1960), and others (cited under the pertinent genera) is eclipsed by the inadequate array of species and features covered, and by the shadow of persistent uncertainties with respect to where the truly generic boundaries lie and, in some cases, with respect to the identification or the documentation of those species that were studied. The extent to which the present work may appreciably improve the view is limited by the lack of evidence as to whether, and at what points, paramorphological features will strengthen or modify the image of any genus as it is here portrayed.

Valuable perspective on the incidence and the variations of a number of anatomical features of 47 species listed under 25 genera of bamboos are presented by Metcalfe (1960). Insofar as the bamboos are concerned, major attention is given in this work to leaf anatomy. The generic perspectives afforded by these recorded data are summarized by Metcalfe (1960:584) as follows: "The anatomical data obtained for the leaves of the various bamboos examined by the present writer have been brought together in Table I. Perusal of this table confirms the opinion already expressed that there are no clear-cut distinctions between any of the genera that have been examined so far as leaf structure is concerned."

Ohki (1934) published a summary of his studies of spodograms of the leaf epidermis in representa-

tive species of Bambusa, Dendrocalamus, Phyllostachys, Pleioblastus, Sasa, Semiarundinaria, and Sinobambusa. Of Ohki’s results, Metcalfe (1960:584) has the following to say:

The facts recorded by Ohki seem to the present writer to support the view that there are no very clear-cut divisions between the genera on the basis of characters revealed in spodograms. On the other hand, variations in the occurrence and distribution of macro-hairs, micro-hairs, and prickle-hairs, variations in the width of the bands of bulliform cells, differences in the number and distribution of papillae on the long-cells have specific diagnostic value. This applies also to quantitive characters such as the dimensions of stomata and prickle-hairs. For the identification of some species it is important to know whether the walls of the basal cells of the micro-hairs are smooth or scabrous, and whether or not the walls of the prickle-hairs bear protuberances.

The hazards of attributing to all members of a taxon (genus or species) a feature whose presence has been demonstrated in a single specimen or a single member has not always been heeded by the taxonomist. Metcalfe (1960:584) observes: "Thus we find uniseriate micro-hairs only in Guaduella oblonga amongst the species examined by the author. Then again, Phyllostachys is the only genus from certain species of which fusoid-cells appear to be absent."

Some of the taxonomic characters most promising for the elucidation of the bamboos at the genus level are to be found in features of structures that are rarely represented at all in extant herbarium specimens—and never adequately so. This lack could be remedied either by extensive travel and repeated visits to wild stands of representative taxa, or by the establishment and maintenance of vast living collections for the same purpose. In either case, the lifetime of one person will not be enough.

The traditional and still prevalent disproportionate emphasis on the importance of the diversity comprehended by features of the reproductive structures as the all-but-exclusive source of fundamental taxonomic characters has resulted in the acceptance of mere fragments of the plant as specimens adequately documenting most known taxa. It has also given us a vast but relatively sterile literary heritage. These unchallenged bad examples, aided by the priority principle embodied in the ICBN have tended to perpetuate—even encourage—undue haste in both the collection of specimens for preservation, and the preparation of their formal description for publication. The body of
uncorrelated literature has become undigestible. The elevation of the level of refinement at which future taxonomic treatments of bamboos may be executed is conditioned upon the improvement of certain procedures. In order to make this progress possible, collectors must adopt the objective of documenting for the taxonomist a more detailed image of each taxon collected. This would involve more deliberation in the selection of the components of the conventional array of pressed specimens. It would provide for more extensive and more sustained field observations, and the recording of the results in the form of notes and sketches and/or photographs to accompany the pressed specimens. It would involve the simultaneous collection of other appropriately selected, preserved, and correlated study materials by way of fostering the progressive development and integration of diversified studies, under interdisciplinary collaboration, of documented materials from a common source for each individual taxon (McClure, 1966b: 6, 147). The study set of any given collector number should be made to represent the plant as completely as possible before duplicate specimens are segregated for distribution.

Plant taxonomy is currently in a period of accelerated evolution. Perspectives on its problems and its methods are changing. Under the stimuli exerted by a developing dissatisfaction with the results achievable through traditional methods, and by the developing interest of specialists and their published studies in several fields ancillary to morphology, perceptive taxonomists are actively seeking new ways to bridge the gaps between the way things are in nature and the ways in which they are pictured in conventional treatises. It is anticipated that, through the gradual accumulation and integration of the results of interdisciplinary collaboration in morphological and paramorphological studies, the present work will be superseded by a greatly improved and more comprehensive portrayal of the bamboos—one that more adequately illuminates the details of their individualities in multidisciplinary depth and clarifies their generic and phylogenetic relationships, both within and beyond the subfamily Bambusoideae.

ABOUT THE KEY.—A key is by many botanists admired on the basis of the conciseness of its leads. Partly for this reason, the array of contrasting features used in botanical keys is, by convenience, kept to a minimum. However, the user of such keys may be misled where exceptions to the impressions created by unduly abbreviated leads are left unmentioned. The negligent perpetuation of loose interpretations of structural complexities can thwart the desire to make an effective key. Inadvertently incorporated ambiguities may betray both the maker of a key and the user of it.

The relatively lavish use of contrasting characters that appears at some points in this key is motivated by practical considerations. Effective definition of the assumed disjunctions between some pairs of closely related bamboo genera demands it. Again, specimens typical of extant herbarium material of most bamboos afford such a sparsely diversified and, in many ways, incongruent representation of the taxonomically critical structures that it is only by means of either a very broad scoop or a net with small meshes that many of them may, with any degree of confidence, be directed into a labeled pigeonhole. Because of limitations of available documented coverage it has not been possible to make genus-wide assessment of the potential of some features as sources of contrasting characters; however, the taxonomically useful array of contrasting characters has been augmented, both by drawing upon several morphological features hitherto neglected and by clarifying others that tradition interprets loosely. Some characters elsewhere given unqualified generic importance have had to be eliminated at certain junctures.

An innovation that seems to serve a useful purpose here incorporates in either lead of a given pair, as occasion arises, mention of one or more characters which, while they do not provide additional contrasts, are common to the taxa designated by that particular lead for subsequent differentiation from each other.

Conventional botanical keys commonly use indentation as the means of matching members of each pair of contrasting leads, and for setting off adjacent pairs from each other, visually. Besides being uneconomical in many ways, this usage occasions avoidable inconveniences and disadvantages. It confronts both the preparer of the manuscript and the typesetter with hurdles that are not always successfully cleared. A key of the design offered here is easier to prepare, easier to set in
type, easier to proofread, and less costly to publish, than one embodying indentation. After a little practice in its use, one needs make no greater ef-

Key to the Recognized Genera of Bamboos Native to the New World

1a. Culms in the vegetative state normally not developing branches ........................................... 2
1b. Culms in the vegetative state normally developing branches ........................................... 5
2a. Flowering culms leafless, the above-ground internodes exceedingly thin walled and pro-
vided with pith septa at close intervals, the lowermost one greatly elongated; branch buds solitary at culm nodes; inflorescence never terminal to a culm, short-peduncled, the rachis deliquescent; spikelets terminating in a depauperate sterile anthecium ................................................................. Glaziophyton
2b. Flowering culms leafy, the above-ground internodes not exceedingly thin walled, and
not provided with pith septa at close intervals, the lowermost one shorter than those
that follow it; branch buds lacking at culm nodes; inflorescence always terminal to a
culm, long peduncled, the rachis evertent; spikelets terminating in a perfect floret
................................................................................................................................. Neurolepis
3a. Primary (first-order) branches (elements of the branch complement) at each midculm
node more than one; stamens 3 .............................................................................................. 4
3b. Primary (first-order) branches (elements of the branch complement) at each midculm
node single; stamens 3 ......................................................................................................... 9
4a. Transitional glumes regularly 4, the first two ("empty glumes") in size and shape clearly
distinct from the second two ("sterile lemmas") .................................................................. 5
4b. Transitional glumes 0–1–2, empty glumes and sterile lemmas not distinguishable .......... 6
5a. Culm internodes lacking a lumen (filled with pith as in Zea mays); initial (primary)
branch buds and primary (first-order) branches at each midculm node typically many
(rarely only 5), of constellate insertion, the middle bud or branch several times as
large as those that accompany it; culms arising from well-developed rhizomes of either
pachymorph or leptomorph form in a given species, or from rhizomes of both forms
in the same plant (as in Chusquea fendleri) ........................................................................ Chusquea
5b. Culm internodes provided with a lumen; initial (primary) branch buds and primary
(first-order) branches at each midculm node usually 3, 1–(rarely) 5, of level insertion,
the middle one dominant but not several times as large as those that flank it; culms
arising from weakly developed pachymorph rhizomes and, in some species, also by
tillering .......................................................................................................................... Swallenochloa, new genus
6a. Inflorescences iterant; terminal segment of each rachis conspicuously elongate; spike-
lets terminating in a rudiment borne on a bristle-like prolongation of the rachilla
behind the palea of the solitary perfect floret .................................................................... Atractantha, new genus
6b. Inflorescences semelant; terminal segment of each rachis not conspicuously elongate;
spikelets terminating in a depauperate sterile anthecium ................................................... 7
7a. Culms scandent; inflorescences capitata ............................................................................... Athroostachys
7b. Culms self supporting, the internodes typically more or less conspicuously sulcate,
inflorescences not capitata ................................................................................................. 8
8a. Inflorescence a raceme; branches at midculm node to 5 ................................................. Apocleda
8b. Inflorescence a panicle; branches at midculm node to 3 ..................................................... Yushania
9a. Primary element of the branch complement at midculm nodes flat, unsegmented, ap-
pressed and wholly adnate to the surface of the culm; second-order branches of
apsidate insertion and displayed in fan-shaped array; inflorescences semelant ................................................................................................................................. 10
9b. Primary element of the branch complement at midculm nodes terete above its base,
segmented and diverging from the culm; and dominant over the fasciculate second-
order branches; inflorescences either semelant or iterant ............................................... 11
10a. Midculm sheaths (as far as known) with the blade very much narrower at its base than
the apex of the sheath proper, abruptly rounded to a constricted base, and more or
less strongly reflexed; the surface of the lower internodes in young culms commonly
shows color mottling; inflorescences typically spicate racemes, the rachis in some species
(as in Merostachys pluriflora) more or less strongly contracted, sometimes producing
a congestion of the spikelets; spikelets typically of secund orientation, either (a)
containing a single perfect flower (as in *Merostachys speciosa*) and terminating in a rudiment borne on a bristle-like prolongation of the rachilla, the latter more or less completely concealed in the narrow, canaliculate sulcus of the palea, or (b) containing two or more perfect flowers (as in *Merostachys pluriflora*), the prolongation of the rachilla then usually more robust than bristle-like, the sulcus of the uppermost fertile palea broader and not canaliculate, and the terminal structure a depauperate (not rudimentary) sterile anthecium; transitional glumes at the base of the spikelet 2, strongly differing in size and shape, both empty, the first an "empty glume," the second a "sterile (empty) lemma;" empty glume, sterile lemma and fertile anthecia all of brittle, extremely fragile consistency and of a typical grayish color at maturity; mature fruit oblong or ovoid, not compressed, the pericarp leathery or crustaceous, thickened toward the base and apex, the sulcus and the basal position of the embryo not manifest externally ................................. *Merostachys*

10b. Midculm sheaths (as far as known) with the blade about as wide at its base as the apex of the sheath proper, broadly triangular and not at all reflexed; the surface of the internodes in young culms typically plain green. Inflorescences typically with either spicate or open racemose branching, the rachis either deliquescent or excurrent (when excurrent, either straight or more or less strongly geniculate; inflorescences with excurrent rachises in some species secund (strongly so in *Rhipidocladum maxonii*; weakly so in *R. racemiflorum* and its allies); spikelets each containing few to several perfect flowers and terminating regularly in a depauperate sterile anthecium; transitional glumes at the base of the spikelet usually 5, rarely 2 or 4, all progressively approaching the first fertile lemma in size and shape, the first two empty, the third rarely and the fourth always (when present) subtending a depauperate flower; glumes and anthecia neither very brittle nor of extremely fragile consistency, at maturity usually representing variously tinted versions of stramineous color, in some species punctate with minute green dots; mature fruit oblong, usually more or less noticeably compressed, the pericarp pergamineous (leathery or crustaceous in *R. verticillatum*), the sulcus and the basal position of the embryo usually more or less clearly manifest externally ................................................................. *Rhipidocladum*, new genus

11a. Rhizomes leptomorph; developed midculm branch complements of restricted insertion, the primary element dominant—in some species (as in *Arundinaria gigantea* ssp. *tecta*, for example) occasionally either suppressed temporarily or remaining solitary; inflorescences semelauctant; stigmas 3 .................................................. *Arundinaria*

11b. Rhizomes pachymorph; stigmas in most cases 2 (often 3 in *Bambusa*) .................. 12

12a. Inflorescences iteruactant, forming pseudospikelets ........................................... 13

12b. Inflorescences semelauctant, not forming pseudospikelets ..................................... 14

13a. Culm branches (at least at lower culm nodes) thorny (except in the unarmed northern forms of *Bambusa amplexifolia* and *B. acuteata*); spikelets proper not pedicellate (the distal segment of the rachis not elongated) .................................. *Bambusa* subgenus *Guadua*

13b. Culm branches all unarmed; spikelets proper rendered pedicellate by the elongated distal segment of the rachis .......................................................... *Elytrostachys*

14a. Primary branch at midculm nodes appressed, not swollen basally, and not bearing buds at its congested proximal nodes; culms and branches in most known species characterized by one or more long internodes followed by several nodes closely crowded together by the suppression (abortion) of the intervening internodes; the culm sheaths and branch sheaths as well as the leaf sheaths each thickened and indurate; leaf blades sessile or subsessile, typically thick, of leathery texture, and broadly rounded at the base (rather grass-like and only perceptibly narrowed at the base in *Myriocladus maguirei*); inflorescences typically of elongate profile, with an excurrent rachis, of open racemose or paniculate branching (a condensed linear panicle in *M. cardonae*), the primary branches of the rachis in some species forming secund racemes; spikelets each containing usually 2 perfect flowers, occasionally 3 and, in at least one species, sometimes up to 5 .................................................. *Myriocladus*

14b. Developed branch complements at midculm nodes with the primary element patent, more or less prominently swollen basally, and potentially proliferating from buds at the congested proximal nodes; the culms, and sometimes their branches, in a few species (as in *Arthrostylidium schomburgkii* and *Aulonemia queko*) with a long internode (usually the first above-ground one of culms) followed by 2 or more nodes
closely crowded together by the suppression (abortion) of the intervening internodes; the culm sheaths and leaf sheaths in a few species (as in *Aulonemia effusa* and *A. deflexa*) thickened, indurate, and provided with leathery or parchment-like blades; leaf blades with well-developed petioles in *A. effusa* and *A. deflexa*; inflorescences either spicate, subspicate, open racemose, purely paniculate, or with both racemose and paniculate branching in the same plant; spikelets each containing few to many perfect flowers

15a. Base of the primary axis typically extending downward beyond the locus of insertion of the prophyllum or lowermost circumcising sheath to form a low, downward-tapered promontory; inflorescence a raceme with zig-zag rachis; plants of tropical or subtropical climates

15b. Base of the primary axis not extending downward into a promontory; inflorescence a panicle (sometimes intermixed with racemose branches in *Colantherelia*) with straight rachises; plants of temperate or cold climates

16a. Sheath at midculm nodes provided with (and abscissing from) a conspicuous persistent girdle

16b. Sheath at midculm nodes typically lacking a conspicuous basal girdle

*Apoclada* McClure

*Figures 1-5*

*Apoclada* McClure, in Reitz, ed., 1967:57.

Plants unicespitose; unarmed. Rhizomes pachymorph. Culm habit unknown, the internodes ± sulcate. Branch complement at each midculm node arising from (what appears to be) more than one primary bud, the primary (first-order) component consisting of more than one axis (2-5) crowded together and inserted in a horizontal line, each primary axis dominant over branches of higher orders potentially arising by proliferation from buds (when these are present) at its proximal nodes. Leaf blades with transverse veinlets typically not at all or only weakly manifest externally.

Inflorescences semelaucant, each typically consisting of but a single spikelet (weakly racemose in *Apoclada arenicola*; some spikelets reduced to a single floret in *Apoclada diversa*). Prophylla usually absent (present in *Apoclada diversa* when a flowering branch is reduced to a solitary spikelet). Transitional glumes of conventional nature typically lacking at the base of each spikelet—when present (e.g., Figure 3b) typically consisting of leaf sheaths bearing reduced blades, but highly diverse (as between species) in form, number, and spatial relation to the first fertile lemma. Spikelets usually made pedicellate by being terminal to a peduncle, sometimes (as occasionally in *Apoclada diversa*) sessile; containing few (rarely but one) to several to many perfect florets, and terminating in a de-pauperate sterile anthecium. Lemma (when sub-

*ETYMOLOGY.*—The name *Apoclada* (Greek, *apo*, separate, and *clados*, branch) alludes to the apparently independent origin and insertion of the primary (first-order) elements of the midculm branch complements.

*TYPE-SPECIES.*—*Apoclada simplex* McClure and L. B. Smith.

*RELATIONSHIPS.*—Aside from certain morphological features of the individual florets and a few features of the vegetative structures that are shared by other bamboo genera of the New World flora, *Apoclada*'s only apparent special relationship to another genus is one that vigorously stirs one's curiosity. I refer to the strong detailed resemblance that links the fruits of *Apoclada simplex* (Figure 5 P-R) to the fruits of the in-other-respects very different taxon, *Rhipidocladum verticillatum* (Figure 42 R-T).
DISTRIBUTION.—As far as the available documentation informs us, all four of the currently recognized species of *Apoclada* are endemic to Brazil, where they are restricted to low elevations near the northern limits of the southern temperate zone. Two of these species are represented only by specimens collected from humid sites, and the other two appear to be restricted to arid habitats.

**Key to the Species of Apoclada**

1a. Plants of humid sites; culm internodes antorse-pubescent; primary axes of branch complement at midculm nodes more or less strongly unequal ........................................ 2

1b. Plants of arid sites; culm internodes glabrous; primary axes of branch complement at midculm nodes subequal, slender, appressed ........................................ 3

2a. Culm internodes with walls of substantial thickness; primary axes of branch complement at midculm nodes robust, divergent; flowering branches all leafy; inflorescences of invariable form ........................................................................................................... 4. *A. simplex*

2b. Culm internodes thin walled; primary axes of branch complement at midculm nodes slender, appressed; flowering branches all leafless; inflorescences of highly variable form ........................................................................................................... 3. *A. diversa*

3a. Primary axes of midculm branch complements without basal buds; flowering branches leafy; keels of palea not perceptibly winged; style densely hispid ................................................................. 2. *A. cannaveira*, new combination

3b. Primary axes of midculm branch complements potentially proliferating from basal branch buds; flowering branches leafless; keels of palea perceptibly winged; style glabrous ................................................................. 1. *A. arenicola*, new species

1. *Apoclada arenicola* McClure, new species

**Figures 1, 2**

Culmi in speciminibus suppetentibus usque 1.1 m alti et 3 mm diametro, omnino glabri, internodiis cavis, medianis (quorum paries crassitudinis mediocris est) elongatis, versus cicatrices nodorum ramiferorum vix vel leviter dilatatis, superficie omnino laevi et dura, primo opaca demum nitida. Culmorum et ramorum primariorum vaginae decidue (in specimine suppetente deficientes, ita incognitae). Rami primarii ad nodos medianos culmorum prodientes plures, tenues, subaequales, appressi, omnino papillati, praecipue versus basin retrorse pubescentes, e nodis suis proximalibus proliferantes. Foliorum vagina arcta, persistens, primo praecipue apicem versus subtilissime et antorse scabriuscula et farinosula et papillata, alibi glabra laevigata nitidaque, secus marginem externam ciliolata; auriculis minutis vel rudimentariis vel obsoletis; setis oralibus confertis, capillaceis, infime cohaerentibus, superne libris, pallidis, levibus, anfractisque, denique cadentibus; ligula interiore perbreve apice convexa, dorso canescenti, maragine dense ciliolata; ligula externo vix ulla, maragine primo dense ciliolata demum glabrescenti et vel denticulata vel erosa vel integra; petiolo circa 1 mm longo, basi puberulo, superne glabro, primo glaucoscenti demum nitido; lamina angustissima, vel planiuscula vel aculeiformi rigidaque, usque ad 9 cm longa et circa (in statu siccato) 1 mm lata, utrinsecus omnino glabra; nervis perpaucis; venulis transversis haud manifestis.

Inflorescentiae ex culmo ab initio efoliato ortae; nonnullae (saltem in specimine suppetente) ad spiculam unicum redactae; vel solitariae vel 2–3 simul inserentes a bractea communi subtentae; prophyllice nullis. Glumae transitionales vulgo 2 (interdum 1 vel 3) usque 3 cm inter se distantes, naviculares, apice vel acuta vel acuminata et breviter aristata, dorso carinata plurinerves et glabrae, substantia subhyalinae fragilesque, 1 ca 10 mm longa, 11 ca 11 mm longa, 111 ca 12 mm longa; gluma transitionalis suprema nonnuncum florum depauoperatum subtendens ubi lemmati fertili similis. Spiculae pedicellatae, usque 4 cm longae, laxe pauciflorae, lanceatae, compressulæ. Rachillae segmenta tarde disarticulantia, 2–3 mm longa, prominenter nervosa, clavata, unilateraliter complanata, apice dilatata, vel omnino vel pro parte puberula. Lemma pergamineum vel papyraceum, usque ad 13 mm longum, lanceatum, plurinerve, superne carinatum et apice breviter mucronatum. Palea lemmate brevior, papyracea, oblonga, dorso
Figure 1.—Apoclada arenicola McClure. A, Leafy vegetative culm (midculm section), × 0.6; B, midculm bud complement, × 6; C, branch complement (basal part), × 6; D, leafy twig, × 1.8; E, apex of leaf sheath and base of leaf blade × ca. 18; F, flowering culm, with rhizome, × 0.6. Drawings A, C, F based on Chase 11886 (US) and B, D, E on Chase 12007 (US).

Figure 2.—Apoclada arenicola McClure. A, Spikelet, × 1.2; B, transitional glume I, × 7.2; C, transitional glume II, × 7.2; D, transitional glume III, × 7.2; E, lemma, × 7.2; F, floret, × 7.2; G, palea, abaxial view of distal portion, × 7.2; H, palea, oblique view, × 7.2; I, lodicule complement, × 15; J, stamen, × 7.2; K, gynoeicum, × 30. All drawings based on Chase 11886 (US).

latissime sulcata, in apicem variabilem vel hebete acuta vel obtusa vel subtruncata et bi- vel quadri-dentata, in plano mediano valde curvata, inter et extra carinas clare nervosa glabraque, secus carinas prominenter alatas ciliis pallidis pulchre ornata. Lodiculae vel opacae vel pellucidae vel diaphanae, margine supra- latae alibi utrinsecus glabrae, anterioribus 2 sub-semiovatis, posteriore lanceata. Antherae usque 6 mm longae, brunneae, apice sub- penicullatae. Ovarium glabrum. Stylus glaber, typice in stigmatibus 2 divisus, nonnumquam (atypice) cum ramo stigmatico tertio abortivo praeditus. Caryopsis incognita.

Culms up to 1.1 m tall and 3 mm in diameter, glabrous throughout, the midculm internodes elongate, scarcely or only lightly flared toward the sheath scar at branch-bearing nodes, hollow, with a smooth, hard surface and walls of medium thickness. Sheaths of the culm and sheaths of primary branches deciduous (lacking in the available specimens). Primary branches produced at midculm nodes several, proliferating from buds at their basal nodes, slender, subequal, appressed, papillate throughout, retrorse-pubescent toward the base. Leaf sheaths tight, persistent, obscurely antrorse-scabrous, perceptibly farinose and papillate near the apex, elsewhere glabrous, smooth, and lustrous, ciliolate on the outer margin; auricles minute, rudimentary or obsolete; oral setae numerous, crowded,
hair-like, cohering basally, free, pale, smooth and wavy above, falling away at length; inner ligule very short, dorsally canescent, apically convex, densely ciliolate on the margin; outer ligule a thin line, its margin ciliolate at first, later glabrescent, then seen as either denticulate, erose, or entire; petiole ca 1 mm long, basally puberulous, glabrous distally, lightly glaucous at first then lustrous; blade very narrow, flattish to aculeiform and stiff, up to 9 cm long and (when dry) ca 1 mm broad, glabrous throughout on both surfaces, the longitudinal nerves very few, strong, with transverse veinlets not at all apparent externally. Flowering culms leafless from the first.

Inflorescences racemose (often reduced to a single spikelet), solitary or emerging in twos or threes and subtended at culm nodes and branch nodes by a common bract; prophylla none. Transitional glumes subhyaline, commonly 2 (sometimes 1 or 3) up to 3 cm distant from each other and from the first fertile lemma, boat-shaped, acute or acuminate and awned at the apex, dorsally keeled and glabrous, i.e. 10 mm long, ii 11 mm long, iii 12 mm long, the uppermost transitional glume sometimes similar to the lemma and subtending a depauperate flower. Spikelets lanceate, pedicellate, up to 4 cm long, lax, compressed, comprising few to several perfect flowers. Rachilla segments tardily disarticulating, 2–3 mm long, curved, D-shaped in cross-section, prominently nerved, flared toward the apex, puberulous to subglabrous throughout. Lemma pergamenous, up to 13 mm long, several-nerved, keeled toward the acuminate apex and terminating in a short awn, dorsally glabrous, densely fringed with pale cilia on the outer margin. Palea shorter than its lemma, papery, oblong, emarginate and bi- or quadridentate at the broadly rounded apex, broadly sulcate dorsally, prominently nerved between and beyond the keels, fringed with pale cilia on the keels, elsewhere glabrous throughout. Lodicules (in the specimen) either opaque or pellucid or diaphanous, ciliate at the apex of the margin, elsewhere glabrous throughout; the anterior 2 sub-semiovate, the posterior one lanceate. Anthers up to 6 mm long, yellow. Ovary glabrous, the style glabrous, typically divided into 2 stigmatic branches, atypically bearing (in addition) an abortive stigmatic branch. Caryopsis unknown.

**Type-collection.**—Brazil, Matto Grosso, between Bonito and Rondonopolis, from a single flowering plant among scattered colonies of plants in the vegetative state growing in sandy soil, 8 iv 1930. Agnes Chase 11886 (holotype: US 1500498, 1500499). Additional specimens seen: between Rondonopolis and Santa Rita do Araguaya, from a plant in the vegetative state, representative of an element common in the local flora for several kilometers along the road, 13 iv 1930, Agnes Chase 12007 (US 1500468 and 1500469).

2. **Apoclada cannavieira** (Alvaro da Silveira) McClure, new combination

**Figure 3**

_Arundinaria cannavieira_ Alvaro da Silveira, 1919:101, fig. 2.

**Type-collection.**—In campis arenosis siccisique in Serra do Caparao (as published; 'Serra do Cabral' as indicated in the field notes that accompany the type-collection) Minas Geraes, ubi sub nomine 'cannavieira,' vulgo cognita est. Floret Novembri. Silveira 644 (holotype: Silveira herbarium), US (duplicate from the type-collection).

3. **Apoclada diversa**

**Figure 4**

_Apoclada diversa_ McClure and Smith, in Reitz, ed., 1967:62, fig. 10e-g.

**Type-collection.**—Brazil, Santa Catarina, Caçador, Rio Caçador, lugares úmidos, 22 i 1946, Swallen 8271 (holotype: US 2152479 and 2383418).

4. **Apoclada simplex**

**Figure 5**

_Apoclada simplex_ McClure and Smith, in Reitz, ed., 1967:59, fig. 10y.

**Figure 3.**—_Apoclada cannavieira_ (Alvaro da Silveira) McClure. A, Upper portion of flowering culm, × 0.6; b, apex of leaf sheath and base of leaf blade, × 12; c, spikelet, × 1.2; d, diagram of longitudinal section of spikelet, × ca. 2.4; e, transitional glume (sterile lemma), × 3.6; f, depauperate floret attached to rachilla segment (transitional glume [k], which subtended bud has been removed), × 6; g, floret, × 2.7; h, lemma, × 2.7; i, palea, × 2.7; j, stamen complement and lodicule complement, × 5.6; k, lodicule complement, × 6; l, stamen, × 3.6; m, gynoeicum, × 14.4. All drawings based on _Alvaro da Silveira_ 644 (US).
Inflorescences semelauctant, spicate racemes; subtending bracts and prophylla always lacking, pulvini at the base of the branches of the rachis usually lacking; transitional glumes 2 or 3, the first and second empty, the third a sterile lemma sometimes subtending a rudiment; spikelets sessile or subsessile, containing few to several perfect florets and terminating in a depauperate sterile antherium; lemma of perfect florets subtending its palea only basally at maturity, palea gaping antically, broadly sulcate and 2-keeled dorsally; lodicules 3, the anterior 2 asymmetrical and paired, the posterior one smaller and symmetrical (exceptionally none, as recorded for \textit{A. cacuminis}). Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit—as far as known (available examples are rare)—an oblong mucronate, sulcate Caryopsis, the pericarp pergamineous, of even thickness throughout, or appreciably thickened apically to form a distinct cap or nodule basal to the stylar column; the sulcus and the basal position of the embryo clearly manifest.

\textbf{ETYMOLOGY.}—The name \textit{Arthrostylidium} (n.), derived from the Greek, \textit{arthron}, joint, and \textit{stylidium}, column, alludes to the readily disarticulating nature of the rachilla, in spikelets of the lectotype and numerous other (but not all) species of the genus.

\textbf{TYPE-SPECIES.}—\textit{Hitchcock} (1927b:307) designated \textit{Arthrostylidium cubense} Ruprecht (1839:27) as the type of the genus (see McClure 1957:199).

\textbf{RELATIONSHIPS.}—Even after the exclusion of 25 of the 43 trivial names that have previously been associated with it, the image of the genus \textit{Arthrostylidium} still contains a few taxa that embody conspicuously deviant features. Since in my present perspective I characterize these features as “maverick” (see glossary for definition), I have not given them significance at the genus level. Some species still retained in the genus (e.g., \textit{Arthrostylidium schomburgki}) share such a feature with \textit{Aulonemia queko}, \textit{Glaziophyton mirabile}, \textit{Rhipidocladum harmonicum}, and several species of \textit{Myriocladus}.

I refer to a disproportionate elongation of at least the first above-ground internode, and usually some internodes of primary branches as well. These elongated internodes are followed by one or more aborted (obsolete) internodes, the successive ones being separated from each other by normal nodes.
FIGURE 5.—Apocladia simplex McClure and L. B. Smith. A, Portion of clump showing rhizomes and base of culms, × 0.12; b, midculm internode, nodes and culm sheath, × 0.6; c, apex of sheath from lower culm node, adaxial aspect, × 1.2; d, apex of sheath from higher node, adaxial aspect, × 1.2; e, midculm complement of leafy flowering branches, × ca. 0.6; f, variant of midculm branch complement, × ca. 0.6; g, apex of leaf sheath and base of blade, × ca. 4.8; h and i, spikelets, showing reduced laminiferous foliage leaf standing in place of a first transitional glume, × 3; j, sterile lemma (either standing empty or subtending a depauperate flower) as a second transitional glume (that can be either a sterile lemma or a fertile lemma), × 6; k, floret from middle of spikelet, × 6; l, palea, × 6; m, lodicule complement, × ca. 18; n, stamen, × 15; o, gynoecium, × 15; p, fruit, embryo side, showing weak indication of the position of the embryo, × 7.2; q, fruit, hilum side, showing the sulcus, × 7.2; r, fruit, longitudinal section, × 7.2. Drawings A, H based on Klein 4108 (US), B-F and I-R on Reitz and Klein 16,355 (US), and G on Klein 4637 (US).

bearing normal sheaths and branch buds (or branches) inserted distichously (cf. McClure, in Maguire, Wurdack, et al., 1964:2). Available specimens of Arthrostylidium fimbriatum show several vegetative features that suggest introgression from (or a possibly recessive genetic heritage shared by) some members of the genus Myriocladus. I retain this species in Arthrostylidium on the basis of the characteristic features of the inflorescence. The inflorescence in Arthrostylidium angustifolium deviates from the spicate form of the inflorescence of the type-species of the genus by substituting a spicate raceme for each spikelet. I retain this species in Arthrostylidium on the basis of a characteristic feature complex of the midculm branch complement. Arthrostylidium excelsum, A. sarmentosum, and A. venezuelae produce spicate racemes with a geniculate rachis (inflorescences technically identical with those of Rhipidocladium harmonicum) but the same characteristic feature complex of their midculm branch complements keeps them in Arthrostylidium.

In terms of the ontogeny and morphology of the midculm branch complements, the taxa I retain in Arthrostylidium display a cline, one extreme of which is found in A. cubense and the other in A. sarmentosum. The central structure of this feature complex is the promontory (Figure 6b), a tapered bulge that extends downward from the locus of initiation of the primordium of the solitary primary bud at midculm nodes. In available speci-
names from either Chusquea or Arundinaria to Arthrostylidium, he continues in a vein that conveys the impression that he does, in fact, consider that known members of these three genera actually form a continuum. Doell seems to have taken this view, since he was led, apparently by Ruprecht’s comparison of Chusquea leptophylla to Arthrostylidium trinii, to publish the combination Arthrostylidium leptophyllum (Nees) Doell (in Martius, 1880:175). Ruprecht’s image of Arundinaria was clearly derived from Nees (1834) and not from Michaux (1803).

It appears that the natural boundary (disjunction) between Arundinaria and Arthrostylidium was obscured for Ruprecht (1839)—and has remained so for other taxonomists, down to the present—by the image of the genus Arundinaria which Nees produced (1834:478–483) when he incorporated it in such morphologically (and generically) divergent species as Arundinaria falcata, A. verticillata, A. amplissima, A. macrostachys, A. pinifolia, A. wightiana, and A. glaucescens. Every one of these species is excluded from Arundinaria by my circumscription of the genus. Hance (1862:235; 1876:340) comments upon the weakness of the published bases for the differentiation of Arthrostylidium and Arundinaria from each other. Major treatises by Munro (1868), Bentham (in Bentham and Hooker, 1883), Hackel (in Engler and Prantl, ed., 1887), and E. –G. Camus (1913) are unanimous in their perpetuation of the earlier failure to establish a clear distinction between the respective groups of New World bamboos that truly represent these two genera.

The Latin notes that follow Ruprecht’s brief formal description of the genus Arthrostylidium (1839:27) read in free translation as follows:

Natives of tropical America. This genus unites the Chusqueas and the Arundinarias. Among the latter especially, fruit-bearing flowers of A[rundinaria] amplissima and A. wightiana absciss, while in the rest [of Arundinaria] and in Chusquea, the flowers adhere tenaciously to the rachilla or “stylidium.” A[rthrostylidium] maculatum, by the sexual difference within the dimorphic spikelets, provides a full notion of the genus, a notion gradually obliterated in the rest [of the species] by way of A[rthrostylidium] cubense.

Apparently begun by Ruprecht in 1839, the search for a natural boundary (disjunction) between Arthrostylidium and “Arundinaria” has remained fruitless for more than 180 years. The sense of futility induced by this perennial failure is revealed dramatically in several taxonomic papers that carry the quest into the 20th century—among them Pilger (in Urban, ed., 1900–1901: 386–387), and Hackel (1903a:67–70). Pilger (in Urban, ed., 1907:289) gave renewed expression to his bewilderment in the following words (translated from the German):

It now seems to me doubtful whether the genus Arthrostylidium has any justification, or should go into Arundinaria. Hackel (1903a:67 ff) has already transferred most of the genus Arthrostylidium to Arundinaria, leaving in Arthrostylidium only the forms with a dorsiventral inflorescence (as in A. Prestoei Munro from the West Indies). I do not believe that this difference is sufficient to justify the genus; a future monograph may well have to unite the two genera.

Hackel’s tentative proposal (1903a:69) to clarify the concept of the genus Arthrostylidium by limiting its content to the taxa represented by A. trinii Ruprecht, A. racemiflorum Steudel, A. prestoei Munro, A. pittieri Hackel—“and perhaps also A. fimbriatum Grisebach”—has been universally and persistently ignored. A wholly different image of the genus was adumbrated by Hitchcock’s (1927b: 807) selection of Arthrostylidium cubense Ruprecht as lectotype. But the boundary between Arthrostylidium and Arundinaria was still left undefined.

Pilger and Hackel both revealed, in print, a mutually held conviction that if the basis for a taxonomic boundary between Arthrostylidium and Arundinaria really exists it must be sought amongst the morphological diversities that characterize the reproductive structures of the respective members of the complex. In his key to bamboo genera Hackel (in Engler and Prantl, ed., 1887:92) proposed the separation of the then current images of Arundinaria and Arthrostylidium solely on the ba-
sis of the (unreliable because unstable) number of transitional glumes (empty glumes alone or empty glumes and sterile lemmas) borne at the base of each spikelet.

The natural boundary between *Arthrostylidium* Ruprecht and *Arundinaria* Michaux still awaits explicit definition. In morphological terms, plants typical of *Arthrostylidium* are distinguishable from plants typical of *Arundinaria* by the possession of pachymorph rhizomes, a unicespitose clump habit, a spicate inflorescence with sessile or sub sessile spikelets, and binate stigmas; while plants typical of *Arundinaria* possess leptomorph rhizomes, a diffuse or pluricespitose clump habit, a paniculate or racemose inflorescence with pedicellate spikelets, and ternate stigmas. The respective areas of the natural distribution of plants of the two genera are disjunct, both in space and in respect to prevailing temperature minima; plants of the genus *Arthrostylidium* being confined to frost-free sites, while the genus *Arundinaria* is made up of frost-hardy plants.

**DISTRIBUTION.**—The twenty named New World species I have retained in the genus *Arthrostylidium* are all endemic to regions with a mesophytic, tropical or subtropical climate. Their aggregate recorded geographic range extends from Brazil, with one known species, to Venezuela, with four known species, to Cuba, with eight known species, and several other Caribbean islands, each with one or two species. Pilger (in Urban, ed., 1900–1901: 337) stresses the narrowly limited known distribution of some of the taxa he calls “island species.”

Annotated Checklist of New World Species Included in the Genus *Arthrostylidium*

As here conceived and circumscribed, the genus *Arthrostylidium* embraces the following named taxa, all of which are endemic to the New World.

1. *Arthrostylidium angustifolium* Nash, 1903:172.
2. *Arthrostylidium cacuminis* McClure, in Maguire, Wurdack, et al., 1964:5.
3. *Arthrostylidium capillifolium* Grisebach, 1862: 531.
*Arundinaria capillifolia* (Grisebach) Hackel, 1903a: 69.
4. *Arthrostylidium cubense* Ruprecht, 1839:28, pl. iv: fig. 13 (Figure 6 A-M).
*Arundinaria cubense* (Ruprecht) Hackel, 1903a:69.
5. *Arthrostylidium distichum* Pilger, in Urban, ed., 1900–1901:342.
6. *Arthrostylidium ekmanii* Hitchcock, 1936:16.
7. *Arthrostylidium excelsum* Grisebach, 1864:529.
*Arundinaria excelsa* (Grisebach) Hackel, 1903a:69.
As represented by currently available herbarium specimens, *Arthrostylidium excelsum* does not appear to be clearly differentiated (disjunct) from *Arthrostylidium venezuelae*.
8. *Arthrostylidium fimbriatum* Grisebach, 1862: 581.
9. *Arthrostylidium haitiense* (Pilger) Hitchcock and Chase, 1917:399.
*Arundinaria haitiensis* Pilger, in Urban, ed., 1907: 288.
10. *Arthrostylidium longiflorum* Munro, 1868:41.
*Arundinaria longiflora* (Munro) Hackel, 1903a:69.
*Guadua exalata* Doell, in Martius, 1880:181.
11. *Arthrostylidium multispicatum* Pilger, in Urban, ed., 1900–1901:341.
*Arundinaria multispicata* (Pilger) Hackel, 1903a: 69.
12. *Arthrostylidium obtusatum* Pilger, in Urban, ed., 1900–1901:340.
*Arundinaria obtusata* (Pilger) Hackel, 1903a:69.
13. *Arthrostylidium pubescens* Ruprecht, 1839:29, pl. iv: fig. 14.
*Arundinaria pubescens* (Ruprecht) Hackel, 1903a: 69.
14. *Arthrostylidium reflexum* Hitchcock and Ekman, in Hitchcock, 1936:19.
15. *Arthrostylidium sargentosum* Pilger, in Urban, ed., 1903:108; Chase, 1914:278, pl. 21.
16. *Arthrostylidium scandens* McClure, in Maguire, Wurdack, et al., 1964:4.
17. *Arthrostylidium schomburgkii* (Bennett) Munro, 1868:41.
*Arundinaria schomburgkii* Bennett, in Schomburgk, 1841:562.
18. *Arthrostylidium simpliciusculum* (Pilger) McClure, new combination.
*Arundinaria simpliciuscula* Pilger, 1920:29.
19. *Arthrostylidium urbanii* Pilger, in Urban, ed., 1900–1901:339.
20. *Arthrostylidium venezuelae* (Steudel) McClure, 1942:172.

Chusquea ? venezuelae Steudel, 1854:357.

*Arunindaria standleyi* Hitchcock, 1927a:79.

As illustrated by currently available herbarium specimens, *Arunindaria standleyi* appears to be only weakly differentiated from *Arthrostylidium venezuelae* by the sparse dorsal vesture of its lemmas in the form of lustrous white appressed or spreading deciduous hairs.

Checklist of New World Species Here Excluded from the Genus *Arthrostylidium*

1. *Arthrostylidium ampliflorum*. See *Rhipido-cladum ampliflorum*.
2. *Arthrostylidium amplissimum*. See *Aulonemia amplissima*.
3. *Arthrostylidium angustiflorum*. See *Rhipidocladum angustiflorum*.
4. *Arthrostylidium aristatum*. See *Aulonemia setigera*.
5. *Arthrostylidium bartlettii*. See *Rhipidocladum bartlettii*.
6. *Arthrostylidium burchellii*. See *Colanthelia burchellii*.
7. *Arthrostylidium effusum*. See *Aulonemia effusa*.
8. *Arthrostylidium geminatum*. See *Rhipidocladum geminatum*.
9. *Arthrostylidium haenkei*. See *Aulonemia haenkei*.
10. *Arthrostylidium harmonicum*. See *Rhipidocladum harmonicum*.
11. *Arthrostylidium leptophyllum* is *Chusquea leptophylla* Nees.
12. *Arthrostylidium longiflorum*. See *Bambusa* (sg. *Guadua*) *longifolia*.
13. *Arthrostylidium maculatum*. See *Aulonemia parviflora*.
14. *Arthrostylidium maxonii*. See *Rhipidocladum maxonii*.
15. *Arthrostylidium pittieri*. See *Rhipidocladum pittieri*.
16. *Arthrostylidium prestoei*. See *Rhipidocladum prestoei*.
17. *Arthrostylidium purpuratum*. See *Aulonemia purpurata*.
18. *Arthrostylidium queko* (as quexo). See *Aulone-mia queko*.
19. *Arthrostylidium racemiflorum*. See *Rhipidocladum racemiflorum*.
20. *Arthrostylidium spinosum*. See *Bambusa* (*Guadua*) *longifolia*.
21. *Arthrostylidium steyermarkii*. See *Aulonemia steyermarkii*.
22. *Arthrostylidium subpectinatum*. See *Aulonemia subpectinata*.
23. *Arthrostylidium trinii*. See *Rhipidocladum par-viflorum*.

**Arunindaria Michaux**

**Figures 7-18**

*Arunindaria* Michaux, 1803, I:73.—McClure, 1957:200.

*Miezia* Persoon, 1805, I:101.—McClure, 1957:205.

*Ludolfa* Wildenow, 1808:320.—McClure, 1957:204.

*Macronax* Rafinesque, 1808:553.—McClure, 1957:204.

*Triglossum* Fischer, 1812:vi.—McClure, 1957:210.

*Pleiocladus* Nakai, 1925:145.—McClure, 1957:207.

*Nipponobambusa* Muroi, 1940:89.—McClure, 1960:194.

*Nipponocalamus* Nakai, 1942:350; 1951:326.—McClure, 1957:206.

The literature that deals with *Arunindaria*—even when the genus is viewed solely in terms of the few New World taxa that I recognize as falling within its natural boundaries—comprises many individual items. Repeated consultation and attentive study of this literature has convinced me that it neither contains nor conveys the documented information needed for the construction of a clear image of the New World components and the natural boundaries of the genus. For this reason, instead of listing all or any major part of it here, I have selected—and reserved for notice in the text—those items that appear to have a clear pertinence to the thread of the present account and to be least likely to confuse the reader.

Plants of diffuse habit (both diffuse and pluricespitose in some species); all axes unarmed. Rhizomes leptomorph. Culms self-supporting, either remaining solitary, or tillering from subterranean buds—with or without the intercalation of a metamorph axis, the internodes fistular, either terete throughout or more or less markedly sulcate—usually so for only a short distance upward from the locus of insertion of a bud or a branch complement, rarely (as occasionally seen in plants of
Arundinaria gigantea ssp. gigantea) lightly so all the way from one node to the next. Primary branch buds at culm nodes solitary, each containing but a single initial primordium. Branch complement at midculm nodes in some species facultative-restricted monoclade, (rarely, either temporarily or permanently, lacking throughout) typically unrestricted monoclade and always of restricted insertion, with the primary member dominant. Leaves (blades of leaf sheaths) petiolate, with transverse veinlets clearly visible on both surfaces initially, but sometimes becoming obscure in old leaves.

Inflorescences semelauctant, generally of open racemose or paniculate branching, sometimes assuming both of these forms, or even reduced to a single spikelet, all in the same plant. Rachis either deliquescent or excurrent, its branches typically not prophyllate, the lowermost primary ones always, the upper ones commonly, subtended by either a small or rudimentary bract, or a line of hairs. Transitional glumes at the base of each spikelet, usually 2 and empty (the first one sometimes lacking), rarely 3, the third (conventionally called a sterile lemma) sometimes empty, more commonly subtending a depauperate flower. Spikelets comprising several to many perfect florets, and terminating acuminate in progressively depauperate sterile florets or empty anhecia. Rachilla segments potentially disarticulating just below the locus of insertion of each fertile lemma. Lemma (when subtending a functional flower) fully embracing the palea only basally at maturity. Palea broadly sulcate and 2-keeled dorsally, the margins not at all or only slightly and partially overlapping. Lodicules 3, the anterior two typically more or less strongly asymmetrical and paired, the posterior one symmetrical and usually smaller (at least either shorter or narrower) than the anterior two. Stamens typically 3, the filaments filiform, free. Stigmas 3. Mature fruit an oblong, sulcate, glabrous caryopsis, terminating apically in the persistent base of the style; the pericarp thin, pigneemous or coriaceous, in some species appreciably thickened at the apex of the fruit; the contours of the basal embryo clearly revealed as a rule in the dry fruit by the embryotegium.

ETYMOLOGY.—The name Arundinaria is derived from the Latin, arundo (arundin-), reed or cane, and the suffix, aria, that signifies belonging to. From 1829 (Kunth, 1829:137) at least until 1861 (Bentham, 1861:438) predominant usage attributed the authorship of the genus Arundinaria to L. C. Richard. In the absence of positive evidence to the contrary, however, Michaux is now generally recognized as the author of it.

TYPE-SPcies.—Arundinaria gigantea (Walter) Muhlenberg (1818).

As basionym, Arundo gigantea Walter (1788), takes precedence over Festuca grandiflora Lamark (1791), and Arundinaria macrosperma Michaux (1803) at the species level, since both Lamark's and Michaux's species are here included in a comprehensive circumscription of Arundinaria gigantea (ICBN 1966:Art. 57).

RELATIONSHIPS.—From the polymorphic neotropical genus, Arthrostylidium (q.v.), numerous species of which have at one time or another been misplaced in Arundinaria, taxa characteristic of Arundinaria are distinguishable by the following invariable combinations of morphological features: leptomorph rhizomes, diffuse or pluricespitose clump habit, and ternate stigmas. Moreover, the respective geographical distributions of the two genera are different and disjunct, and are correlated with distinctive ecological adaptations. As far as known, plants of the genus Arthrostylidium are confined to frost-free sites, while the genus Arundinaria comprises plants that are frost-hardy.

Included by some authors in Arundinaria, the recognized components of the Old World genus Thamnocalamus are set off from this genus by the combination of pachymorph rhizomes, unicespitose clump habit, and ternate stigmas. Moreover, the respective geographical distributions of the two genera are different and disjunct, and are correlated with distinctive ecological adaptations. As far as known, plants of the genus Arthrostylidium are confined to frost-free sites, while the genus Arundinaria comprises plants that are frost-hardy.

Of the known African species at present allocated to Arundinaria, A. alpina K. Schumann (at least) is excluded from this genus by its pachymorph rhizomes, unicespite clump habit, and binate stigmas; cf Yushania sg. Oatea, p. 116.

DISTRIBUTION.—The known New World components of the genus Arundinaria constitute the polymorphic type-species whose natural distribution is limited to continental United States. They are represented principally in North American, British, and European herbaria by specimens gathered in Alabama, Arkansas, Delaware, Florida, Illinois, Indiana, Kentucky, Louisiana, Maryland, Missis-
sippi, Missouri, North Carolina, Ohio, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia.

A map of southeastern United States showing, by counties, the observed incidence of stands of native *Arundinaria*—under the name *Arundinaria tecta* applied in a comprehensive sense—is presented by West (1935:258, fig. 1). Owing to the difficulties involved in reconciling incongruities and inconsistencies between various published taxonomic usages—difficulties augmented by the fragmentary nature of most of the available preserved specimens—it is not yet possible to construct authentic maps of the precise distribution of stands of the respective subspecific entities herein recognized. A general idea of the pattern of their distribution, however, may be derived from Gilly's map (1943, fig. 1) by assuming a rough (but not precise) correspondence between Gilly's "Mississippi-type" and my *A. gigantea* ssp. *gigantea*; between Gilly's "Atlantic-type" and my subspecies *tecta*; and between Gilly's "Intermediates" and my subspecies *macroesperma* (cf. Figure 16).

Known Old World taxa that I recognize as members of the genus *Arundinaria* are found in China proper, Hainan Island, northern India, Japan, Korea, Madagascar, Nepal, the Ryukyu Archipelago, Sikkim, Taiwan, Tibet, and northern Vietnam.

The New World Component of the Genus *Arundinaria*.—The only known New World bamboos embraced by my circumscription of the genus *Arundinaria* are those included in its polymorphic type-species, *Arundinaria gigantea* (Walter) Muhlenberg, sensu lato. The development of an improved idea of the geographical boundaries of the genus and its known content requires, therefore, a critical examination of taxa that have hitherto been assigned to it from the bamboo floras of the Old World, as well as those of the New.

During the interval since *Arundinaria* was first described and given monotypic status by Michaux in 1803, the number of species assigned to the genus increased spectacularly. The inventory of names linked to it in the taxonomic literature grew from the initially solitary entry, *Arundinaria macroesperma* Michaux, to a total of about 376, counting only binomials. The inclusion of trinomials swells the number of its published nomenclatural diversities to about 482. Of the New World component of this total, I have excluded the taxa represented by 50–odd names listed on page 36 et seq.

As a result of interim studies and revised judgments published by other authors, many of the Old World species originally (or at one time) incorporated in the genus *Arundinaria* have subsequently been made either the respective types, or components, of the following genera: *Brachystachyum*, *Chimonobambusa*, *Indocalamus*, *Neosasamoria*, *Oreocalamus*, *Pseudosasa*, *Sasa*, *Sasaella*, *Sasamorpha*, *Semiarundinaria*, *Sinarundinaria*, *Sinobambusa*, *Thannocalamus*, and *Yushania*. All of the bamboos that have since been allocated to these genera are endemic to Old World areas.

Annotated Checklist of New World Elements Included in the Genus *Arundinaria* (as herein defined)

*Arundinaria gigantea* (Walter) Muhlenberg, 1813: 14. Basionym: *Arundo gigantea* Walter, 1788:81. *Arundo tecta* Walter, 1788:81.
**Festuca grandiflora** Lamarck, 1791:191. *Arundinaria macroesperma* Michaux, 1803: I:74.
**Triglossum bambusinum** Fischer, 1812:6. *Arundinaria tecta* (Walter) Muhlenberg, 1813:14.
**Arundinaria bambusina** (Fischer) Trinius, 1820: 97.
**Miegia pumila** Nuttall, 1837:149 [illegitimate name].
**Arundinaria tecta** β *pumila* Ruprecht, 1839:22.
**Arundinaria tecta** γ *distachya* Ruprecht, 1839:22.
**Arundinaria tecta** δ *colorata* Ruprecht, 1839:22.
**Arundinaria macroesperma** α *arborescens* Munro, 1868:15.
**Arundinaria macroesperma** β *suffruticosus* Munro, 1868:15.
**Arundinaria macroesperma** β *tecta* Wood, 1871: 404.
**Arundinaria gigantea** tecta (Walter) Scribner, in Kearney, 1893:478.
**Arundinaria tecta** var. *decidua* Beadle, in Bailey, 1914:446.

*Given the present unsatisfactory state of their description, their documentation, and their typification, vis-à-vis the highly polymorphic character of the populations here included under *Arundi-
Arundinaria gigantea, sensu lato, it is my judgment that proposals for a more refined formal disposition of the taxa represented by these names should be deferred until comprehensive studies on a broad disciplinary spectrum in field and laboratory have improved present perspectives.

Proposed Taxonomic Revision

of the Type-species of Arundinaria

The relegation by Hitchcock (1935:29 [1951:27]) of the name Arundinaria macrosperma Michaux to synonymy under Arundinaria gigantea (Walter) Muhlenberg appears to be referable to an earlier tentative decision expressed in the following paragraph quoted from page 156 of a paper entitled "Types of American Grasses" (Hitchcock, 1908).

Arundinaria gigantea (Walter) Muhlenberg, "Gramen altissimum ramosum a Virginia ad Floridam & in occidentalibus juxta fluviis ab Illinoensibus ad ostium Misissipi [sign for undershrub]." The specimen is fragmentary and one can not be certain which species of Arundinaria it represents. Michaux probably included the large and the small canes in one species. As he described the plants as being very high, we may retain this name for the tall cane, as is done in our manuals.

Hitchcock's disposition of the matter of synonymy appears to have been influenced by the reiterated allusion to size—in the trivial name, gigantea, of one taxon, and in the description of the other, macrosperma, as "altissima." In other words, it is based upon an interpretation of Michaux's description of the monotypic genus Arundinaria, and not upon an interpretation of the lectoholotype by completing the image of its botanical source (cf. Rickett and Camp, 1950). At the same time, however, the taxon represented by Arundinaria tecta (Walter) Muhlenberg was maintained by Hitchcock as a distinct species.

In present perspectives it appears that the taxa represented by the binomials Arundinaria gigantea (Walter) Muhlenberg, Arundinaria tecta (Walter) Muhlenberg, and Arundinaria macrosperma Michaux embody, respectively, three components of a polymorphic array of populations (cf. Figures 16, 17). As shown by their purest available typifications, Arundinaria gigantea and Arundinaria tecta are clearly set off from each other by distinctive combinations of strongly contrasting morphological and ontogenetic features (Figure 15). The lectotype and isotype of the taxon Arundinaria macrosperma are seen as representing a plant that falls within the series of variants (putative nothomorphs) that form a cline bridging the morphological and ontogenetic divergency that exists between Arundinaria gigantea and Arundinaria tecta (Figures 17, 18). Circumstantial evidence of the biological relationships of these three taxa supports the proposal that they be treated taxonomically as members of a single polymorphic species.

When the circumscription of Arundinaria macrosperma Michaux is interpreted as including the type of Arundo gigantea Walter, the adoption of the name Arundinaria gigantea (Walter) Muhlenberg in place of Arundinaria macrosperma Michaux for the type-species of the genus Arundinaria (Hitchcock, 1935:29 [1951:27]) has the sanction of the International Code of Botanical Nomenclature (see Lanjouw et al, ed., 1966: Art. 57). This precedent determines the binomial to be adopted when the three taxa now under discussion are treated as subspecies under one specific name.

In present perspectives, any specimen that bears a recorded origin indicating nativity to continental United States, and that shows features of both subspecies gigantea and subspecies tecta—even though it is otherwise incomplete—may be determined as subspecies macrosperma.

The subspecific identification placed on incomplete specimens that show only features characteristic of either subspecies gigantea or subspecies tecta should be followed by a query (?), since the name of the subspecific taxon to which the character of the missing structure(s) would carry the identification, by way of the key, must remain uncertain in such cases. Where, on account of the incompleteness of a specimen, uncertainties arise as to its correct subspecific disposition, it may with propriety be filed tentatively as Arundinaria gigantea, sensu lato. However, the possibility that more intensive field studies in the United States may bring to light native plants specifically distinct from Arundinaria gigantea, as this taxon is here circumscribed, should not be ignored.

Concerning the Typification

of Arundo gigantea, Arundo tecta, and Arundinaria macrosperma

Of all of the many previously published treatises
Key to the Herein Recognized Subspecies of *Arundinaria gigantea*, sensu lato

1a. Rhizomes without air canals; typically of steadily diageotropic growth, i.e., normally not turning up at the apex to form a culm. Plants of diffuse habit, the culms normally solitary and not tillering. Midculm sheaths each shorter than the corresponding internode; deciduous. Primary axis of midculm branch complements not constricted basally, lacking a “neck” (see glossary). The lowest bud (or secondary branch) of midculm pleioclade branch complements inserted but a short distance above the base of the first internode of the primary branch and (in contrast to those inserted at its succeeding nodes) not subtended by a conventional sheath. The primary and secondary axes of midculm branch complements relatively short and slender, all appressed basally and then curving strongly away from the culm. Culms with their leafy branch complements fully developed present a narrowly linear profile. Leaf blades pubescent on the abaxial surface; subglabrous on the adaxial. Lemmas dorsally hirsute with antrorse hairs and minutely hispidulous or scaberulous; the exposed exterior surface pale green (not tinted with wine) and more or less conspicuously glaucous when fresh; transverse veinlets clearly manifest externally. Lodicles typically subopaque, fringed with marginal cilia, and supplied with numerous vascular traces. Pistils lacking the uncinate rudimentary stylar branch that is regularly present on the pistil in the neotype of subspecies *tecta*. Fruits narrowly conical apically and terminating in the persistent base of the style (Figures 7-11). ........................................................... 1. subspecies *gigantea*

1b. Rhizomes with air canals forming a continuous and unbroken cylinder; apical growth commonly diageotropic (horizontal) for only a short distance, then directed upward to form a culm. Plants of diffuse habit (culms arising from lateral buds of the rhizomes normally remaining solitary) and also pluricespitose as a result of the tillering of culms (principally those that are apical to rhizomes). Midculm sheaths each longer than the corresponding internode; not deciduous. Primary axis of midculm branch complements constricted basally into an obconical “neck” consisting of usually 2 or 3 very short internodes with budless sheath-bearing nodes (Figure 12a), followed by more elongated internodes each bearing basally a secondary member of the branch complement (or a bud) subtended by a conventional sheath. The primary and secondary axes of midculm branch complements elongate, appressed basally, then ascending and, when fully developed, curving broadly away from the culm. Culms with their leafy branch complements fully developed present a lanceolate profile. Leaf blades densely pubescent on both surfaces. Lemmas dorsally glabrous or nearly so, the exposed exterior surface tinted with wine, and not glaucous when fresh; transverse veinlets not at all manifest or only barely perceptible. Lodicles thin, transparent, with glabrous margins and vascular traces weakly to scarcely manifest. Pistils all showing the unciform rudiment that becomes a conspicuous feature in mature fruits. Fruit dome-shaped apically, terminating in a short beak, and regularly bearing (just below the base of the beak, and directly above the tip of the sulcus) a usually more or less strongly unciform rudiment—apparently representing a supernumerary style or stylar branch (Figures 12-14) *............................. 2. subspecies *tecta*, new status

1c. Rhizomes with air canals either present or absent; when present, either continuous or discontinuous; other individual morphological and ontogenetic features appearing in diverse recombinations of either identical or intermediate expressions of the same contrasting features that (in characteristic combinations described above) clearly differentiate subspecies *gigantea* and subspecies *tecta* ....... 3. subspecies *macrosperma*, new status

*Edna Rema Walker (1906) reports and illustrates the occurrence of rudimentary style-branches in a number of species of grasses, including *Oryza sativa*. See also Arber, 1934, fig. 88. I have not found any published notice of the occurrence of this feature in any bamboos.

Munro’s monograph (1868)—Hitchcock’s publications (1905, 1908) proposing lectotypes for *Arundo gigantea* Walter and *Arundinaria macrosperma* Michaux, are the only ones that are recognizable...
as representing a disciplined conformity to the spirit and the letter of the pertinent references in the International Code of Botanical Nomenclature.

In the selection of a neotype for *Arundo tecta*, and living plants (hypotypes, sensu Frizzel, 1938: 653) to supplement the original images of subspecies *gigantea*, *tecta*, and *macrosperma*, I have followed the stipulations of the International Code of Botanical Nomenclature (1966) as set forth in note 3 under Art. 7; and in paragraphs 5, 4, and 5 under the heading, Guide for the determination of types (Lanjouw, et al., ed., 1966:71). The protolog pertaining to each of these three taxa lacks a precise indication of type-locality. However, I believe that the plants selected present details that authentically supplement the sketchy images of these taxa provided by their respective protologs. According to Ewan (1969:198) "Thomas Walter's new species in his *Flora Caroliniana* (1788) are generally assumed to be descriptions of plants that grew about his plantation at the mouth of the Santee River. But we must remember that John Fraser was Walter's advocate and 'well spring in the wilderness' who brought plants for Walter to study and describe."

In the present limited state of our knowledge of the component living plants, and in the restricted perspective afforded by their fragmentary representation in extant herbarium specimens, the apparently clinal nature (composition) of presumably hybrid populations from which these three taxa have been selected renders their more refined systematic treatment infeasible as yet (cf Böcher, 1963:11-12, 1967:258; Stebbins, 1940; Heiser, 1949; and Allan, 1949).

1. *Arundinaria gigantea* ssp. *gigantea*

Holotype.—Walter Herbarium (BM); Walter s.n. The specimen is a mere fragment of a sterile, leafy axis—apparently the tip of a young culm—with the distal branch complement in an early stage of development. A ticket attached to the specimen bears the name, *Arundo gigantea*, but no other annotation.

The feature-combination characteristic of *Arundinaria gigantea* ssp. *gigantea*—as elaborated in the descriptive key—is based on the following speci-

mens: Vegetative state: McClure (LU 15140) collected 18 April 1928 from a homogeneous, apparently natural stand growing in and adjacent to a swamp at the side of a small stream on the Old Shaker Farm, near Lebanon, Warren County, Ohio; and McClure 21321 (US) yielded by plants from the same source maintained under cultivation as MBG 2784. Flowering state: Winteringer 7214 (US) "Low ground west of Sandusky, Alexander Co., Illinois. 7 July, 1951." Fruiting state: Bain 117 (US) "River banks, Tennessee. 1892;" and Bush 198 (US) "Common in woods. Eagle Rock, Missouri. May 31, 1898."

Swallen 6717 (US 2078084-2078089)—illustrated in Hitchcock, 1935 [1951, fig. 1], as *Arundinaria gigantea* (Walter) Muhlenberg—and D. M. Moore, s.n. (US 2206426-2206430) are relatively complete specimens that appear at first sight to represent typical *A. gigantea* ssp. *gigantea*. On closer examination, however, both of these collections show evidence of minor introgression of genetic influence from subspecies *tecta*. This is expressed inconspicuously in such tectoid features as a noticeable vinous tinting of the lemma and the palea, and the development, sooner or later, of negative geotropism in each rhizome, whereupon it turns upward apically to form a culm from its growing point. Strict application of the formula provided by the descriptive key identifies the plants represented by these two specimens as members of the clinal series embraced by *A. gigantea* ssp. *macrosperma*. They may be visualized, however, as occupying positions morphologically and genetically (and therefore taxonomically) very near to *A. gigantea* ssp. *gigantea*.

2. *Arundinaria gigantea* ssp. *tecta* (Walter)

McClure, new status

*Figures 12-14, 15a, 16c*

*Arundinaria tecta* (Walter) Muhlenberg. 1813:14; 1817:191. *Arundo tecta* Walter, 1788:81.

*Figure 7.—Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Basal section of mature culm with section of rhizome attached, × 0.6; b, middle section of mature culm at end of first season, × 0.6; c, base of midculm branch complement, × 2.4; d, apex of leaf sheath with petiole and base of leaf blade, × ca. 6; e, cross-section of rhizome, showing lack of air canals, × ca. 12. All drawings based on McClure Bamboo Garden specimen no. 2784 (US).
Neotype.—Walter's type has not been found. However, the living plant to which his brief characterization led me, has presented both the vegetative and the reproductive stages of its ontogeny, and many facets of its potential morphological diversity. The feature-combination characteristic of *A. gigantea* ssp. *tecta*—as elaborated in the descriptive key—is based on *McClure 22000* (US), a series of specimens yielded by plants in a natural stand growing in and adjacent to a swamp lying between Stony Run Creek and the Pennsylvania Railroad, near Friendship International Airport, Anne Arundel County, Maryland, and by plants from the same source maintained under cultivation, as MBG 2762. They were collected over a period of years both at the original site, and from plants taken from the same source and maintained under cultivation, since 1955. This series of specimens constitutes the exclusive documentation of the characterization of subspecies *tecta* presented in the descriptive key.

Plants growing in the wooded swamp reach a maximum height of about 2.5 m. These have remained in a sterile (vegetative) state ever since my observations were initiated in 1952. Other sterile plants of the same taxon growing in upland clay soil on the opposite side of the railroad (until they were destroyed by earth fill) reached a maximum height of about one meter. Plants growing along the edge of the swamp push their rhizomes into the original gravel ballast along the railroad, where they produce culms 0.5 to 1.0 m tall. Here and there among these latter, little patches of culms in a depauperate condition may be found in flower every year. However, I have never found fruits produced in that situation. The reproductive organs in every floret are always more or less completely destroyed by the larvae of insects that pass this stage of their life cycle within the antheria.

Another specimen, preserved in the Richard Herbarium (P) and labeled “ex Herb. E. Drake” supplements slightly the fragmentary representation (and the diversity) of the feature-combinations that appear in the image of the taxon *Arundinaria macrosperma* Michaux provided by the lectotype and the isotype. The species label bears the inscrip-

3. *Arundinaria gigantea* ssp. *macrosperma* (Michaux) McClure, new status

**Figure 16b**

*Arundinaria macrosperma* Michaux, 1803, I:74 [as to type].

Type (elig. Hitchcock, 1908:156).—(P) “Herbier de l'Amerique Septentrionale d'Andre Michaux.”

“Gramen altissimum ramosum [Michaux's symbol for undershrub]. Hab. a Virginia ad Floridam et in occidentalibus [a phrase is here crossed out and illegible] juxta fluvios ab Illinoensibus ad ostium Mississipi [Michaux's symbol for perennial plant].”

The specimen is a leafy flowering branch with leaf blades and florets detached.

Isotype (nunc elig.).—A specimen that quite clearly represents a duplicate from the same Michaux collection as that which yielded the lectotype is preserved at the Paris Herbarium. A printed label on the sheet bears the following information:

MUSEUM D'HISTOIRE NATURELLE DE PARIS

herbier d’Antoine Laurent de Jussieu.

Donné au Museum par les enfants d’Andrien de Jussieu en 1857. Catal. no. 2881.

The label (made in Paris by the elder Jussieu) bears the following annotations:

Arundinaria Mich. en Dew.

**Figure 8.**—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Midculm section of young culm, × 0.6; B, tip section of young culm, × 0.6; C, culm sheath from midculm node, with blade not reflexed, × 3; D, culm sheath from higher level, with blade reflexed, × 3; E, Walter's type of *Arundo gigantea* (from British Museum photo), × ca. 0.4.

All drawings based on McClure Bamboo Garden specimen no. 2784 (US).
tion "Arundinaria macrosperma [Michaux] Caroline. m." With the possible exception of the word "macrosperma"—which appears to have been inserted by a different hand—this inscription is in the handwriting of Michaux. The specimen gives the plant from which it came a recognizable relationship to subspecies tecta.

A sterile specimen, McClure 21320 (US), and a fruiting specimen, McClure 21664 (US), represent a plant taken from the wild near the Ogeechee River, about 12 miles south of Savannah, Georgia, in the vegetative state, by David Bisset. I received a division of it in 1942 and maintained it under cultivation (as MBG 2803) until August 1948, when it flowered, bore fruits and died. The inflorescences match those of the lectotype and isotype of Arundinaria macrosperma. The fruits of this plant are similar in shape to the fruits of the neotype of subspecies gigantea but differ in their much larger average size and in the infrequent incidence of the unisemiform rudimentary style branch.

McClure 22018 (US) represents a plant secured from the wild near Travelers Rest, South Carolina, through the good offices of Robert A. Young, and maintained under cultivation (as MBG 2782) from 1948 to the present. The plant, which has remained steadily in the vegetative state, combines expressions of morphological features characteristic, respectively, of subspecies gigantea and subspecies tecta, and some that are intermediate. The rhizomes (as in ssp. gigantea) lack air canals, but (as in ssp. tecta) turn up apically to form a culm. The culms (as in ssp. tecta) proliferate from subterranean buds to form either culms or rhizomes. The primary axis of midculm branch complements (as in ssp. gigantea) lacks a basal "neck" but the component members of the complement (as in ssp. tecta) are more elongate and not so strongly curved away from the culm. The leaf blades are, on the average, larger than those of either typical subspecies gigantea or typical subspecies tecta.

The revised taxonomic dispositions embodied in the nomenclature proposed here for these three subspecific components requires a postscript to my paper (McClure, 1963a) entitled "A New Feature in Bamboo Rhizome Anatomy." The plant therein called Arundinaria gigantea (Walter) Muhlenberg, whose rhizomes lack air canals (cf. Figure 7E), is herein classified (and described in the key) under the name Arundinaria gigantea ssp. gigantea. Its documenting number is incorrectly given (McClure, 1963) as MBG 2792; however, the origin of the plant is correctly given there; its correct number is MBG 2784. The plant (MBG 2762) therein called Arundinaria tecta (Walter) Muhlenberg, whose rhizomes show continuous air canals (cf. Figure 18E) is herein classified (and described in the key) as Arundinaria gigantea ssp. tecta. The unnamed specimens (Biltmore 1405, and Radford and Wood 6879-A) cited therein and described as having air canals discontinuous in the rhizomes, are now recognized as falling within my circumscription of Arundinaria gigantea ssp. macrosperma.

In the limited perspective provided by their fragmentary representation in extant specimens of the conventional sort, these three subspecies are usually not clearly differentiated from each other in herbaria. For the identification of complete plants or complete specimens, however, the descriptive key is believed to be adequate and reliable.

As they appear in nature, and as they are characterized in the descriptive key (p. 25), plants of subspecies macrosperma probably comprise the numerically dominant element of Arundinaria gigantea, sensu lato. This subspecies is here interpreted (circumscribed) as embracing plants (all apparently of hybrid origin) that embody, respectively, diverse recombinations of either identical or intermediate expressions of the same contrasting features that (in characteristic combinations) clearly differentiate subspecies gigantea and subspecies tecta, the putative genetical parents.

The union, under one specific name, of the morphologically and genotypically distinct but obviously (at least ostensibly) interbreeding members of sympatric populations has the sanction of precedent. In the present case it has other defenses as well. It affords a framework for facilitating the practical disposition (identification and filing) of the fragmentary specimens of this species that

Figure 9.—Arundinaria gigantea (Walter) Muhlenberg ssp. gigantea. a, Young leafy sterile culm with section of rhizome attached, × 0.6; b, young leafless flowering culm, × 0.6; c, whole sheath on midculm node of young culm shoot, × 0.6; d, apex and blade of culm sheath from upper node of young culm, showing reflexed sheath blade, × ca. 1.8. All drawings based on D. M. Moore s.n., Arkansas, USA, 2 August 1947 (US).
predominate numerically in herbaria. Assigning subspecific status to the three components portrayed in the descriptive key provides a means of giving greater depth of focus to floristic and ecological field studies such as those carried out by West (1935). For example, West's identifications and descriptions of the geographic areas within which the existence of "canebrakes" is recorded by him are extremely valuable. Apparently, however, no effective effort was made, either to document the observed "ecological forms" by means of annotated voucher specimens or to correlate their distribution with that of the nine different "habitats" (ecological complexes) and the eight different floristic associations ("forest types") within which they were observed to occur. Hopefully, such ecological and floristic emphasis will also encourage collectors to cultivate an awareness of the potential taxonomic importance of morphological and ontogenetic diversities that await documentation, and to exercise the discipline necessary to give due attention to them in preparing specimens, whether these are intended for identification only or for permanent preservation.

West (1935:255) maintained that the *Arundinaria gigantea* and *Arundinaria tecta* of the manuals are indistinguishable. "It is believed that the two so-called species of the manuals are in reality ecological forms of the same species ... when both types are planted side by side in the greenhouse or in the open, they soon become indistinguishable."

I have had under observation for at least ten years, both in the wild and in cultivation under essentially identical conditions, plants I recognize as representing *Arundinaria gigantea, Arundinaria tecta,* and *Arundinaria macrosperma,* respectively. They have retained their distinguishing features as described in the key and as documented by voucher specimens cited here under the corresponding subspecies.

Plants from different natural stands of either subspecies *gigantea* or subspecies *tecta* rarely match each other in all details of their ontogeny and their gross morphology. The persistence of observed minor differences between a number of variants of both subspecies *gigantea* and subspecies *tecta* when the plants were grown for a number of years under essentially identical conditions appears as evidence that the genotypic heterogeneity that characterizes hybrid populations may embrace the whole content of this polymorphic species—lightly so in the most divergent taxa (ssp. *gigantea* and ssp *tecta*) and more profoundly so in the diverse components of subspecies *macrosperma* that form a cline between the first two subspecies.

Observations Concerning the Taxonomic Utility of Certain Structures and Their Contrasting Features

I find that certain features that have been used by others to differentiate taxa identified, respectively, as *Arundinaria gigantea* and *A. tecta* are taxonomically undependable at both the species level and the subspecies level.

**Maximum Culm Height.**—The impression given by many local floras and incidental treatises is that plants of two recognizable bamboo taxa native to the United States may be distinguished from each other by the maximum height attained by their culms. Maximum culm heights given for plants referred to in the literature—either as *gigantea* or as *macrosperma*—range from 7.6 to 12 meters (Nuttall, 1837:149; Mitford, 1896:165; Hitchcock, 1936:19 [1951:27]) and those given for plants—referred to either as *tecta* or as *macrosperma* range up to 4.6 meters (Nuttall, 1818, I:39; Mohr, 1901:103). However, I have not found published culm heights above 5.5 meters documented in any case by reference to field notes accompanied by voucher specimens. Among the field notes accompanying specimens of more than 300 collections examined personally, I found less than a dozen that bear an indication of the height of the culms of the plant from which the specimen was taken. And in no case have I found field notes recording a maximum height greater than 5.5 meters, regardless of how the specimen was identified.

The existence today of canebrakes containing culms at least 7.6 meters tall is not in doubt. During

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**Figure 10.**—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea.* a, Leafy culm tip, × 0.6; b, branch complement from node high on culm, with leafy and leafless flowering branches (with many spikelets shattered), × 0.6; c, base of midculm branch complement, × 2.4; d, apex of leaf sheath with petiole and base of leaf blade, × ca. 4.8. All drawings based on D. M. Moore s.n., Arkansas, USA, 2 August 1947 (US).
the second world war I saw in a hardware store in Savannah, Georgia, 7.6-meter-long culms of a native bamboo on sale as fishing poles. I also have a photograph taken in 1905 or 1906 which shows a stand of native bamboo in Louisiana, the culms of which are estimated (on the scale of a man on horseback included in the picture) to be at least 7.6 meters tall. In the absence, however, of documentation by means of adequate voucher specimens, it is impossible to assess the taxonomic pertinence of these published and unpublished observations. In the following paragraph C. A. Brown (1929:817) discusses what he considers to be the ecological significance of differences in culm size observed in different stands—all of which he includes in a comprehensive “Arundinaria tecta.”

One might inquire as to the reason for the difference in size between the small woody canes the size of a lead pencil and only a few feet [ca. 1 m] tall and the large woody canes one to one and a half inches [2.5–3.8 cm] in diameter and up to thirty feet [9m] tall. It has been noticed that there are many patches of this small type. The only explanation that can be offered is that there must be some difference in soil or moisture conditions which hinders the growth of these plants.

West (1935:255 and fig. 1) follows Brown in recognizing only one genotype, in adopting for it the name *Arundinaria tecta* (in a comprehensive sense), and in suggesting that plants producing tall culms owe their superior stature to a pheno-typic response to favorable environmental conditions, especially those conditions that are related to edaphic factors. It appears that plants with very tall culms (illustrated by Harper 1928, fig. 18) have been reported only from the Gulf States. The answer to the question “Does culm size have any taxonomic significance?” remains to be discovered by means of additional field studies, documented by comprehensive, fully annotated specimens. There is no significant difference between subspecies *gigantea* and subspecies *tecta* with respect to the observed maximum heights of culms found in stands of plants of these two taxa which are growing under similar ecological conditions at the northern limits of their currently known distribution. I have had these stands under intermittent observation for 40 years and 16 years, respectively. In the light of morphological and ontogenetic evidence that hybridization has taken place between plants representing these two taxa, it seems possible—even probable—that at least some of the plants with very tall culms may embody what is commonly known as hybrid vigor.

**APPENDAGES OF CULM SHEATHS AND LEAF SHEATHS.**—The morphological expression of the appendages—ligules (*inner and outer*), auricles, oral setae, and blades—apical to culm sheath and leaf sheaths is often more or less variable even as between specimens taken from the same plant. This variability is due, in large part, to ontogenetic factors related to the age of the whole plant, the age range as between young and old culms in the same plant, and the point of origin within the plant and on the culm from which the specimen was taken (see McClure, 1966b:6, par. 1).

**VESTURE OF VEGETATIVE STRUCTURES.**—The incidence, patterns of distribution, and persistence of trichomes in the bamboos are subject to influence by so many (generally unrecorded) variables that it is often difficult to find consistent patterns of vesture in a given structure, as represented by preserved specimens. Pertinent variables that are generally ignored during the collection of bamboo specimens are age (or stature) of the plant; environment and relative vigor of the plant; position on the culm and relative age of the culm from which a given specimen is taken. Weathering, spontaneous abscission, or abrasion, may erase trichomes that were originally present on some structures.

**Loci of Insertion of Inflorescences.**—Until recently (Hitchcock, 1935:29, key) supposed distinct differences in the loci of insertion of inflorescences was commonly offered as a means for the differentiation of two elements of the New World component of *Arundinaria* recognized (but inadequately characterized) under the names *A. gigantea* (Walter) Muhlenberg ssp. *gigantea*.

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**Figure 11.—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. 1. Spikelet with pedicel and inflorescence branch subtended by a small bract, × 1.8; a, base of spikelet showing transitional glumes 1 and 2 and sterile lemma, × 1.8; c, transitional glume 1 (normal), × 3.6; b, transitional glume 2 (variant), × 3.6; e, transitional glume 2 (sterile lemma), variant, × 3.6; r, floret, × 3.6; g, fertile lemma (normal), × 3.6; h, fertile lemma with stipule-like appendages, × 3.6; i, stipule-like appendage, × 10.8; j, palea, × 3.6; k, lodicule complement showing dorsal surface, × 7.2; l, lodicule complement from another flower showing adaxial surface, × 7.2; m, gynoecium and androecium, × 7.2; n, fruit, hilum side, × 7.2; o, fruit, embryo side, × 7.2. All drawings based on D. M. Moore, s.n., Arkansas, USA, 2 August 1947 (US).**
Arundinaria (or A. macrosperma) and A. tecta. It appears that C. A. Brown (1929:316) was the first to focus attention upon the confusion that may result from reliance upon this feature as a source of contrasting characters to support a traditional pattern of taxonomic segregation. I have observed that this is one of the features whose expression—in Arundinaria as well as in many other genera—may change progressively during successive stages of the flowering of a plant or may differ as between very young and very old parts of the plant. Its reliability for the differentiation of taxa of any category must be tested by means of exhaustive and sustained field studies.

**Transitional Glumes Incident at the Base of Each Spikelet.**—Variable also are the transitional glumes at the base of the spikelets. Gilly (1943:301, figs. 2-A, 2-M) illustrated, as characteristic (typical) of his Atlantic type and his Mississippi type, empty glumes that are distinguished, respectively, by size, shape, vesture, marginal ciliation, and venation. These differences, which really exist, are ostensibly of genotypic origin. However, I have found the empty glumes to be not consistently uniform, in their number or in their morphological expression, either in duplicates from the collections cited by Gilly, or in the plants I have chosen as typical, respectively, of the subspecies I distinguish under *Arundinaria gigantea*, sensu lato.

**Lodicules.**—Michaux (1803:74) gave the genus *Arundinaria* but 2 lodicules, which he designated as “appendices.” He, and those who subsequently have quoted this number, apparently overlooked the posterior member of the trio that I have always found to be present in members of this genus. On account of its slightly more distal insertion, however, the posterior lodicule often remains attached to the palea and hidden inside of it, when a floret is dissected. Members of the lodicule complement in *Arundinaria* (and in other genera as well) are subject to such a diversity of unpredictable variabilities that it is often very difficult to discover features that embody expressions sufficiently reliable for descriptive purposes.

**The Sty lar Axis.**—In the neotype of *Arundinaria gigantea* ssp. *tecta*, the fusion of two of the three stylar branches sometimes extends upward to a point noticeably beyond the level at which the first one became free. The appearance produced by this deviation from the usual manner in which branches of the style are disposed may have lent deceptive support to a description that characterizes the genus *Arundinaria* as embracing taxa having two styles (or stylar branches) and taxa having three styles (or stylar branches). Published 139 years ago by Nees (1834:478) this incorrect characterization of *Arundinaria* is still widely copied in the current literature. The error appears to have had its origin in Nees’ allocation to the genus *Arundinaria* (where the number of stylar branches or stigmas is always 3) of several species of other genera (see below the list entitled New World species excluded from the genus *Arundinaria* as herein defined) where the number of stylar branches or stigmas is always 2.

The array of morphological, anatomical, and ontogenetic features whose taxonomic utility I have explored may not complete the list of potentially useful ones. It remains to be seen whether comprehensive studies in anatomy and other disciplines, correlated with intensive field studies, will improve the present taxonomic perspectives on this heterogeneous complex of closely related but distinguishable entities between which biological (genetic) isolation apparently has not yet been fully established.

Reeder (1957, fig. 29) illustrated, in cross-section and sagittal section, the embryo of a fruit from a plant of bamboo native in Ann Arundel County, Maryland, documented under MBG 2762, and identified as *Arundinaria tecta*. Gould (1960:873) reported for a plant from a stand of bamboo native in Walker County, Texas, identified as *Arundinaria gigantea*, a chromosome count of “n equals 24.”

**Checklist of New World Species Excluded from the Genus Arundinaria**

(as herein defined)

The apparently general acceptance of the con-
A. rhizome turned upward apically and terminating in a simple inflorescence, × 0.6; b, leafy and leafless flowering branches from tip of rhizome, × 0.6; c, apex of sheath and reflected blade from midculm node, × 3; d, apex of leaf sheath showing petiole and base of blade, × 6; e, cross-section of rhizome, showing one of the peripheral air canals, × ca. 12. All drawings based on McClure Bamboo Garden specimen no. 2762 (US).
40. *Arundinaria pubescens* is *Arthrostylidium pubescens* Ruprecht.
41. *Arundinaria queko*. See *Aulonemia queko*.
42. *Arundinaria radiata*. See *Aulonemia radiata*.
43. *Arundinaria ramosissima*. See *Aulonemia ramosissima*.
44. *Arundinaria rhizantha*. See *Colanthelia rhizantha*.
45. *Arundinaria schomburgkii* is *Arthrostylidium schomburgkii* (Bennett) Munro.
46. *Arundinaria setifera*. See *Aulonemia haenkei*.
47. *Arundinaria setigera*. See *Aulonemia setigera*.
48. *Arundinaria simpliciuscula*. See *Arthrostylidium simpliciusculum*.
49. *Arundinaria sodiroana*. See *Aulonemia sodiroana*.
50. *Arundinaria standleyi*. See *Arthrostylidium venezuelae*.
51. *Arundinaria trianae*. See *Aulonemia trianae*.
52. *Arundinaria ulei*. See *Aulonemia ulei*.
53. *Arundinaria urbanii*. See *Arthrostylidium urbanii*.
54. *Arundinaria verticillata*. See *Rhipidocladum verticillatum*.
55. *Arundinaria viscosa*. See *Aulonemia viscosa*.

**Athroostachys Bentham**

*FIGURES 19, 20*

_Athroostachys_ Bentham, in Bentham and Hooker, 1883:1208.—Hackel, in Engler and Prantl, 1887:93.—McClure, 1957:200.

_Athroostachys_ [sic] Bentham, 1881:134 [nomen nudum].—McClure, 1957:199.

Plants unicespitose, unarmed. Rhizomes pachymorph. Culms clambering (teste Gardner), the internodes terete and fistular. Primary branch buds at culm nodes apparently solitary (not seen). Initial branch primordia at each midculm node more than one. Branch complement at a midculm node unrestricted pleioclade, the initial component axes (three in _Glaziou_ 13325; illustrated in Figure 19a) each arising from an apparently independent initial primordium, all inserted at approximately the same level, subequal or the middle one noticeably dominant. Leaf blades with transverse veinlets not manifest externally.

Inflorescences semelauctant, solitary, contracted, short-peduncled panicles of capitate or subcapitate form, each inserted at or near the apex of a usually leafy twig, and subtended by a laminiferous sheath; the primary branches of the percurrent rachis inserted distichously in obscurely secund orientation, very short, not prophyllate, either unbranched or bearing one or two subequal short branches; the lowermost primary branches each subtended by a bract, the uppermost one or more not so subtended, the branches of higher orders mostly so subtended; the bracts varying from the liguliform caudate unawned foliar organ up to 3 cm long that subtends the lowermost primary branch, down to short, awned scales 0.5 mm long that subend branches of the higher order. Transitional glumes 2, empty, approximate. Spikelets pedicellate, each containing a single perfect flower, the rachilla potentially disarticulating just below the locus of insertion of the fertile lemma, distally prolonged behind the palea and bearing a depurate sterile anthecium. Lemma of perfect florets free. Spikelets pedicellate, each containing a single perfect flower, the rachilla potentially disarticulating just below the locus of insertion of the fertile lemma, distally prolonged behind the palea and bearing a depurate sterile anthecium. Lemma of perfect florets freely embracing its palea only basally at maturity. Palea gaping antically, narrowly sulcate and 2-keeled dorsally. Lodicles 3, the anterior 2 asymmetrical and paired, the posterior one symmetrical and much smaller. Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit unknown.

**ETYMOLOGY.—**The name _Athroostachys_ (derived from the Greek, _athros_, crowded, and _stachys_, spike) ostensibly alludes to the condensed paniculate branching of the capitule inflorescence.

**TYPE-SPECIES.—**_Athroostachys capitata_ (Hooker) Bentham (in Bentham and Hooker, 1883:1208). _Merostachys capitata_ Hooker (1840:pl. 273–274); Munro (1868:50); Doell (in Martius, 1880:216); Ekman (1913:64). _Chusquea fimbriata_ Steudel (1854:338). Cotypes of _Merostachys capitata_: Gardner 136 (BM); _Tweedie 1324_ (BM); type of _Chusquea fimbriata_: Riedel s.n. (P).

As a result of my own experience, I can understand the difficulty evidently encountered by Bentham in determining the categories to which to...
assign the successive sections of each ultimate branch of the inflorescence and the several sheathing structures that precede the fertile lemma in this bamboo. Having identified as a first empty glume, the bract that subtends the pedicel of a spikelet, and having equated the pedicel, so subtended, to an elongated rachilla, Bentham (in Bentham and Hooker, 1883:1209) wrote as follows: “spicululis re vera sessilibus, sed ob rachillam supra glumam infimam productam pedicellatae apparent.” That is to say “the spikelets are really sessile, but they appear to be pedicellate on account of the elongation of the rachilla beyond the first glume.”

Doell encountered similar difficulties. In his description (in Martius, 1880:216) of the type-species of the genus Athroostachys (under Merostachys capitata Hooker) Doell not only referred to the spikelets as sessile, he gave them two rudimentary empty glumes and two sterile lemmas!

Munro (1868:50) recognized the spikelets of Merostachys capitata as pedicellate, but he saw the two empty glumes as sterile lemmas—by convention called, at that time, “flosculi stelres.”

In his original description of Merostachys capitata, Hooker confessed uncertainty as to its generic affinity, but his recorded observations do not contain the errors noted above.

Under Merostachys capitata, but without designating types, Doell (in Martius, 1880:217) described two variants of Athroostachys capitata, distinguishing them on the basis of width of leaf blades: a latifolia (presumably representing the typical form of the species) and β angustifolia. Munro (1868:50) intimates that the type of Chusquea fimbriata Steudel represents a plant with the character of the latter variant. He adds, however, that it is not clear whether the sterile, leafy branches of the Riedel specimen belong with the flowering branches or not.

Relationships.—I do not find clear evidence of a close affinity between Athroostachys and any other known genus. The strong resemblance of the very prominent radiate oral setae, borne on its leaf sheaths (Figure 19a), to those of many species of Merostachys may have exerted an influence in favor of the initial allocation of the type-species of Athroostachys to the genus Merostachys. This superficial resemblance, however, plus noticeable similarities in a few technical features of the reproductive apparatus, does not add up to a clear indication of close phylogenetic affinity between the type-species of Athroostachys and members of the genus Merostachys.

Distribution.—Recorded only from Brazil, the single known species of Athroostachys has been collected in the immediate vicinity of the city of Rio de Janeiro; near Jacarehy in the state of Paraná; and near Villa Maria in the state of Mato Grosso.

Atractantha McClure, new genus

Figures 21-23

The defects of conventional procedures prevalently followed in the documentation of bamboos for taxonomic purposes are impressively demonstrated by the extreme incompleteness of the first two (and the only available) collections representing this very distinct, hitherto undescribed genus. Representation, in herbaria, of the individual component taxa apparently has not been improved in comprehensiveness during the thirty years that have passed since the first specimen was brought to light!

Plantarum habitus non adhuc relatus. Rhizomatia non adhuc visa (?pachymorpha). Culmi in speciminius suppetenibus haud satiis representati; internodiis teretibus, vel inanibus vel efistulosis. Ramorum complementarum (in speciminius suppetentibus) axes componentes primum prodicti plures, ad circa libram inserti, unusquisque ex pri-mordio distincto enascens (gemmis intactis primordios primos includentibus non adhuc visis); uno alios plus minusve valde dominantli; ramorum com-

Figure 15.—Young culms and roots of Arundinaria gigantea (Walter) Muhlenberg ssp. gigantea (A) and A. gigantea ssp. tecta (Walter) McClure (B) compared. Aa, Base of culm and section of rhizome, with roots, × 0.3; Ab, young culm, full height at age 3 months, showing branches already well developed, × 0.15; Ac, cross-section of root from rhizome, to show air canals, × 15; Ad, cross-section of root from culm base, to show air canals, × 15; Bb, base of culm and section of rhizome, with roots, × 0.6; Bb, young culm, full height, with branches not yet developed, × 0.3; Bc, cross-section of root from rhizome, to show air canals, × 30; Cd, cross-section of root from culm base, to show air canals, × 30. Drawings Aa—Ad based on McClure Bamboo Garden specimen no. 2784 (US), Bb—Bd on McClure Bamboo Garden specimen no. 2762 (US).
components, each arising from a distinct initial
one of the primary components more or less
nodes unrestricted pleioclade when fully developed,
primordium. The branch complement at midculm
ments (at least those seen) containing several initial
articulantes, unaequaeque flosculam perfectam
fra et proxime locum lemmatis insertionis dis-
dis segment0 terminali pro pedicel10 spiculae con-
solitariam habentes, rhachilla post paleam pro-
vulgo praeditae hic nullae. Spiculae deciduae, in-
with transverse veinlets weakly to not at all mani-
complement (exemplified in the isotype specimen of A.

Foliorum lamina venulis transversis extus vel in-
firme vel haud manifestis.

Inflorescentiae iterauctantes, vel capitatae vel
diffusae, earudem ramorum insertione aut dis-
ctica aut sympodiali, rhachidum ramificationibus
omnibus et bracteatis et prophyllatis, omnis rhachi-
dis segmento terminali pro pedicello spiculae con-
sistenti. Glumae transitionales ad basin spicularum
vulgo praeditae hic nullae. Spiculae decidueae, in-
fra et proxime locum lemmatis insertionis dis-
articulantes, unaequeaeque flosculam perfectam
solitariam habentes, rhachilla post paleam pro-
longata in setam gracilem anathceo rudimentario
terminatam. Lemma fertile maturitate saltem pa-
leam suam basi tantum circumentam. Palea apice
bifurcata, dorso sulco angustissimo instrueta, an-
tice leviter imbricata. Lodiculae 3, antiores 2
seae aequales, plus minusve valde asymmetriceae
atque geminatae, posteriorisymmetriceae et anterior-
ribus aliquanto minore. Stamina 3, filamentis fili-
formibus liberisque. Stigmata typice 2 (atypice et
rarissime 3). Fructus maturus adhuc non inventus.

Plants of as yet unrecorded habit. Rhizomes not
yet seen, ?pachymorph. Culms not adequately rep-
resented in the available specimens; the internodes
terete, either fistular or efistular. Branch comple-
ments (at least those seen) containing several initial
components, each arising from a distinct initial
primordium. The branch complement at midculm
nodes unrestricted pleioclade when fully developed,
one of the primary components more or less
strongly dominating the others, all inserted in close
order at approximately the same level. Leaf blades
with transverse veinlets weakly to not at all mani-
fest, externally.

The pachymorph character of the rhizomes (which
are neither represented in the available specimens nor described
by the collector) may be surmised from the strong resem-
blance of the inflated base of the primary axis of a branch
complement (exemplified in the isotype specimen of A. ra-
diate) to a pachymorph rhizome (see McClure 1966b:58,
last paragraph).

It has not been possible to ascertain with certainty from
the available specimens whether the independent primary
primordia incident at each culm node are originally enclosed
in a common prophyllum as one primary bud, or whether
each independent initial primordium corresponds to an in-
dependent primary bud.

Inflorescences iterauctant, of either capitulate or
diffuse form, their branching pattern either dis-
tichous or sympodial, each axis the bracteate and
prophyllate rachis of a pseudospikelet, the terminal
segment of each rachis serving as the pedicel of an
abssicile spikelet. Transitional glumes at the base
of each spikelet none. Spikelets each made pedi-
cellate by the segment of the rachis it terminates,
each spikelet typically containing but a single per-
fuse flower, and disarticulating promptly at ma-
turity just below the locus of insertion of the
lemma, the rachilla prolonged behind the pala in
a bristle-like structure bearing a minute rudiment
of a sterile anathecium. Lemma in functional florets
embracing its pala only basally at maturity. Palea
apically bifurcate, lightly imbricate antically, dor-
sally sulcate, the sulcus very narrow or subtubular.
Lodicules 3, the anterior 2 more or less strongly
asymmetrical, paired and equal, the posterior one
symmetrical and somewhat smaller (at least either
shorter or narrower). Stamens 3, filaments filiform,

The ostensible (approximate) position of the transitional
glumes is here (and in Elytrostachys, q.v.) occupied by what
I now classify as bracts.
Arundinaria gigantea, sensu lato

![Diagram of Arundinaria gigantea, sensu lato, showing putative phylogenetic relationships.](image)

**Figure 17.**-Arundinaria gigantea, sensu lato. Diagrammatic representation of the putative phylogenetic relationships of the principal New World components of the genus Arundinaria. The arrows suggest putative contemporary potential for further introgression or hybridization. The question marks and the broken lines raise the question, "Are there any existing stands of 'pure' gigantea and 'pure' tecta?"

**Figure 18.**-Arundinaria gigantea, sensu lato. Schematic portrayal of some of the quantitative and qualitative relationships visualized as existing between the strongly divergent populations herein categorized as subspecies gigantea and subspecies tecta, respectively, and the populations of intermediates (putative nothomorphs) herein given taxonomic status as subspecies macroperma, based on Arundinaria macroperma Michaux (as to nomenclatural lectotype). The apparent absence of either a clear morphological discontinuity, or an absolute barrier to the exchange of genes, as between the populations comprising these three groups of plants, they are herein interpreted as constituting a polyphyletic species, and given the formal, comprehensive name, Arundinaria gigantea, sensu lato.

**Figure 19.**-Athrostachys capitata (Hooker) Bentham. A, Basal portion of young plant in the vegetative state, showing two culms and the rhizomes to which they are terminal, × 0.6; B, midculm node and branch complement showing three primary branches of independent origin, derived from the primordial meristem enclosed within the prophyll; leaf sheaths with auricles and oral setae not only much less conspicuously developed but of different morphological configuration; empty bracts preceding the base of the terminal segment of each rachis none or one; the slender, spindle-like form of the anthecia; and the number of stamens in each flower limited to 3. While the recorded geographical range of bamboos of the genus Atractantha is limited to the state of Bahia, Brazil, the recorded
geographical range of bamboos of the genus *Elytrostachys* extends from Venezuela to Nicaragua.

**DISTRIBUTION.**—The recorded geographical distribution of the two known species of the genus *Atracanthantha* is limited to the state of Bahia, Brazil. It appears that nothing concerning the ecological features of their respective natural habitats was recorded by the collectors of the only available specimens.

**Key to the Known Species of Atracanthantha**

1a. Leaf blades up to 10.5 cm long and up to 1.0 cm broad; leaf sheaths hispid and hispidulous at first; internodes of leafy twigs hirsute; inflorescences diffuse, their ultimate branches curved; rachises of sympodial insertion, each bearing a bud at a single proximal node; bud-subtending bracts laminiferous ..........................1. *A. falcata*, new species

1b. Leaf blades up to 19.5 cm long and up to 3.5 cm broad; leaf sheaths glabrous from the first; internodes of leafy twigs glabrous; inflorescences capitate, their ultimate branches straight; rachises of distichous insertion, each bearing a bud at each of 2 proximal nodes; bud subtending bracts without leaf blades ...............2. *A. radiata*, new species

1. *Atracanthantha falcata* McClure, new species

*Figure 21*

Plantarum habitus non adhuc relatus. Culmi in specimine suppetenti neque satis representati neque descripti, itaque ignoti. Vaginae culmi et vaginae ramorum primariorum in specimene suppetenti deficientes. Vagina foliorum arcta, initio hispida hispidulaque demum subglabrescens; versus apicem tantum nervis interdum debiliter manifestis; auriculis vel subnullis vel sat evolutis glebosisque; setis oralibus paucis, e basi ad apicem sensim angustatis, omnino glabris vel basin versus versus sparsissime antrorse hispidulaque; ligula interiore subnulla, truncata; ligula exteriore truncata, margine primo sparse et minuttissime ciliolata denique glabrescenti; petiolo vix 2 mm longo, pagina adaxiali hispidulo pagina abaxiali hirsuto; lamina usque 10.5 cm longa et 1.0 cm lata, linear lanceata, apice acuta, bassi rotundata, basin versus utrinsecus sparsissime hirsuta, alibi utrinsecus primo antrorse hispidula, denique sensim glabrescenti; costa mediana et tribus paribus nervorum secundariorum pagina abaxiali sat prominulis; pagina adaxiali inter omnem nervos propinquos profunde et angustissime sulcata, prope marginem externam costa alata penitus instructa; venulis inversis extus haud manifestis.

Inflorescentiae ramos ramuloseque vel foliigeros vel aphyllous terminantes, ob rhachidibus ramificationibus insertionibus sympodialis falcatae diffusaeque. Bractae e quoque rhachidi proditae pleraeque 2, altera gemmam subtendenti altera vacua, approximatae, laminiferae, paucinerves, substantia indurata sed fragilis, dorso sparsim puberulae. Spiculae usque 15 mm longae, maturitate cadentes; ubi unaquaque spicla delapsa reliquit est segmentum terminale rhachidis a bractea persistenti fere omnino vestitum. Glumae transitioales nullae. Anthecia papyracea, glabra nitidaque, nervis extus vix vel haud manifestis. Leuma usque 15 mm longum, lanceatum, attenuate acuminatum. Palea lemmate brevior, secus margines sulci angustissimi antrorse ciliata. Lodiciue diaphaneae, angustae, margine apicem versus sparsim ciliolatae. Antherae apice emarginatae, basi profunde divisae, ubi desiccatae brunneaes. Ovarium vel omnino glabrum vel apice tantum hispidulum. Stylus antrorse hispidulus. Fructus maturus adhuc non visus.

*Figure 20.—* *Elytrostachys capitata* (Hooker) Bentham. A, Diagram of the branching system of the inflorescence; B, a primary branch of the inflorescence, terminating in a spikelet, and bearing two secondary branches each terminating in a single somewhat immature spikelet, × ca. 3; C, a secondary branch subtended by a bract and bearing a solitary spikelet, × ca. 3; D, transitional glumes of a mature terminal spikelet, × ca. 3; E, hermaphrodite floret and (at left) depauperate (sterile) anthecium of a mature terminal spikelet, × ca. 3; F, component structures of a secondary branch of the inflorescence (schematic); G, floral parts in immature state (gynoeicium not visible), × ca. 12; H, mature lodicule complement (the narrow symmetrical one is the posterior member), × ca. 18; I, stamen, × ca. 12; J, gynoeicium, unmodified, × ca. 12; K, gynoeicium, immature fruit stage, × ca. 12. All drawings based on Glaziou 20155 (F).
Plants of unrecorded habit. Culms neither represented nor described in the available specimen. Culm sheaths and sheaths of the primary axes of branch complements lacking in the specimen. Leaf sheaths tight, hispid and hispidulous at first, at length subglabrous; nerves sometimes weakly discernible toward the apex only; auricles either subobsolete or somewhat developed and lumpy; oral setae few, tapered, glabrous throughout or sparsely and antrorse scaberulous basally, very fragile, sooner or later broken off; the inner ligule truncate, not at all or barely exserted; the outer ligule truncate, sparsely ciliate on the margin at first, at length glabrescent and entire; petiole scarcely 2 mm long, hispidulous on the adaxial surface, and hirsute on the abaxial; the blade up to 10.5 cm long and 1.0 cm broad, linear-lanceolate, apically acute, basally rounded, sparsely hirsute on both surfaces at the base, elsewhere antrorse hispidulous at first, then gradually glabrescent on both surfaces; the conventional midrib and three pairs of secondary nerves moderately prominent on the abaxial surface, narrowly and deeply sulcate between all adjacent nerves of the adaxial surface, with a winglike rib from base to tip near the outer margin and, at the same time, the midrib obsolete toward the apex on this surface; transverse veinlets not at all manifest on either surface.

Inflorescences terminating leafy and subleafless branches of all orders; of diffuse, falcate branching, the rachis branches of sympodial insertion. Bracts at the base of each rachis commonly 2, approximate, laminiferous, few-nerved, of indurate but brittle substance, sparsely puberulent dorsally, one mate, laminiferous, few-nerved, of indurate but persistent bract. Transitional glumes at the base of each rachis almost completely clothed in a persistent bract. Transitional glumes at the base of each spikelet none. Anthecia papyraceous, glabrous and lustrous, without externally discernible nerves. Lemma up to 15 mm long, lanceate, attenuately acuminate. Palea shorter than the lemma, the sulcus very narrow, with its edges marked by a row of antrorse cilia. Lodicles diaphanous, narrow, sparsely ciliate on the margin apically. Anthers dark brown when dry, sagittate basally and emarginate apically, the tip of each half curving outward. Ovary glabrous throughout or antrorse hispidulous apically. Style antrorse hispidulous. Mature fruit not yet seen.

Etymology.—The trivial name, falcata, alludes to the curvature that characterizes the branches of the inflorescences. This curvature is construed as induced by the sympodial nature of the branching of the individual rachises.

Holotype.—In the U.S. National Herbarium (no.2040296) collected in a “carrascal” [forest of small trees] at Esplanada, Bahia, Brasil, sometime during 1950-51, by Geraldo Pinto (no. 0681).

2. Atractantha radiata McClure, new species

FIGURES 22, 23

Plantarum habitus collectore neglectus. Culmi in specimine suppediti neque satis representati neque descripsti, ita ignoti. Vaginae culmi et vaginae ramorum primariorum in specimine suppediti deficientes. Vagina foliorum arcta, dorso glabra, opaca, nervis vix aut haud manifestis; auriculis vel nullis vel ad lineam reductis; setis oralibus crebris, superne saltam anfractis, omnino glabris, propter substantiam fragilissimam mox effractis; ligula intemериес ca 1.0 mm longa, dorso granulata, apice asymmetrica, margine integra; ligula exteriore arcuata, angusta, margine primo minute ciliolata demum glabrescenti; petiolo usque 5 mm longo, gracili omnino glabro; lamina usque 18 cm longa et 3.5 cm lata, lanceata, apice acuminata, basi inaequaliter vel rotundata vel subdeltoidea, utrinsecus glabra vel faciei abaxiali pro parte subtiliter puberula; nervis pluribus, validis, tertiaribus a secundaribus haud facile distinguendis, venulis transversis perpaucis inter se late distantibus.

Inflorescentiae capitatae, in ramis ramulos is foliiferis insertae ubi et terminales et laterales, rhachidum ramificationes insertione distichae. Rhachidum segmentum terminale usque 10 mm longum,

Figure 21.—Atractantha falcata McClure. a, Culm internode with branch complement of leafy and leafless flowering axes, × 0.6; b, base of branch complement, × ca. 3; c, apex of leaf sheath and base of leaf blade, × ca. 6; da and db variations in structures forming terminal portion of a flowering twig, diagramatic; r, laminiferous bract from base of a branch of the inflorescence; f, floret, × 6, c, lemma, × 6; h, palea (right) and prolongation of the rachilla (left), × 6; i, lodicule complement, × 15; j, stamen, × 6; k, gynoecium, × 30. All drawings based on Pinto 0681 (US).
apice usque 1.0 mm diametro dilatatum, omnino glabrum laevigatum nitidumque. Bracteae gemmam subtendentes in nodis basalibus omnibus rhachidis vulgo 2, glabrae, substantia delicatissima, infima 2–3 mm, superiore usque 5 mm longa, non laminiferae. Spiculae usque 19 mm longae, omnes maturitate caducae, rhachidi sua tum conspicua relicta apicaceque nuda. Glumae transitionales nullae. Anthecia papyracea, dorso glabra nitidaque, nervis extus hauud manifestis. Lemma usque 17 mm longum, lanceatum, attenuate acuminatum. Palea lemmate parum longior, secus latera sulci angusti ciliolis antrorsis crebris ornata. Lodiculae minimae angustae diaphanae acuminatae secus marginem superne ciliolatae. Anthereae apice obtusae basi conspicue sagittatae, ubi desiccatae vinaceae. Ovaryum superne pilosum. Stylus vel conspicue vel inconspicue hispidulus. Stigmata typice 2 (atypice et rarissime 3). Fructus maturus adhuc non visus.

Plants of unrecorded habit. Culms neither adequately represented nor described in the available specimens. Culm sheaths and sheaths of the primary axis of branch complements lacking in the specimen. Leaf sheaths tight, glabrous, dull, the nerves scarcely or not at all visible externally; auricles either lacking or reduced to a line; oral setae crowded, curved distally, glabrous throughout, very fragile and soon broken off; the inner ligule ca 1.0 mm long, dorsally granulate, apically asymmetrical, the margin entire; the outer ligule arcuate, narrow, the margin minutely ciliolate at first, then glabrescent; petiole up to 5.0 mm long, slender, glabrous throughout; blade up to 18 cm long and 3.5 cm wide, lanceate, acuminate, rounded or subdeltoid at the asymmetrical base, either glabrous on both surfaces, or partly and minutely puberulous on the abaxial surface; many-nerved, the nerves strong, the tertiary ones not easily distinguished from the secondary ones; transverse veinslets few and far removed from each other.

Inflorescences capitate, terminal and lateral to leafy branches and leafy twigs, the branches (rachises) of distichous insertion. Bracts at the base of each rachis typically 2, approximate, glabrous and of very delicate substance, not laminiferous, soon disintegrating, the lowermost one 2–3 mm, the uppermost up to 5 mm long; each subtending a bud. Spikelets up to 19 mm long, readily falling away at maturity, each leaving conspicuous and naked the apex of the terminal segment of its rachis; the latter glabrous, smooth and lustrous, up to 10 mm long and (at its slightly flared apex) up to 1 mm in diameter. Anthecia papery, glabrous and shining throughout, the nerves not at all visible externally. Lemma up to 17 mm long, lanceate, attenuately acuminate. Palea a little longer than the lemma, the margins of the sulcus close together and densely fringed with antorse cilia. Lodicules diaphanous, very small, narrow, the margin apically ciliate. Anthers sagittate basally, obtuse apically, dark purple when dry. Ovary apically pilose. Style conspicuously or inconspicuously hispidulous. Stigmas typically 2, atypically and very rarely 3. Mature fruit not yet seen.

ETYMOLOGY.—The trivial name, radiata, alludes to the radiate orientation of the rachises of the capitate inflorescence.

HOLOTYPE.—In the U. S. National Herbarium (nos. 1910764, 1910765, and 2146781) collected at "Estrada de Bom Gosto a Olivença, Estado da Baía, Brasil, March 15, 1943," by Ricardo de Lemos Fróes (no. 19947). Additional material examined: an isotype from the same collection on loan from the herbarium of the Instituto Agronômico do Norte, Belém, Pará, Brazil (IAN no. 15373).

Aulonemia Goudot

Figures 24–26

Aulonemia Goudot, 1846:75.
Matudacalamus Maekawa, 1961:344.

Plants unicepsitate, unarmed. Rhizomes pachymorph. Culms of small or medium stature and self-supporting, to very tall and upright, the apex erect, nodding, pendulous or scandent; each midculm node bearing a single initial (primary) branch bud, the prophyllum elongating simultaneously with the germination of the bud. Branch complement at midculm nodes typically comprising but a single initial (primary) axis, this dominant over axes of higher orders that may proliferate promptly.
or tardily from usually functional buds borne at its own proximal nodes. Sheath at midculm nodes typically lacking a well-marked (conspicuous) basal girdle; the auricles and oral setae (varying from species to species) entirely lacking to well developed and scaberulous to entirely glabrous. Leaf blades with transverse veinlets not at all to weakly to sometimes strongly manifest externally.

Inflorescences semelauctant, forming typically open panicles, the typically solitary, pulvinate or epulvinate primary ramifications with subtending bracts generally small, obsolete or lacking entirely. Spikelets few-flowered to many-flowered, terminating in a depauperate sterile anthecium. Transitional glumes 2 or 3; when three the uppermost one usually recognizable as a “sterile lemma.” Lemma in functional florets embracing its palea only basally at maturity. Palea broadly sulcate and 2–keeled dorsally, the margins not at all or barely imbricate. Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit (as far as known) an oblong or subfusciform, sulcate, apically micronate caryopsis, the pericarp pergamineous, glabrous, of uniform thickness throughout or sometimes appreciably thicker apically, the sulcus and embryotegium clearly manifest.

ETYMOLOGY.—The name Aulonemia, a Latinized combination of the Greek words, aulos (ancient name of a flute made from a shin bone) and nemos (a forest with pasture for cattle) alludes to (1) the musical instruments (called, in the vernacular, “queko”) made by the native inhabitants from tips of plants of the same species (cf. Goudot, 1846:75, et seq.; R. W. Brown, 1954:112, 554). The terminal element, nemos, makes the natural gender of the word Aulonemia neuter; however, the vernacular trivial name, queko, does not reveal a choice of gender by Goudot. In the absence of any other precedent, Aulonemia was given the feminine gender by McClure and L. B. Smith (in Reitz, ed., 1967:47) when they attached to it the trivial name, lanciflora.

TYPE SPECIES.—Aulonemia queko Goudot.

RELATIONSHIPS.—The array of 24 species here incorporated in Aulonemia imparts to the genus an admittedly polymorphic content. Some of the arms of marked diversity recognizable within the genus as I have circumscribed it involve species that show individual features suggesting the presence of genetic elements shared by several other genera. Aulonemia humillima alone is superficially grass-like in appearance. My study of fragmentary specimens and brief field notes provided by the solitary extant collection of Aulonemia hirtula suggests to me that it probably joins Aulonemia queko in being distinguishable from the other known species of the genus by the possession of relatively large culms with greatly elongated internodes, each followed by two or more nodes, the adjacent ones separated from each other by an aborted subobsolete inter-node. This pecularity—without apparent linkage with any other stable attribute—also appears as a stable attribute of each plant in Glaziophyton mirabile, in a few species of Arthrostylidium (cf. McClure, in Maguire, Wurdack, et al., 1964:2), and quite generally in the known species of Myriocladus. Aulonemia effusa apparently is joined by Aulonemia deflexa in combining other vegetative features that suggest a phylogenetic heritage shared by members of Myriocladus, viz., the frequently delayed germination of primary branch buds at culm nodes and/or the branch bud at the proximal nodes of primary branches (a feature ostensibly related to the strongly indurated vegetative foliar appendages) and the closely appressed culm branches, each comprising conspicuously elevated numbers of short internodes and crowded foliiferous nodes. Aulonemia subpectinata shows a facultative but not obligate tendency to delay the germination of midculm branch buds, and to postpone proliferation from buds at the proximal nodes of the initial branch at midculm nodes. Aulonemia laxa and A. viscosa share this tendency. These two species also share with other species of Aulonemia, and with some species of both Arthrostylidium and Bambusa, a more or less conspicuous vinous tinting or macula-
tion of either vegetative structures alone or reproductive structures alone, or both. To accommodate one of these last two species, Maekawa has proposed (1961:344) the recognition of a monotypic genus, Matudacalamus. In the perspective resulting from my studies in the field and in various herbaria, Matudacalamus laxus Maekawa appears to be a member of one of the several nondisjunct arms of diversity that make up the polymorphic natural genus, Aulonemia. Maekawa expresses the opinion that the "wavy, smooth" oral setae of the leaf sheaths, and the "one-at-a-node" culm branches are two critical features that set off Matudacalamus from other genera he mentions as related to it. However, neither one nor both of these features—nor any other combination of morphological features at present available to me—appears to supply either a reliable (stable) basis, or a justification, for segregating Matudacalamus from Aulonemia at the genus level. The mingling of racemose branching with the paniculate branching of the inflorescences of Aulonemia purpurata gives it a striking resemblance to the branching typical of the inflorescence in Colanthelia cingulata. The type-specimen of A. purpurata, however, does not include any feature that shows other affinities in that direction.

**Distribution.**—The named species here incorporated in Aulonemia gives the genus an aggregate recorded geographical and altitudinal range extending from Brazil, with 10 species at 800-2800 m, through Bolivia, with one species at about 3200 m; Peru, with four species at 1500-3000 m; Ecuador, with one species at 1800-3000 m; Colombia with three species at 2800 m; Guyana, with one species at about 2700 m; Costa Rica, with one species at 1800-2700 m; to Mexico, with one species at about 2200 m.

**Annotated Checklist of Bamboos Here Recognized as Belonging in the Genus Aulonemia**

1. *Aulonemia amplissima* (Nees) McClure, new combination.

*Arundinaria amplissima* Nees, 1834:479.

*Arthrostylidium amplissimum* (Nees) McClure, in Steyermak, et al., 1951:33.

My dissections of florets from the type-collection reveal the number of stigmas to be regularly 2–instead of 3 as recorded by Nees (1834:479) and as reiterated by Ruprecht (1839:27). The number of stigmas is correctly given by Munro (1868:26) and by later authors.

2. *Aulonemia aristulata* (Doell) McClure, new combination.

*Arundinaria aristulata* Doell, in Martius, 1880:165.

*Sieglungia aristulata* (Doell) Kuntze, 1898, III (3): 341.

*Arundinaria mucronata* Munro ex E.-G. Camus, 1912:244.

3. *Aulonemia deflexa* (N. E. Brown) McClure, new combination.

*Arundinaria deflexa* N. E. Brown, 1901:75.

4. *Aulonemia effusa* (Hackel) McClure, new combination.

*Arthrostylidium effusum* (Hackel) McClure, in Steyermak, et al., 1951:31.

5. *Aulonemia glaziovii* (Hackel) McClure, new combination.

6. *Aulonemia goyazensis* (Hackel) McClure, new combination.

*Arundinaria goyazensis* Hackel, 1903a:71.

7. *Aulonemia haenkei* (Ruprecht) McClure, new combination.

*Arthrostylidium haenkei* Ruprecht, 1839:27.

*Arundinaria haenkei* (Ruprecht) Hackel, 1903:69.

*Arundinaria setifera* Pilger, 1905: 145.

8. *Aulonemia herzogiana* (Henrard) McClure, new combination.

*Arundinaria herzogiana* Henrard, in Herzog, 1921: 75.

9. *Aulonemia hirtula* (Pilger) McClure, new combination.

*Arundinaria hirtula* Pilger, 1921:445.

**Figure 24.**—*Aulonemia queko* Goudot. 

A, Leafy flowering branch, \( \times \) 0.6; b, junction of leaf sheath and leaf blade, \( \times \) ca. 1.8; c, insertion of lowermost branch of inflorescence, \( \times \) ca. 6; d, spikelet, \( \times \) 1.5; e, transitional glumes I, II, and III, \( \times \) 3.6; f, sterile lemma, \( \times \) 3.6; g, floret, \( \times \) 3.6; h, fertile lemma, \( \times \) 3.6; i, palea, \( \times \) 3.6; j, lodicule complement, \( \times \) 7.2; k, stamen, \( \times \) ca. 6; l, gynoecium, \( \times \) ca. 12; m, stigmatic processes, greatly enlarged. All drawings based on Goudot no. 1 (P).
10. *Aulonemia humillima* (Pilger) McClure, new combination.

*Arundinaria humillima* Pilger, in Engler and Prantl, 1906:100.

11. *Aulonemia laxa* (F. Maekawa) McClure, new combination.

*Matudacalamus laxus* F. Maekawa, 1961:345.

12. *Aulonemia parvispora* (Presl) McClure, new combination.

*Guadua parviflora*, J. S. Presl, in K. B. Presl, 1825–1835, I (4–5):257.

13. *Arthrostylidium maculatum* Ruprecht, 1839:28.

14. *Arundinaria maculata* (Ruprecht) Hackel, 1903a:69.

15. *Aulonemia paurophora* (McClure) McClure, new combination.

*Arthrostylidium paurophorum* McClure, 1942:170.

16. *Aulonemia radiata* (Ruprecht) McClure and L. B. Smith, in Reitz, ed., 1967:56.

17. *Arundinaria radiata* Ruprecht, 1889:25.

18. *Aulonemia setigera* (Hackel) McClure, new combination.

*Arundinaria glaziouii* var. *macroblephara* E.-G. Camus, 1913, I:41.

Available specimens from collections supplementing the holotype represent this taxon as a species embracing plants somewhat diverse in respect to mature stature and habit, size, shape, texture, and vesture of leaf blades, disposition of the peripheral branches of the inflorescence, and degree of development of awns and dorsal prickles on the lemmas. The wide altitudinal range of the natural distribution of plants, which I recognize as belonging to this species, suggests that some of the phenotypic diversities noted may be ecotypic in origin. More detailed studies in field and laboratory may, however, reveal the existence of genotypic bases for some of the observed diversities.

In 1950 I had an opportunity to visit the type-locality of *Aulonemia queko* near La Trocha in the region of Colombia called Quindio. I found no sign of either the original forest, or the bamboo described by Goudot as *Aulonemia queko*. The mountainside is clothed instead with a beautiful carpet of *Pennisetum clandestinum* Hochstetter ex Chiovanda, a grass native to Africa. I eventually decided that specimens of a plant I had collected in Ecuador (McClure 21429) and in Peru (McClure 21450) represent *Aulonemia queko*, in spite of minor deviations with respect to some of the features given this species by Goudot. This ended my own quarter-century of puzzlement over the riddle presented by Goudot's deliniation of *Aulonemia queko*. It appears that Hackel's action (in Engler and Prantl, 1887) in making *Aulonemia* a synonym of *Arthrostylidium* was induced by Ruprecht's (1889) broad circumscription of *Arthrostylidium*. Again, Hackel's (1903a) transfer of *Alonemia queko* to *Arundinaria* apparently was suggested by Nees' (1834) image of *Arundinaria*. The anguished efforts of Hackel (1903a) and Pilger (in Urban, 1900–1901) to find bases for distinct and stable generic images of the diverse elements that had been, at one time or another, placed in *Arthrostylidium* and *Arundinaria* are brought into focus elsewhere (p. 19).

I identify as representing a species of *Elytrostachys* the specimen *Fendler 2496* (a leafy twig in the vegetative state, preserved at Kew) cited by Munro (1868:46) in his treatment of *Aulonemia queko*. It seems likely that Munro's modification of Goudot's spelling of the specific epithet from queko to quexo misled Hackel (in Engler and Prantl, 1887). In 1903a, however, Hackel restored the original spelling in the combination, *Arundinaria queko*.

16. *Aulonemia radiata* (Ruprecht) McClure and L. B. Smith, in Reitz, ed., 1967:56.

17. *Arundinaria radiata* Ruprecht, 1889:25.

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16. *Aulonemia radiata* (Ruprecht) McClure and L. B. Smith, in Reitz, ed., 1967:56.

17. *Arundinaria radiata* Ruprecht, 1889:25.

18. *Aulonemia setigera* (Hackel) McClure, new combination.

**FIGURE 25.—*Aulonemia queko* Goudot. A, Seedling plant, \( \times 0.6 \); b, twinned culm sheaths, \( \times \) ca. 0.6; c, sterile leafy branch, \( \times 0.6 \); d, apex of leaf sheath and base of leaf blade. \( \times 1.5 \). Drawing A based on McClure 21429A (US), b, c, d on McClure 21429 (US).**
Arundinaria setigera Hackel, 1903a:73.
Arthrostylidium aristatum Glaziou ex E.-G. Camus, 1913, 1:67.

19. Aulonemia sodiroana (Hackel) McClure, new combination.
Arundinaria sodiroana Hackel, 1930a:70.

On the basis of the similarity of the inflorescences in their respective type-specimens, Arundinaria sodiroana was by Hitchcock and Chase made a synonym of Arundinaria patula. Plants of the two taxa may be distinguished, however, even in the nonflowering state by the distinctly prominent fimbriation of the outer margin of the leaf sheaths present in A. sodiroana but lacking in A. patula.

20. Aulonemia steyermarkii (McClure) McClure, new combination.
Arthrostylidium steyermarkii McClure, in Steyermark, et al., 1951:31.

21. Aulonemia subpectinata (O. Kuntze) McClure, new combination.
Arthrostylidium subpectinatum O. Kuntze, 1891, II:760.

22. Aulonemia trianae (Monro) McClure, new combination.
Arundinaria trianae Munro, 1868:25.
Arundinaria multiforma Doell, in Martius, 1880:166.

23. Aulonemia ulei (Hackel) McClure and L. B. Smith, in Reitz, ed., 1967:57.
Arundinaria ulei Hackel, 1903a:75.

Species sedis mihi etiam nunc incertae manet.

24. Aulonemia viscosa (Hitchcock) McClure, new combination.
Arundinaria viscosa Hitchcock, 1927a:79.

Checklist of New World Species Here Excluded from the Genus Aulonemia

1. Aulonemia cingulata. See Colanthelia cingu-

lata.

2. Aulonemia intermedia. See Colanthelia inter-

media.

3. Aulonemia lanciflora. See Colanthelia lanci-

flora.

Bambusa Schreber, Subgenus Guadua (Kunth)
Hackel

Figures 27–29

Genus Guadua Kunth, 1822a:150; 1822b:254.—Ruprecht, 1899:38 [1840:128].—Munro, 1868:70.—Doell, in Martius, 1880:176.—Bentham, in Bentham and Hooker, 1883:1210.—McClure, 1957:203.

Bambusa (Guaduae) Nees, in Martius, 1829:532.

Bambusa Sect. II Guadua, Hackel, in Engler and Prantl, 1887:95.

Bambusa (Guadua) Hackel, 1908c:194.

Plants typically unicespitose and typically armed. Rhizomes pachymorph, the rhizome neck in some species more or less elongated (exceptionally, as in McClure 21438 and 21438-A, to 5 m or more). Culms self-supporting below and apically nodding, pendent, or clambering; internodes cylindrical or terete, in some species shallowly to more or less deeply sulcate above the point of insertion of a bud or a branch complement; hollow, occasionally subsolid (teste Doell, in Martius, 1880:186), exceptionally (as commonly in Bambusa amplexifolia) multiflustral in the lower part of the culm. Branch buds at culm nodes typically solitary, lacking in the midculm range (in plants of some taxa at mature stature). Midculm branch complements lacking in mature plants of some species (as in some strains of Guadua angustifolia; see Bambusa guadua), facultative restricted monoclade in others; in most species unrestricted monoclade, of restricted insertion (the insertion rarely gremial, as in Guadua spinosa; see Bambusa swalleniana) the component axes more or less strongly unequal, the primary axis always dominant. Branches (at least those at lower nodes of the culms) typically thorny in all known species (see exception noted under Bambusa amplexifolia). Leaves (leaf sheath blades) with transverse veinlets not at all visible to more or less clearly manifest externally.

Inflorescences iterauctant, developing by way of pseudospikelets, the primary pseudospikelets either pedunculate or sessile, and forming sparse to more
or less densely crowded, sometimes capitate aggregations, lateral or terminal to leafy or leafless axes. Spikelets typically comprising several perfect florets (only 2 in *Bambusa capitata*) and either tapering apically through progressively reduced sterile anthers, or terminating abruptly in a single depauperate antherodium; the rachilla potentially disarticulating immediately below the locus of insertion of each fertile lemma, and in some species also below a sterile lemma. Transitional sheathing organs inserted between the uppermost bud-subtending bract and the first fertile lemma 0–2 (~3). [In some species of *Bambusa* subgenus *Guadua*, and in other genera in which branches of the inflorescences form pseudospikelets, sheathing structures occasionally reported as “sterile lemmas” sometimes prove to be bracts that are inserted at a level below the base of the spikelet proper, and subtend prophyllate buds that are easily mistaken for abortive florets. Cf. Munro 1868, pl. 5: fig. 4 (such a bud) and fig. 5 (a floret) both referred to by Munro (1868:153) as “flosculi fertilis.”] Lemma in functional florets fully embracing its palea only basally at maturity. Palea sulcate and 2–keeled dorsally, the keels typically more or less prominently winged (not more noticeably winged in *Burchell 7642* [cotype of *Guadua refracta* Munro] than in some species of the Old World genus *Bambusa*), the margins typically not at all or only barely imbricate. Lodicules typically 3, the anterior 2 asymmetrical and paired (sometimes connate), the posterior one symmetrical and smaller. Stamens 6 (3 in *Guadua spinosa*; see *Bambusa swallowiana*), the filaments filiform, free. Style terminating in 2 or 3 (rarely 4) stigmas or (exceptionally) undivided. Mature fruit an oblong or lagenoid, mucronate or distinctly not more noticeably winged in *Burchell 7642* (cotype of *Guadua refracta* Munro) than in some species of the Old World genus *Bambusa*. It also appears that subgenus *Guadua* and subgenus *Bambusa* are not sharply disjunct, with respect to features of the gross morphology of either their vegetative or reproductive structures or with respect to their geographical endemism.

The name *Guadua* is the Latinized version of a vernacular term used by aboriginal natives of Ecuador and Colombia to designate plants of this subgenus.

**Type-species.**—McClure (1957:203) designated *Guadua angustifolia* Kunth as type-species of the genus *Guadua*. This species therefore becomes the type of subgenus *Guadua* of the genus *Bambusa*, but under the name *Bambusa guadua* Humboldt et Bonpland (Figure 27).

**Relationships.**—Bamboos hitherto allocated to the genus *Guadua* have no close relatives among known members of other New World genera. However, their common technical image is very similar to that of members of the Old World genus *Bambusa*. Kunth (1822a:150) failed to cite any morphological feature to differentiate his genus *Guadua* from Schreber’s genus *Bambusa*. The first promising effort in this direction was made by Munro (1868:76) in these words: “The upper palea in *Guadua* has the keels much more distinctly and broadly winged than in any *Bambusa*.” However, the trivial taxonomic significance Munro attached to this feature is clearly apparent in the following sentence: “This genus is kept up by most authors; but I am unable, in the absence of a perfect fruit, to point out any good distinction, except a well-marked one in geographical distribution, between it and *Bambusa*.” Munro then lists the features proposed by other authors as distinctive of *Guadua* as a genus, and shows that not one of them provides *Guadua* with a clearly distinct morphological relation to *Bambusa*. My own observation is that the keels of the palea are not more noticeably winged in *Burchell 7642* (cotype of *Guadua refracta* Munro) than in some species of the Old World genus *Bambusa*. It also appears that subgenus *Guadua* and subgenus *Bambusa* are not sharply disjunct, with respect to features of the gross morphology of either their vegetative or reproductive structures or with respect to their geographical endemism.

By 1829 Nees (in Martius, p. 582) had already made “Guaduace” an uncategorized division of the genus *Bambusa*. This proposal was more fully developed by Nees in *Linnaea* (1834:465).

In 1887 Hackel (in Engler and Prantl, p. 95) proposed the formalization of the status of *Guadua* as Section II under *Bambusa*; in 1903 he (1903c: 194) continued the subordination of *Guadua* under...
the genus *Bambusa* and proposed the elevation of its status from section to subgenus.

**Distribution.**—As documented at present, the recognized New World components of this arm of the genus *Bambusa* exhibit an aggregate recorded distribution extending from Mexico to all countries of Central and South America, excepting Chile. They reach their greatest spontaneous development under mesophytic conditions in frost-free areas at elevations not known to greatly exceed 1500 m. Some species show a remarkable tolerance of, or ability to thrive in, soil that is saturated with water. I have observed that, in the general vicinity of Chinchiná, Department of Caldas, Colombia, plants of *Bambusa guadua* occupy, spontaneously, practically every available type of ecological niche.

*Guadua philippinensis* Gamble, an Old World species of diverse, as yet incompletely known, affinities, is known only by the type-collection (*C. V. Piper* 473). This collection was made 15 May 1911, at Mati, District of Davao, Island of Mindanao. No information concerning the ecological setting of the plant has come to light.

Agrostologists who find it difficult to accept Hackel's disposition of the genus *Guadua* here adopted may be helped by the following words of Davis and Heywood (1963:106) quoted from their treatment of the category "genus": "When in doubt as to whether to accord generic rank to a group, there is much to be said for the subgenus as a suitable category; it draws attention to the group in the classification, and at the same time allows people to continue to use the old binomial." Final emphasis added.

**Annotated Checklist of Binomials**

**Recognized Herein as Belonging to the Subgenus Guadua**

**New World Bamboos**

Improved perspectives resulting from the development of more complete images of the taxa represented by some of the binomials in the suggested synonymies may give occasion for future revision in some cases.

1. *Bambusa aculeata* (Ruprecht) Hitchcock [as *Bambos*], 1913:387 (Figure 28 k, l).

*Guadua aculeata* Ruprecht ex Fournier, 1881:150. *Guadua aculeata* var. *liebmanniana* E.—G. Camus, 1913, 1:112.

*Guadua inermis* Ruprecht ex Fournier, 1881.129. *Guadua intermedia* Ruprecht ex Fournier, 1881:130.

*Bambusa aculeata* appears to represent a northern extension of *Bambusa guadua* (*Guadua angustifolia*) clearly distinguishable from the latter only by means of vegetative features. I have not been able to distinguish *Guadua inermis* from *Guadua aculeata* by means of inflorescences in their respective type-collections. Contrary to an assertion in the original description of *Guadua inermis*, the lemma in the type-specimen are entirely glabrous, just as they are in the type of *Guadua aculeata*. If Fournier's descriptive term "inermis" and the vernacular name "caña mansa" quoted by him are authentic, then *Guadua inermis* may prove to be an unarmed form of *Guadua aculeata* from the northern range of that species. I do not at present see any basis for giving a distinctive taxonomic status to either *Guadua inermis* or *Guadua aculeata* var. *liebmanniana*.

In 1877 Fournier (p. 198) published a paper entitled "De la modification des envelopes florales des Graminées suivant le sexe de leurs fleurs" in which he referred to the spikelets of *Guadua aculeata* Ruprecht as embodying "a form of polygamy." When, however, Fournier cited *Guadua aculeata* as the source of an illustrative example, this binomial had not yet been validated or given taxonomic content by the publication of a formal description.

For descriptions of this same phenomenon as observed in bamboos of the genera *Schizostachyum* and *Gigantochloa*, among others, see McClure (1934:54ff; 1966b:100, 117) and Arber (1934:193). Instead of being considered as a reliable source of taxonomic characters, however, this morphological deviation should perhaps be seen simply as representing progressive transitional morphogenetic
changes in sexual expression that become potential during the later stages of the ontogeny of indeterminate (iterauctant) inflorescences in several bamboo genera.

2. *Bambusa amplexifolia* (Presl) Schultes f., in Roemer and Schultes, 1830:1348.

*Guadua amplexifolia* Presl, 1830:256.

Plants of *Bambusa amplexifolia* are very thorny throughout most of the known range of the species (which extends from Venezuela and Colombia to Mexico) but progressively less thorny forms appear from El Salvador northward, and a completely unarmed form is found in the State of Sinaloa (specimen at US under McClure 21200). No mention of thorns appears in the original description of this species, the type of which was collected by Haenke from an unrecorded locality in Mexico. Cf. similar notes regarding *Guadua* inermis under *Bambusa* aculeata.

3. *Bambusa barbata* Trinius, 1835:627.

*Nastus barbatus* (Trinius) Ruprecht, 1839:41, pl. 17.

4. *Bambusa capitata* Trinius, 1835:626; 1836, III: pl. 337.

*Schizostachyum capitatum* (Trinius) Ruprecht, 1839 [1840: 136–137, pl. 17, fig. 46.]

*Guadua ? capitata* (Trinius) Munro, 1868:81.

Chromosome counts of 2n=ca. 36 and 2n=46 were reported by Gould and Soderstrom (1967, under 1961, Art. 64.)

5. *Bambusa distorta* Nees, 1834:470.

*Guadua distorta* (Nees) Ruprecht, 1839:113, pl. 16; fig. 59.

6. *Bambusa glazioii* Hackel, 1903:c:194.

*Guadua glazioii* (Hackel) E.—G. Camus [as glazioii], 1913, I:108.

7. *Bambusa glomerata* (Munro) McClure, new combination.

*Guadua glomerata* Munro, 1868:79.

Non invalidatus by *Bambusa glomerata* Royle ex Munro (1868:147) [nom. nud. ex sched.] as synonynm of *Dendrocalamus strictus* Nees. Cf. icBN, 1961, Art. 64.

8. *Bambusa guadua* Humboldt et Bonpland, 1808:63, pl. 20 (Figures 27, 28a-j, 29).

*Guadua angustifolia* Kunth, 1822b:253.

*Nastus guadua* (Humboldt et Bonpland) Sprengel, 1825, vol. 2:113.

9. *Bambusa latifolia* Humboldt et Bonpland, 1808:67, pl. 21.

*Guadua latifolia* (Humboldt et Bonpland) Kunth 1822:254.

The description under the name *Guadua latifolia* in Munro (1868:78), and the illustration under the same name in Doell, in Martius, (1880:pl. 49), are based on Spruce 1954, a collection that appears to represent a species quite distinct from the plant represented by the nomenclatural type of *G. latifolia*.

*Nastus latifolia* [] (Humboldt et Bonpland) Sprengel, 1825, II:113.

10. *Bambusa longifimbriata* (E.—G. Camus) McClure, new combination.

*Guadua longifimbriata* E.—G. Camus, 1913, I:113.

A specimen from the type-collection of this species (*Glaziou 5717*) (US from C, where it is labeled *Guadua refracta* Munro) differs from the type of the latter species by having the keels of the palea prominently winged.

11. *Bambusa longifolia* (Fournier) McClure, new combination.

The basionym of the combination *Arthrostylidium longifolium* (Fournier) E.—G. Camus (1913, I:68) is *Arundinaria ? longifolia* Fournier (1881:131) the type of which is a sterile Liebmann specimen cited by Fournier as "Jicaltepec, Aprili, Lieb." In his description of *Arthrostylidium longifolium*, Camus (1913, I:68) combines with his verbatim French translation of Fournier's description of *Arundinaria longifolia* a description, in French, of a flowering...
specimen which he illustrates and cites as “Las Sedas. Altitude 2000 m. (Pringle).” Available material from the type and other collections of *Arundinaria longifolia* Fournier matches specimens of *Arthrostylidium spinosum* Swallen (1938:6) whose type I identify as a species of *Bambusa* subgenus *Guadua*. The name now becomes *Bambusa longifolia*. The Pringle specimen cited by Camus (of which I have three sheets available at US) turns out to be a duplicate of Pringle 6742. This I identify as belonging to the newly described subgenus *Otatea* of the genus *Yushania*. Meanwhile numerous specimens of bamboos pertaining to this new subgenus are filed in herbaria around the world under the name “*Arthrostylidium longifolium* (Fournier) E.-G. Camus.”

12. *Bambusa macrostachya* (Ruprecht) McClure, new combination.
*Guadua macrostachya* Ruprecht, 1859:39, pl. 15: fig. 35.

13. *Bambusa maculosa* Hackel, 1903c:196.
*Guadua maculosa* (Hackel) E.-G. Camus, 1913: I:106.

14. *Bambusa paniculata* (Munro) Hackel, 1903c: 195.
*Guadua paniculata* Munro, 1868:85.

15. *Bambusa paraguayana* (Doell) Bertoni, 1918: 159.
*Guadua paraguayana* Doell, in Martius, 1880:179.

16. *Bambusa refracta* (Munro) McClure, new combination.
*Guadua refracta* Munro, 1868:84.

17. *Bambusa spinosissima* Hackel, 1903c:197.
*Guadua spinosissima* (Hackel) E.-G. Camus, 1913; 1:112.

18. *Bambusa superba* (Huber) McClure, new combination.
*Guadua superba* Huber, 1904:479.

19. *Bambusa walleniana* McClure, new name.
*Guadua spinosa* (Swallen) McClure, 1954:82 (not

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**SMITHSONIAN CONTRIBUTIONS TO BOTANY**

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20. *Bambusa tagoara* Nees, in Martius, 1829:532. *Guadua tagoara* (Nees) Kunth, 1834:611.

21. *Bambusa tessmannii* (Pilger) McClure, new combination.
*Guadua tessmannii* Pilger, 1924:124.

22. *Bambusa tomentosa* (Hackel and Lindman) McClure, new combination.
*Guadua tomentosa* Hackel and Lindman, in Lindman, 1900:20, pl. 12.

23. *Bambusa trinii* Nees, 1834:469. *Guadua trinii* (Nees) Nees ex Ruprecht, 1839:40, pl. 15, fig. 38.

24. *Bambusa riograndensis* Dutra, 1938:147, fig. 1. *Guadua riograndensis* (Dutra) Herter, 1941:49.

25. *Bambusa venezuelae* (Munro) McClure, new combination.
*Guadua venezuelae* Munro, 1869:86.

26. *Bambusa virgata* Trinius, 1835:624. *Guadua virgata* (Trinius) Ruprecht, 1839:40.

27. *Bambusa weberbaueri* (Pilger) McClure, new combination.
*Guadua weberbaueri* Pilger, 1905:152.

28. *Bambusa philippinensis* (Gamble) McClure, new combination.
*Guadua philippinensis* Gamble, 1913:208.

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**OLD WORLD BAMBOOS**

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**Checklist of Names of Congeneric New World Taxa of Unresolved Specific Status**

1. *Bambusa chacoensis* Rojas, 1918:157.
2. *Guadua fascicularis* Doell, in Martius, 1880:186.
3. *Guadua lindmani* E.-G. Camus, 1913:1113.
*Guadua sp.*, Lindman, 1900:22, pl. 11c.
4. *Guadua polyclados* Doell, in Martius, 1880:182.
Annotated Checklist of New World Species Here Excluded from the Subgenus Guadua

1. *Guadua exalata* Doell (in Martius, 1880:181) is *Arthrostylidium longiflorum* Munro (1868:41).

2. *Guadua ? flabellata* Fournier (1881:131). *Arundinaria flabellata* (Fournier) McClure (in Maguire, Wurdack, et al., 1964:162), species sedis mihi etiam nunc incertae; fortasse ad genus *Yushaniam* subgenus *Otateam* attinit.

3. *Guadua pallescens* Doell (in Martius 1880:186) syn. *Bambusa pallescens* (Doell) Hackel (1908:160), identified by Bentham (in Bentham and Hooker, 1883:1210) as *Bambusa pallida* Munro, is *Bambusa tuloides* Munro (1868:93), an Old World species naturalized in Brazil.

4. *Guadua parviflora* J.S. Presl (in K. B. Presl, 1830:257). See *Aulonemia paroiflora* (Presl) McClure.

5. *Guadua perligulata* Pilger (in Diels, 1937:8) is *Chusquea perligulata* (Pilger) McClure, new combination.

**Chusquea Kunth**

Figures 30, 31

*Chusquea Kunth, 1822a:151; 1822b:254; 1829:138; 1833:427.*—Nees, 1834:484.—Endlicher, 1836:102.—Ruprecht, 1839:30 [1840:120].—Munro, 1868:52.—Doell, in Martius, 1880:194.—Bentham, in Bentham and Hooker, 1883:1209.—Hackel, in Engler and Prantl, 1887:93.—McCullogh, in Swallen, 1955:86; 1957:202.

*Rettbergia* Raddi, 1823:17.—Nees, in Martius, 1829:535.—Nees, 1834:486.—McClure, 1957:207.

*Dendrogrrostis* Nees [as subgenus], 1834:487.—McClure, 1957:202.

Plants of unicespite or multicespite or diffuse habit; either unarmed throughout or (as in *C. fendleri* Munro; cf. McClure, 1966b, fig. 15) the culms armed by a ring of short, sharp, aborted roots at several of their lower, above-ground nodes. Rhizomes either wholly pachymorph (as in most known species) or wholly leptomorph (as in *C. simpliciflora* Munro) or both pachymorph and leptomorph in the same plant (as in *C. fendleri*). Culms either self-supporting below and broadly arched or clambering above (as in *C. scandens* Kunth), or wholly dependent upon external support from other vegetation (as in *C. simpliciflora* Munro); the internodes pithy to the very center and (as in *Zea mays* L.) lacking a natural lumen, cylindrical or terete, in most species shallowly sulcate for some distance above the locus of insertion of a complement of buds or branches—rarely (commonly in some variants of *C. pinifolia* Nees) sulcate or noticeably flattened all the way from one node to the next. [In some species, as in *C. pittieri* Hackel, the pith in old culms may become shrunken or broken down, leaving an irregular central passage without a membrane-lined inner surface. This same change may explain discrepant descriptions of *C. uruguayensis* Arechavaleta, whose culms are described by Arechavaleta (1897:546) as solid, and by Parodi (1941:334) as hollow.] Branch complement at midculm nodes unrestricted pleio-clade, the initial components—developed from separate primary buds of two size categories in constellate insertion, the smaller ones usually many (rarely only 2)—comprising axes of two size categories (major and minor) the major ones solitary and (when developed) strongly dominant (similar in form to the mother culm and, particularly in scandent species, often approaching it in size) the minor ones (rarely only 2) usually numbering several to many and, when many hiding the large central bud from sight when it does not germinate. Leaves (leaf sheath blades) with transverse veinlets in some species (as in *C. lanceolata* Hitchcock) clearly evident, in others obscure, and in most species not at all manifest, externally.

Inflorescences semelauctant, terminal to leafy or leafless branches, or to the culm itself, typically with a strong, variously branched central axis, usually paniculate, rarely either racemose or capitulate; prophylls and bracts usually lacking entirely, bracts subobsolete in a few species (e.g., *C. bambusaeoides* (Raddi) Hackel). Transitional glumes at the base of the spikelet usually 4 (rarely 5, as sometimes in *C. bambusaeoides*): I and II "empty glumes" (these in some species sub obsolete), III, IV and (V) "sterile (empty) lemmas." Spikelets typically containing but one perfect floret—occasionally 2 in some species (e.g., *C. andina* Philippi, teste Munro (1868:58); and *C. tenella* Nees, teste Nees (1884:493); specimens under *McClure 21292* (*C. oxylepis* (Hackel) Ekman) commonly show an aborted floret in the axil of transitional glume IV ("sterile lemma" IV)—the rachilla...
very short and not prolonged behind the palea of the terminal perfect floret. [My personal impression in this regard agrees with that expressed by Bentham (in Bentham and Hooker, 1883:1209) in Latin: “According to Doell, the rachilla in C. tenella and other species [of this genus] is prolonged beyond the apical floret a condition which we have not seen in our specimens.” (Emphasis added by F. A. M.)] Fertile lemma fully embracing its palea only basally at maturity. Palea gaping antically, in most species dorsally convex, narrowly sulcate and more or less noticeably 2-keeled toward the usually emarginate or bidentate or bimucronate apex, rarely (as in C. capitata Nees) very similar to its lemma, i.e., compressed and 1-keeled (not sulcate) dorsally and apically entire. Lodicules 3, the anterior two appreciably asymmetrical and paired, the posterior one symmetrical and smaller. Stamens 3, the filaments filiform, free. Stigmatic branches 2, one of them rarely (as sometimes in C. scandens Kunth, for example) divided above the point of its union with the other one. Mature fruit (rarely found) a small, oblong or fusiform caryopsis with a longed beyond the apical floret a

Plants of the closely related genus Swallenochloa, are distinguished from plants of the genus Chusquea by the relatively weak development of their rhizomes; the usually stiff, erect culm habit; the hollow structure of the culm internode; the typically horizontal and level (not constellate) insertion of branch buds at culm nodes, and the correspondingly different branching habit of the culm; the more or less strongly xeromorphic (leathery) texture of the leaf blades. The very narrow profile of the inflorescences of Swallenochloa is not diagnostic, however.

The existence of noticeable affinities or similarities between members of the genus Chusquea and members of the genus Arundinaria is suggested by Trinius (1835:617), Baillon (1894:253), and Beadle (in Bailey, 1914:449). As far as the reproductive apparatus is concerned, similarities between members of these highly dissimilar genera are limited to some aspects of the lodicules and the stamens. As far as elements of the vegetative apparatus are concerned, the only noticeable similarities are shown by those species of the respective genera that share the following three features: (1) lepto-morph rhizomes; (2) leaf blades with conspicuous transverse venation; and (3) frost-hardiness. These three features are not known to be associated in any species of any one of the other bamboo genera of the New World. I do not construe their association together in exceptional species of Chusquea to be evidence of a close phylogenetic relationship or affinity between the two genera, Chusquea and Arundinaria.

Nees (1834:467, 468) gave Chusquea Kunth four subgenera: (1) Platonia (Kunth) with C. (Platonia) elata (Kunth) listed as type; (2) Chusquea with C. scandens Kunth listed as type; (3) Rettbergia (Raddi) with C. (Rettbergia) gaudichaudii Kunth listed as type; and (4) Dendragrostis Nees with C. (Dendragrostis) pinifolia Nees listed as type. Subsequent authors have not maintained taxonomic status for the subgenera proposed by Nees. The originally monotypic content of Platonia Kunth (non Platonia Martius) was restored by Meisner

Figure 30.—Chusquea scandens Kunth. A, Leptomorph rhizome turning up to form a culm, × 0.6; B, lower segment of a small culm with buds, × 0.6; C, midculm node showing complement of branch buds, front view, × 1.2; D, same, in profile, × 1.2; E, apex of culm sheath, abaxial view, × 1.2; F, apex of culm sheath, adaxial view, showing ligule; G, midculm node with fully developed branch complement, × 0.6; H, auxiliary branch, showing leaves at apex, branch sheath, and a complement of branches emerging extravaginally, × 0.6; I, apex of leaf sheath with petiole and base of leaf blade, × 12. All drawings based on McClure 21414 (US).
Inflorescence with persistent transitional glumes ("emptying a primary branch, branches of secondary order, × 0.6; c, terminal ramifications of inflorescence with persistent transitional glumes ("empty glumes" 1 and II), × 7.5; d, spikelet with its pedicel, × 7.5; e, transitional glumes III and IV ("sterile lemmas"), × 7.5; f, lemma, × 7.5; g, palea, × 7.5; h, lodicule complement, × 9; i, stamen, × 7.5; j, gynoecium, × 9; k, terminal branches of inflorescence, × 7.5; l, fruit, embryo side, × 7.5; m, fruit, hilum side, × 7.5; n, fruit, embryo side, × 7.5; o, fruit, hilum side, × 7.5; p, fruit, embryo side, × 7.5; q, diagram of spikelet. Drawing A-J based on McClure 21414 (US), K on Bonpland 3386, type-species (P), l, m on Fosberg 22386 (US), and n-p on McClure 21292 (US).

(1843, I:426; 1843, II:325) to its original status as genus, with a new name, Neurolepis.

As I visualize the natural boundaries of the genus, Chusquea embraces taxa that give it a polymorphic composition. One arm of this diversity induced Raddi to publish Rettberga as a monotypic genus. As observed by Nees (in Martius, 1829:536) a number of the features attributed to the type-species of Rettberga by Raddi (1823:18, pl. 1: fig. 1) suggest faulty observation on the part of its author. Subsequent study of numerous available specimens collected from the type-locality confirms the opinion—first expressed tentatively by Nees (in Martius, 1829:536) and tacitly affirmed by Kunth (1830:331), Ruprecht (1839:34), Munro (1868:67), and Doell (in Martius, 1880:207)—that the type-species of Rettberga does not fall outside the natural boundaries of the genus Chusquea. However, the trivial name of the type-species of Rettberga (R. bambusoides [as bambusaeoides] Raddi) was not formally incorporated in the genus Chusquea until its claim to priority over C. gaudichaudii Kunth was given expression in the combination C. bambusoides (Raddi) Hackel (in Wettstein, ed., 1908:81).

Chusquea bambusoides is joined by C. capituliflora, C. sellowii, and C. capitata to form a clearly recognizable but apparently not clearly disjunct arm of diversity, in which C. capitata stands most sharply distinguished from other members of the genus by the form of the palea, which here approaches that of the lemma. Another arm of diversity is rendered clearly disjunct from Chusquea proper principally by distinctive features of the vegetative apparatus. It is represented by Chusquea depauperata, C. spicata, C. subtessellata, and C. weberbaueri which now constitute the published content of the genus Swallenochloa, q.v.

Chusquea pinifolia (Nees) Nees (1834:490). Arundinaria pinifolia Nees (in Martius, 1829:525), represents a taxon of special interest. Its polymorphic character finds expression in the following validly published names: C. bacuifera Alvaro da Silveira (1919:99), C. heterophylla Nees (1885:488) with three variants named by Doell (in Martius, 1880:207), and C. pinifolia var. heterophylla (Nees) Hackel (in Wettstein, ed., 1908:82). Since, however, they apparently have not been shown to represent morphologically disjunct entities, they are currently regarded as synonyms of a highly polymorphic C. pinifolia. In the habit of the plants, the form of the midculm branch complement, and the form of the inflorescences, some of the divergent forms of C. pinifolia bear superficial resemblance to members of the genus Swallenochloa. Their basic morphology, however, keeps plants of this taxon clearly within the natural limits of the genus Chusquea, their aggregate range in distribution extending from slightly above sea level to elevations (in the midtropics) reaching 3200 m, in generally mesophytic sites between about 47°S latitude and Mexico, and on islands adjacent to this area.

Distribution.—Documented in herbaria by specimens of more than 100 described species, the genus Chusquea is represented by one or more of these in the indigenous flora of every country of the New World from Mexico to Chile and Argentina, and that of many of the islands as well.

The aggregate altitudinal coverage recorded for its members carries the genus from approximately sea level to the lower limit of perpetual snow. According to Munro (1868:61) Jameson (in the field notes to a collection under Jameson 9) recorded the altitudinal range of Chusquea fendleri in Ecuador as "a litore usque ad 12,000 ped. s. m." Chusquea scandens Kunth was collected by W. H. Camp (E–1778 and E–1824, US) in Ecuador at an elevation of 11,000 ft (3300 m) and C. andina Philippi was collected by Germain in Chile "ad limitem nivis perpetuae" (Munro, 1868:58).

Ranges of tolerance and of requirements, in terms of ecological factors, are not adequately recorded either in the available field notes or in the literature; but the entire gamut covered by members of the genus Chusquea must be very comprehensive. According to Brade (1956) as re-
viewed by F. Markgraf (1958) the zone occupied by *Chusquea pinifolia* (Nees) Nees is recognizable on Itatiaia at elevations ranging from 2000 to 2400 meters. [Hackel (in Wettstein, ed., 1908:82) gives the altitudinal range of *C. pinifolia* on Itatiaia as 1300 m to 2750 m.] The meteorological station at 2200 meters recorded an annual rainfall (as the average for a period of 20 years) of 2417 mm (roughly 95 in) and a temperature range between an average low of 7° and an average high of 11° C; extremes recorded: -6° and 35° C. Brade lists the following taxa that appear along with *Chusquea pinifolia* as characteristic of the vegetation of this high tableland: *Cortaderia modesta*, *Paepalanthus*, *Xyris*, *Sisyrinchium*, *Clematis*, *Fuchsia*, *Buddleia speciosa*, *Fragaria chiloensis*, *Valeriana*, *Mikania*, and *Erigeron*.

Weberbauer (1911 [1945:146]) summarizes his notes on the ecological role of *Chusquea* in the vegetation of Peru as follows (trans. by FAM):

*Chusquea* is a genus characteristic of the cloud forest ("Ceja de la Montaña"); in the north it extends over to the western side of the Andes. In its true center of distribution it sends out extensions that reach down as far as the tropical forest. The shrubby species of the genus *Chusquea* exert a conspicuous influence on the physiognomy of the plant formations of the cloud forest, and here and there occupy large areas, suppressing other plants. Their slender branches, from whose nodes emerge masses of twigs and dense foliage, support themselves on other woody plants, from which they hang down in beautiful curves.

It should be borne in mind that Weberbauer's concept of the genus *Chusquea* included the species treated herein under *Swallenochloa*, q. v. These are referred to by him as "shrubby species" (vide infra.). On the other hand, his concluding sentence refers to species I retain in *Chusquea*.

Annotated Checklist of Bamboo Here Recognized as Belonging to the Genus *Chusquea*

1. *Chusquea abietifolia* Grisebach, 1864:529. *Arundinaria (Arthrostylidium?) microclada* Pilger, in Urban, ed., 1907:289.

   Apparently this taxon is known only by vegetative material from the type-locality; the nomenclatural type-collection remains undesignated. Pilger's uncertainty as to the correct generic disposition of this taxon is patent.

2. *Chusquea acuminata* Doell, in Martius, 1880: 204.

3. *Chusquea tenuis* Glaziou ex E.-G. Camus, 1913, 1:90.

4. *Chusquea affinis* Munro ex E.-G. Camus, 1913, 1:80, pl. 60: fig. B.

6. *Chusquea anelytroides* Ruprecht ex Doell, in Martius, 1880:206.

7. *Chusquea argentia* Parodi, 1941:339, pl. 24: fig. 4.

8. *Chusquea bambusoides* (Raddi) Hackel, in Wettstein, ed., 1908:81.

*Retterbia bambusaeoides* Raddi, 1823:18, 57, pl. 1: fig. 1.

9. *Chusquea gaudichaudii* Kunth, 1829:138. Nomen nudum.

10. *Chusquea gaudichaudii* Kunth, 1830:331–332, pl. 78.

*Nastus bruneus* A. N. Desvaux, 1831:211.

*Nastus bruneus* and some other collections have the awns of the empty glumes antrorse ciliate or antrorse scabrous on the dorsal keel of the awn. This is a variable character.

11. *Chusquea carinata* Desvaux, 1881:132.

12. *Chusquea carinata* var. *minor* McClure and Smith, in Reitz, ed., 1967:25.

13. *Chusquea capituliflora* var. *pubescens* McClure and Smith, in Reitz, ed., 1967:28.

14. *Chusquea culeou* Desvaux, in Gay, 1854:450.
16. Chusquea culeou forma longiramea Parodi, 1941:343.
17. Chusquea cumingii Nees, 1835:487.
18. Chusquea decolorata Munro ex Parodi, 1945:65–66.
19. Chusquea deficiens Parodi, 1941:335–338, figs. 2,3, and pl. 22.
20. Chusquea delicatula Hitchcock, 1927b:309–310.
21. Chusquea discolor Hackel, 1903b:155.
22. Chusquea dombeiana Kunth, 1832:553, pl. 191.
23. Chusquea fasciculata Doell, in Martius, 1880:202–203, pl. 54.
24. Chusquea fendleri Munro, 1868:61.
25. Chusquea fernandeziana R. A. Philippi, 1873:577–578. [May be the same as C. Zigulata Munro.]
26. Chusquea galeottiana Ruprecht ex Munro, 1868:59.
27. Chusquea gracilis McClure and Smith, in Reitz, ed., 1967:43–44, pl. 8i-k.
28. Chusquea heydei Hitchcock, 1927a:80–81.
29. Chusquea huantensis Pilger, 1920:29–30.
30. Chusquea ibiramae McClure and Smith, in Reitz, ed., 1967:40–42, pl. 8d-f.
31. Chusquea inamoena Pilger, 1905:150–151.
32. Chusquea jamesonii Steudel, 1854:337.
33. Chusquea juergensii Hackel, 1909a:325–326.
34. Chusquea lanceolata Hitchcock, 1935:145–146.
35. Chusquea lehmannii Pilger, 1899:35–36.
36. Chusquea leptophylla Nees 1835:489. Arthrostylidium trini sensu Steudel, 1854:336, in part, non Ruprecht, 1889:119. Arthrostylidium (?) leptophyllum (Nees) Doell, in Martius, 1880:175–176.
37. Chusquea liebmannii Fournier, 1881:132.
38. Chusquea ligulata Munro, 1868:62.
39. Chusquea linearis N. E. Brown, 1901:76. [Probably equals C. pinifolia (Nees) Nees.]
40. Chusquea longifolia Swallen, 1940:210.
41. Chusquea longipendula Kuntze, 1898, III (8):348–349.
42. Chusquea lorentziana Grisebach, 1874:249–250.
43. Chusquea macrostachya R. A. Philippi, 1896:350–351.
44. Chusquea mexicana Hackel, 1902:256.
45. Chusquea meyeriana Ruprecht ex Doell, in Martius, 1880:203–204. C. meyeriana is closely related to C. acuminata Doell but differs in the pubescent leaf blades, prominent external ligule, reflexed inflorescence branches, and smaller spikelets.
46. Chusquea mimosa McClure and Smith, in Reitz, ed., 1967:37.
47. Chusquea montana R. A. Philippi, 1864:298–299.
48. Chusquea muelleri Munro, 1868:65.
49. Chusquea nelsonii Scribner and Smith, 1897:16.
50. Chusquea nigricans R. A. Philippi, 1865:323–324.
51. Chusquea oligophylla Ruprecht, 1839:124, pl. 7: fig. 23.
52. Chusquea oxylepis (Hackel) Ekman, 1913:65, pl. 4: fig. 6 (Figure 31~p).
53. Chusquea palenae R. A. Philippi, 1896:350.
54. Chusquea paruipora R. A. Philippi, 1896:349–350.
55. Chusquea perligulata (Pilger) McClure, new combination. Guadua (?) perligulata Pilger, in Diels, 1937:57–58.
56. Chusquea pittieri Hackel, 1903b:153–154.
Chusquea maurofernandeziana Hackel ex Pittier, 1892:64, nomen nudum.

Chusquea maurofernandeziana Hackel ex E.-G. Camus, 1913, i:86, pl. 56c.

61. Chusquea polyclados Pilger, 1905:147.

62. Chusquea polychlaena Hackel ex Pittier, Hackel ex E.-G. Camus, 1913, I:86, pl. 56c.

63. Chusquea polychlaena Pilger, 1905:148-149.

64. Chusquea pubescens Steudel, 1854:337.

65. Chusquea pubespissa Pilger, 1905:147.

66. Chusquea quila Kunth, 1830:329-330, pl. 77.

67. Chusquea quila var. laxiflora Desvaux, in Gay, 1854:447.

Chusquea intermedia Steudel, in Lechler, 1857:52, nomen nudum.

Chusquea quila var. longipila E.-G. Camus, 1913, i:198, fig. 61a, nomen nudum.

66. Chusquea ramosissima Lindman, 1900:24.

Chusquea phacellophora Pilger, 1923:456.

67. “Chusquea” rollotii Berry, 1929: 2-3.

This is a fossil species described from fragmentary remains in lithified gray shale of the late Tertiary (Colombia).

68. Chusquea scandens Kunth, 1822:254 (Figures 30, 31 A-M).

Nastus chusque Humboldt, Bonpland, and Kunth, 1816, I:201.

Bambos chusque Poiret, 1817:494.

Chusquea jamesonii Steudel, 1854:537.

Chusquea quitensis Hackel, in Sodiro, 1889:484, nomen nudum.

Chusquea quitensis Hackel, 1903b:154.

Chusquea quitensis var. patentissima Hackel, 1908:161.

Chusquea meyeriana var. patentissima (Hackel) E.-G. Camus, 1913, i:94.

69. Chusquea simplificiflora Munro, in Martius, 1880:200.

70. Chusquea sellowii Ruprecht, 1839 [1840:125, pl. 11: fig. 26].

71. Chusquea serrulata Pilger, 1898:719-720.

72. Chusquea simpliciflora Munro, 1868:54.

Chusquea simplicifolia Munro ex Hemsley, in Godman and Salvin, ed., 1885:587, error for C. simpliciflora Munro.

73. Chusquea sneidernii Asplund, 1939:797-799, fig. 2.

74. Chusquea spadicea Pilger, 1899:35.

75. Chusquea spencei Ernt, 1872:262.

76. Chusquea spinosa Fournier, 1881:131.

77. Chusquea straminea Pilger, 1905:147-148.

78. Chusquea sulcata Swallen, 1940:209.

79. Chusquea swallenii McClure and Smith, in Reitz, ed., 1967:44-45, 48, figs. a-c.

80. Chusquea tarmensis Pilger, 1905:151.

81. Chusquea tenella Nees, 1834:492-493.

82. Chusquea tenella var. latifolia Dutra, 1938:146.

83. Chusquea tenuiflora R. A. Philippi, 1859:206.

Chusquea ciliata R. A. Philippi, 1864:299.

84. Chusquea tenuiglumis Doell, in Martius, 1880:199-200.

85. Chusquea tenuiglumis var. laxiuscula Doell, in Martius, 1880:200.

86. Chusquea tenuiglumis var. subcytindrica Doell, in Martius, 1880:199-200.

87. Chusquea tonduzii Hackel, 1903b:155.

88. Chusquea tuberculosa Swallen, 1931:14.

Chusquea hispida McClure, 1942:179, fig. 7.

89. Chusquea uliginosa R. A. Philippi, 1859:207.

90. Chusquea uniflora Steudel, 1854:337.

91. Chusquea urelytra Hackel, 1903b:158.

92. Chusquea uruguayensis Arechavaleta, 1897:546-547.

93. Chusquea valdiviensis E. Desvaux, in Gay, 1854:446.

94. Chusquea virgata Hackel, 1903b:156-157.

95. Chusquea ? wettsteinii Hackel, in Wettstein, ed., 1908 [1906:21-22].

96. Chusquea wilkesii Munro, 1868:68.

Checklist of Species Here Excluded from the Genus Chusquea

1. Chusquea amplopaniculata Steudel (1854:337) is Dinochloa scandens (Blume) O. Kuntze.

2. Chusquea aristata. See Neurolepis aristata.

3. Chusquea depauperata. See Swallenochloa depauperata.

4. Chusquea fimbriata. See Athroostachys capitata.

5. Chusquea glomerata Munro (1868:50) (as synonym of Merostachys capitata Hooker). See Athroostachys capitata.

6. Chusquea humilis. See Swallenochloa spicata.

7. Chusquea simplicissima. See Swallenochloa spicata.

8. Chusquea spicata. See Swallenochloa spicata.
9. *Chusquea subtessellata*. See *Swallenochloa subtessellata*.
10. *Chusquea tessellata*. See *Swallenochloa tessellata*.
11. *Chusquea venezuelae*. See *Arthrostylidium venezuelae*.
12. *Chusquea weberbaueri*. See *Swallenochloa weberbaueri*.

**Invalid Species of *Chusquea***

1. *Chusquea caamanoi* Sodiro (1881:11). *Nomen nudum*.

**Colanthelia** McClure and E. W. Smith, new genus

**Figure 32**

Plants unicespitose, unarmed. Rhizomes pachy-morpha. Culms of small to medium stature and erect or decumbent, to very tall and scandent, the nodes prominent with a narrow crest, each midculm node giving rise to but a single initial bud; the prophyl-lum of the bud growing while the bud germinates, the primordium producing a single (segmented, terete) primary axis, this dominant over the axes of secondary order usually proliferating promptly from buds typically present at its own proximal nodes. Sheath at midculm nodes provided with (and abscising from) a conspicuous persistent girdle (basal expansion zone). Leaf blades with trans-verse veinlets as a rule not manifest externally.

Inflorescences semelauctant, either paniculate or racemose (sometimes showing in the same specimen forms intermediate or intermixed between these two forms), part or all of the inflorescences (or even whole flowering branches) in a given specimen sometimes reduced individually to barely more than a solitary spikelet. Transitional glumes typi-cally 2, rarely 1 or 3. Spikelets usually pedicellate, typically many-flowered (few-flowered in *Colanthelia lanciflora*), very narrow and fragile, terminating apically in a more or less strongly depauperate sterile anthecium. Fertile lemma fully embracing its palea only basally at maturity. Palea 2–keeled and broadly sulcate dorsally, gaping ventrally. Rachilla segments (owing to their fragility at the nodes) easily disarticulating at maturity. Lodicules typi-cally 3, the anterior 2 more or less asymmetrical and paired, the posterior one symmetrical and usually smaller. Stamens 3, the filaments filiform and free. Stigmas 2. Fruit not yet available.

**ETYMOLOGY.**—The name *Colanthelia* (f.) is coined from the Greek *kolos*, shortened, and *anthele*, “plume or panicle of a reed” (R. W. Brown, 1954). It alludes to a tendency common to all of the currently recognized species of the genus. There is a noticeable to strongly manifested tendency toward a progressive reduction of the reproductive structures from weak panicules to simple racemes and, in some cases, even from whole flowering branches all the way to little more than solitary spikelets.
Figure 32.—Colanthelia cingulata (McClure and L. B. Smith) McClure. A, Rhizome and culm bases, × 0.6; b, branch complement from midculm range, in flowering state, × 1.2; c, culm sheath from above midculm range, with developing branch complement, × 0.9; d, apex of leaf sheath and base of leaf blade, × 7.2; e, paniculate inflorescence terminating a leafy flowering branch, × 0.6; f, progressively depauperate leafy and leafless flowering branches, × 0.6; g, flowering branch terminating in an inflorescence with mixed paniculate and racemose branching, × 0.6; h, spikelet with its pulvinate pedicel, × 2.4; i, transitional glumes, × 6; j, floret, × 6; k, lamina, × 6; l, palea, × 6; m, lodicule complement, × 12; n, stamen, × 6; o, gynoecium, × 12. Drawings a–f, g–o based on Reitz and Klein 9679 (US), and f on Dasén 18011 (US).

Type-species.—Colanthelia cingulata (McClure and L. B. Smith) McClure.

Relationships.—Affinity toward Aulonemia is weakly suggested by the nature of the midculm branch complement; this possible affinity is reinforced by the occurrence of paniculate inflorescences in some species. Among available examples, a specimen of Aulonemia haenkei (US 1256334) from Peru shows an occasional flowering branch reduced to little more than a solitary spikelet. The feature to which the name Colanthelia alludes also comes to light here and there in members of other genera. Among bamboos of the Old World genera a few similarly reduced flowering branches sometimes appear in specimens of Chimonobambusa marmorea. Other attributes (e.g., racemose inflorescences) suggest affinity toward Arthrostyletium. Such divergent attributes are connected by intermediate expressions to form clines, both from one species to another and (in some cases) within the same specimen. In the available material representing the genus Colanthelia, the morphological gamut of the reproductive apparatus reaches from leafy to leafless branches, each terminating in either a panicle, a raceme, a combination between those two forms, or a single spikelet. Pertinence to the genus Colanthelia (among the known bamboo genera of the New World) is made plain in its known members (even in their vegetative state) by the overall delicacy of the plant, with distinctively small leaf blades, combined with pachymorph rhizomes, prominent narrow-crested midculm nodes, a wide girdle at the base of the sheath at each node, and the unarmed complements with the primary element clearly dominant. With the exception of Colanthelia lanciflora, all known members of the genus have more or less distinctively long and narrow spikelets with more or less clearly exposed slender, elongate segments.

Distribution.—As far as their natural distribution is a matter of record, all of the known species of Colanthelia are confined to Brazil. Three species have been reported from Santa Catarina, and one each from Minas Gerais, Paraná, Rio Grande do Sul, and São Paulo. The recorded altitudinal range extends from 30 m for Colanthelia cingulata, to 550 m for C. intermedia, to 710 m for C. gracillima, and to 1600 m for C. lanciflora.

Annotated Checklist of Recognized Species of the Genus Colanthelia

1. Colanthelia burchellii (Munro) McClure, new combination.
2. Colanthelia cingulata (McClure and L. B. Smith) McClure, new combination (Figure 32).
3. Colanthelia distans (Trinius) McClure, new combination.
4. Colanthelia intermedià (McClure and L. B. Smith) McClure, new combination.
5. Colanthelia lanciflora (McClure and L. B. Smith) McClure, new combination.
6. Colanthelia macrostachya (Nees) McClure, new combination. Arundinaria macrostachya Nees, 1834:481.
7. Colanthelia rhizantha (Hackel) McClure, new combination. Arundinaria rhizantha Hackel, 1909a:323.

Elytrostachys McClure

Figures 33–35

Elytrostachys McClure, 1942:173, figs. 4–6; 1957:202.

Plants unicespitose; unarmed. Rhizomes pachymorph. Culms self-supporting below, typically weak
and pendulous or clambering above; the internodes cylindrical, hollow. Branch buds at culm nodes solitary, each containing but a single initial primordium. Branch complements at midculm nodes of either restricted or gremium insertion, unrestricted monoclaude, consisting typically of one strong, central axis and a tuft of more slender ones arising from lateral buds at proximal nodes of the initial primordium, these latter buds sometimes germinating precociously while the apical growth of the initial primordium remains inhibited. Leaves (leaf sheath blades) typically with transverse veins; leaflets not at all or only weakly manifest externally; oral setae few, rigid, erect or spreading, slender except at the bulbous base, scabrous.

Inflorescences iteructant, terminating leafy or leafless axes, of diffuse form, each axis the bracteate and prophyllate rachis of a pseudospikelet, the terminal segment of each rachis serving as the pedicel of a spikelet. Transitional glumes at the base of each spikelet none. [The conventional position of the transitional glumes is here (and in Atractantha, q. v.) occupied by what I now classify as bracts. When, in 1942, I first described and illustrated the genus Elytrostachys, I identified and labeled these structures as being glumes. However, in the perspective achieved more recently through a re-study of the structures in this transitional zone in the inflorescence of species of Elytrostachys in comparison with their counterparts in species of Atractantha, I now see them in both genera as empty bracts that are terminal to the series of bracts that subtend buds, rather than as empty glumes that precede the lemmas. The elongated terminal segment of the rachis that follows the two short internodes that precede the elongated terminal segment of each rachis it terminates, and each typically containing but a single perfect floret (sometimes 2 in E. clavigera), promptly disarticulating at maturity immediately below the locus of insertion of a fertile lemma, the rachilla prolonged behind the terminal perfect palea in a bristle-like segment bearing a minute rudiment of a sterile antherium. [When the spikelet contains but a single perfect floret, the prolongation of the rachilla is bristle-like and bears a minute rudiment; but when the spikelet contains more than one perfect floret, the prolongation of the rachilla behind the palea of the terminal perfect floret may be more robust than bristle-like, and then will bear a sterile antherium more substantial than rudimentary.] Lemma in functional florets fully embracing its palea only basally at maturity. Palea gaping antically, dorsally canaliculate in spikelets containing but a single perfect floret, broadly sulcate in the lower floret when the spikelet contains two perfect florets. Lodicules 3, subequal or unequal, the anterior 2 asymmetrical and paired, the posterior one symmetrical and smaller. Stamens 6, the filaments filiform, free. Stigmatic branches 2. Fruit a fusiform or lagenoid, rostrate, sulcate caryopsis, the pericarp coriaceous, of even thickness below, thickened at the apex, the basal position of the embryo clearly manifest.

ETYMOLOGY.—The name Elytrostachys, formed from the Greek elytra (combining form of elytron) sheath, cover (elytra = wing-cover of beetles) and stachys, spike, alludes to a fancied resemblance of the lemmas to the wing-cover of a beetle.

TYPE SPECIES.—Elytrostachys typica McClure.

RELATIONSHIPS.—The only known New World genus to which Elytrostachys appears to be closely related is Atractantha. These two genera share the following features: inflorescences of a peculiar form characterized by rachises with long terminal segments, each of which serves as the pedicel of an abscissile spikelet; the absence of the transitional glumes commonly found at the base of each spikelet, and the presence, in their stead, of a bract inserted on each of the two short internodes that precede the elongated terminal segment of each rachis; each spikelet typically containing but a single perfect floret followed by a rudiment of a sterile antherium borne on the tip of a bristle-like prolongation of the rachilla. From known members of Atractantha, known members of Elytrostachys differ in the following features: midculm

FIGURE 33.—Elytrostachys clavigera McClure. A, Portion of a seedling plant, x 0.6; b, culm sheath at midculm node of young culm shoot, x 0.6; c, midculm node and basal part of a typical branch complement, x 0.6; d, leafy twig with terminal inflorescence, x 0.6; e, two nodes from upper part of leafless flowering culm, x 0.6. All drawings based on McClure 21478 (US).
branch complements of restricted or gremial inser-
tion, each arising from a solitary branch bud con-
taining but a single initial primordium; auricles

Key to the Species of Elytrostachys

1a. Leaf blades scabrous toward the base on the upper surface; laminiferous bracts silky-
pubescent in part; bladeless empty bracts (originally called empty glumes) 1 to 14 mm, 
11 to 18 mm long; terminal segment of rachis to 17 mm long and pubescent in part; 
lemma to 17 mm long; ovary hispidulous toward apex ..................................1. E. clavigera

1b. Leaf blades glabrous on both surfaces; laminiferous bracts glabrous; bladeless empty 
bracts (originally called empty glumes) 1 to 15 mm, 11 to 30 mm long; terminal segment 
of the rachis to 65 mm long and entirely glabrous; lemma to 23 mm long; ovary entirely 
glabrous .............................................................................................................2. E. typica

Glaziophyton Franchet

Glaziophyton Franchet, 1889:277.—McClure, 1957:208. 
Arundinaria sect. Glaziophyton (Franchet) Hackel, in Engler 
and Prantl, 1897:46.—Lamson-Scribner, 1899:9. 

Plants multicespite, unarmed. Rhizomes pachy-
morph, the neck of an occasional one much elong-
ated, thus creating an opening between tufts of 
culms arising either by tillering, or from a cluster 
of rhizomes with short necks. Culms strictly erect, 
the internodes (in leafless, juncoid culms) cylindrical, 
the hollow interior partitioned by numerous 
thin but firm septa of pith without vascular tissue, 
the first above-ground internode disproportionately 
elongate, the upper ones very short to obsolete; 
juncoid culms in the vegetative state normally 
branchless and leafless—only after burning (teste 
Glaziou) do small secondary culms arise by tillering 
from the stumps and emit leafy branches. Branch 
buds at the nodes of these secondary culms solitary. 

Vegetative branch complements of restricted insertion, unrestricted or facultatively restricted monoclade, with the median (primary) one dominant (those present in the only extant leafy specimens, Glaziou 8999 and 17914, not fully developed). Leaf sheaths with auricles and oral setae weakly developed or obsolete. Leaf blades with transverse veins manifest to superficial view, more prominently so on the abaxial surface. Culms in the flowering state leafless; the very slender, elongate, subequal, highly ramified flowering branches borne in basally 
pressed pleioclade complements each arising from a 
soleitary bud and inserted at one of the close-set 
distal nodes of the culm and producing gigantic, 
nodding, apically pendulous inflorescences (up to 1 m long, teste Franchet).

Inflorescences semelauclant, effusely branched 
panicles with a deliquescent rachis, the branches of 
all orders solitary, very slender and wiry, each sub-
tended by a bract, and each bearing a 2-keeled
prophyllum at its basal node. Transitional glumes at the base of the spikelet 0–3; I and II “empty glumes”; III (when present) a “sterile lemma” that is either empty or subtends a rudimentary flower. Spikelets petiolate, each containing 2 (1–3) perfect flowers and terminating in a small, loosely convolute sterile anthecium (an occasional spikelet contains several progressively depauperate florets above the perfect ones); the rachilla segments somewhat elongate, potentially disarticulating immediately below the locus of insertion of each lemma including the terminal, reduced one (s). Palea gaping antically, dorsally sulcate and 2–keeled. Lodicules 3, the anterior two asymmetrical and paired, the posterior one symmetrical and smaller. Stamens 3, the filaments filiform, free. Stigmas 2. Fruit unknown.

ETYMOLOGY.—The name of this bizarre, monotypic genus honors its discoverer, Auguste François Marie Glaziou (1833–1906), a French botanist and plant collector, who made excellent specimens and critical observations of this plant in the field during a period of 15 years. Glaziou passed on his observations to Franchet, apparently by oral communication.

TYPE-SPcies.—Glaziophyton mirabile Franchet, the sole known representative of the genus.

RELATIONSHIPS.—Greslania Balansa (genus of Old World bamboos endemic on mountaintops in New Caledonia) resembles Glaziophyton superficially in the branching habit of the inflorescence (with each branch of the inflorescence subtended by a bract and bearing a prophyllum at its basal node) and in the manifest tessellate venation of the leaf blades, but differs profoundly in having the flowering culms leafy, with efiistular internodes, and in the presence of 6 stamens and 3 stigmas in each flower.

The disproportionate elongation of a single lower internode of every culm—a feature of the type-species of Glaziophyton—is a vegetative character shared by most species (including the type) of Myriocladus and several species of Arthrostylidium (e.g., A. schomburgkii). The peculiar, juncoid nature of the septate lumina of the culm internodes in the type-species of Glaziophyton apparently has no close counterpart in any known species of bamboo. Glaziophyton shows spikelet characters similar to those of Myriocladus, and features within the florets that link it in a general way with Merostachys, Myriocladus, and Arthrostylidium. The genus Glaziophyton, however, stands without any obviously close affinities among the bamboos.

Glaziou assumed the existence of juncoid affinities in this plant, and on the field label of his first collection (Glaziou 8999, 7 June 1877) he wrote a tentative (unpublished) binomial, placing it in the genus Juncus. Franchet, however, in his discussion of its relationships, compared Glaziophyton mirabile to cyperaceous plants, such as Scirpus lacustris and Cyperus articulatus. It is of interest to note that both Juncus effusus Linnaeus and Glaziophyton mirabile Franchet have been recorded from the same geographical area and at approximately the same elevation, in Brazil.

DISTRIBUTION.—Extant specimens indicate an endemism restricting this species to open, dry mountain tops in the general vicinity of Rio de Janeiro.

Glaziophyton mirabile poses interesting problems for the serious student of the genetic, as well as the physiological, bases of morphogenesis. During a period of 15 years, Glaziou observed repeatedly that the sterile culms were all typically juncoid, without branches and without foliage leaves. When the sterile culms were destroyed by burning, however, secondary culms or tillers arising from the stumps produced leafy branches. Flowering was observed on leafless juncoid culms only.

We have here what appears to be an extremely exaggerated expression of an ontogenetic feature found in some other bamboos (e.g., Bambusa arundinacea) where culms in the flowering state regularly lack foliage leaves from the first. In Glaziophyton mirabile, however, the phenetic gap between the flowering state and the vegetative state of the plant is very much more extreme morphologically, more persistent, and apparently deep-rooted genetically. The only ecological condition that is known to trigger the production of shoots bearing leafy ramifications is a bizarre one, namely, burning of the aerial part of plants previously re-
FIGURE 30.—Glaziophyton mirabile Franchet. A, Habit of underground part of plant: rhizomes with elongated necks (shown in broken outline), double circles represent the stumps of severed culms, greatly reduced; b, sterile leafless culm (partly in longitudinal section, to show pith distumps of severed culms, greatly reduced; after burning, x 0.6; c, tip of leafless sterile culm, showing close-set budless nodes, x ca. 5; d, f, culm sheaths (apical portion only) from nodes 8 and 13 of sterile culm, abaxial and adaxial aspects, respectively, x 4.8; f, stumps of burned leafless plant, with leafy culms that developed by tillering, after burning, x 0.6; g, foliage leaf and part of its sheath, abaxial aspect, x 1.8; h, junction of foliage leaf and its sheath, adaxial aspect, x 1.8; i, portions of two mature flowering branch complements, the latter with an intact rudimentary bud which when present, is the lemma of a sterile floret. Spikelets sessile or subsessile, usually containing but a single perfect flower (in some species now and then 2–as in an isotype of Merostachys speciosa, teste Munro (1868:48)—in others regularly 2; rarely—as in M. pluriflora—2–5 and exceptionally, as in M. polyantha, even up to 10) and terminating in a rudimentary or more or less depauperate sterile anthecium. Rachilla segments potentially disarticulating immediately below the locus of insertion of a fertile lemma. (When the spikelet contains but a single perfect floret, the prolongation of the rachilla is bristle-like and bears a minute rudiment; when the spikelet contains more than one perfect floret the prolongation of the rachilla behind the palea of the terminal perfect floret may be more robust than bristle-like, and then may bear a sterile anthecium more substantial than rudimentary.) Florets more or less strongly inflated, the lemma fully embracing the palea only basally at maturity, the palea gaping antically, narrowly to broadly sulcate and 2–keeled dorsally. Lodicles 3, in some species subequal and subsimilar, elsewhere the anterior 2 asymmetrical and paired, the posterior one smaller and symmetrical. Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit a mucronate or weakly rostrate, oblong or ovoid Caryopsis with a thin, coriaceous or crustaceous pericarp of even thickness or more or less strongly thickened toward the base and toward the apex; in the absence of both a sul-

maining in the unbranched, perennially leafless state. How long will the “satiated curiosity” of technically equipped persons ignore the challenge to investigate this enigma—in depth!

Merostachys Sprengel

FIGURE 37

Merostachys Sprengel, 1825, II:129.—Endlicher, 1836–1840: 102.—Ruprecht, 1839:36.—Munro, 1868:46.—Doell, in Martinez, 1880:207.—Benth, in Bentham and Hooker, 1883: 1209.—Hackel, in Engler and Prantl, 1887:98.—McClure, 1957:205.

Brasitiocalamus Nakai, 1933:10.—McClure, 1957:201.

Plants unicospitos, unarmed. Rhizomes pachymorph. Culms self-supporting in the lower part, the slender, sometimes long-attenuate upper part nodding, pendulous or clambering; internodes cylindrical, typically hollow, exceptionally, as in some as yet unidentified species, ephistulose or filled with pith. Primary branch buds solitary at mid-culm nodes, each bud giving rise to but a single initial (primary) axis. Branch complement at mid-culm nodes monoclad, with its primary element solitary, flat, unseparated, roughly ovate or cor-
cus and an embryotegium, the respective positions of the hilum and the embryo are not manifest externally.

Etyymology.—The name, Merostachys, formed from the Greek, meros, part (partial, or incomplete) and stachys, spike, alludes to the secund (one-sided) profile of the inflorescence.

Type-Species.—Merostachys speciosa Sprengel.

Relationships.—Rhipidocladum is the only bamboo genus toward whose members bamboos of the genus Merostachys show any strong or striking resemblance. This resemblance is shown most spectacularly by the manner of development and form of the branch complement at midculm nodes (Figures 37c, 42a). However, the form of the sheaths (Figures 37b, 42b) at midculm nodes of the young culms in active growth (insofar as these are known for plants of either genus) provides a convenient means of establishing the generic affinity of a given plant. Otherwise a deceptive technical resemblance between members of Merostachys and members of Rhipidocladum is manifested only where certain features of the reproductive structures appear in exceptional combinations. The fact that in Merostachys the thickening of the pericarp of the fruit proceeds simultaneously from both apex and base may provide an additional item of difference between Merostachys and Rhipidocladum. Thus occasions for confusion or uncertainty as to generic affinity or generic discontinuity may involve those species of Rhipidocladum having pectinately second, spicate inflorescences (e.g., R. maxonii) or those species of Merostachys (e.g., M. pluriflora and M. polyantha) having spikelets that contain several perfect florets and terminate in a robust (not bristle-like) rachilla segment bearing a sterile anthecium more substantial than rudimentary. Specimens of such mutually imitative members of Merostachys and Rhipidocladum, however, may be sorted to genus if, in addition to the midculm branch complement, they both contain intact or complete examples (in good condition) of sheaths from midculm nodes.

I do not find any support for the opinion expressed by Hackel (1909a:327) that Merostachys is related to Chusquea.

Distribution.—The 25 species of Merostachys tentatively recognized here give the genus an aggregate but discontinuous distribution extending from Argentina to Guatemala and British Honduras, at moderate elevations and up to 1500 meters. As far as known today, the genus reaches its fullest development and greatest diversity in Brazil, where 20 described species are found. Outlying stands of single species have been reported from Argentina, Uruguay, Paraguay, Peru, Guatemala, and Honduras; two species have been recognized in Venezuela.

Annotated Checklist of Species of the Genus Merostachys

1. Merostachys anomala Dutra, 1938:151, fig. 3. [See Merostachys multiramea.]
2. Merostachys argyronema Lindman, 1900:22, pl. 15.

The Guatemalan plant referred to this species by McClure (in Standley and Steyermark, ed., 1955:207) is known only in the vegetative state. It probably represents a species distinct from M. argyronema, whose vegetative features are, as yet, insufficiently known.

3. Merostachys bradei Pilger, 1927:114. [See Merostachys pluriflora.]
4. Merostachys brevistipa Munro, 1868:49.
5. Merostachys burchellii Munro, 1868:51.

This species was initially described by Munro on
the basis of a single collection consisting of sterile specimens under *Burchell 3243* (K). Dutra (1938: 151) described, under the same name, a flowering specimen purporting to supplement Munro's image of that species without, however, citing any specimen to document his description. But, in his introductory statements, Dutra made reference to the flowering, in 1907, of a plant identified by him as *Merostachys burchellii* Munro. A flowering specimen collected in that same year by Dutra under no. 513 bears (at US) a tentative identification as *Merostachys burchellii* Munro. It may represent the same collection as the uncited specimen on which Dutra based the (emended) description of *M. burchellii* referred to above. Judged by its vegetative features, however, Dutra 513 is very different from *Burchell 3243*, the type of *Merostachys burchellii* Munro. It is closely related to (but not identical with) Dutra 518 (US), type-collection of *Merostachys anomala* Dutra (q. v.), collected in 1906 in the same general locality.

6. *Merostachys ciliata* McClure and Smith, in Reitz, 1967:71, pl. 12b-h.

7. *Merostachys claussenii* Munro, 1868:48.

? *Merostachys claussenii* ß *mollior* Doell, in Martius, 1880:214.

Ekman (1913:64) expressed the opinion that Doell's type of ß *mollior* is identical with Munro's type of *M. claussenii*. Ekman supports this opinion by the assertion that Claussen 399 "is indeed a duplicate of the original plant," i.e., is actually a duplicate from the Claussen collection cited by Munro. This assertion is neither verified nor supported by my observation that Munro's specimen of "Claussen, Minas Geraes" (frag. ex K at US) is clearly distinguishable from Doell's type (Regnell III n. 1425—frag. et photo ex S at US) on the basis of features of the spikelets alone. The discrepancy between Ekman's interpretation and the way things look to me suggests the need for a re-evaluation of the evidence as to whether more than one recognizable taxon is involved here.

8. *Merostachys exserta* Munro ex E. –G. Camus, 1913, I:74, pl. 44A.

This is a species of which I have not seen a specimen. The type (P) cited by Camus as "Auguste de Saint-Hilaire, 1816 à 1821; Cat. D, no. 713," is annotated by Munro (teste Camus) with the words "Spica exserta ab affinisibus distat; spicula brevi M. Fischeriannae approximat."

9. *Merostachys fischeriana* Ruprecht ex Doell, in Martius, 1880:215.

10. *Merostachys fistulosa* Doell, in Martius, 1880:209, pl. 55.

11. *Merostachys glauca* McClure and Smith, in Reitz, 1967:74, pl. 12n.

12. *Merostachys kunthii* Ruprecht, 1839:37, pl. 10: fig. 30.

*Merostachys speciosa* sensu Kunth, 1830:333, pl. 79. [Non Sprengel, teste Ruprecht.]

13. *Merostachys maguireorum* McClure, in Maguire, Wurdack, et al., 1964:5.

14. *Merostachys multiramea* Hackel, 1909a:326.

*Merostachys anomala* Dutra, 1938:151, fig. 3.

15. *Merostachys neesii* Ruprecht, 1839:37, pl. 10: fig. 31.

*Merostachys speciosa* sensu Nees, in Martius, 1829:527. [Non Sprengel, teste Ruprecht.]

16. *Merostachys pauciflora* [as *pauciflorus*] Swallen, 1943:469, fig. 1.

17. *Merostachys petiolata* Doell, in Martius, 1880:216.

18. *Merostachys pluriflora* Munro ex E. –G. Camus, 1913, I:77.

*Bambusa pubescens* Doell, in Martius, 1880:189, pl. 51: E. –G. Camus, 1913, I:124. (Non Loddiges ex Lindley, 1835, III:357.)

*Brasilocalamus pubescens* (Doell) Nakai, 1933:10.

*Merostachys bradei* Pilger, 1927:114.

A catalog of the hitherto unassembled series of amazing and amusing taxonomic inadvertencies by which the history of this species has become complicated may prove instructive to the prospective student of the bamboos. Having projected "Bam-busa" as the proper repository for a specimen from Gaudichaud's collection no. 97, Doell (in Martius, 1880) proceeded (certainly by inference rather than on the basis of direct evidence) to include in the illustration of his *Bambusa pubescens* a floral diagram showing six stamens. When Doell's otherwise authentic plate, and his description (including the statement "stamina 6") caught the eye of Dr. Nakai, the latter saw what he took to be a new genus, and proceeded (Nakai 1933) to christen it *Brasilocalamus*. Not having examined a specimen of the type-
species, however, Nakai failed to detect Doell’s error in giving it six stamens. At an earlier (unrecorded) date, Munro had already annotated (at P) another specimen from the same Gaudichaud collection with the following words: "Merochys sp. indescr. M. pluriflora nov. sp. M. Kunthii Ruppr. affinis distinct spicae florculos hermaphrod [itis] 3–5." E. –G. Camus (1913, I:77) published Munro’s manuscript name, with a description consisting solely of the Latin annotation associated with it. Camus failed to take account of the fact that this name is based upon a specimen from the same collection that yielded the type of Bambusa pubescens Doell. Consequently, the latter name also appears in the Camus work (1913, I:124) along with a full reproduction of Doell’s description of it translated into French. Camus apparently overlooked the fact that Bambusa pubescens Doell (in Martius, 1880) is a later homonym of Bambusa pubescens Lodidge in Lindley (1885) which name appears (Camus, 1913, I:152) in a list of synonyms under Dendrocalamus strictus. In 1927 Pilger described Merochys bradei as new to science, on the basis of a specimen from a different collection of M. pluriflora. An English translation of Pilger’s notes in German reads as follows:

The new species is distinguished by the short, thick, spikes, as well as by the 2–3 fully developed flowers with normal lemma and palea [in] short, thick, downy spikelets. E. –G. Camus (1913, I:77) mentions a M[erochys] pluriflora Munro without a full description ("les épillets pluriflores"); but that species, which cannot be considered as properly published, can hardly be identical with my new species because that one is considered to be nearly related to M. Kunthii. The rudiments of glumes below the two empty glumes cited by Eichler in Flora Brasiliensis were not observed in our species.

A formal description of the following species, apparently new to science, is included here because by adding a member in which the number of antheria in its apically indeterminate spikelets sometimes reaches the unprecedented figure of ten, it dramatically extends the current circumscription of a genus whose type-species has one-flowered spikelets terminating in a bristle-like prolongation of the rachilla bearing a rudiment.

19. Merochys polyantha McClure, new species
Culmi 6–8 m alti (teste A. Lima); internodia teretia, cava, parietibus tenuibus, extus infra unum-
2, alia vel alia aliquando rudimentum (velut gemmam dormantem) foventi; 1 ca 4 mm longa, anguste triangula, acuminatissima, valde carinata, cetera enervosa, dorso invalide appresso-hirtula, secus margines valde ciliata; II 6–9 mm longa, ovata, acuminata, 5-nervia et valde carinata, extus valde hirtula, marginibus versus apicem tunc tantum incalide ciliolata. Flosculi in spiculis proximalibus usque 10, eis in spiculis succedentibus gradatim paucioribus; flosculo terminali vel plus minusve depaupe-rato vel etiam in statu rudimentario dirempto. Anthoeciorum elementae utraeque crustaceae, extus plus minusve dense strigosae, sews margines apicotem versus antrorse-ciliatae. Rhachillae segmenta usque 4 mm longa, semiclaviformia, omnino molliter antrorse pubescentia. Lemma flosculi infimi usque 20 mm longum, flosculorum sequentium gradatim redactum, anguste lanceolatum, apicem versus 5-nervium naviculareque, alibi enervium. Palea vulgo vel lemmam aequans vel parum brevior, raro parum longior; oblongo-lanceolata, late sulcata, omnino enervia, apice et profunde et anguste bilobata. Lodiculae dimensionibus formaque variabilissimae, textura tenuissimae, deorsum interdum opacae, vel enerviae vel invalide paucinerviae, omnino glabrae vel margine (apice saltem) obscure ciliolatae. Antherae atropurpureae, versus basin apicemque parum attenuatae. Ovarium, stylus et rami styli infra stig mata omnino glabri. Fructus non adhuc inventus.

Culms 6–8 m tall (teste A. Lima) the internodes terete, hollow, thin-walled, more or less heavily coated at first with white powder and densely clothed in a narrow zone immediately below each node with retrorsely appressed lustrous white hairs, elsewhere sparsely strewn with papillae each tipped with a minute retrorse hook; ultimately seen as yellowing green in color, variegated with longitudinally elongated vinaceous stipules. Culm sheaths deciduous, upon abscission leaving a rather prominent persistent girdle densely clothed outside and fringed basally with retrorsely appressed lustrous white hairs; the sheath proper ciliate on the outer margin, apparently entirely glabrous abaxially; auricles and oral setae prominently developed, the auricles narrow, tortuous, dull, and glabrous abaxially, densely hirtellous adaxially, the oral setae 10–12 mm long, spreading from crowded loci of insertion on the margin and on the adaxial sur-

dace of the auricles, lustrous, very sparsely and obscurely antorse-scabrous throughout, crisped distally; ligule short, truncate or slightly arcuate apically, minutely and irregularly denticulate and ciliolate on the margin; blade deciduous (not seen). Leaf sheaths proper (represented on flowering twigs only in the available specimens) minutely corrugated (quasi-uncate) longitudinally, densely fringed with lustrous hairs on and near the outer margin; the proximal sheaths in a given series glabrous, the distal ones strewed (on the exposed surface at least) with retrorsely uncinate papillae; auricles and oral setae approximately as seen on the culm sheaths; inner ligule not exerted, the outer ligule narrowly linear, subglabrous to densely ciliate on the margin; petiole up to 8 mm long, dorsiventrally compressed, entirely glabrous to densely antorse-hispidulous throughout on both surfaces; blade up to 150 x 35 mm, oblong-lanceolate, asymmetrical and broadly rounded or cordate at the base, asymmetrically and abruptly acuminate at the apex, abruptly becoming ovate-acuminate and greatly reduced in size at the proximal and distal extremes of every leafy flowering twig, concolorous and glabrous or nearly so on both surfaces; longitudinal nerves all salient on the abaxial surface only, the midrib distinguishable only toward the base of the blade; secondary nerves 5–8 on each side of the midrib; tertiary nerves up to 8 in the first space on each side of the midrib, the number in each successive internerve space reduced progressively, commonly 2 next to each margin of the blade; transverse veinlets visible only on the abaxial surface, adjacent ones in a given space 1.5 to 4.0 mm distant from each other.

Inflorescences congested secund spicate racemes terminal to usually leafy axes; peduncle scarcely to slightly exerted, densely canescence apically; rachis 25–65 mm long, lightly curved, densely strigose; bract subtending the lowermost spikelet ovate, acute and apiculate apically, dorsally many-nerved and prominently keeled, glabrous throughout on the back and on the margins, up to 10 mm long, those subtending successive spikelets progressively reduced, the distal ones either rudimentary or obsolete. Spikelets somewhat compressed, narrowly triangular, of indeterminate growth apically, of solitary but crowded, alternate and distichous insertion at intervals of 1.5 to 4.0 mm from the base
of the raceme upward in each row; spikelets in each raceme up to 26, the basal one up to 55 mm long, the successive ones progressively reduced in length to about 20 mm, followed by sometimes seven or eight abruptly and progressively depauperate to rudimentary ones; pedicels almost obsolescent, each prominently pulvinate on the external side only; transitional glumes normally two, one or the other sometimes subtending a bud-like rudiment; 1 about 4 mm long, narrowly triangular, acuminate, prominently keeled, otherwise without visible nerves, weakly appressed hirtulous dorsally and strongly ciliate on the margins; I 6-9 mm long, ovate, acuminate, 5-nerved and strongly keeled, hirtulous dorsally and weakly ciliate on the margin toward the apex only. Elements of the anthecia both crustaceous, more or less densely strigose on the outer surface, antorse-ciliolate on the margins apically. Rachilla segments up to 4 mm long, semiclaviform, softly pubescent throughout with antorse hairs. Lemma in the lowermost floret up to 20 mm long, progressively reduced in the succeeding florets, narrowly lanceolate, 5-nerved and strongly boat-shaped toward the apex, elsewhere without manifest nerves. Palea commonly as long as the lemma or a little shorter, rarely a little longer; oblong-lanceolate, broadly sulcate, lacking manifest nerves, deeply and narrowly bilobed at the apex. Lodicles of variable form and dimensions, of delicate texture, sometimes opaque at the base, always translucent above, either weakly few-nerved or nerveless, glabrous throughout or obscurely ciliolate on the margin toward the apex only. Anthers dark purple, lightly attenuate toward the base and at the apex. Ovary, style and branches of the style (below the stigmas at least) entirely glabrous. Fruit not yet found.

COTYPES (= syntypes, sensu Frizzell 1933:647).—Herbarium Bradeanum no. 22857, leg. Flavia Torgo (s.n.) 19 viii 1926; and Herb. Kew, leg. A. Lima (= Dárdano de Andrade-Lima) no. 62-4122, 24 viii 1962 (ex Instituto de Pesquisas Agronômicas Seção de Botânica, São Paulo, no. 13192), both collections taken simultaneously from the same flowering plant (teste A. Lima): “Serra de Mongaguá, pr. Praia Grande, Municipio Mongaguá, São Paulo, Brasil, a sombra da mata no alto da serra (100-120 m). 6-8 m. Fl. roxoescuro. Caule c/p eq. aculeos cuticulares (?) volt. p/base.” Plants shaded by forest at the summit of a hill 100-120 m above sea level—culms 6-8 m tall, with minute cuticular hooks on the lower internodes; flowers dark red. [Vernacular name:] 'taquara miju.’” Notes ex A. Lima. Both cited specimens seen. Photographs of both cotype specimens, and a duplicate of the specimen collected by A. Lima are on deposit at the U.S. National Herbarium.

RELATIONSHIPS.—Merostachys polyantha differs from the closely related M. pluriflora in the more robust development of the inflorescences, spikelets, anthecia and the auricles, and oral setae; as well as in the greater maximum number (up to 26) of spikelets in each raceme; the greater maximum number (up to 10) of florets in each spikelet; the shape and vesture of the parts of the anthecia; and the much broader, oblong-lanceolate shape of the midrange leaf blades.

DISTRIBUTION.—Merostachys polyantha is known as yet by only two collections taken, simultaneously (teste A. Lima), from a single source: Serra de Mongaguá, prope Praia Grande, Municipio São Paulo, Brasil. Its nearest known relative, Merostachys pluriflora, has been collected near Iguape, State of São Paulo, and on the Island of Santa Catarina, State of Santa Catarina.
27. *Merostachys ternata* Nees, in Martius, 1829: 529.
28. *Merostachys vestita* McClure and Smith, in Reitz, 1967:72, pl. 12 i–j.

The following authors offer additional information on some of the species of *Merostachys* listed above: Doell, in Martius, 1880:207–218; McClure, in Swallen, 1955:207–209; McClure and Smith, in Reitz, ed., 1967:63–75; Metcalfe, 1960:564, 586–588; Munro, 1868:47–52; Nees, in Martius, 1829:527–531; Parodi, 1936:242–244; Ruprecht, 1839:36–38.

**Annotated Checklist of Excluded Species**

Erroneously Allocated to the Genus *Merostachys*

1. *Merostachys capitata* Hooker, 1840:273. [See *Aethrostachys capitata*.

2. *Merostachys racemiflora* (Steudel) Fournier, 1881:131. [See *Rhipidocladum racemiflorum*.

3. *Merostachys sikokianus* (Makino) Nakai, in Hara, 1935:74. [A Japanese plant of the genus *Sedum*—Crassulaceae.]

**Myriocladus** Swallen

*Figures 38–40*

*Myriocladus* Swallen, in Steyermark, et al., 1951:34, fig. 4; in Maguire, Wurdack, et al., 1957:237–239.—McClure, 1957:205.

Plants, unisepitous, unarmed. Rhizomes pachymorph. Culms self-supporting, the internodes tere, in some species hollow, in others eistular, the lowermost above-ground one usually disproportionately elongated and followed by one to several more or less completely suppressed (obsolete) ones with the intervening nodes crowded closely together. Branch buds at culm nodes solitary. Branch complements restricted monoclade, the successive ones sometimes brought deceptively closely together by the suppression of culm internodes. The primary element of branch complements apparently never proliferating from any bud at its proximal nodes, this perhaps due to suppression of the buds by powerful physical pressure exerted by the very thick, rigid sheaths that subtend them. [A proximal internode of the single component branch is also (as in the culm) commonly elongate and followed by one to several suppressed (obsolete) ones with the intervening nodes crowded closely together, making the corresponding sheaths strongly imbricate.] Leaves (blades of leaf sheaths) petiolate or subessile, the transverse veinlets usually obscure or invisible externally or (as in *M. paludicolus*) more or less conspicuously manifest on both surfaces.

Inflorescences semelautant, terminating leafy or leafless branches and (in some species) the culms as well; generally long and narrow, of diverse branching habit, racemose to paniculate, usually with part or all of the branches of secund orientation and lacking both prophylla and subtending bracts. Spikelets either pedicellate, subpedicellate or sessile, containing 2 (1–5) perfect florets, and terminating in a depauperate sterile anthersium. Rachilla segments short, potentially disarticulating immediately below the locus of insertion of the first only, or (in some species) each of the fertile lemmas. Transitional glumes typically 3: 1 and 11 “empty glumes,” 11 a “sterile lemma” that is either empty or subtends a rudimentary flower. Fertile lemma fully embracing its palea only basally at maturity, the palea broadly sulcate dorsally, the margins gaping basally and lightly overlapped above. Lodicles 3, either subsimilar in shape or the anterior 2 more or less noticeably asymmetrical and paired, the posterior one symmetrical and slightly smaller. Stamens 3, the filaments filiform, free. Style very short, terminating in two stigmas. Mature fruit a mucronulate or weakly rostrate, fusiform caryopsis with a thin membranaceous pericarp of even thickness, the sulcus and the basal position of the embryo clearly manifest.

**Etymology.**—The name *Myriocladus*, formed from the Greek, *myrios*, numberless, and *clados*, branch, ostensibly alludes to the profuse ramification of the inflorescences.

**Type-Species.**—*Myriocladus virgatus* Swallen.

**Relationships.**—Certain of the striking generic features of *Myriocladus* are shared by individual...
members of other genera. A disproportionately elongate proximal above-ground culm internode followed by two or more obsolete internodes is a feature shared by Glaziophyton mirabile, by Aulonemia queko, and by a number of species of Arthrostylidium, including A. schomburgkii. The strongly thickened and indurate culm sheaths, branch sheaths and leaf sheaths with leathery blades, and the (sometimes irregular) incidence of solitary and appressed branches at culm nodes—features characteristic of all known species of Myriocladus—are found also in Aulonemia de: flexa and A. effusa, and in all known species of Greslania. Probably because some species of both genera have sessile leaf blades Myriocladus has been said to resemble (be related to?) Neurolepis (Swallen in Steyermark, et al., 1951:34). However, in its over-all combination of vegetative and reproductive features, Myriocladus is clearly disjunct from all other bamboo genera.

Distribution.—The twenty known species of Myriocladus are known only from the sandstone tablelands region of Venezuela. They occupy generally mesophytic, rarely swampy habitats, at recorded altitudes ranging from 1025 m to 2500 m.

Checklist of New World Bamboos Described Under the Genus Myriocladus

1. Myriocladus affinis Swallen, in Maguire, Wurdack, et al., 1957:244, fig. 3f.
2. Myriocladus cardonae Swallen, in Steyermark, et al., 1951:35.
3. Myriocladus confertus Swallen, in Maguire, Wurdack, et al., 1957:248, fig. 4c; in Maguire, Steyermark, Wurdack, et al., 1957:397. (Figures 38, 39b)
4. Myriocladus churumensis Swallen, in Steyermark, 1967:182.
5. Myriocladus distansiflorus Swallen, in Maguire, Wurdack, et al., 1957:248, fig. 4d.
6. Myriocladus exsertus Swallen, in Maguire, Wurdack, et al., 1957:242, fig. 3c.
7. Myriocladus gracilis Swallen, in Maguire, Steyermark, Wurdack, et al., 1957:393, fig. 74.
8. Myriocladus grandifolius Swallen, in Maguire, Wurdack, et al., 1957:245, fig. 5h.
9. Myriocladus longiramosus Swallen, in Maguire, Wurdack, et al., 1957:243, fig. 3e.
10. Myriocladus maguirei Swallen, in Maguire, Wurdack, et al., 1957:239, fig. 3b.
11. Myriocladus neblinaensis Swallen, in Maguire, Wurdack, et al., 1957:240, fig. 1.
12. Myriocladus paludicolus Swallen, in Maguire, Wurdack, et al., 1957:246, 248, fig. 4b.
13. Myriocladus paraquensis Swallen, in Maguire, Wurdack, et al., 1957:246, figs. 3i, j.
14. Myriocladus parvensis Swallen, in Maguire, Wurdack, et al., 1957:244, fig. 3g.
15. Myriocladus purpureus Swallen, in Maguire, Wurdack, et al., 1957:248, fig. 4e; in Maguire, Steyermark, Wurdack, et al., 1957:397.
16. Myriocladus simplex Swallen, in Maguire, Wurdack, et al., 1957:242, fig. 2.
17. Myriocladus steyermarkii Swallen, in Maguire, Wurdack, et al., 1957:247, fig. 5a; 395.
18. Myriocladus variabilis Swallen, in Maguire, Wurdack, et al., 1957:248, fig. 4a; in Maguire, Steyermark, Wurdack, et al., 1957:396.
19. Myriocladus virgatus Swallen, in Steyermark, et al., 1951:34, 35, fig. 4. (Figures 39aa–AC, 40)
20. Myriocladus wurdackii Swallen, in Maguire, Wurdack, et al., 1957:248, fig. 4f; in Maguire, Steyermark, Wurdack, et al., 1957:398.

Neurolepis Meisner

Figure 41

Neurolepis Meisner, 1843, I:426, II:925.—Pilger, in Engler and Prantl, 1906:21.—McClure, 1957:206.

Platonia Kunth, 1829:139 [non Rafinesque, 1808, nec Martius, 1829].—Nees, 1834:486.
Planotia Munro, 1868:70.—Bentham, in Bentham and Hooker, 1883:1209.—Hackel, in Engler and Prantl, 1887:93.

Plants typically unicespitose, exceptionally—as in N. aristata (Munro) Hitchcock—forming dense, more or less extensive thickets; unarmed. Rhizomes pachymorph, relatively slender. Culms self-supporting, typically unbranched in the vegetative state, the internodes fistular and cylindrical or terete. Leaf blades typically coarse and grass-like, petiolate or sessile, persistent or articulated with the leaf
sheath, the transverse veinlets not at all visible to clearly manifest.

Inflorescences semelauctant, each terminal to an unbranched culm, broadly to narrowly paniculate with a strong excurrent rachis, the branches appressed or spreading, commonly only one order of the branches (the first or the last or, in some species, none) showing second orientation; prophylla lacking; subtending bracts commonly lacking or obsolete. Transitional glumes at the base of the spikelet 4 (~5, as in N. angusta Swallen): i and ii "empty glumes," iii and iv (~v) "sterile (empty) lemmas." Spikelets pedicellate, typically containing but one perfect floret (the terminal one), the rachilla very short, articulated immediately below the loci of insertion of either the first sterile lemma only, or both the fertile and the sterile lemmas, and not prolonged behind the palea of the terminal perfect floret. Fertile lemma sometimes embracing its palea fully, but as a rule only basally so at maturity. Palea gaping antically, dorsally convex, in some species with an entire apex and not at all sulcate, elsewhere showing a very short, narrow sulcus terminating in an emarginate or bimucronulate apex. Lodicles 3, subequal or the anterior two appreciably asymmetrical and paired, the posterior one symmetrical and smaller (at least either shorter or narrower). Stamens typically 3—exceptionally 4, 5, 6 as in Cuatre-casas 14813 (US) (N. aristata (Munro) Hitchcock— the filaments filiform, free. Stigmas 2. Mature fruit an oblong, straight caryopsis with a uniformly thin, glabrous, dry pericarp, the sulcus abbreviated distally and proximally, the basal position of the embryo clearly to weakly manifest. [Examples of mature fruits known to me only from a specimen (US) identified by Soderstrom as Neurolepis elata (Kunth) Pilger, collected in Colombia by Cuatre-casas (no. 11522). These are extremely minute 2.0—2.5 mm long) but well formed.]

ETYMOLOGY.—The name Neurolepis, coined from the Greek words, neuron, nerve, and lepis, scale, apparently alludes to the strong, keel-like median nerve of the empty glumes in the type-species of this initially monotypic genus.

TYPE-SPECIES.—Neurolepis elata (Kunth) Pilger (in Engler and Prantl, 1906:21); Platonia elata Kunth (1830:327, pl. 76).

RELATIONSHIPS.—Plants comprised by Neurolepis share the following features with plants comprised by the genus Swallenochloa hollow culm internodes, a similar spikelet structure, and inflorescences with branches in secund orientation. Plants of the genus Neurolepis differ from plants of the genus Swallenochloa most conspicuously in their coarse, grass-like appearance and generally restricted radial development, besides bearing very much larger inflorescences that are confined to the terminal position on culms devoid of lateral branches. Ostensibly allied to Chusquea by a similar spikelet structure and (in some species) by certain features of the inflorescence, members of the genus Neurolepis differ from members of the genus Chusquea most conspicuously in bearing an inflorescence only at the tip of an unbranched culm, and in the incorporation of the following vegetative features: the generally coarse, grass-like (not bamboo-like) appearance of the plant (due to the shape and dimensions of the leaf blades, plus the lack of a strong differentiation between culm sheaths and leaf sheaths); the relatively slender form of the pachymorph rhizomes; and culms with hollow internodes but no lateral branches.

When Kunth (1829:139) published the genus Platonia, he stated that it differs from Chusquea only in a peculiar habit. However, on page 327 of the same work (1830), he said of Platonia elata Kunth—basionym of Neurolepis elata (Kunth) Pilger—"Cette plante présente tous les caractères du genre Chusquea; mais elle en diffère tellement par son port, que je n'ai pas hésité à en former un genre particulier." Nees (1834:486) reduced Neurolepis (as Platonia Kunth) to the rank of subgenus under Chusquea. Ruprecht (1839:80), who did not include Neurolepis (Platonia elata Kunth) in his monograph, expressed the opinion that Platonia in its true nature is very far from Chusquea: "Platonia vero natura sua valore a Chusquea distat."
Freier's study (1945:103) of Neurolepis pittieri and *N. aristata* reveals a bambusoid type of leaf anatomy in both species. It seems to me, however, not unlikely that intensive comparative studies of the known members of the genus *Neurolepis*, undertaken on a broader interdisciplinary basis, may result in their being given a revised disposition within the subfamily Bambusoideae, possibly as a tribe distinct from the "true bamboos."

The genus was treated briefly by Soderstrom (in Maguire, et al., 1969) and a key given to the nine species which he recognized. Gould and Soderstrom (1970) reported a chromosome count of $2n = 48$ for a specimen of *N. aperta* from Colombia.

**Distribution.**—Species of *Neurolepis* have been reported from an area that embraces sites in Peru, Ecuador, Colombia, Venezuela, and the island of Trinidad. All are reported from relatively high elevations (2900–4500 m); some of them inhabit ecological formations characterized as "páramo."

According to Munro (1868:73) *Chusquea aristata* Munro [= *Neurolepis aristata* (Munro) Pilger] was collected in Colombia by Goudot, who recorded for it the local name "Chusquea de Páramo." Notes by Jameson, collector of the type-specimen of *Chusquea aristata* Munro [= *Neurolepis aristata* (Munro) Hitchcock] are quoted by Munro (1868:61) as follows: 'It is a tall reedy grass, found only on the Eastern chain of the Andes. At 13,000 feet [ca. 4000 m] it makes its appearance, in irregular patches; at 15,000 feet [5000 m] it completely covers the whole surface, forming what the natives call a 'carizal,' impenetrable to man or beast. It continues upwards nearly to the limits of perpetual snow.'

**Annotated Checklist of Recognized Species of the Genus Neurolepis**

1. *Neurolepis angusta* Swallen, in Maguire, Wurdack, et al., 1957:249.

2. *Neurolepis aperta* (Munro) Pilger, in Engler and Prantl, 1906:21.

3. *Neurolepis aristata* (Munro) Hitchcock, 1927b:313 (Figure 41A).

4. *Neurolepis diversiglumis* Soderstrom, in Maguire, et al., 1969:16–18, 20.

5. *Neurolepis elata* (Kunth) Pilger, in Engler and Prantl, 1906:21.

6. *Neurolepis nobilis* (Munro) Pilger, in Engler and Prantl, 1906:21.

7. *Neurolepis glomerata* Swallen, in Maguire, Wurdack, et al., 1957:399.

8. *Neurolepis nigra* Swallen, 1957b:400.

9. *Neurolepis mollis* Swallen, 1931:14.

10. *Neurolepis pittieri* McClure, 1942:181, fig. 8 (Figure 41B-N).

11. *Neurolepis virgata* (Grisebach) Pilger, in Engler and Prantl, 1906:21.

12. *Neurolepis densiflora* Swallen, in Maguire, Steyermark, Wurdack, et al., 1957:399.

13. *Neurolepis ingens* (Pilger) Pilger, in Engler and Prantl, 1906:21.

14. *Neurolepis densiflora* Swallen, in Maguire, Steyermark, Wurdack, et al., 1957:399.

15. *Planotia acuminatissima* Munro, 1868:72.

16. *Planotia stipelii* Pilger, 1898:720.

17. *Planotia tessellata* Pilger, 1898:720.

18. *Neurolepis acuminatissima* (Munro) Pilger, in Engler and Prantl, 1906:21.

19. *Neurolepis stipelii* (Pilger) Pilger, in Engler and Prantl, 1906:21.

20. *Neurolepis tessellata* (Pilger) Pilger, in Engler and Prantl, 1906:21.

21. *Neurolepis weberbaueri* Pilger, 1921:446.

22. *Neurolepis diversiglumis* Soderstrom, in Maguire, et al., 1969:16–18, 20.

23. *Neurolepis elata* (Kunth) Pilger, in Engler and Prantl, 1906:21.

24. *Planotia elata* Kunth, 1830:327, pl. 76.

25. *Planotia nobilis* Munro, 1868:72.

26. *Neurolepis glomerata* Swallen, in Maguire, Wurdack, et al., 1957:399.

27. *Neurolepis nigra* Swallen, 1957b:400.

28. *Neurolepis mollis* Swallen, 1931:14.

29. *Neurolepis pittieri* McClure, 1942:181, fig. 8 (Figure 41B-N).

30. *Neurolepis virgata* (Grisebach) Pilger, in Engler and Prantl, 1906:21.

31. *Planotia virgata* Grisebach, 1864:530.

32. *Neurolepis densiflora* Swallen, in Maguire, Steyermark, Wurdack, et al., 1957:399.

33. *Neurolepis ingens* (Pilger) Pilger, in Engler and Prantl, 1906:21.

34. *Planotia acuminatissima* Munro, 1868:72.

35. *Planotia stipelii* Pilger, 1898:720.

36. *Planotia tessellata* Pilger, 1898:720.

37. *Neurolepis acuminatissima* (Munro) Pilger, in Engler and Prantl, 1906:21.

38. *Neurolepis stipelii* (Pilger) Pilger, in Engler and Prantl, 1906:21.

39. *Neurolepis tessellata* (Pilger) Pilger, in Engler and Prantl, 1906:21.

40. *Neurolepis virgata* (Grisebach) Pilger, 1921:446.

41. *Neurolepis diversiglumis* Soderstrom, in Maguire, et al., 1969:16–18, 20.

42. *Neurolepis elata* (Kunth) Pilger, in Engler and Prantl, 1906:21.

43. *Planotia elata* Kunth, 1830:327, pl. 76.

44. *Planotia nobilis* Munro, 1868:72.

45. *Neurolepis glomerata* Swallen, in Maguire, Wurdack, et al., 1957:399.

46. *Neurolepis nigra* Swallen, 1957b:400.

47. *Neurolepis mollis* Swallen, 1931:14.

48. *Neurolepis pittieri* McClure, 1942:181, fig. 8 (Figure 41B-N).

49. *Neurolepis virgata* (Grisebach) Pilger, in Engler and Prantl, 1906:21.

50. *Planotia virgata* Grisebach, 1864:530.

51. *Neurolepis acuminatissima* (Munro) Pilger, in Engler and Prantl, 1906:21.

52. *Neurolepis stipelii* (Pilger) Pilger, in Engler and Prantl, 1906:21.

53. *Neurolepis tessellata* (Pilger) Pilger, in Engler and Prantl, 1906:21.
apice penduli; internodiis cylindricis, intus fistulosis. Ramorum complementum ad nodos medianos culmorum insertum; eiusdem axi primario planato, subtriangulato, ad culmi superficiem appresso adnatoque, neque cylindrato neque segmentato; axibus secundariis numerosis, gracilibus, subaequalibusque, margine axis primarii insertis, ita ordinatone rhipidiforme sese ostendentibus. Foliorum lamina venulis transversis in speciebus plerisque extus vulgo haud manifestis, alibi plus minusve clare visibilius.

Inflorescentiae semelauctantes, ramificatione typice racemosa, rachidi vel percurrenti vel deliquescenti; spiculae insertione et orientatione diversae; prophyllis bracteisquenullis. Glumae transitionales (glumae vecuae et lernmata sterilia) numero diversae atque nonnumquam inconstantes. Spiculae vel sessiles vel subessiles vel pedicellatae, flosculos hermaphroditos vel paucos vel plures continentes, apice in ananthecio depauperato sterilique terminantes. Lemma fertile maturitate saltem partiendo, subtriangulato, ad culmi superficiem apresso, vel apice penduli; internodiis cylindricis, intus fistulosis. Ramorum complementum ad nodos medianos culmorum insertum; eiusdem axi primario planato, subtriangulato, ad culmi superficiem appresso adnatoque, neque cylindrato neque segmentato; axibus secundariis numerosis, gracilibus, subaequalibusque, margine axis primarii insertis, ita ordinatone rhipidiforme sese ostendentibus. Foliorum lamina venulis transversis in speciebus plerisque extus vulgo haud manifestis, alibi plus minusve clare visibilius.

Inflorescentiae semelauctantes, ramificatione typice racemosa, rachidi vel percurrenti vel deliquescenti; spiculae insertione et orientatione diversae; prophyllis bracteisque nullis. Glumae transitionales (glumae veceae et lernmata sterilia) numero diversae atque nonnumquam inconstantes. Spiculae vel sessiles vel subessiles vel pedicellatae, flosculos hermaphroditos vel paucos vel plures continentes, apice in anathceciio depauperato sterilique terminantes. Lemma fertile maturitate saltem partiendo, subtriangulato, ad culmi superficiem apresso, vel apice penduli; internodiis cylindricis, intus fistulosis. Primary branch buds (when present) at midculm nodes, solitary, each containing a single initial primordium. Branch complement at midculm nodes monoclade, of restricted insertion, the primary element neither cylindrical nor segmented, but thin, roughly triangular, appressed and more or less strongly adnate to the surface of the culm, the secondary axes numerous, slender, subequal, arising from primordia formed on the margin of the flat, primary element, of close-set apsidate insertion, with a fan-like pattern of orientation. Leaves (blades of leaf sheaths) with transverse veinlets in most species not at all (or scarcely) manifest, but in an occasional one more or less clearly visible externally.

Inflorescences semelauctant, typically of racemose branching, the rachis either deliquescent, or percurrent and straight or zigzag, the spikelets inserted and oriented in diverse patterns. Excepting the lowermost one, bracts subtending primary branches usually obsolete or lacking; typical prophylls lacking. Transitional glumes (empty glumes and sterile lemma) 2 or 3 (rarely 4) the uppermost one often subtending a depauperate flower, the others empty. Spikelets comprising few to several perfect florets, and terminating in one or more progressively depauperate sterile antheria. Rachilla segments possessing at maturity the potential for disarticulating just below the locus of insertion of each fertile lemma. Lemma (when subtending a functional flower) fully embracing the palea only basally at maturity. Palea broadly sulcate and 2-keeled dorsally, the margins not at all or only slightly and partially overlapping. Lodicules typically 3, the anterior two asymmetrical and paired, the posterior one smaller (at least shorter or narrower) and symmetrical (all three symmetrical and subequal in R. parviflorum; exceptionally -2, -1, -0 as recorded for R. ampliflorum). Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit (as far as known; available examples are rare) an oblong, subfusiform, sulcate, apically mucronate Caryopsis lightly compressed and lightly curved or asymmetri-
cal in the dorsiventral plane; pericarp pergaminoues (crustaceous in *R. verticillatum*), glabrous, of uniform thickness; the sulcus and embryotegium weakly to strongly manifest.

**Etymology.**—The name *Rhipidocladum*, derived from the Greek, *rhipis*, fan, and *klados*, branch, alludes to the fan-like pattern formed by members of a mature midculm branch complement in all of the bamboos herein allocated to the genus.

**Type-species.**—*Rhipidocladum harmonicum* (Parodi) McClure, new combination. *Arthrostylidium harmonicum* Parodi (1944:478, fig. 1).

**Relationships.**—The combinations of morphological features used herein to define *Rhipidocladum* places this genus between *Merostachys* and *Arthrostylidium*, with some of its features indicating affinities toward *Merostachys* and other features indicating affinities toward *Arthrostylidium*. The taxa I have allocated to *Rhipidocladum* are perfectly uniform in terms of the ontogeny and morphological development of the midculm branch complements and are, in this aspect, indistinguishable from the taxa I have retained in *Merostachys*. However, a comparison of the shape and orientation of the blade borne on culm sheaths representing their midculm range, insofar as these features have been documented, suffices to distinguish plants of taxa allocated to the genus *Rhipidocladum* (Figure 42a) from plants of taxa retained in the genus *Merostachys* (Figure 37b).

As *Merostachys* and *Rhipidocladum* are here circumscribed, the component species of both genera show a considerable range of variation in morphological features of their inflorescences. The range of these diversities is the more marked in *Rhipidocladum*, where at one extreme it embraces deceptive simulations of *Merostachys* and at the other, *Arthrostylidium*. Fournier (1881:131) was misled by this latter case into transferring Steudel’s *Arthrostylidium racemiflorum* to *Merostachys*.

As shown in the key below, the species currently allocated to *Rhipidocladum* embrace, in their inflorescences, six distinct patterns of insertion and orientation of the spikelets. An intimation of ostensible relationship between *Rhipidocladum* and *Merostachys* appears in the noticeable to marked secund orientation of the spikelets in the spicate racemes of seven species of *Rhipidocladum*.

*Rhipidocladum* and *Arthrostylidium* coincide here and there (compare *R. harmonicum* with *Arthrostylidium venezuelae*, and *R. urbanii* with *A. cubense*) with respect to certain forms assumed by the inflorescences. As mentioned above, however, the respective members of these two genera are readily distinguishable by the characteristics of their midculm branch complements.

**Distribution.**—The eleven named species comprehended by the present circumscription of the genus *Rhipidocladum* represent taxa that occupy open or forested mesophytic situations at low to moderate altitudes in frost-free areas, from Mexico to Brazil and Bolivia.

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**Key to Recognized Species of *Rhipidocladum***

| Step | Description                                                                 | Species                                                                 |
|------|-----------------------------------------------------------------------------|-------------------------------------------------------------------------|
| 1a   | Rachis deliquescent; spikelets pedicellate                                   | *R. verticillatum*, new combination                                      |
| 1b   | Rachis excurrent; spikelets sessile or subsessile                            |                                                                        |
| 2a   | Spikelets inserted on the rachis in predominantly binate clusters           |                                                                        |
| 2b   | Spikelets of monate (solitary) insertion                                     | *R. geminatum*, new combination                                         |
| 3a   | Rachis geniculate (at least in its distal portion); spikelets in distichous orientation | *R. harmonicum*, new combination                                         |
| 3b   | Rachis not genculate; spikelets in secund orientation                        |                                                                        |
| 4a   | Spikelets oriented within a single plane giving a banneret-like form to each inflorescence | *R. maxonii*, new combination                                           |
| 4b   | Spikelets not oriented within a single plane                                 |                                                                        |
| 5a   | Spikelets 4-5 cm long; the rachilla not disarticulating promptly at maturity | *R. ampliflorum*, new combination                                        |
| 5b   | Spikelets not exceeding 2.5 cm in length; the rachilla disarticulating promptly at maturity | *R. angustiflorum*, new combination; *R. bartletti*, new combination; *R. parviflorum*, new combination; *R. pittleri*, new combination; *R. prestoei*, new combination; *R. racemiflorum*, new combination. |
The six names (in couplet 5b) represent Hackel's (1903a:69) image of the genus *Arthrostylidium* as tentatively adumbrated but not typified by him (see p. 19). The corresponding binomials label several closely related taxa that are poorly represented by their type-specimens, and but weakly differentiated from each other by their protologs. Numerous currently available specimens represent these and similar taxa too incompletely and too incongruently to support confident decisions with respect to the existence of either suspected synonyms or possible specific or subspecific novelties.

Annotated Checklist of Recognized Species of *Rhipidocladum*

1. *Rhipidocladum ampliflorum* (McClure) McClure, new combination. *Arthrostylidium ampliflorum* McClure, 1942: 167, fig. 1.
   **Holotype.**—*Karsten s. n.* (US). Specimens examined include the holotype and elements of the holotype collection (US ex LE, US ex W).
   **Distribution.**—Venezuela.

2. *Rhipidocladum angustiflorum* (Stapf) McClure, new combination. *Arthrostylidium angustiflorum* Stapf, 1913: 268.
   **Holotype.**—"Communicated by Messrs. Sander & Sons, Bruges, 3rd May, 1912" (K). Specimens examined include the type-collection (US ex K).
   **Distribution.**—"Tropical America."

3. *Rhipidocladum bartlettii* (McClure) McClure, new combination. *Arthrostylidium bartlettii* McClure, 1954: 81.—McClure in Swallen 1955: 38.
   **Holotype.**—*Bartlett 12154* (US). Specimen examined, the holotype.
   **Distribution.**—Guatemala.

4. *Rhipidocladum geminatum* (McClure) McClure, new combination. *Arthrostylidium geminatum* McClure, 1942: 169, fig. 2.
   **Holotype.**—"Jahn 125" (=Jahn 11, teste Dra. Zoraida Luces de Febres) (VEN). Specimen examined, the holotype.
   **Distribution.**—Venezuela.

5. *Rhipidocladum harmonicum* (Parodi) McClure, new combination (Figure 42A-q).

6. *Rhipidocladum maxonii* (Hitchcock) McClure, new combination. *Arthrostylidium maxonii* Hitchcock, 1927a: 80.
   **Holotype.**—*Maxon 8154* (US). Specimens examined include the holotype and *Standley and Torres 50981* (US); *Standley and Valerio 49781* (US).
   **Distribution.**—Ecuador; Peru.

7. *Rhipidocladum parviflorum* (Trinius) McClure, new combination. *Arundinaria parviflora* Trinius, 1835: 619.
   **Holotype.**—"in sylvis pr. Ypenêma Bras." [Riedl 189] (LE).
   *Arthrostylidium trini* Ruprecht, 1839: 29.
   **Holotype.**—"in sylvis Brasiliae pr. Ypenêma Bras. Riedl!* [189] (LE). Specimens examined include *Macedo 4555* (US); *Regnell ser. III no. 1420* (US ex Regnell herbarium); *Riedl 189* (US ex LE); *Soderstrom 979* (US); *Tamayo 2718* (US ex VEN).
   **Distribution.**—Brazil; Venezuela.

8. *Rhipidocladum pittieri* (Hackel) McClure, new combination. *Arthrostylidium pittieri* Hackel, 1903a: 75.
   **Holotype.**—*Pittier 7193* (W). McClure, in Swallen, 1955: 40.
   *Arundinaria pittieri* (Hackel) E. & G. Camus, 1913, I: 40.
   Specimens examined include *Grant 1036* (US ex A); *Heyde and Lux 4302* (US); *Pittier 7193* (US); *Standley 78356* (US).
DISTRIBUTION.—Costa Rica, Guatemala, Nicaragua.

In his original description of *Arthrostylidium pittieri*, Hackel (1903a:76) gives this species only 2 lodicules but 3 stigmas; however, a specimen from the type-collection—Pittier 7193 (US)—shows lodicules typically 3 and stigmas typically 2. Some lodicules in this specimen show an abnormality in the form of a style-like apical prolongation which is terminated by several (often 3) bristles. It seems unlikely that this structure was misconstrued by Hackel as the pistil. The occasional appearance, however, of morphological anomalies in the pistil itself (e.g., a supernumerary stigmatic branch) might be responsible for the erroneous impression recorded by him for this species.

9. *Rhipidocladum prestoei* (Munro) McClure, new combination.

*Arthrostylidium prestoei* Munro, 1895:186.

**HOLOTYPE.**—Prestoe [Trinidad Botanical Garden Herbarium no. 1675] (K).

*Arundinaria prestoei* (Munro) Hackel, 1903d:516.

Specimens examined include *Broadway 4922* (US ex TRIN); *Prestoe* [Trinidad Botanical Garden Herbarium no. 1675] (US ex B [compared with type at Kew by Agnes Chase]).

**DISTRIBUTION.**—Trinidad.

10. *Rhipidocladum racemiflorum* (Steudel) McClure, new combination.

*Arthrostylidium ? racemiflorum* Steudel, 1854:336.

**HOLOTYPE.**—Ghiesbrecht 234 (?LE).

*Merostachys racemiflora* (Steudel) Fournier, 1881:131.

Specimens examined include *Brother Angel 721* (US); *Camp E-3814* (US); *Curran 198* (US); *Davidson 1297* (F); *Ghiesbrecht 234* (US ex LE, US ex P); *Liebmamn 144* (US ex C); *McClure 21221* (US); *Molina 8072* (US ex EAP); *Skutch 3806* (US).

**DISTRIBUTION.**—Canal Zone, Colombia, Costa Rica, Ecuador, Honduras, Mexico, Panama.

11. *Rhipidocladum verticillatum* (Nees) McClure, new combination.

*Arundinaria verticillata* Nees, in Martius, 1829:523.—Kunth, 1834:483, pl. 155, 156; 1835:348.—Ruprecht, 1839:25, pl. 3: fig. 7.—Munro, 1868:28.—Doell, in Martius, 1880:166.

*Ludolphia verticillata* (Nees) Willdenow, 1833:25.

**HOLOTYPE.**—Sellow s.n. (B). Specimens examined include *Glaziou 20148* (US ex P; US ex C), (F); *Sellow s.n.* (US ex B; US ex LE).

**DISTRIBUTION.**—Brazil.

*Swallenochloa* McClure, new genus

**FIGURES 43-45.**

Plantae unicespitoseae, inermes. Rhizomata pachymorpha. Culmi sese sustinentes, in speciebus pleurocoryfe adhuc saltam cognitis rigide erecti; internodiis fistulosis, supra locum insertionis vel ramorum vel gemmarrum complementi tantum vel breviter vel prorsus sulcatis, alibi teretibus. Ramorum complementum ad nodos culmorum medianos insidens raro absens, nonnumquam monocladum, typice solutum pleiocladum, axibus primaris vulgo 3 (usque 5), ad libram conflerissime insertis et ex gemmis discretis, unoquoque mostem vel demum ex gemmis ad nodos proximos suos proliferanti. Foliorum lamina venulis transversis in speciebus nonnullis hauud visibilibus alibi plus minusve clare manifestis.

Inflorescentiae semelauctantes, typice confertim paniculatae, lineares et secundae; rhachidi percurrenti; ramis omnibus brevibus, plus minusve valde appressis; prophyllis bracteisque nullis. Glumae transitionales imo spiculae insidentes 4: I et II "glumae vacuae," III et IV "lemmata (vacua) sterilia." Spiculae plerque florem perfectam unicam terminalemque continent; rhachilla post paleam hauud producta. Anthoeciorum fertilium maturorum lemma paleam suam imo tantum circumnectans. Palea antice hians, saltam apicem versus vulgo et sulcata et nonnumquam plus minusve manifeste bicarinata, dorso alibi convexa. Lodiculæ 3, duabus anterioribus aequalibus, plus minusve valde asymmetricis et congruentem gynoecium, posteriori sym-metrico et aliquantum minore. Stamina 3, filamentis filiformibus liberisque. Stigmata 2, quorum unum nonnumquam sed rarissime supra basin suam in duas partes divisum. Fructus maturus non inventus.

**FIGURE 43.—Swallenochloa subtessellata** (Hitchcock) McClure. A, Leafy flowering branch complement, × 0.6; b, apex of leaf sheath and base of leaf blade, × 3; c, base of branch complement high on culm, × 3; d, tuft of ultimate branches of inflorescence with transitional glumes attached, × 7.2; e, spikelet, × 7.2; f, sterile lemma i, × 7.2; g, sterile lemma ii, × 7.2; h, fertile lemma, × 7.2; i, palea, × 7.2; j, lodicule complement, × 25; k, stamen, × 15; l, gynoecium, × 50. All based on *Tonduz 3367*, type-species (US).
Plants unicespitose, unarmed. Rhizomes pachymorph. Culms self-supporting, the internodes typically fistular, either terete or lightly to strongly sulcate above the locus of insertion of a complement of buds or branches. Branch complement at midculm nodes rarely lacking, occasionally monoclade, typically unrestricted pleioclade, the initial components most commonly 3 in number (rarely to 5), unequal (each of independent origin, i.e., developing from a separate primary bud), of level insertion (with their bases close together in a horizontal row) the middle one dominant, each usually proliferating from buds at its proximal nodes. Leaves (leaf sheath blades) with transverse veinlets not at all evident or more or less clearly manifest externally.

Inflorescences semelauctant, commonly terminal to the culm as well as to leafy or leafless lateral axes, typically linear in profile, compact-paniculate, the rachis percurrent, the primary branches of secund orientation, those of all orders usually short and more or less strongly appressed; prophylls and bracts lacking throughout. Transitional glumes at the base of the spikelet 4: I and II “empty glumes” in some species sub-obsclete; III and IV “sterile (empty) lemmas.” Spikelets typically containing but one perfect floret, the rachilla very short, potentially disarticulating immediately below the locus of insertion of the first sterile lemma and of any fertile lemma, and not prolonged behind the palea of the terminal floret. Fertile lemma fully embracing its palea only basally at maturity. Palea gaping antically, sulcate and weakly to strongly bicarinate for a short distance at the usually emarginate or bidentate or bimucronate apex, dorsally convex elsewhere. Lodicles 3, the anterior two typically asymmetrical and congruently paired, the posterior one smaller (at least either shorter or narrower) and symmetrical. Stamens 3, the filaments filiform free. Stigmas 2, one of them sometimes (but rarely) divided above the point of its origin as observed in one flower of *Weberbauer 4415*, (type-collection of *S. weberbaueri*). Mature fruit unknown.

**Etymology.**—The name *Swallenochloa* commemorates the initial recognition of this genus by Dr. Jason R. Swallen, well known for his extensive field studies of New World grasses, and for his numerous contributions to the taxonomy of the Gramineae.

**Type-species.**—*Swallenochloa subtessellata* (Hitchcock) McClure.

**Relationships.**—Members of *Swallenochloa* share with members of *Chusquea* and members of *Neurolepis* a basically similar spikelet structure. Beyond this, *Swallenochloa* touches each of the other two at a few points where one or two technical features exceptional in one genus are shared by one of its members with a member of one of the other genera. Examples follow. A specimen under Pittier 3069 (US 677457)—cited by Hitchcock (1927a:81) as *Chusquea subtessellata* Hitchcock, now *Swallenochloa subtessellata* (Hitchcock) McClure, from which it differs in several technical details—appears to conform to the other members of *Swallenochloa* in all generic aspects except the profile and dimensions of the strongly chusqueoid inflorescence. Specimens of an undescribed species of *Chusquea*, under McClure 21234 (US) have the satellite buds and branches at midculm nodes reduced to two, as is usual in *Swallenochloa*, but in all other technical respects the material clearly falls within the natural boundaries of *Chusquea*. A whole plant under Fosberg 20856 (US 273832) shows unbranched culms with hollow internodes and a terminal inflorescence as in *Neurolepis*, but the nature of its foliage places it clearly in *Swallenochloa*.

Bamboos of the genus *Swallenochloa* differ most conspicuously from bamboos of the genus *Chusquea* by combining inflorescences of linear profile with distinctive features of the vegetative organs, including hollow culm internodes, primary complement of buds or branches at midculm nodes comprising fewer members, presenting several markedly distinctive morphological aspects, and foliage leaves

**Figure 44.**—*Swallenochloa subtessellata* (Hitchcock) McClure. A, Habit of leafy flowering branch showing tessellation of leaf blades, × 0.6; b, sheath subtending flowering twigs (left) and detached blade (right), × 12; c, apex of leaf sheath and base of leaf blade, × 7.2; d, tuft of ultimate branches of inflorescence with transitional glumes attached, × 7.2; e, spikelet (without pedicel and transitional glumes), × 7.2; f, sterile lemma 1, × 7.2; g, sterile lemma 11, × 7.2; h, fertile lemma, × 7.2; i, palea, oblique aspect; j, palea, dorsal aspect, × 7.2; k, lodicule complement, × 15; l, stamen, × 15; m, gynoeceum, × 50. All drawings based on Pittier 3069, a variant form of the species, (US).
generally showing definitely xeromorphic structure, texture, and habit.

Swallenochloa subtessellata (as Chusquea subtessellata) is by Niilo Virkki (1963) given a chromosome number 2n = 36. Janaki Ammal (1959) gives three species of Chusquea the chromosome number of 2n = 48.

The genus Swallenochloa shares the following features with the genus Neurolepis: hollow culm internodes, a similar spikelet structure, and a strong tendency to secund orientation in the branches of the inflorescences. However, members of Swallenochloa differ from members of Neurolepis most conspicuously in the dense and extensive development of individual plants, the freely branched culms; the smaller size, bamboo-like shape, xeromorphic texture, and upright habit of the foliage leaves; and the very much smaller and generally more compact inflorescences, which are not confined to the terminal position on the culms.

Among the many available specimens that clearly belong to the genus Swallenochloa but remain unidentified as to species, certain features of the reproductive structures show a high incidence of intergradation. For this reason, the differentiation and definition of species or other subgeneric taxa on the basis of typical conventional herbarium specimens presents difficulties at many points. The high incidence of abortive or distorted structures in the spikelets of many of the variants, and the scarcity of normal, mature fruits suggest (1) the possibility of a hybrid origin for the genus or the continued but only partially successful introgression between its members, and (2) the existence of insects or fungi whose parasitic activities may be responsible for the widespread incidence of distortion shown by the spikelets. As matters now stand, so great is the incidence of variation and distortion in the spikelets, and so obscure are the bases for these diversities, that it is difficult to determine with confidence a suitable taxonomic disposition for many of the available collections.

The genera Chusquea, Neurolepis, and Swallenochloa represent groups of species that are closely related in the essential features of the reproductive apparatus, members of Chusquea leading in the diversity of form expressed in the branching of the rhizomes, culms, and inflorescences. From the other bamboo genera of the New World flora, these three are set off, as a group, by the regular appearance in their members of two usually empty "sterile lemmas" following the second "empty glume" at the base of the spikelet, and by the termination of the spikelet in a perfect floret, without a prolongation of the rachilla behind it. Chusquea is unique among the three in the efistulose structure of all segmented vegetative axes; in the universal presence of more than one branch bud at midculm nodes; and in the constellate insertion of the branch buds and members of the branch complement at midculm nodes. Species of Chusquea show, in aggregate, the most extreme range of ecological tolerance, or preference. Neurolepis recedes from the other two members of the group in the coarse, grass-like character of the plant; the usually large, persistent leaf blades; the universal lack of branching in the aerial range of the vegetative part of the culm; and the usually rather weak development of the rhizome system. At least some species of Neurolepis are found at relatively high altitudes and in ecological formations characterized as páramo. Species of Swallenochloa form dense thickets, consisting of erect culms with hollow internodes, branch buds and branches at midculm nodes in level (not constellate) insertion. Their natural distribution is confined to high altitudes, commonly in ecological formations some of which are characterized as páramo.

The sharing by Swallenochloa, Chusquea, and Neurolepis of features not found elsewhere among New World bamboos raises questions as to the phylogenetic relationship of these three genera. Could Swallenochloa be the product of introgression between members of Chusquea and Neurolepis that

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Figure 45.—Swallenochloa tessellata (Munro) McClure. A, Small leafy flowering culm, × 0.6; B, leafy flowering culm with its pachymorph rhizome, × 0.6; C, midculm complement of three branch buds, × 3; D, base of midculm complement of three independent primary branchlets, × 3; E, apex of leaf sheath and base of leaf blade, × 6; F, secondary branch of inflorescence, bearing three pedicellate spikelets, × 3; G, spikelet, × 6; H, two transitional glumes, × 6; I, two "sterile (empty) lemmas," × 6; J, "fertile lemma," × 6; K, palea, × 6; L, lodicule complement, × 12; M, stamen, × 6; N, gynoeclium, × 24; O, rhizome and base of culms, × 0.6; P, cross-section of rhizome, × 5.4. Drawing A based on Triana 306, type-species (US); B, F-N on Schultes 18771 (US), C, P on Garcia-Barriga 11643-A; D, E on Garcia-Barriga 11684 (US), and O on Soderstrom 1339 (US).
are, or have been, sympatric in the high altitudes where the three genera meet today?

**DISTRIBUTION.**—Originally allocated to the genus *Chusquea*, the five bamboos currently recognized as species of *Swallenochloa*, together with numerous collections representing as yet undescribed congeneric diversities, are all endemic to the New World. Their aggregate geographic range of distribution extends from Bolivia and Brazil to Costa Rica, and embraces areas distinguished by characteristic complexes of ecological factors locally given distinctive names such as “páramo,” “sub-páramo,” etc. Recorded altitudinal limits fall between 2700 m and 4000 m above sea level. The highest density of incidence appears in Colombia.

Fosberg (1944) describes in extensive and vivid detail the plant life and the ecological features of the Páramo de Sumapaz of Colombia where he collected a species of *Swallenochloa* referred to as follows (1944:230).

Another grass (*Chusquea weberbaueri*) is locally abundant and conspicuous. It, too, is very stiff, but it usually forms colonies rather than bunches, and its blades are flat and lanceolate. It is not climbing like other species of its genus. In exposed situations it is low but erect, 6 or 8 decimeters tall when not in fruit, and in very unfavorable situations it even fruits at 1 or 2 decimeters. Usually the spikes make it somewhat taller. In wetter places it becomes a meter or more tall, and in sheltered spots, it forms small cane-brakes up to 3 or 4 meters deep and very hard to push one’s way through.

The field notes that accompany the specimen (Fosberg 20856, US 2181792) read as follows: Colombia: “Cordillera Oriental, Dept. Cundinamarca, Cordillera de las Cruces, Páramo de Sumapaz. Common everywhere on páramo slopes; rough páramo plateau with wet forest running up the sides to about 3500 m, brush, up to 3650 m. [Plants] varying greatly in size. Aug. 19, 1934.” The specimen represents an apparently undescribed species of *Swallenochloa*.

Weberbauer in his monumental work entitled *El Mundo Vegetal de los Andes Peruanos* (1911 [1945: 146]) says of three species of *Swallenochloa* (under the names *Chusquea spicata*, *C. depauperata*, and *C. weberbaueri*) that “these dwarf forms occupy peat bogs and open grasslands at elevations between 3200 and 3500 meters” and that “with them are associated members of the curious genus *Neurolepis*, whose ensiform leaves emerge from the base of the stem and reach, in *N. weberbaueri*, a length of 2.5 meters.”

The present published content of the genus *Swallenochloa* is limited to five recognized species that were originally allocated to the genus *Chusquea*.

**Key to Currently Recognized Species of Swallenochloa**

1a. Transitional glumes I and II (“empty glumes”) subobsolete; branches of inflorescence entirely glabrous .................................................. 1. *S. depauperata*, new combination

1b. Transitional glumes I and II (“empty glumes”) about 1 mm or more in length; branches of inflorescence more or less noticeably to densely strigose ................................. 2

2a. Branches of inflorescence heavily waxy; spikelets tinted with wine ........................................................... 3

2b. Branches of inflorescence not noticeably waxy; spikelets of stramineous hue ........................................................... 4

3a. Transitional glume IV (upper sterile lemma) almost as long as the lemma, and showing 2 well-developed veins on each side of the midrib ... 3. *S. subtessellata*, new combination

3b. Transitional glume IV (upper sterile lemma) less than ¾ as long as the lemma, and showing only one well-developed vein on each side of the midrib .................................................. 4. *S. tessellata*, new combination

4a. Anthecium dull; pale stramineous; awn of lemma glabrous  ........................................................... 2. *S. spicata*, new combination

4b. Anthecium lustrous; dark stramineous; awn of lemma antrorse-scabrous .................................................. 5. *S. weberbaueri*, new combination

Annotated Checklist of Recognized Species of the Genus *Swallenochloa*

1. *Swallenochloa depauperata* (Pilger) McClure, new combination.

*Chusquea depauperata* Pilger, 1905:149.

**HOLOTYPE.**—Weberbauer 3709 (B).

**DISTRIBUTION.**—Peru.

2. *Swallenochloa spicata* (Munro) McClure, new combination.

*Chusquea spicata* Munro, 1868:60.
The name *Yushania*, *yu*, jade, and *shan*, mountain, is a Latinized form of the two components of the Chinese name (in the National dialect) of the type-locality of *Y. niitakayamensis*, type-species of the genus. A renowned geographical feature of Formosa (the Island of Taiwan), Yushan is known in Japanese as Niitakayama, and in English as Mount Morrison.

**Etymology.**—The name *Yushania*, *yu*, jade, and *shan*, mountain, is a Latinized form of the two components of the Chinese name (in the National dialect) of the type-locality of *Y. niitakayamensis*, type-species of the genus. A renowned geographical feature of Formosa (the Island of Taiwan), Yushan is known in Japanese as Niitakayama, and in English as Mount Morrison.

**Type-species.**—*Yushania niitakayamensis* (Hayata) Keng f. (see McClure, 1959:209). Based on

**Yushania K. H. Keng**

**Figures 46, 47**

*Yushania* K. H. Keng, 1957:355.

Plants unarmed, compactly unicespitose at first; mature clumps of pluricespitose habit in *Y. niitakayamensis* and of diffuse (open) habit in *Y. aztecorum*. Rhizomes pachymorph, the rhizome neck in *Y. niitakayamensis* and in *Y. aztecorum* becoming, in plants of mature stature, up to ca 50 cm long. Culms of small or medium stature, self-supporting; each midculm node bearing a single initial branch bud; margins of the prophyllum not fusèd; the initial primordium giving rise (simultaneously or nearly so and apparently before the germination of the bud) to typically three growing points, these becoming three subequal primary axes with a common base. The germination of each primary branch bud is accompanied by the apparently simultaneous elongation of its prophyllum. Branch complement arising at midculm nodes with the first three component axes typically dominant over any axes that proliferate from buds at their proximal nodes. Sheath at midculm nodes typically lacking a well-marked basal girdle. Leaf blades with transverse veinlets not at all to weakly to sometimes strongly manifest externally.

Inflorescences semaelauctant, forming contracted to more or less prolifically branched panicles, their branches epulvinate and eprophyllate, with subtending bracts (excepting the somewhat well-developed basal one) small to rudimentary to obsolete. Spikelets few-flowered to several-flowered, each terminating in a depauperate sterile anthecium. Transitional glumes typically 2, empty. Lemma of fertile florets embracing its palea only basally at maturity. Palea broadly sulcate and 2–keeled dorsally, the margins not at all or barely imbricate. Lodicules 3, the anterior 2 more or less asymmetrical and paired, the posterior one smaller and symmetrical. Stamens 3, the filaments filiform, free. Stigmas 2. Mature fruit, as far as known, a subfusiform, sulcate apically mucronate carypsis, the pericarp pergaminoæous, glabrous, of uniform thickness, the suclus and the embryotegium clearly manifest.
Arundinaria niitakayamensis Hayata (1907:79).

Relationships.—The simultaneous or subsimultaneous emergence, at midculm nodes, of more than one primary branch in Yushania recalls a similar feature in Apoclada. In Apoclada, however, the several primary axes of the midculm branch complement apparently do not have a common base, and the respective primordia from which they arise are apparently not initially enclosed in a common prophyllum (bud scale) as they are in Yushania.

Members of Yushania as the genus is herein circumscribed, resemble members of the genus Aulonemia in the paniculate form of the inflorescence. Plants allocated to Yushania, however, differ most basically from plants allocated to Aulonemia in terms of ontogeny (and certain details of the form) of the midculm branch complement. In members of the genus Yushania, the primordium of the initial bud at midculm nodes, while still enclosed in the prophyllum, gives rise to typically 3 initial growing points in quick succession. This situation suggests the presence of the phenomenon conventionally referred to as the "telescoping" of an axis—actually the shortening of the interval between the loci of emergence of the successive growing points produced by a body of primordial tissue. A satisfactory description of the distinctive sequence of events that produces the midculm branch complement that is characteristic of members of the genus Yushania awaits the intervention of anatomical studies designed to supplement the results achievable by way of gross morphology.

Distribution.—In the Chinese text that follows his Latin diagnosis of the genus, K. H. Keng (1957: 356) says of the Old World component of Yushania: "Of this genus only the type species is known at present. It is native of Taiwan, and is found also on Luzon, P.I., and in the mainland Chinese provinces of Szechuan and Yunnan." The known distribution of the New World component of the genus (subgenus Otatea) extends from Mexico to Honduras. Both the Old World component and

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**Key to Subgenera of Yushania**

1a. Culms proliferating from buds at their subterranean nodes; inflorescences with few spikelets; lemma weakly or not at all awned; palea acutely bifid apically; bamboos endemic to areas of the Old World

1b. Culms not proliferating from buds at their subterranean nodes; inflorescences with numerous spikelets; lemma conspicuously awned; palea obtuse apically; bamboos endemic to areas of the New World

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**Figure 46.** Yushania aztecorum McClure and E. W. Smith. A, Diagram of a portion of the rhizome system (greatly reduced) of a plant of mature stature, with culms and roots omitted from the rhizomes proper: the rhizome necks are naturally budless and rootless. In young plants of the species illustrated, the necks are shorter than the rhizomes proper, but as a plant approaches its mature stature the necks of the midculm range (apex of ramification at this level, leaf blades in profile, × 0.6; c, midculm internodes (greatly reduced) showing the shallow groove (sulcus) that extends upward from the locus of insertion of each primary bud: d, midculm node, showing the solitary primary branch bud with its prophyllum intact, × 1.5; e, primary branch bud at a midculm node, with the prophyllum removed, revealing three growing points, each a prophyllate but unsubtended bud, × 1.5; f, diagram of the pattern of the loci of insertion of the prophylla of the three branch buds portrayed in e, in relation to the prophyllum of the initial primordium (the body of special meristematic tissue from which the three buds emerge), × 4.8; g, base of a midculm branch complement, showing the initial components in an early stage of development, with sheaths removed, × 0.9; h, midculm branch complement with the initial components fully developed, × 1.2; i, base of midculm branch complement in a later stage of development, after the production of axes of higher orders following the germination of buds at the proximal nodes of the initial component axes, × 1.2; j, nonflowering leafy branches (distal portion only) from culms of relatively advanced age, showing solitary nature of ramification at this level, leaf blades in profile, × 0.6; k, leaf sheath apex with petiole and base of a narrow leaf blade, × 7.2; l, culm sheath from midculm range (apex only), adaxial aspect (left) and abaxial aspect (right), × 0.9. All drawings based on McClure 21204 (US).
the New World component of the genus Yushania embrace taxa still requiring intensive study in field and laboratory to determine their infrageneric status. The much-needed monographic treatment of the genus should, in my opinion, be deferred pending the completion of such studies.

**Subgenus Ostatea McClure and E. W. Smith, new subgenus**

Culmi e gemmis suis subterraneis haud prolife-
rentes; inflorescentiae spiculas multas gaudentes;
lemma aristatum dorso dense strigosum; palea apice
obtusa; plantae in terris occidentalis indigenae.

**ETYMOLOGY.**—The name *Ostatea* is a Latinized
form of the vernacular name *otate* (corrupted form
of a word from the Nahuatl, language of the Az-
tecs) by which some native bamboos (more par-
ticularly those pertaining to this subgenus) are
currently known and referred to in Mexico.

**TYPE-SPECIES.**—*Yushania aztecorum* McClure and
E. W. Smith.

### 1. Yushania (Ostatea) aztecorum McClure and
E. W. Smith, new species

**Figures 46, 47 A-M**

Plantae initio conferte caespitose demum sensim
aperientes. Rhizomatum collum initio (in plantis
staturea juvenant) rhizomate proprio suo brevis,
demum (in plantis staturea adultae) rhizomate
proprii multo longius. Culmi usque ad 6 m alti
et 2.5 cm diametro; internodia glabra, in plantis
juvenibus intus fustica, in plantis adulti fistulosa,
ea supra nodos medianos ramiferos sulcata. Ra-
chorum complementum ad nodos medianos oriens
initio axes primarios 3 subequales subcoaetaneos-
que vulgo capiens; axes ordinum superiorum a
primarii valde superati. Vagina internodia culmi
fovens dorso initio setis castaneis fragilis vel sparse
vel dense vestibata, demum calvecens sed papillis
persistentibus conspersa; auriculae et setae orales
vel nullae vel invalide evolutae; ligula arcuata,
margine pro parte ciliata et pro parte crasse fim-
biata; lamina appressa et late vel anguste trian-
gula; vaginae ad nodos inferiores culmorum
orientes haud deciduas, in situ demum fatiscentes.

Vagina foliorum prominenter nervos-striata, inter
nervos plus minusve dense usque haud papillata,
vel omnino glabra vel hic illic vel omnino
puberula; auriculae et setae orales vel vix uallae vel
nullae; ligula interior et ligula exterior dimensioni-
bus, forma, margine vesturaque maxime variabiles;
lamina foliorum vel lanceolata cum nervis secun-
dariis usque 3–4, vel lineari-lanceolata usque li-
nearis et nervos secondarios vulgo 1–2 praebens;
venulae transversae extus haud usque clare mani-
festae; pubescentia laminae charactere, crebretate,
et distributione maxime variabilis.

Inflorescentiae ramos et ramulos vel foliiferos vel
efoliatis terminantes; pedunculus, rhachis et radii
scaberuli; bracteae sat minima nonnunquam ob-
soleta. Spiculae omnino pallide strigosae, laxae,
usque ad 4 cm longae, flosculos 3–7 fungentos ca-
pientes, ubi maturae sat friabiles. Glumae transi-
ionales typice 2, lanceolatae, valde carinatae, apice
in aristan scabram ca 2.5 mm longam terminantes;
i (dempta arista): 2.5–3.5 mm longa, nervos secun-
darios 1–2 praebens; ii (dempta arista): 3.5–4.5
mm longa, nervos secundarios 2–3 praebens. Rachillae
segmentum unumquidque dimidium lemmatis sui
superantia, omnino scabrosa, gracilia, apice subito
dilatato conspicue ciliata. Lemma floscularum

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**Figure 47.—Yushania aztecorum** McClure and E. W. Smith
(A–M) and *Yushania sp.* (N). A, Examples of leaf blades
showing the range in size and shape encountered within a
single population. The largest lanceolate one was taken from
a young flowering culm. The long, narrow one represents
an associated form borne by older culms in both the vege-
tative state and in a weakly flowering state. The several
progressively smaller ones were taken from flowering
branches borne on culms of progressively more advanced
age, × 0.6. B, Leaf sheath apex with petiole and base of a
broad leaf blade, × 7.2; C, flowering branch—one of three
initial component axes of a branch complement high on a
young culm—with several contracted and leafless flowering
branches arising from buds at the proximal nodes of the
initial axes, × 0.6; D, tip of a flowering branch from a culm
of relatively advanced age, characterized by a pronounced
reduction in the size of the foliage leaf and the inflorescence
proper, × 1.2; E, spikelet, × 1.8; F, transitional (empty)
glomerules, × 6; G, floret, × 6; H, lemma, × 6; I, palea, × 6; J,
lodicule complement, × 12; K, stamen, × 6; L, gynoecium,
× 12; M, seedling, × 0.6; N, fruit, embryo side, showing
embryotegium (left), and hilum side (right), showing the
sulcus (conventionally referred to as a hilum), × 7.2. Draw-
ings A–M based on McClure 21204 (US) and N on Ortega
[4341](US).
fungentium lanceolatum usque (dempta arista scabra 2.5 mm longa) 9 mm longum, prominenter carinatum, alibi nervos secundarios 2-3 praebens. Palea usque 9 mm longa, oblonga, apice integra truncata, inter et secus carinas strigosa, nervis secundariis extus haud manifestis. Lodicae subopaeae, nervosae, utrinque glabrae, apice ciliis albidis ca 0.5 mm longis fimbriatae; duae anticae (demptis ciliis) usque ad 1.5 mm longae, leniter asymmetricae et gemmatae, quasi pulvinatae; postica (demptis ciliis) usque ca 1.0 mm longa, elliptica. Antherae maturitate stramineae, 5-6 mm longae. Ovarium glabrum. Fructus non adhuc inventus.

Plants at first compactly cespitose, becoming diffuse in habit as they mature. Neck of rhizomes at first shorter than the rhizomes proper, becoming longer in successive annual innovations, and eventually much longer than the rhizomes proper as the plant approaches its mature stature. Culms up to 6 m tall and 2.5 cm in diameter, with glabrous internodes pith-filled in young plants and hollow in plants of mature stature; internodes above ramiferous midculm nodes sulcate. Branch complement at midculm nodes at first typically comprising 3 subequal primary axes that emerge simultaneously or nearly so and dominate axes of higher orders that develop subsequently from buds at their own proximal nodes. Culm sheaths at lower (unbranched) nodes of the culms (Figure 46 B, L) not at all deciduous, slowly disintegrating in place. Leaf sheaths prominently nerved- striate, more or less densely to not at all papillate between the nerves; glabrous throughout to puberulous here and there or puberulous throughout; auricles and oral setae weakly developed to lacking entirely; inner and outer ligules highly variable in size, shape, margin, and vesture. Blade of leaf sheath varying in shape from lanceolate with up to 3-4 secondary nerves, to linear with 1-2 secondary nerves, the transverse veinlets not at all to clearly manifest externally; pubescence of the leaf blade highly variable in character, density and distribution.

Inflorescences terminating leafy or leafless branches and twigs; peduncle, rachis, and ramifications scaberulous; bracts rather small and sometimes obsolete. Spikelets up to 4 cm long, comprising 3-7 functional florets, obscurely and palidly strigose throughout, open, more or less noticeably zig-zag at maturity. Transitional glumes typically 2, lanceolate, strongly keeled, terminating in a scaberulous awn about 2.5 mm long; I (without the awn): 2.5-3.5 mm long, with 1-2 secondary nerves; II (without the awn): 3.5-4.5 mm long, with 2-3 secondary nerves. Rachilla segments slender, each more than half as long as its lemma, conspicuously ciliate at the abruptly dilated apex, elsewhere slender and scaberulous; readily disarticulating at maturity. Lemma of functional florets lanceolate, up to 9 mm long (without the ca 2.5 mm long scaberulous awn), prominently keeled, with 2-3 secondary nerves. Palea up to 9 mm long, oblong, entire and truncate apically, strigose along the keels and between them; secondary nerves not manifest externally. Lodicae subopaque, nerve, glabrous on both faces, fimbriate apically with cilia about 0.5 mm long, the two anterior ones about 1.5 mm long without the cilia, weakly asymmetrical and paired, apparently pulvinate at anthesis, the posterior one elliptical, up to about 1.0 mm long without the cilia. Anthers stramineous at maturity, 5-6 mm long, the connective not exserted. Ovary glabrous. Fruit not yet found.

Holotype.—F. A. McClure 21204 (US), collected at about 450 m on La Dispensa, an elevated area inland from Rosario, State of Sinaloa, Mexico, 5 August 1943. Vernacular name Otaté.

Relationships.—The foregoing description is based principally upon the most complete available specimen, McClure 21204 (US). It is supported in this and that detail by specimens from thirty-five other collections, the bulk of which are too fragmentary for confident infrageneric taxonomic disposition.

Distribution.—Field notes accompanying available specimens of thirty-six collections of members of the subgenus Otatea examined are generally meager. Most commonly encountered in herbaria are specimens from Mexico where, as observed by the senior author of this subgenus, plants of this subgenus often occupy relatively (seasonally?) dry sites, sometimes in association with cacti. Specimens collected in El Salvador and Honduras are more rarely seen. Plants we recognize as belonging
to the subgenus *Otatea* have been collected at reported elevations from 200 m to 2700 m in Mexico and Central America.

2. *Yushania (Otatea) acuminata* (Munro) McClure, new combination

*Arundinaria acuminata* Munro, 1868:25.
Figure 48.—Chart of Generic Characters. **Fruit:** view from embryo side (left), view from hilum side (right). **Stigma:** number of stigmas. Number in parentheses indicates that the number is of rare occurrence. **Stamen:** number of stamens. Number in parentheses indicates that the number is of rare occurrence. **Spikelet Apex:** Diagrammatic representation of the apical element of a spikelet. Male-female sign indicates a perfect floret. All others indicate empty florets reduced to varying degrees, in some cases quite depauperate. **Br Subt:** branches of the inflorescence (at least the lowermost ones) subtended by a bract. **Br Proph:** Branch prophyllum; plus indicates each branch of the inflorescence is subtended by a prophyllum at its basal node. **Infl Br:** type of inflorescence branching. Pan, panicle or paniculate; Rac, raceme or racemose; Con to Ope, congested to open; Sec, secund; Sol, solitary; Spi, spicate; Div, diverse; Cap, capitulate; Dif, diffuse; Dig, digitate. **Infl Dev:** inflorescence development. S, semelauctant; I, iterauctant. **Rhizome:** L, leptomorph; P, pachymorph; LP, leptomorph and pachymorph condition existing within the same plant. Dotted lines indicate that the rhizome system has not been seen but assumed to be pachymorph. **Midculm Prophyllum and Primordium:** Primary buds at midculm node consisting of the initial primordium (solid black triangle) covered by the prophyllum (cone). The single initial primordium represented by zig-zag lines indicates that it gives rise to a specialized primary element with buds of apsidate insertion. Dotted lines indicate what the situation is assumed to be, although not seen. **Initial (Primary) Branch:** Either lacking, a single dominant one, three or more subequal ones, or many subequal ones arising from a primary element in apsidate fashion. Open triangles represent buds capable of germination while the black dots represent buds which do not germinate. **L/S Int:** Long/short internodes. In plants of those genera marked with both a plus and a circle, there is a tendency for culms to have elongated internodes followed by shortened internodes. A question mark within the circle indicates that this feature possibly may not be present in some culms.
| Fruit | Stigma | Stamens | Spikelet Apex | Br. Subt. | Br. Proph. | Infl. Br. | Infl. Dev. | Genus | Rhizome | L/S | Midculm Prophyllum and Primordium | Initial (Primary) Branch |
|-------|--------|---------|---------------|----------|-----------|----------|-----------|-------|---------|-----|---------------------------------|------------------------|
|       | 3 3    | 0 0     | Pan Rac       |          |           |          |           | Arundinaria | L     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Con Ope Pan   |          |           |          |           | Chusquea    | L P   |         | 0   |                                 | 0                      |
| Not yet known | 2 3 | 0 0 | Sec Con Pan |           |           |          |           | Swallenochloa | P     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Pan Sec Rac   |          |           |          |           | Neurolepis   | P     |         | 0   |                                 | 0                      |
| Not yet known | 2 3 | 0 0 | Pan Rac Sol |           |           |          |           | Myriocladus  | P     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Pan          |          |           |           |           | Yushania (Otatea) | P |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Pan          |          |           |           |           | Aulonemia    | P     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Spi Rac      |           |           |           |           | Arthrostylidium | P   |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Div          |           |           |           |           | Rhipidocladum | P     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Sec           |           |           |           |           | Merostachys  | P     |         | 0   |                                 | 0                      |
|       | 2 3    | 0 0     | Sol          |           |           |           |           | Apoclada     | P     |         | 0   |                                 | 0                      |
| Not yet known | 2 3 | + 0 | Cap          |           |           |           |           | Athroostachys | P     |         | 0   |                                 | 0                      |
| Not yet known | 2 3 | + + | Dif          |           |           |           |           | Glaziophyton | P     |         | 0   |                                 | 0                      |
| Not yet known | 2 3 | + + | Cap or Dif |           |           |           |           | Atractantha  | P     |         | 0   |                                 | 0                      |
|       | 2 6    | + +     | Dif          |           |           |           |           | Elytrostachys | P     |         | 0   |                                 | 0                      |
|       | 4 3 2 1 | + +   | Dif or Cap   |           |           |           |           | Bambusa (Guadua) | P |         | 0   |                                 | 0                      |
Glossary

The following terms are defined with special reference to the usages adopted by the author for describing various characteristics of the bamboo plant. Most of these first appeared in the glossary of McClure (1966b:295–318), reprinted in Taxon (McClure 1966a: 220–235). In that glossary newly coined terms were indicated by an asterisk (*); others, indicated by a dagger (†), were given new or extended meanings to describe conditions not satisfactorily covered by conventional usage, or by botanical glossaries.

Some of the following definitions incorporate more or less drastic modifications that, in the present dissertation, are given precedence over the definition of the same terms that appear in the above publications. For example, the content given the terms monoclade and pleioclade in the earlier glossary has been drastically changed. When unqualified (standing alone) these terms now refer exclusively and to the first order element(s) of a branch complement. The qualifying adjectives “restricted” and “unrestricted” refer to their potential for proliferation from buds (if any exist) at the proximal nodes of their first order elements. Any modified, or newly added, terms are indicated by a double asterisk (**) in the present glossary.

Abaxial (L. ab, away from; axis). Away from an axis; designates that surface of an appendage (such as a culm sheath or a sheath blade) which faces, in a structural sense, away from the axis on which it is inserted or relies for support. The terms abaxial and adaxial (q.v.) should be employed instead of upper and lower, or dorsal and ventral, whose use—with reference to the two faces of a foliage leaf or a reflexed sheath blade, for example—is apt to perpetrate ambiguity, and so cause confusion. This is because the orientation of such a structure may vary—in time, and from one botanical entity to another—especially among the bamboos. Therefore, neither upper and lower, nor dorsal and ventral, will always be correlated reliably with anatomical dorsiventrality, to which important structural basis all pertinent observations must be oriented unmistakably in order to satisfy the requirements of scientific discipline, dependability, and clear thinking. Cf. Adaxial.

Abscissile (L. abscissilis, from abscissus, cut off). Susceptible of being cut off or disarticulated by the formation of an abscission layer; applies to the petiole of a deciduous leaf or, as in many bamboos, to the segments of a rachilla. See Deciduous.

Acropetal (Gr. akron, the highest point; L. peto, I go toward). Progressing toward an apex, as when the development or emergence of appendages on any axis takes place serially in the direction of the apex of the axis. Cf. Basipetal.

Acropetally (adv.) Toward an apex.

Adaxial. Toward an axis; designates that surface of an appendage which faces, in a structural sense, toward the axis on which it is inserted, or relies for support. Cf. Abaxial.

Adnate (L. adnascor, I grow to). “Attached the whole length” (Jackson, 1949). “Congenitally grown together; said especially of unlike parts” (Webster, 1959). Used herein as applying to any degree or extent of union between the tissues of unlike parts. See Connate.

Adventitious (L. adventitius). Occurring in a location other than the usual one. In the bamboos, and in other grasses as well, the principal complement of roots is adventitious, arising at the nodes of culms and rhizomes, and not from the primordial root. In the genus Chusquea; for example, adventitious branch buds arise independently, both at the right and at the left of the one at the usual site, which is median to the base of a subtending culm sheath. See Constellate.

Amphimorph (Gr. amphi, both; morphè, forms). Embracing both of two distinct forms. Example: The same plant of Chusquea fendleri gives rise to culms from both pachymorph and leptomorph rhizomes.
**Ananthous** (*L. anathus*). Lacking a flower; "transitional glumes," and "sterile lemmas" are ananthous.

**Anastomosis** (Gr. *anastomosis*, a new outlet). "Union of one vein with another, the connection forming a reticulation" (Jackson, 1949).

**Androecium** (Gr. *androes*, male; *oikos*, house). The stamen complement of a flower. I have not followed Arber (1934:152 et passim) in adopting the spelling (andraeecium) advocated by Kraus (1908). R. W. Brown (1954), Jackson (1949), and Nybakken (1959) all give androecium. Cf. Gynoecium.

**Anthecium** (Gr. *anthos*, flower; *oikos*, house). The protective structure in the Gramineae, which is formed by the lemma and palea and which, typically, encloses a single flower.

**Antically,** anticiously (L., forward, in front). Toward the front; introrsely or adaxially. Jackson (1949) records diverse and even antonymous definitions of antical, mentioning the synonymous use of introrse as "occasional." The bamboo palea often gapes antically.

**Apo Paypalda** (Gr. *apo*, separate; *klados*, branch). A bamboo genus; the name alludes to the independent origin of the primordial elements of midculm branch complements, a feature that appears in distinctive expression in this taxon.

**Apsidate** (L. *ipsis*, arch). In convex arcuate array; characterizes the pattern of insertion of the secondary component (second-order axes) of a monoclade branch complement, as exemplified by members of the genera *Merostachys* and *Rhipido cladum*, q. q. v. See Constellate; Gremial; Level; Restricted.

**Assimilation tissue.** Mesophyll; the interior ground tissue of a leaf blade.

**Awned.** Bearing a bristle-like apical appendage called an awn (OE). The empty glumes of the spikelet in the type and some other species of *Neurolepis* are awned. In *Streptochaeta* (a genus of grasses related to bamboos), the lemma terminates above in a very long, apically coiled structure called an awn (*L. arista*) by Nees (1834), the author of the genus; Trinius called it a tail (*L. cauda*). The distinctions between the ways in which the different types of sheathing structures or their foliar appendages terminate apically are not sharp. Technical terms (such as apiculate, awned, cuspidate, and mucronate) and their conventional definitions do not clearly distinguish the diverse expressions that are a part of the morphological intergradation that baffles efforts at hard-and-fast categorization here, as in many other facets of plant structure.

**Bamboo** (*bambu, a vernacular word of undetermined Oriental origin*). The wood of bamboo culms; a plant so classified.

**Bamboos.** A taxonomic group of plants comprising the tribe Bambuseae of the Bambusoideae, a subfamily of the Gramineae; living plants, or culms (stems) severed from plants of this group.

**Basipetal** (L. *basis*, base; *petto*, I go toward). Progressing toward a base, as when the development or emergence of appendages on any axis takes place serially in the direction of the base of the axis. Cf. Acropetal.

**Basipetally** (adv.). Toward a base.

**Binate** (as applied to pleioclade midculm branch complements). Typically consisting of only two axes or branches, e.g., typical midculm branch complement in the Old-World genus *Phyllostachys*.

**Blade** (AS. *blaed*, leaf). "The limb or expanded portion of a leaf" (Jackson, 1949). In the bamboos, a thin, expanded, chlorophyll-bearing, sessile or petiolate, apical appendage (lamina) of a sheath proper. See Leaf.

**Bottlebrush** (*bottle brush, a brush of cylindrical shape*, with the bristles uniformly distributed on the axis and oriented approximately at right angles to it). A borrowed term, given a slightly modified form, and used here (in the adjectival sense apparently not recorded in dictionaries) to describe the approximate pattern of distribution and orientation of the proliferations of the stigmatic surface in certain bamboos, a pattern loosely called plumose or aspergilliform by some authors. Cf. Dendroid.

**Bract** (L. *bractea*, a thin plate of metal). A foliar organ of the rachis of bamboo inflorescences. Circumcingent bracts subtend branch buds and branches of the rachis in all bamboo genera with iterautant inflorescences, but at one or more of the basal nodes immediately above the prophyllum they are usually empty. Bracts are usually rudimentary or obsolete in most bamboo genera with semelautant inflorescences; in *Glasiophyton*, however, they are well developed and circumcingent.

**Branch complement.** The monoclade or pleioclade array of primary branches (first-order axes) that develops at a single midculm node. A complete definition of each recognized type of branch complement includes (1) the mode or pat-
tern of insertion of its primary (or secondary) components or axes (see Insertion); and (2) its potential (restricted or unrestricted) for proliferation from buds at the proximal nodes of its primary (first-order) component (s).

**Branch sheaths.** The sheathing organs borne singly at each node of an aerial vegetative branch of any order (except the culm itself), excluding the neck sheaths and the leaf sheaths.

**Bud** (ME. *budde*). “The nascent state of a flower or branch” (Jackson, 1949). In the usage here adopted, the term bud is applied only to those primordial vegetative or reproductive branches that (1) are enclosed in a prophyllum, and (2) have a resting stage. Those (such as branch primordia in determinate inflorescences generally; and root primordia, for example) that lack either one or both of these features are referred to simply as primordia. Branch primordia in the determinate inflorescences of *Glaziophyton*, *Greslania*, and some other genera are prophyllate, but they apparently have no resting stage.

**Bud, primary.** A primary bud is one whose initial primordium produces the primary (first-order) element (axis) in any series of branches of ascending order. It appears that, in the members of some bamboo genera a solitary primary bud may incorporate more than one initial primordium, and that each of these initial primordia normally produces an independent first-order element of a pleio-clade branch complement. See Primordium, initial.

**Callus.** A growth consisting internally of undifferentiated pith-like parenchyma that in some bamboos forms an external ridge at the junction of two structures (as, for example, at the locus of insertion of a sheath upon its axis). Holttum (1958: 15, fig. 3) applies the term to what Hackel (1899: 716) calls the “exterior (outer) ligule” of the leaf sheath, and what Pilger (in Diels 1937:57) calls a collar. In that structure the tissue is usually of a firmer nature, and is brought into prominence by the abscission of the petiole. See Cupule; Girdle; and “outer ligule” under Ligule.

**Caryopsis** (Gr. *karyon*, a nut; *opsis*, likeness). “A one-celled, one-seeded, superior fruit, with a pericarp united to the seed” (Jackson, 1949, as cariopsis). A caryopsis is indehiscent, i.e., the pericarp does not open to liberate the seed. In some bamboos (*Melocanna baccifera*, for example) the seed is free from the pericarp at maturity. The separability of the pericarp from the seed has been much used by agrostologists as a taxonomic feature, but mature caryopses of bamboos are rarely available for comparison.

**Cataphyll** (Gr. *kata*, down; *phyllon*, leaf). “The early leaf forms of a plant or a shoot, as cotyledons, bud-scales, rhizome scales, etc.” (Jackson, 1949). “Any rudimentary scalelike leaf which precedes the foliage leaves, as a bud scale, etc.” (Webster, 1959). As herein used, the term designates the sheaths that are incident at the lowermost nodes of any vegetative axis of a bamboo plant. In cataphylls the sheath proper is smaller in all dimensions than it is in the sheaths borne at the more distal nodes of the same axis, and its appendages are all rudimentary or obsolete.

**Centrifugally** (L. *centrum*, center; *fugo*, I flee from). Outward from a center.

**Centripetally** (L. *centrum*, center; *peto*, I go toward). Toward a center.

**Cespitose** (L. *caespes*, a sod; *caespitosus*, forming a more or less compact clump or tuft). Describes the normal clump habit of bamboos with pachymorph rhizomes, except where the rhizome neck is very much elongated and the primary culms proliferate by tillering or by way of short-necked rhizomes as in the Old World bamboo currently known as *Yushania niitakayamensis*. See Diffuse; Pluricepsitose; Unicepsitose.

**Character** (L.). “An instrument for marking, character” (Webster, 1959). “The technical difference whereby allied forms are distinguished, as ordinal, generic, specific, and so on” (Jackson, 1949). “A member of mutually exclusive dates” (Kendrick and Proctor, 1964:66). Any distinctive form or behavior, or characteristic feature of demonstrable reliability (constancy) for purposes of recognition or for the composition of a formal description or for the construction of a key for the differentiation of similar or related taxa. Constant features serve in some cases alone as recognition characters, in other cases as members of a set of regularly associated constant features. Webster's definition of the term character, as used by biologists ("Bot. & Zool. A feature or peculiarity (as of structure, color, form or size) possessed by the individuals of a variety, species or other category, and by means of which they may be recognized or differentiated; as a specific character, a generic character, etc. An inherited character is regarded as the
observable effect of a gene or genes”) makes feature a synonym of character. I differentiate these two terms with the objective of promoting clear thinking in relation to taxonomic procedures. It is my position that a *feature* does not become a *character* in the taxonomic sense until it can be shown to be dependable for use in the differentiation of two similar or related taxa. See Feature.

**CHARTACEOUS** (L. *charta*, paper; *-aceus*, made of, or belonging to). Paperlike; papery.

**CIRCUMAXIAL** (L. *circum*, around; *axis*). Completely around an axis; describes the typical reach of the locus of insertion of a sheathing appendage, or an assemblage of adventitious roots. Jackson’s (1949) definition, under Circumaxile, is limited to the special sense, “surrounding a central axis which separates when the fruit splits open.”

**CIRCUMCINGENT** (L. *circum*, around; *cingens*, girding). Characterizes a sheathing appendage (e.g., a bract or a prophyllum) with respect to the reach of its locus of insertion when this completely encircles an axis.

**CIRCUMNUTATION** (L. *circum*, around; *nutans*, wavering). The circular movement that commonly takes place in the distal portion of a growing axis, causing the apex to follow a spiral path as elongation proceeds.

**COLLARET** (Arber 1934:309). The girdle or callus at the base of a leaf sheath. See CALLUS; GIRDLE.

**CONGRUENT** (L. *congruens*, conformable). In agreement; consistent; harmonious. Applied to herbarium specimens, of different but allied bamboo species, which show a range of corresponding characters that can be compared. Incongruent specimens show different ranges of characters and thus are sometimes useless as evidence of distinctions between species.

**CONNATE** (L. *connatus*, born at the same time). “United, congenitally or subsequently” (Jackson, 1949), in reference to the union of members of a set of homologous parts (such as the filaments in a stamen complement) that takes place in some bamboos. See ADNATE; DIADELPHOUS; MONADELPHOUS; TRIADELPHOUS.

Connective (L. *connectivum*). A very narrow strip of tissue upon the approximately opposite sides of which the two parts of an anther (that is, the two pairs of locules) are inserted longitudinally. Jackson (1949) describes the connective as “distinct from the filament,” of which it appears to be an apical extension.

**CONSTELLATE** (L. *constellatio*, a cluster of fixed stars; a constellation). Arranged in a constellation-like cluster; characterizes (1) the pattern of insertion of the primary components (first-order axes) of a pleioclade branch complement as exemplified by members of the genus *Chusquea* (where the central element is several times as large as the auxiliary ones that flank it), as well as where component first-order elements are subequal, as in *Athyrostachys*; and (2) the pattern of insertion of the bud complement from which such a branch complement arises. See APSIDATE; GREMIAL; LEVEL; RESTRICTED.

**CORNIFORM** (L. *cornu*, horn). Shaped like a horn.

**CULM** (L. *culmus*, stalk, stem). A segmented aerial axis that emerges from a rhizome, and forms a part of a gramineous plant; the term is used most commonly with special reference to bamboos. Syn.: halm, haulm, haum.

**CULM NODE** (L. *nodus*, knot). “The ‘knot’ of a grass stem” (Jackson, 1949). The term node is generally applied in a loose, comprehensive sense to that complex locus—the junction of adjacent internodes in a segmented axis of a gramineous plant. Hackel (in Lamson-Scribner and Southworth, 1890:2, 3) stressed the importance of the “constantly overlooked” difference between the culm nodes and the sheath nodes in non-bambusoid grasses. However, neither Hackel’s description nor his illustration does justice to the distinctive features of these structures as they appear in the bamboos. Culm node is here defined with special reference to that level within the node (sensu lato) where secondary elongation (intercalary growth) takes place, and where branch buds and adventitious roots are inserted. Each culm node (sensu stricto) is located just above a sheath node (q.v.), from which it is usually distinguishable by the transverse thickening or ridge (the “supranodal ridge” of some authors) that appears at the level of insertion of a bud or a branch complement. Branch node and rhizome node should be similarly differentiated, respectively, from the corresponding sheath nodes. See SHEATH NODE.

**CULM SHEATH.** One of the sheathing organs borne singly at each node of a bamboo culm, below the level at which the sheaths of foliage leaves take their place. Kurz (1876:268) anticipates this usage with “halm-sheath.” The transition between culm
sheaths and foliage leaves may be rather abrupt or very gradual.

Culm shoot. Bamboo shoot; a young culm in any stage of its development short of maturity in height. See Shoot.

**Cupule.** The cup-shaped depression that marks the locus of insertion of the petiole upon the leaf sheath (McClure, 1941:33–34). The cupule is apparent, of course, only after the leaf has fallen away. See Callus; Ligule.

**Cuspidate** (L. cuspidatus, from cuspis, a point, especially the point or head of a spear [Marchant and Charles, 1958]). “Tipped with a cusp” (Jackson, 1949). Terminating in a small, hard point; used herein in this sense to characterize the apex in bamboo caryopses where the indurated conical base of a slender style persists at maturity.

**Cymbiform** (L. cymbiformis; cymba, boat). Boat-shaped, like the lemma in many bamboos, especially when it is keeled.

**Deciduous** (L. deciduus). Abscissile; falling away; “falling in season” (Jackson, 1949). The term applied especially to organs (the culm sheaths in some bamboos) or parts that become cut off at or near the locus of their insertion by development of a special layer of cells (an absciss layer), or by the formation of a cleavage plane along a well-defined line of separation. In many bamboos several of the distal internodes of leafy twigs (as well as the individual leaves) are deciduous. They fall away after the leaf blades have fallen, upon the formation of a transverse rift at a node—usually the most distal node bearing a bud—this bud having already produced a new leafy twig. See Persistent.

**Declined** (L. declinatus, turned aside). “Directed obliquely” (Jackson, 1949); describes the habit or orientation of the culms in some species of bamboos.

**Deliquescent** (L. deliquescent, melting away, disappearing). Becoming dispersed or expended, as when the main axis of any structure (the rachis of an inflorescence of Aulonemia quexo, for example) loses its identity among its own branches, or “loses itself by repeated branchings” (Jackson, 1949). See Excurrent.

**Dendroid** (Gr. dendron, tree, -oid, having the form of). Treelike; bearing branches of more than one order; describes the pattern of proliferation of the stigmatic surface in certain bamboos.

**Degauperate** (L. depauperatus, impoverish- ed). Reduced in size or functional efficiency, or both; the term characterizes whole plants, or individual parts or organs thereof such as florets, pseudospikelets, whose development is impeded or restricted by adverse conditions, external or internal.

**Dermogramme** (Gr. derma, skin; gramma, something drawn). A French term used by Prat (1936:178) to designate any example of his diagrammatic illustrations of the cellular details of the structure of the epidermis of any grass or bamboo. See Spodogram.

**Determinate** (L. determinatus, having fixed limits). Of limited growth; characterizes an axis, or a system of immediately related axes (a determinate inflorescence, for example), whose development or potential for development is confined to a single, definitely limited “grand period of growth,” after which no meristem usually persists. The occasional persistence of meristem at the tip of individual rachillas sometimes prolongs the grand period of growth in a determinate inflorescence atypically. A rachilla may then continue to produce new florets until the spikelet is greatly elongated—to as much as a foot, while its normal length would be 3 to 4 inches. Again, this meristem may revert to the vegetative state, proliferating to produce a leafy axis. Both of these teratic phenomena have been observed in Arundinaria dolichantha. See Proliferation; Semelauctant. Cf. Indeterminate.

**Diadelphous** (Gr. dis, twice; adelphos, brother). Having “two groups of stamens”; cognate with Diadelphia, the name of “a Linnean class having the stamens in two bundles of brotherhoods” (Jackson, 1949). Diadelphous describes the condition of a stamen complement of a flower when its members have their filaments connate to form two distinct groups. In the bamboos, the relative numbers of stamens in the respective groups may vary from one genus to another. Cf. Monadelphous; Triad- elphous.

**Diageotropic.** Adjectival form derived from diageotropism, which is defined under Geotropism.

**Diaphragm** (Gr. diaphragma, a partition wall). The transverse internal layer of parenchyma found at the level of every sheath node. It is reinforced by the crossing over and anastomosis of vascular bundles, and forms a rigid structural element that lends strength (mechanical resilience) to the segmented vegetative axes of bamboos. “A dividing membrane or partition” (Jackson, 1949).
**Diffuse** (L. diffusus, spread out). Growing in open array; characterizes the normal mature clump habit of most bamboos with leptomorph rhizomes, and also those whose pachymorph rhizomes have a greatly elongated neck and solitary culms, e.g., *Bambusa* sp. (McClure 21438-A) of Peru. (See McClure, 1966b:27, fig. 10:5).

Distal (L. disto, I stand apart). Remote; far out; designates loci of insertion, or structures, situated at or near the tip of an axis. Cf. Proximal.

Distichous (L. distichus, consisting of two rows). "Disposed in two vertical ranks, as the florets in many grasses" (Jackson, 1949). Distichous also describes the pattern of insertion of buds and branches, and the sheathing appendages on all segmented axes, both vegetative and reproductive, of the bamboo plant. As tacitly recognized by agrostologists, but generally not mentioned in published definitions, the two ranks are normally inserted on opposite sides of an axis but are sometimes secund.

Distichy (substantive of L. distichus). Arber's (1934) word for the two-ranked arrangement of buds, branches, and sheathing appendages generally characteristic of segmented axes in the Gramineae. See Distichous.

**Dominant** (L. dominans). Superior in size among several associated objects of a class or kind, as the primary axis among members of a pleioclade midculm branch complement in *Bambusa vulgaris*, or the trees that overtop all others in a forest.

**Embryotegium** (Gr. embryo, foetus, tega, a covering). The embryotega of Stearn (1966). Literally, embryo cover; the "little shield" (Sp. escudete) of Parodi (1961); to be distinguished from the scutellum, which is a part of the embryo itself. "A callosity in the seed coat of some seeds near the hilum, and detached by the protrusion of the radicle on germination" (Jackson, 1949). Since Jackson's definition is based on the nature of the embryotegium in the seed proper, it is not strictly applicable to its nature in a Caryopsis. Hackel (in Lamson-Scribner and Southworth, 1890:20, fig. 6) describes and illustrates the embryotegium in a Caryopsis (without, however, giving it a technical name) as "a place where the embryo lies covered only by the pericarp, and plainly visible on the outside." The position of the embryotegium is clearly visible in Caryopses with a thin pericarp as in bamboos of certain genera such as *Bambusa* and *Arundinaria*. In some genera, including *Melocanna* (Stapf, 1904a, pl. 45: fig. 3, pl. 47: fig. 40), and *Ochlandra*, where the pericarp is thick, the embryotegium is ordinarily not externally recognizable (cf. Figure 37 o).

**Empty glumes.** Revision of McClure's (1966a:225) definition. See Transitional glumes.

**Endosperm** (Gr. endo, within; sperma, seed). "The nutritive tissue formed within the embryo sac" [of a seed] (Webster, 1959)—referred to by earlier writers as "albumen" (Jackson, 1949). In some bamboos the embryo consumes the endosperm as fast as it is formed (Stapf, 1904a). The stored endosperm in some bamboos (*Arundinaria gigantea*) is granular and starchy, in others (*Apoclada simplex*) it appears to be waxy or glutinous, not granular.

**Excurrent** (L. excurrens, running out). Extending through, as when the main axis of any structure (the rachis of the paniculate inflorescence in *Indocalamus sinicus*, for example) maintains its identity among its own branches; "where the stem remains central, the other parts being regularly disposed round it" (Jackson, 1949). Cf. Deliquescent.

**Facultative** (Fr. facultatif, from L. facultas, capability). "Of such a character to admit of existing under various forms or conditions; of happening or not happening, etc." (Webster, 1959). "Occasional, incidental, as opposed to obligate" (Jackson, 1949). Describes the freedom, or potential faculty, to give expression to one or the other of two or more states, forms, products or features; possessed by (1) the proximal buds of the primary branch in certain bamboos with respect to germination or continued dormancy (*Aulonemia effusa*) (see Key, p. 8); or (2) the apical meristem of the developing axes in certain bamboos (*Arundinaria gigantea* ssp. tecta; *Semiarundinaria fastuosa*) to produce either a culm or a rhizome.

**Feature** (ME. feture; L. factura). "The . . . form or outward appearance of anything" (selected from Webster, 1959). In conventional discourse (and in technical papers as well) the term "feature" is often used in the sense here given "structure" (e.g., eyes, nose, mouth, chin—individual component structures of a countenance). In the present work the technical meaning of feature is restricted to characteristic aspects (such as form, size, number, color, behavior) of various structures or parts thereof. It is my position that a feature does not become a character in the taxonomic sense until it can be
shown to be invariable (dependable) and either unique to a given taxon or a member of a set of contrasting features that distinguish two similar or related taxa. Cf. Character.

Fibrous (L. fibra, thread, filament). Numerous, slender, and not conspicuously tapered; the meaning of the term as conventionally used to describe the gross aspect of the roots of bamboos and other grasses, a definition apparently not recorded in dictionaries or glossaries. Jackson's (1949) definition of the term is not applicable here.

Fistulose (L. fistula, a pipe). Hollow; having a lumen; characterizes the internodes of culms and branches in most bamboos.

Floret (dim. OFr. flor, flower). One of the units into which a spikelet breaks up when the rachilla segments disarticulate. Regardless of whether the rachilla segments are abscissile or not, a floret consists of (1) a segment of the rachilla, (2) the lemma that is inserted upon it, (3) a branch (the axis of a flower) subtended by the lemma, (4) a prophylllum (the palea) of the axis of the flower, and (5) the parts of the flower that are inserted on its axis. Attention is directed especially to the fact that the gramineous floret includes structures from axes of two orders while the flower is confined to a single axis. The distinction between floret and flower is not always observed in published works on agros-tology. The loose use of the two terms interchangeably is to be avoided. Cf. Flower.

Flower (OFr. flor). That portion of a branch of the rachilla that is distal to its own prophylllum (the palea), together with the reproductive organs (androecium or gynoecium or both) borne by it. The lodicules, when present, are included in this concept of the flower, but the palea is not. Cf. Floret.

Flowering Branch. A leafy or leafless segmented axis that bears one or more inflorescences. A flowering branch is distinguishable from an inflorescence proper in that it retains all of the morphological characteristics of the vegetative state, with the sole exception that in some cases it does not produce foliage leaves. The inflorescence proper, on the other hand, always has morphological features peculiar to it that are not found on the flowering branch proper. In describing and illustrating bamboos, some authors fail to distinguish the two. Arber (1934:108) characterizes a leafless flowering bamboo as a "truly gargantuan inflorescence." Cf. Inflorescence.

Foliar organ. See Sheathing organ.

**Free (ME. fre). "Not adhering, the reverse of adnate" (Jackson, 1949). Here given the sense of non-connate, in reference to the filiform filaments of the stamens in certain bamboos.

Fugaceous (L. fugax, fleeting). Promptly deciduous; "soon perishing" (Jackson, 1949).

Fusiform (L. fusus, spindle). Spindle-shaped; circular in cross-section, thickest in the middle and tapering toward each end. See Subfusiform.

Geniculate (L. geniculatus, with bended knee). "Bent abruptly at an angle, like the bent knee" (Webster, 1959). When a growing culm adjusts the direction of its orientation (as in situations where negative geotropism operates to effect the restoration of a fallen or deflected culm to an upright posture), the adjustment takes place through differential elongation in the upper and lower portions, respectively, of the zone of intercalary growth immediately above a node, and the node involved becomes geniculate.

Geotropism (Gr. gē, the earth; plus tropism, defined by Webster (1959) as "the innate tendency of an organism to react in a definite manner to external stimuli"). A physiological potential, and the consequent act, involved in the assumption and maintenance of a particular direction of growth by an axis or organ with reference to the force of gravity, or to the centrifugal force generated by rapid circular motion. As commonly used, geotropism ambiguously embraces (and confuses) two component phenomena: the visible physical response, and the more fundamental, invisible response, which is physiological. Jackson's (1949) definition: "the force of gravity as shown by curvature in nascent organs of plants" is incomplete. Three distinct classes of geotropic responses are recognized: positive, negative, and transverse. The last named is called diageotropism.

**Germination (L. germen, an offshoot, sprout, bud). A term usually restricted to the beginning of growth of the embryo of a seed; here extended to the beginning of growth of a temporarily dormant axillary bud on a bamboo culm.

**Girdle (AS. gyrdel, belt; Latin equivalent, cingulum). A conspicuous horizontal band of special tissue occupying a position basal to the culm sheath proper in some bamboos (e.g., Melocalamus
compactiflorus and some scandent species of Chusquea). It is expansible in all directions as long as the corresponding intercalary zone of the embraced internode is in active growth, and it takes on an asymmetrical form at geniculate nodes. Upon the abscission of the sheath, this band remains attached at the culm nodes. The distinction between a girdle and a sheath callus (q.v.) is not always clear, being based principally upon their relative vertical dimension (area). Cf. CALLUS; SHEATH CALLUS.

**GLUME** (L. gluma, a hull or husk). "The chaffy, two-ranked members of the inflorescence of grasses and similar plants" (Jackson, 1949). Excepting prophylla, this very general definition ostensibly embraces all of the sheathing appendages of the inflorescence, including the bracts that, in some cases, subtend its branches. As shown elsewhere, the application (meaning and usage) of the terms lemma and palea and bract has become rather generally standardized. However, in those cases where it is difficult to distinguish empty glumes and sterile lemmas from each other, I have proposed to cover both categories with the comprehensive term transitional glumes, q.v.

**GREMIAL** (L. gremialis, of a lap or bosom). "Growing in a pollard-like cluster" (R. W. Brown, 1954). Sheathing organs at successive nodes of an axis are imbricate when each one exceeds, in length, the internode it embraces.

**INDETERMINATE** (L. indeterminatus, unlimited). "Not terminated absolutely" (Jackson, 1949). Continuing apical growth characterizes an individual axis as indeterminate. The term is here given another connotation (namely, iterautcant) with particular reference to the continuing ramification of a system of immediately related axes, as exemplified by the indeterminate inflorescences of certain bamboos. In such inflorescences, the buds at the proximal nodes of each new order of branches bear fresh bodies of meristem. The development of new branches from these buds may be continuous (or intermittent and reactivated on a seasonal basis) for a period lasting in some cases for several successive years. Each branch of an indeterminate inflorescence (an axis with its appendages) has the appearance of a spikelet. Because of this, it is called a pseudospikelet. Each pseudospikelet has its own independent grand period of growth. The active period of the meristem at the apex of the rachilla that terminates each pseudospikelet is limited. Thus, while the branching of indeterminate bamboo inflorescences is of a continuing nature, each individual branch is apically determinate in its growth. See ITERAUTANT; PSEUDOSPIKELET; cf. DETERMINATE.

**INFLORESCENCE**. A discrete aggregation of spikelets associated with a common primary rachis or a common peduncle. Exceptionally, an inflorescence may comprise but a single spikelet. I know of no
exception to the rule that the inflorescence in a given bamboo genus is uniformly either semelauca
tant or iteraucauent (q.v.) in its manner of develop-
ment. The occurrence of individual features of an
intermediate (incongruous) nature is rare. Cf.
FLOWERING BRANCH; see also INFLORESCENCE, ITER-
AUCAUNT; INFLORESCENCE, SEMELAUCAUNT.

**INFLORESCENCE, ITERAUCAUNT.** An inflores-
cence in which typically both the initiation and the
termination of growth takes place in serial sequence
in the flowering axes of successively higher orders,
each branch possessing residual meristematic tissue
in the form of basal branch primordia (buds) that
continue the expansion of the inflorescence as long
as physiological conditions in the adjacent tissues
are favorable to their germination and growth.

**INFLORESCENCE OF MIXED BRANCHING.** An in-
florescence with peduncles proliferating (duplicat-
ing themselves indefinitely from nascent or dormant
prophylate branch buds) the rachises of determinate
branching (without nascent or dormant
branch buds) and with the development of all
spikelets simultaneous or nearly so (e.g., the Old
World genus *Chimonobambusa*).

**INFLORESCENCE, SEMELAUCAUNT.** An inflores-
cence in which typically the initiation of growth is
simultaneous or nearly so in all axes, and the termi-
nation of growth is likewise simultaneous or nearly
so; and no meristematic tissue remains afterwards
in the form of dormant buds.

**INSERTION (L. insertio, a putting in).** The
mode, pattern, or locus of attachment of an organ
or a part. With a view to characterizing the several
patterns of insertion herein distinguished with re-
spect to the component first- (or second-) order axes
of a midculm branch complement, the following
terms have been selected and defined: APSIDATE,
CONSTELLATE, GREMIAL, LEVEL, and RESTRICTED.

**ITERAUCAUNT (L. iterum, again; auctans, grow-
ing).** Embracing more than one grand period of
growth, as the mode of development of the succes-
sive orders of the branches of an inflorescence com-
posed (as in bamboos of the genera *Bambusa,
Elytrostachys*, and *Atractantha*) of pseudospikelets
(q.v.). Cf. SEMELAUCAUNT; INDETERMINATE.

**LEAF (AS).** Foliage leaf; bamboo leaf; the
chlorophyll-bearing, usually petiolate, blade of a
leaf sheath proper. This concept of leaf, in the
sense bamboo leaf, includes the petiole when it is
present, but excludes the leaf sheath proper. Leaf

is here defined in this circumscribed sense in order
to avoid a commonly encountered ambiguity occa-
sioned by its indiscriminate use in the literature.
The word is commonly used by agrostologists, with-
out modification or qualification, to refer to any
one of the morphologically, anatomically, and func-
tionally divergent forms of sheathing organs borne
on the several kinds of vegetative axes of a bamboo
plant. This imprecise use of the term, in disregard
of the importance of the manifest differences thus
loosely covered by it, apparently is due to the
generalized and unqualified nature of the definition
of “leaf” given by Jackson (1949): “the principal
appendage or lateral organ borne by the stem or
axis.” The use of the term “leaf” for the petiolate
leaf blade as distinct from the leaf sheath in bam-
boos has ample precedent in Munro’s “folia” which
is described separately from “vagina.” I think that
we may rationalize this usage by postulating that,
in the grasses, the sheath is a distinct organ or
structure inserted between the leaf proper and the
axis from which it emerges (or on which it is in-
serted). We may continue with the postulate that
the girdle (where it appears) is a structure inserted
between the sheath proper and the sheath node.
Cf. SHEATH; LEAF SHEATH; see also SHEATHING OR-
GAN.

**LEAF SHEATH.** One of the leaf-bearing sheaths
inserted at the distal nodes of each aerial segmented
axis whether culm, branch, or twig. The conspicu-
ous part of a leaf sheath is the usually petiolate
blade, inserted at the apex of the sheath, just below
the ligule. Cf. LEAF; SHEATH.

**LEMA (Gr., a husk).** The glume that sub-
tends a flower. Lemmas that subtend normally con-
stituted and developed flowers are conventionally
called fertile lemmas, to distinguish them from
sterile lemmas, whose subtended flowers are de-
pauperate or obsolete. See TRANSITIONAL GLUMES.

**LEPTOMORPH (Gr., leptos, slender, and
morphé, form).** Characterizes the rhizomes proper
(of a bamboo plant) when they are long and slen-
der, and have the following associated characteris-
tics: a cylindrical or subcylindrical form, with a
diameter typically less than that of the culms
originating from it; internodes longer than broad,
relatively uniform in length, symmetrical or nearly
so, rarely solid, typically fistulose, the usually nar-
row central lumen interrupted at each node by a
diaphragm; nodes in some genera usually somewhat
elevated or inflated, in others not; lateral buds in the dormant state boat-shaped, with a distally oriented apex. Cf. PACHYMORPH.

**LEVEL (L. libella, a water level or plumb level).** Even, horizontal. Characterizes the pattern of insertion of the primary components (first order axes) of a pleioclade branch complement, as exemplified by members of the genus *Apoclada.*

**LIGULATE.** Having a ligule.

**LIGULE (L. ligula, a little tongue).** A thin, apical extension of a sheath proper, adaxial to the locus of insertion of the sheath blade (or leaf petiole). The outer rim of the little cup revealed by the abscission of the petiole of a foliage leaf is sometimes referred to as the “outer ligule,” especially when it is conspicuously developed, as it is in some variants of *Arundinaria gigantea* ssp. *tecta.* The term “inner ligule” is then applied to the adaxial structure conventionally known simply as the ligule. The ligule is reduced to a mere line, or is even lacking entirely, in the culm sheaths of certain species of bamboos.

**LOCUS (L., place).** The locale in which some event takes place, or where something is to be found. Locus is here given the connotation, point, or line, or area, principally in the phrase “locus of insertion.” See INSERTION.

**LODICULE (L. lodicula, a small coverlet).** One of the small, usually thin, delicate and transparent structures (by some authors referred to as “scales”) inserted usually in a single whorl of 3, immediately below the stamens in the bamboo flower. The lodicules are relatively large, opaque, and parchment-like in the flowers of known species of *Streptochaeta.* Their number is variable in some bamboos (up to 12 or more in *Ochlandra stridula*); in known species of *Gigantochloa,* typical lodicules are lacking entirely.

**LUMEN (L., opening).** “The space which is bounded by the walls of an organ, as the central cavity of a cell” (Jackson, 1949); the central cavity of a hollow internode of any segmented axis of a bamboo plant.

**MAVERICK.** Nonconformist (see Webster, 1959). A term borrowed here (see page 15 et passim) for the purpose of characterizing ontogenetic and/or morphological features that appear to range alone, as if moving in independent trajectories. Maverick features appear at random as discrepancies (phenotypic diversities) among the other features of one or more species of different genera that are otherwise more or less distantly related, or at least phenotypically disjunct. I was at first inclined to credit their presence in such discrepant settings as due to recent introgressions of unlinked genes. More recently I have considered the possibility that they come from a common ancestor by way of recessive genes.

**MBG.** McClure Bambo Garden, Bethesda, Maryland, U.S.A. See also P.I.

**MERISTEM (Gr. meristos, divisible).** A body of tissue in which cell division and differentiation are active or potential.

**METAMORPH (Gr. meta, implying change; morphē, form).** Of intermediate form; a term proposed here to designate certain underground portions of segmented axes, whose transitional character cannot be clearly indicated by the use of existing conventional terms. See METAMORPH I; METAMORPH II.

**METAMORPH I.** A transitional axis that occupies a position between the culm neck and the base of the culm proper, where no clearly defined rhizome intervenes; in some cases doubtfully distinct from an elongated culm neck.

**METAMORPH II.** A transitional axis intermediate in form and position between the apex of a rhizome (either pachymorph or leptomorph) and the culm into which the rhizome is transformed apically. It appears where the transformation of the apex of a rhizome into a culm takes place gradually and not abruptly.

**METAMORPHOLOGICAL (Gr. meta, beyond, plus morphological).** Pertaining to the techniques, the areas of investigation, or the data of disciplines other than morphology.

**MONADELPHOUS (Gr. monos, one; adelphos, brother).** United in a single brotherhood; an adjective cognate with Monadelphia, the name of “a Linnean class in which the anthers are united by their filaments into a single brotherhood” (Jackson, 1949), and conventionally used to describe the stamen complement of a flower when all of its members are united by their connate filaments. Cf. DIADELPHOUS; TRIADELPHOUS.

**MONOCARPIC.** See MONOPERIODIC.

**MONOCLADE (Gr. monos, one; klados, branch).** Characterizes those branch complements that contain only one primary axis. See BRANCH COMPLEMENT; MONOCLADE, RESTRICTED; MONOCLADE, UNRESTRICTED. Cf. PLEIOCLADE.
Monoclade, Restricted. Characterizes those monoclade branch complements whose primary axis is incapable of proliferating basally, for lack of buds at its proximal nodes. When buds are present at the proximal nodes of the solitary axis of a monoclade branch complement but remain dormant, such a branch complement is referred to herein as facultative restricted monoclade.

Monoclade, Unrestricted. Characterizes those monoclade branch complements whose solitary primary axis is capable of proliferating basally from buds at its proximal nodes.

Monoperiodic (Gr. monos, one; periodos, a completed course). Having but a single reproductive cycle within the lifetime of a plant; characterizes bamboos (such as Bambusa arundinacea) that flower but once, then perish. Monocyclic suggests itself for use in the sense here given the newly coined term, monoperiodic, but it already bears the disqualifying connotation annual, with reference to the life span of a plant—besides indicating sets of parts (such as sepals and petals) that comprise but a single whorl or cycle. In the interest of clarity, the term monocarpic, commonly used to indicate the monoperiodic character of certain bamboos, should be reserved (with its orthographic variants; see Jackson, 1949) for reference to a pistil comprising but a single carpel. Cf. Polyperiodic.

Monopodial (Gr. monos, one; pous, podos, foot). Having the form of a monopodium, which is defined by Jackson (1949) as “a stem of a single, and continuous axis.” This term was used earlier (McClure, 1925) to designate the type of rhizome described as leptomorph (q.v.). Cf. Sympodial.

Morphogenesis (Gr. morphē, form; genesis, beginning or origin). “The production of morphological characters” (Jackson, 1949). As defined here, morphogenesis connotes not only its external manifestations but also, and primarily, the nature and sequence of events in the program of genic monitoring of physiological states associated with the emergence of the structural features that determine the characteristic form of a plant.

Mucronate (L. mucronatus, pointed). “Possessing a short, straight point, as some leaves” (Jackson, 1949). Cf. Cuspidate; Muticous.

Muticous (L. muticus, docked). “Blunt, awnless” (Jackson, 1949); used primarily (when applicable) to describe the apex in small sheathing appendages on the various axes of the bamboo inflorescence.

Neck (AS. hnecca). The constricted basal part, characteristic of all, or most, of the segmented vegetative axes of a bamboo plant.

Neck Sheath. One of the reduced, bladeless sheaths that clothe the constricted proximal part, the neck, of various vegetative axes in the bamboo plant. Neck sheaths are sometimes referred to as Cataphylls.

Nothomorph (Gr. nothos, hybrid; morphos, form). “Applied to any hybrid form, whether F₁, segregate or back-cross” (International Code of Botanical Nomenclature, Article H.5). Cf. Figures 17 and 18.

Obsolete (L. obsoletus, worn out). “Wanting or rudimentary; used of an organ which is scarcely apparent or has vanished” (Jackson, 1949).

Obterete. Circular in cross-section, tapering progressively from one end to the other, and smallest at the proximal end (for example, a rhizome neck). Cf. Terete.

Oval. “Having the solid figure or lengthwise outline of an egg; popularly elliptical or ellipsoidal. Bot. broadly elliptical” (Webster, 1959). “A body or figure in the shape of the long section of an egg, or popularly an ellipse” (Webster, 1959).

Ovate. “Shaped like an egg; oval” (Webster, 1959). “With an outline like that of a hen’s egg cut in two lengthwise, the broader end downward” (Bailey, 1914; Jackson, 1949).

Ovoid and Ovate. The terms “ovoid” and “ovate” are used in diverse senses. The original botanical sense of ovate appears to be [that of] Bailey (1925) and Jackson (1949) but it has (under popular influence) drifted to mean elliptic or ellipsoidal (Stearn, 1966; Webster, 1959).

Pachymorph (Gr. pachys, thick; morphē, form). Term proposed by McClure to describe the rhizome proper (of a bamboo plant) when it is short and thick, and has the following associated characteristics: a subfusiform (rarely subspherical),
usually more or less curved (rarely straight) shape, with a maximum thickness typically somewhat greater than that of the culm into which it is always transformed, apically; internodes broader than long, asymmetrical (longer on the side that bears a bud), solid (apparently never fistulose); nodes not elevated or inflated; lateral buds solitary, in the subcircular margin and an intramarginal apex. Cf. Leptomorph.

Palaea (L., [a piece of] chaff). The prophyllum of the axis of a gramineous flower. Jackson's (1949) definition: "the inner bract or glume in grasses, called 'Palet' by North American writers" is too vague to be useful. See Prophyllum.

Panicle (L. panicula, a tuft). A determinate inflorescence with branches of more than one order. Jackson's definition of panicle is not applicable here.

**Paniculate** (L. paniculatus, tufted). Inflorescences with branches of more than one order, the rachis excurrent or deliquescent. See Panicle.

**Paramo** (Sp., from L. paramus, teste Larousse, in Augé and Gisbert, 1949:697). "Extensive treeless regions that dominate the summits of the Andean cordillera from the upper limit of the forest—an elevation of 3800 m (locally 3220 m)—up to the level of permanent snow (4700 m);" teste Cuatrecasas (1959:249) where distinctive ecological, vegetational, and floristic features of the páramo are described at length—in Spanish.

Parenchyma (Gr. parenchein, to pour in beside). Fundamental tissue; ground tissue; a tissue, such as pith, composed of thin-walled, undifferentiated, isodiametric cells (adapted, from Jackson, 1949).

Pedicel (L. pedicellus, dim. of pes, foot). The stalk of a spikelet, that is, the distal segment or internode of the axis immediately below the glumes that marks the base of a spikelet. The ultimate branches of a determinate inflorescence are all pedicels, since each terminates in a spikelet. In spicate racemes, and in pseudepikelets, the pedicels are usually very short. Cf. Peduncle; Rachis.

Pedicellate. Having a pedicel.

Peduncle (L. pedunculus, dim. of pes, foot). The stalk of an inflorescence, that is, the unbranched segment of the inflorescence axis that is immediately below the rachis. In determinate inflorescences, the first sheathbearing node below the first branch of the inflorescence is here taken arbitrarily as marking the base of the peduncle, and the locus of insertion of the first branch of the inflorescence as marking the apex. In those rare cases where a determinate inflorescence includes only one spikelet, the peduncle is not distinguishable from the pedicel. In indeterminately branching inflorescences, the peduncle is usually very short. An exception appears where the primary pseudo-spikelet is terminal (instead of lateral) to a flowering branch. Here the peduncle is more elongate. Cf. Pedicel; Rachis.

Pedunculate. Having a peduncle.

**Percurrent** (L. percurrent, passing through). Used here in a sense identical with that given Excurrent.

**Perfect.** Signifies the presence, within an anthecium, of a flower containing a normally developed complement of sexual elements, both staminate and pistillate. Same as hermaphrodite.

Pergameneous (L. pergamina, parchment). "Like parchment in texture" (Jackson, 1949).

Persistent (L. persistens, remaining in place). Not deciduous; applies to organs that remain in place after they have fulfilled their natural functions (for example, the culm sheaths of Arundinaria gigantea ssp. tecta).

Pinnate (L. pinnatus, feathered). "Featherlike" (Webster, 1959). Having lateral appendages distributed in two continuous series inserted, respectively, on opposite sides of an axis and antrosely oriented; a borrowed term used here to describe the pattern of insertion and orientation of the proliferations of the stigmatic surface in certain bamboos. Jackson (1949) and Webster (1959) both confine the botanical application of the term pinnate to the arrangement of the leaflets on the rachis of a compound leaf.

Pistil (L. pistillum, a pestle). See Gynoeicum.

**Pleioclade** (Gr. pleion, more; klados, branch). Characterizes those branch complements that contain more than one independent primary (first-order) axis. See Branch complement; Pleioclade, restricted; Pleioclade, unrestricted. Cf. Monoclade.

**Pleioclade, restricted.** Characterizes those pleioclade branch complements whose component axes are incapable of proliferating basally for lack of buds at their proximal nodes.

**Pleioclade, unrestricted.** Characterizes those pleioclade branch complements whose component...
axes are capable of proliferating basally from buds at their proximal nodes.

**Pleioency** (Gr. pleion, more; genos, birth). "An increase from the parental unit, as by branching or interpolation of members" (Jackson, 1949); a general term for the particular examples described under Proliferation and Pleioclade, as pertaining to vegetative axes, and under Indeterminate, as pertaining to reproductive axes.

**Plicate** (L. plicatus, folded). "Folded into plaits, usually lengthwise" (Jackson, 1949); marked by longitudinal ridges suggesting a prior condition of being folded like a collapsible Chinese fan; an appearance shown by some bamboo leaf blades.

**Pluricespitosus** (L. pluris, of more; caespitosus, from caespes, a tuft). Characterizes the clump habit of a bamboo plant that embraces more than one tuft of culms, all tufts belonging to an individual plant being connected by subterranean axes as in *Arundinaria gigantea* ssp. tecta. Cf. Unicespitosus.

**Polycarpic.** See Polyperiodic.

**Polyperiodic** (Gr. polys, many; periodos, a complete course). Having many reproductive periods, alternating with vegetative periods, within the lifetime of one plant; characterizes bamboos (such as plants of the known species of *Phyllostachys*) that flower repeatedly (and usually periodically) during an indefinite life span. Polycyclic suggests itself for use in the sense here given polyperiodic, but is rejected because of its long-established use with reference to the occurrence of an indefinite number of whorls of parts, such as sepals or petals in a flower. Pleiocyclic is already burdened with the connotation perennial, which is incompatible as a meaning alternate to that here given polyperiodic. Moreover, monocyclic, which would pair with the pleiocyclic, already means annual, in reference to the life span of a plant. In the interest of clarity, the term polycarpic, sometimes used to indicate the polyperiodic character of certain bamboos, should be reserved (with its orthographic variants) for reference to pistils with numerous carpels (see Jackson, 1949). Cf. Monoperiodic.

**Precocious** (as applied to the proliferation of the branch primordium at midculm nodes). Elaborating secondary branch primordia before the rupture of the bud-scale (prophyllum) that accompanies the "germination" of the branch bud.

**Primary.** The first (initial) element in a series of related axes or structures of a given category, as branch buds or branches.

**Primituin.** "Ancestral" in the sense of L. L. Forman (1964:390 footnote).

**Primordial** (L. primordialis). "First in order of appearance" (Jackson, 1949). See Primordium.

**Primordium** (L., the beginning). An axis or an outgrowth of an axis in its earliest recognizable condition, or in an early dormant state. In the bamboos, a branch primordium borne on a segmented vegetative axis is always enclosed in a prophyllum; an adventitious root primordium is never so enclosed. See Prophyllum.

**Primordium, initial.** An initial primordium is a body of undifferentiated meristem which, when enclosed by a prophyllum and remaining dormant, forms part of a primary bud; it then constitutes an incipient axis of the first order. When inserted at a culm node, its first potential is to give rise to a primary element of a branch complement. See Bud, Primary.

**Proliferation** (L. proles, offspring; fero, I bear). "Bearing progeny as offshoots" (Jackson, 1949). The term is brought into focus here with reference to the rapid multiplication of members of a branch complement by the prompt awakening of buds at the proximal nodes of the component members. The proliferation of the culm itself by the same process (without the intercalation of a rhizome) is called stooling or tillering. Proliferation should not be confused with proliferation, which Jackson (1919) differentiates as "The production of terminal or lateral leaf buds in a flower." An example of proliferation is cited under Determinate. See also Pleioency.

**Promontory** (a physiographic term described by Webster, 1959). I have borrowed this term to describe the tapered bulge that extends downward from the locus of initiation of the primordium of the primary bud at midculm nodes in all of the known species I here include in the genus *Arthrostylidiun*. See Gremial.

**Prophyllate.** Bearing a prophyllum (q.v.).

**Prophyllum** (L. prophyllum, first leaf). A sheathing organ, usually 2-keeled and inserted circumaxially at the first (proximal) node of a branch. In vegetative axes, and in inflorescences of indeterminate branching, the prophyllum at first surrounds the branch primordium to form a bud. Jackson's
(1949) definition of prophyllum limits it to what is now generally called a palea. Prophylla are by some authors called bracts, or bracteoles. See PALEA; BUD.

Proximal (L. proximus, nearest). Basal; situated at or near the base of an axis or an organ; designates loci of insertion, or structures, so situated. Cf. DISTAL.

Pseudospikelet (L. pseudo, false; by extension, superficially resembling; spicula, spikelet). A spikelet-like branch of an iterauctant (indeterminately branching) inflorescence. See INDETERMINATE.

Pulvinus (L., cushion). A tropical organ (L. trópicus, pertaining to a turning) associated with movement of differential growth. Pulvini usually manifest themselves as dome-shaped eminences, commonly in pairs, strategically located in relation to the organ with whose orientation they are concerned—at or near the base of the leaf petiole, for example, or a branch of an inflorescence. Pulvini function through one or the other of two physiological mechanisms: changes of turgidity and differential growth.

**Quinate (as applied to pleioclade midculm branch complements).** Typically consisting of only five axes or branches.

Raceme (L. racemus, a bunch of grapes). A semelauctant gramineous inflorescence with a single order of (usually solitary) branches. Jackson's (1949) definition is not applicable here. A raceme in which some of the branches emerge in fascicles of two or three may be characterized (interpreted) as a paniculate raceme, if the extra branches in each fascicle are taken to be secondary ones arising subcutaneously from the base of a primary one. *Arthrostachys capitata* (Figure 19c) bears paniculate racemes in which all branches are relatively short. This gives the inflorescence a capitulate superficial appearance. A spicate raceme is one of which the pedicels are so short that the inflorescence resembles a spike.

Rachilla, rhachilla (Gr. dim. of rachis, q.v.). The axis of a spikelet in any gramineous plant. Jackson (1949) defines rachilla vaguely as "secondary axis in the inflorescence of grasses."

Rachis; rhachis (Gr. rhachis, backbone). The primary axis of an inflorescence; its position is terminal to the peduncle.

Reduced. Subnormal in size; connotes also (in some applications) either a failure to fulfill a normal function, or a diminution in the expected number of parts in a set (of stamens, for example). Cf. Depauperate.

**Restricted (L. restrictus).** Characterizes (1) a branch complement—either monoclade or pleioclade—as unable to proliferate from buds at proximal nodes of its first-order component member(s); and (2) the locus and the mode of insertion of a monoclade branch complement, regardless of whether the primary component (first-order) axis is dominant or not.

Rhizome (Gr. rhízóma, a mass of roots). An individual component branch of the subterranean system of segmented axes that constitute the “chassis” (popularly referred to as the “rootstock”) of a bamboo plant. A rhizome consists of two parts: the rhizome proper and the rhizome neck. Two distinct types of rhizome are differentiated: leptomorph and pachymorph (q.v.).

Rhizome sheath. The husklike sheathing organ inserted at each node of a rhizome proper (as distinct from the rhizome neck).

**Secondary.** Of higher order in a given system of related axes. Example: the branches that arise by proliferation from buds basal to the primary branch at midculm nodes in *Arthrostylidium*. Cf. Subsidiary.

**Secund** (L. secundus, following). “Arranged on one side only; unilateral, as flowers in some racemes, spikes, etc.” (Webster, 1959). Applied to “parts or organs directed to one side only, usually by torsion” (Jackson, 1949). The term comes into use in the description of bamboo inflorescences with an excurrent rachis, where the modification of the rachis, either by torsion or by asymmetrical development, causes all of the spikelets, or branches, to be oriented more or less strongly toward each other on one side of the rachis, and away from each other on the other side of it. In actual practice, the term may be applied either to the inflorescence as a whole, or to the parts (spikelets or branches) whose orientation is the focus of attention.

Semelauctant (L. semel, once; auctans, increasing, growing). Embracing but a single grand period of growth. A determinate bamboo inflorescence may be said to be semelauctant. See DETERMINATE; ITERAUCTANT.

Sensus lato; sensu stricto (L.). In a broad sense; in a restricted sense; expressions used to in-
dicate the intended scope of a given application of a scientific name or a scientific term.

Sheath (ME. sheethe). A sheathing organ, the basal part of which, the sheath proper, completely surrounds the vegetative axis on which it is borne, its locus of insertion being circumaxial. In its simplest form (as in typical neck sheaths and rhizome sheaths) the sheath proper terminates apically in a short, hard point. In its fully elaborated form—that characteristic of examples in the middle of any series—the sheath proper usually terminates above in a ligule, at the base of which is inserted a more or less expanded laminar appendage referred to in a comprehensive sense as the sheath blade. In addition, the sheath proper commonly bears, at or near each extremity of the locus of insertion of the blade, a tuft of bristles (oral setae). These may be borne either directly on the sheath proper or on the margin of an auricle. When there is a pair of auricles (one on each side) the two may be similar and subequal, or they may be unequal in size and dissimilar in shape. To avoid the ambiguity occasioned by a commonly encountered indiscriminate usage of the term leaf (q.v.) to refer to any one of the diverse forms of sheaths borne on the vegetative axes of the bamboo plant, two expedients are followed: (1) the adoption of the differential terms rhizome sheath, neck sheath, culm sheath, branch sheath, leaf sheath, and prophyllum (q.v.); and (2) the differentiation of the sheath proper from its appendages. A clear precedent for this effort to avoid ambiguity is found in the now fairly common adoption of a precise terminology to differentiate the several types of sheathing structures borne on the reproductive axes of the bamboo plants, as bracts, prophylla, glumes, lemmas, and paleas. See Sheathing Organ.

Sheath blade. A distinct foliar part, the lamina, that is appended apically on the laminiferous culm sheaths proper and branch sheaths proper in any series. A sheath blade is distinguishable from a leaf, first of all by the relatively proximal position of the sheath proper of the former on any aerial vegetative axis, while leaf sheaths are always inserted at the distal nodes of any culm or branch. Sheath blades are always sessile, while the leaf blades are petiolate (in all known bamboos except some species of Neurolepis). Moreover, characteristic differences in shape are usually quite marked. The strong divergence in form, as between leaf blades and sheath blades in the bamboos, is one of the commonest and most useful of the gross morphological distinctions between members of the Bambusoideae and those of other grasses. See Leaf.

Sheath callus (L. callus, hard skin). A somewhat prominent ring of parenchymatous (not hard) tissue which remains at a sheath node after the abscission of a sheath (of a culm, especially) in some bamboos (Phyllostachys nidularia, for example). Cf. Girdle.

Sheath node. The circumaxial locus of insertion of a sheath on any vegetative axis of a gramineous plant (elaborated after Hackel, in Lamson-Scribner and Southworth, 1890: fig. 1). The sheath node is marked externally by a more or less prominent offset in the surface of its axis. At the level of each sheath node the crossing over and anastomosis of fibrovascular bundles take place through a diaphragm which marks the internal boundary between adjacent internodes. Cf. Culm Node; see Diaphragm.

Sheath scar (Gr. eschara, mark). Jackson (1949) defines Scar as “a mark left on a stem by a separation of a leaf, or a seed by its detachment; a cicatrix.” In the bamboos, a sheath scar is a narrow, transverse, circumaxial trace, the locus of abscission of a sheath proper. A sheath scar marks the position of a sheath node (q.v.).

Sheathing organ. Any sheathing structure inserted at a node of any vegetative or reproductive axis in a gramineous plant. Among the bamboos, distinguishable types of sheathing organs are rhizome sheaths, neck sheaths, culm sheaths, branch sheaths, leaf sheaths, prophylla, bracts, empty glumes, lemmas, and paleas. Unless used, and interpreted, with discretion, the often-encountered term foliar organ is apt to be ambiguous, since it may be construed as referring either to a sheath proper alone, to a sheath proper with all of its appendages, to the blade only, or to a bladeless sheathing structure, such as a prophyllum. See Leaf.

Shoot (noun, from AS. scēolan, to move rapidly). “(1) A young growing branch or twig; (2) the ascending axis; when segmented into dissimilar members it becomes a stem” (Jackson, 1949). See Culm shoot.

Silica bodies; also silica corpuscles (G. Kieselkörper). Bodies of silica that are secreted and persist within the cells of various tissues of the plant.
particularly any epidermal layer. In both size and shape, they range widely. At one extreme, they are small, lack characteristic shape, and occur solitarily or in small numbers within a given cell. At the other extreme, they may be large enough individually to fill a cell more or less completely (see Silica cells) and have a characteristic shape. Metcalfe (1960:xlii, fig. 1) lists 20 “types” (forms) of silica bodies, some of which are illustrated. He states (p. xx) that “the silica-bodies in silica-cells assume very characteristic forms when the grass leaf is mature, and are of considerable value for diagnostic and taxonomic purposes.” Ohki’s (1932:73f) key to Japanese genera of bamboos refers to the occurrence of “silica corpuscles” in the long epidermal cells of the leaf in Dendrocalamus [D. latiflorus] and in the articulation (bulliform) cells of the leaf in Sinobambusa [S. tootsik] and Chimonobambusa [Ch. quadrangularis].

Silica cells. Epidermal short cells each of which is more or less completely filled by a single silica body (Metcalfe, 1960:xx).

Spicate (L. spicatus, bearing spikes or ears). Having some or all of the characters of a spike (q.v.). A spicate raceme is a raceme in which the pedicels are so short that the inflorescence resembles a spike.

Spike (L. spica, an ear of grain). In the bamboos, a spike is a determinate inflorescence in which the sessile or sub sessile spikelets are inserted on a solitary rachis. Since the distinction between a spike and a spicate raceme is, in the terms of their definitions, only a matter of the relative length of “sub obsolete” pedicels, it is sometimes difficult to choose between these terms for the description of a given inflorescence (as in some species of the genus Merostachys, for example). According to Jackson’s (1949) definition (not applicable here) a spike is an “indeterminate inflorescence with flowers sessile on a common elongated axis.” A loose interpretation of Jackson’s definition of a spike has resulted in the occasional misapplication, in the literature, of the term spike to a spikelet (q.v.) of bamboo.

Spikelet (L. spicula, little spike). A basic structural component of every normal gramineous inflorescence, comprising a segmented axis (the rachilla) and its appendages. The appendages (beginning with the lowermost) are: empty glumes (usually two, rarely more, sometimes only one, rarely lacking entirely), lemmas (either variable or invariable in number, according to the taxon involved), and branches of the rachilla (one subtended by each lemma), each bearing a palea and the parts of a flower. In some taxa, one or more of either the distal or the proximal lemmas, or both, may be sterile by virtue of either being empty or subtending an incompletely developed flower. See Floret; Flower. [Empty glumes=transitional glumes.—ed.]

**SPODOGRAM (Gr. spodos, ashes; gramma, something drawn). The “ash picture” of a plant part, such as leaf epidermis, which is revealed on a slide prepared by the following method: the plant part is burned to the white-ash stage and the product transferred intact to a glass slide and mounted in an agent such as aniline or Canada balsam. Spodograms were used for purposes of plant classification by Molish (1920) and for identification of bamboos by Ohki (1932).

Sporadic (Gr. sporadikos, dispersed). “Widely dispersed or scattered” (Jackson, 1949); dispersed, or irregular, in time, as when the individual plants of a given generation of bamboos (from seeds of a common origin) enter the reproductive phase at different times, or at irregular intervals. In either case, the flowering is said to be sporadic (Gamble, 1896:viii). Cf. Gregarious.

Stoma (Gr. mouth, opening; pl., stomata). A functional organ found commonly, but not everywhere, in the epidermis that covers photosynthetic tissues. A stoma consists of two guard cells and (in the bamboos, as far as known) two subsidiary cells (Porterfield, 1987). Changes in the turgor of the guard cells result in the opening and closing of a slitlike aperture (the stoma of Jackson, 1949) between them.

**Style. The description of the style as a separate or distinct structure encounters difficulties which grow out of peculiarities in the ontogeny of the gynoecium. In many bamboos, the stigmas are at first sessile at the apex of the ovary and there is no discernible style. Usually, a style develops later, but rarely (as in Bambusa multiplex), the stigmas remain sessile. It does not appear useful or logical to call these separate styles. The style when it appears seems to be an outgrowth of the pericarp; but only by means of anatomical studies of the pistil (gynoecium) at different successive stages in its development can the details of the origin, structure, and relationships of the compo-
ment structures traditionally given independent names and status be clarified.

Sub- (L.). A prefix indicating either an approximation or some reservation or limitation in the use of the term with which it is combined, as in sub-distal, suberect, subfamily, subfusiform.

**Subequal** (as applied to the transitional glumes of a spikelet, or the component axes of a midculm branch complement). Nearly, but not quite of equal size.

Subfusiform. Of a shape suggesting the concept fusiform, but not corresponding to it precisely; the approximate general shape of a pachymorph rhizome. See Fusiform.

**Subsidiary.** Of the same order but of smaller size; example: smaller members of the complement of initial (primary) buds or branches at midculm nodes in *Chusquea* and *Swallenochloa*. Cf. Secondary.

Subsidiary branches. Branches of higher order arising from buds at the base of a dominant primary branch.

Subtend (L. subtendo, I stretch underneath). To precede on a common axis, as a foliar organ precedes (subtends) a bud or branch inserted immediately above it.

**Sulcate** (L. sulcatus, furrowed). "Grooved or furrowed" (Jackson, 1949); as where the otherwise approximately cylindrical shape of the surface of the internode of a segmented axis is modified by one or more longitudinal depressions. In most bamboo genera the palea in functional florets is sulcate with a single longitudinal dorsal depression. The furrow or groove that marks, on the exterior of the caryopsis in many bamboos, the interior locus of the attachment of the seed to the pericarp. Cf. Hilum.

Suture (Fr., from L. sutura, from suere, to sew). "A junction or seam of union; a line of opening or dehiscence" (Jackson, 1949).

**Sympodial** (Gr. sym or syn, together; pous, podos, foot). Having the form of a symposium; for example, a system of related axes wherein successive branches assume the role or position of effective leadership or dominance so that the axis of a symposium is composite; a term used earlier (McClure, 1925) to designate the branching habit of the type of rhizome described herein as pachymorph (q.v.). Cf. Monopodial.

**Tardy** (as applied to the proliferation of the branch primordium at midculm nodes). Elaborating secondary branch primordia after the rupture of the bud scale (prophyllum) that accompanies the germination of the branch bud.

**Taxon** (neo-Gr., from taxis, arrangement). "A taxonomic group or assemblage of plants or animals having certain characteristics in common, which we take as evidence of genetic relationship, and possessed of some degree of objective reality" (Rickett, 1958). Rickett adds, "We can use the word wherever we can use 'taxonomic group' in referring to the characteristics, dynamics, distribution, or uses of such an assemblage." Morton (1957) cautions that "where the words 'taxonomic group' cannot be appropriately substituted, the word taxon is misused."

**Teretic** (Gr. teras, teratos, monster, wonder). Abnormal; teratological, in the sense of conventional usage, with particular reference to marked deviations from the normal, or expected, morphological expression. See teratic example of proliferation under Determinate.

**Terete** (L., teres, well-turned). Circular in cross-section, tapered progressively from one end to the other, and smallest at the distal end or tip (for example, a small bamboo culm). Cf. Oterete.

**Ternate** (as applied to pleioclade midculm branch complements). Typically consisting of only three axes or branches.

**Testa** (L., covering, in a poetical sense of the substantive). The outer coat of a seed.

**Tillering.** "Throwing out stems from the base of a stem" (Jackson, 1949); proliferation of a culm from its basal (subterranean) buds, without the intercalation of a rhizome proper.

**Traçant** (Fr., running, creeping). Ranging widely and freely; a term used by the Rivieres (1879:321 et passim) to characterize (1) the slender, elongate type of rhizome herein called leptomorph (q.v.), and (2) the bamboos that spread by this means.

**Transitional glumes.** A term newly coined to designate those sheathing structures that occupy the physiologically transitional zone located immediately below the first fertile lemma of a bamboo spikelet. In many of the tribes of conventional grasses, and in some bamboos, it is possible to focus on one or more features that reveal a clearly perceptible distinction between two categories of structures in this zone, namely, empty glumes and sterile lemmas (q.v.). Agrostologists generally have
made the most (in some cases too much) of these structures as sources of taxonomic characters. In many bamboos, either the total number or the number of members of each category (or both of these features) found in a given spikelet may vary as between spikelets in a single specimen. Again, in some species, one may look in vain for a clear distinction (disjunction) between “empty glumes” and “sterile lemmas.” In such cases, their taxonomic value may be greatly reduced. For this reason, in describing bamboo genera, I have adopted the expedient of treating both categories as members of a single morphological category, namely, transitional glumes. Besides avoiding a certain psychological difficulty that arises in some cases this emphasizes the existence of physiological gradients, and places in proper perspective the frequent appearance of morphological gradients, in place of the sharp (abrupt) morphological transitions sought by the taxonomist.

**Triaedelphous** (Gr. treis, three; adelphos, brother). Having “filaments in three brotherhoods”; an adjective cognate with Triadelphia; the name of “a Linnean order of plants with their stamens in three sets” (Jackson, 1949), and conventionally used to describe the stamen complement of a flower when its members have their filaments connate to form three distinct groups. In bamboos with triadelphous androecia, the three “brotherhoods” commonly comprise one, two, and three stamens, respectively. Cf. Monadelphous; Diadelphous.

**Tufted** (as applied to the component pleioclade branch complements at midculm nodes of a bamboo). Indicates more or less profuse branching from the basal nodes of the primordial branch. The component axes of tufted branch complements may be subequal, or unequal (with the primordial axis [branch] more or less strongly dominant).

**Turgidity** (L. turgidus, inflated). Turgor, turgescence; the firmness imparted by “the distention of a cell or cellular tissue by water or other liquid” (Jackson, 1949).

**Unequal** (as applied to the transitional glumes of a spikelet, or the component axes of a midculm branch complement). Of more or less strongly disparate size.

**Unicespitose** (L. unus, one; caespitosus, from caespes, a tuft). Characterizes the clump habit of a bamboo plant that embraces but a single, more or less compact, tuft of culms—as in Bambusa (Guadua) amplexifolia. Cf. Pluricespito.

**Unilateral** (L. unilateralis, from unus, one; latus, a side). One-sided. See Secund.

**Unisulcate**. Provided with, or marked by, a single horizontal groove. See Sulcate; Hilum.

**Unrestricted**. Characterizes a branch complement (monoclade or pleioclade) as possessing the potential for proliferating by way or buds at the proximal nodes of its component first-order member(s).

**Versatile** (L. versatilis, adaptable, turning with ease from one thing to another). Applied herein to a rhizome system capable of producing both leptomorph and pachymorph axes, as in some species of Chusquea. Versatile is elsewhere (Jackson, 1949) “turning freely on its support, as many anthers on their filaments.”

**Zygomorphic** (Gr. zygos, yoke; morphē, form). Symmetrically divisible by a single plane; “used of flowers which are divisible into equal halves in one plane only, usually the anteroposterior” (Jackson, 1949). Normal bamboo flowers conform to this restricted criterion for zygomorphy (see McClure, 1966b:114). According to Jackson (1949), “Sachs extends the meaning to such flowers as may be bisected in any one plane.”

**Vernation** (L. vernatio, renewal). “The disposition or method of arrangement of foliage leaves within the bud” (Webster, 1959). Jackson’s (1949) definition, “the order of unfolding of leaf buds,” is not applicable here. In most known bamboos, the developing leaf blades are individually rolled up tightly along their long axis, with one edge at the center of the roll.

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