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

F. A. McCLURE

(EDITED BY THOMAS R. SODERSTROM)

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*F. A. McClure*

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## 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.

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## 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 knowledgeable 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  
Smithsonian Institution  
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 Benthams, 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 *iterauctant* (indeterminate) and *semelauctant* (determinate). *Iterauctant* 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 understanding 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 subtropics, 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 indispensable 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 Japanese 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 specialized 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 itercaucant 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 exhaustively 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 3D, 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 (Holtum, 1955) that sympodial branching of the stem predominates 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 distinguished 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) remarked 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 gramineous 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

*Smithsonian Institution*  
*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.



# Contents

	<i>Page</i>
Preface, by Edward S. Ayensu .....	iii
Foreword, by R. E. Holtum .....	v
Acknowledgments, by F. A. McClure .....	ix
Introduction .....	1
Key to the Recognized Genera of Bamboos Native to the New World .....	6
<i>Apoclada</i> McClure .....	8
<i>Arthrostylidium</i> Ruprecht .....	15
<i>Arundinaria</i> Michaux .....	21
<i>Athroostachys</i> Bentham .....	40
<i>Atractantha</i> McClure, new genus .....	42
<i>Aulonemia</i> Goudot .....	53
<i>Bambusa</i> Schreber, Subgenus <i>Guadua</i> (Kunth) Hackel .....	61
<i>Chusquea</i> Kunth .....	69
<i>Colantheia</i> McClure and E. W. Smith, new genus .....	77
<i>Elytrostachys</i> McClure .....	79
<i>Glaziophyton</i> Franchet .....	83
<i>Merostachys</i> Sprengel .....	87
<i>Myriocladus</i> Swallen .....	94
<i>Neurolepis</i> Meisner .....	97
<i>Rhipidocladum</i> McClure, new genus .....	101
<i>Swallenochloa</i> McClure, new genus .....	106
<i>Yushania</i> K. H. Keng .....	113
Glossary .....	122
Literature Cited .....	140

FRONTISPIECE: 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 (Gramineae: 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. The new demands for evidence from other disciplines means that in order to be up-to-date the collector must abandon the idea that the conventional leafy flowering specimens are sufficient for purposes of

description and classification. He must have in mind not only the morphologist but the anatomist, cytologist, chemist, geneticist, biochemist, ecologist, etc., so that material for the study of each entity in as many disciplines as possible may be available under the same herbarium voucher.

In some cases, the nomenclatural type of a genus (especially where its choice was fortuitous) represents a species that is morphologically peripheral to the main body of the currently recognized components of the genus. In any case, the depth of presently attainable taxonomic perspectives varies from genus to genus. For this reason, the emphasis on phylogeny is uneven, tentative, and of necessity extremely limited in this treatment of the genera. During the course of the phylogenetic diversification of bamboo taxa, some of the characteristic expressions of different individual features (conventionally referred to as "characters") have recombined (in disregard of quasi-generic boundaries). This may be due to the persistence of genetic compatibility within populations of related plants, or between groups of related species, some of which have already acquired combinations of morphological features of such strong divergence as to suggest, respectively, either specific or generic segregation by the taxonomist.

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 iterant (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 on 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 quantitative 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 *Guadaluella 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 fea-

tures 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-

fort, either to follow the path that leads to the right name, or to retrace one's steps in case one loses his way.

### 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 .....3
- 2a. Flowering culms leafless, the above-ground internodes exceedingly thin walled and provided 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 antherium .....*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 excurrent; 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 3), 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 .....*Swallemochloa*, new genus
- 6a. Inflorescences iterauctant; terminal segment of each rachis conspicuously elongate; spikelets 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 semelauctant; terminal segment of each rachis not conspicuously elongate; spikelets terminating in a depauperate sterile antherium .....7
- 7a. Culms scandent; inflorescences capitate .....*Athroostachys*
- 7b. Culms self supporting, the internodes typically more or less conspicuously sulcate, inflorescences not capitate .....8
- 8a. Inflorescence a raceme; branches at midculm node to 5 .....*Apoclada*
- 8b. Inflorescence a panicle; branches at midculm node to 3 .....*Yushania*
- 9a. Primary element of the branch complement at midculm nodes flat, unsegmented, appressed and wholly adnate to the surface of the culm; second-order branches of apsidate insertion and displayed in fan-shaped array; inflorescences semelauctant .....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 semelauctant or iterauctant .....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 antherium; 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 antheria 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 antherium; transitional glumes at the base of the spikelet usually 3, 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 antheria 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. *tracta*, for example) occasionally either suppressed temporarily or remaining solitary; inflorescences semelautant; stigmas 3 ..... *Arundinaria*
- 11b. Rhizomes pachymorph; stigmas in most cases 2 (often 3 in *Bambusa*) .....12
- 12a. Inflorescences iterant, forming pseudospikelets .....13
- 12b. Inflorescences semelautant, 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. aculeata*); 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 ..... *Elytostachys*
- 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 .....15
- 15a. Base of the primary axis typically extending downward beyond the locus of insertion of the prophyllum or lowermost circumcinct sheath to form a low, downward-tapered promontory; inflorescence a raceme with zig-zag rachis; plants of tropical or subtropical climates .....*Arthrostyloidium*
- 15b. Base of the primary axis not extending downward into a promontory; inflorescence a panicle (sometimes intermixed with racemose branches in *Colantheia*) with straight rachises; plants of temperate or cold climates .....16
- 16a. Sheath at midculm nodes provided with (and abscising from) a conspicuous persistent girdle ..... *Colantheia*, new genus
- 16b. Sheath at midculm nodes typically lacking a conspicuous basal girdle ..... *Aulonemia*

### *Apoclada* McClure

#### FIGURES 1-5

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

Plants unispitose; unarmed. Rhizomes pachymorph. Culm habit unknown, the internodes  $\pm$  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 semelautant, 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 3D) 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 depauperate sterile anthecium. Lemma (when sub-

tending a functional flower) embracing its palea only basally at maturity. Palea broadly sulcate and 2-keeled dorsally, the margins not at all or only slightly and partly overlapping. Lodicules typically 3, the anterior 2 asymmetrical and paired, the posterior one smaller and symmetrical. Stamens normally 3 (exceptionally as sometimes observed in *Apoclada diversa*, varying from 3 to 6 in spikelets from the same specimen), the filaments filiform, free. Stigmas 2. Mature fruit (known only in *Apoclada simplex*) an oblong or subfusiform, sulcate, mucronate caryopsis, the pericarp glabrous, appreciably thickened and crustaceous, the sulcus broad, the basal position of the embryo weakly manifest externally.

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 antrorse-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. cannavieira*, 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, superficiei omnino laevi et dura, primo opaca demum nitida. Culmorum et ramorum primariorum vaginae deciduae (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 antrorse 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 liberis, pallidis, levibus, anfractisque, denique cadentibus; ligula interiore perbreve apice convexa, dorso canescenti, margine dense ciliolata; ligula exteriori vix ulla, margine primo dense ciliolata demum glabrescenti et vel denticulata vel erosa vel integra; petiolo circa 1 mm

longo, basi puberulo, superne glabro, primo glaucescenti 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 unicam redactae; vel solitariae vel 2-3 simul insertae a bractea communi subtentae; prophyllis nullis. Glumae transitionales vulgo 2 (interdum 1 vel 3) usque 3 cm inter se distantes, naviculares, apice vel acutae vel acuminatae et breviter aristatae, dorso carinatae plurinerves et glabrae, substantia subhyalinae fragilesque, I ca 10 mm longa, II ca 11 mm longa, III ca 12 mm longa; gluma transitionalis suprema nonnunquam florem depauperatum subtendens ubi lemmati fertili similis. Spiculae pedicellatae, usque 4 cm longae, laxae pauciflorae, lanceatae, compressulae. 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),  $\times 0.6$ ; B, midculm bud complement,  $\times 6$ ; C, branch complement (basal part),  $\times 6$ ; D, leafy twig,  $\times 1.8$ ; E, apex of leaf sheath and base of leaf blade  $\times$  ca. 18; F, flowering culm, with rhizome,  $\times 0.6$ . Drawings A, C, F based on *Chase 11886* (US) and B, D, E on *Chase 12007* (US).

latissime sulcata, in apicem variabilem vel hebetere acuta vel obtusa vel subtruncata et bi- vel quadridentata, 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 suprema ciliolatae alibi utrinsecus glabrae, anterioribus 2 sub-semiovatis, posteriore lanceata. Antherae usque 6 mm longae, brunneae, apice subpenicillatae. 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, ciliate on the outer margin; auricles minute, rudimentary or obsolete; oral setae numerous, crowded,

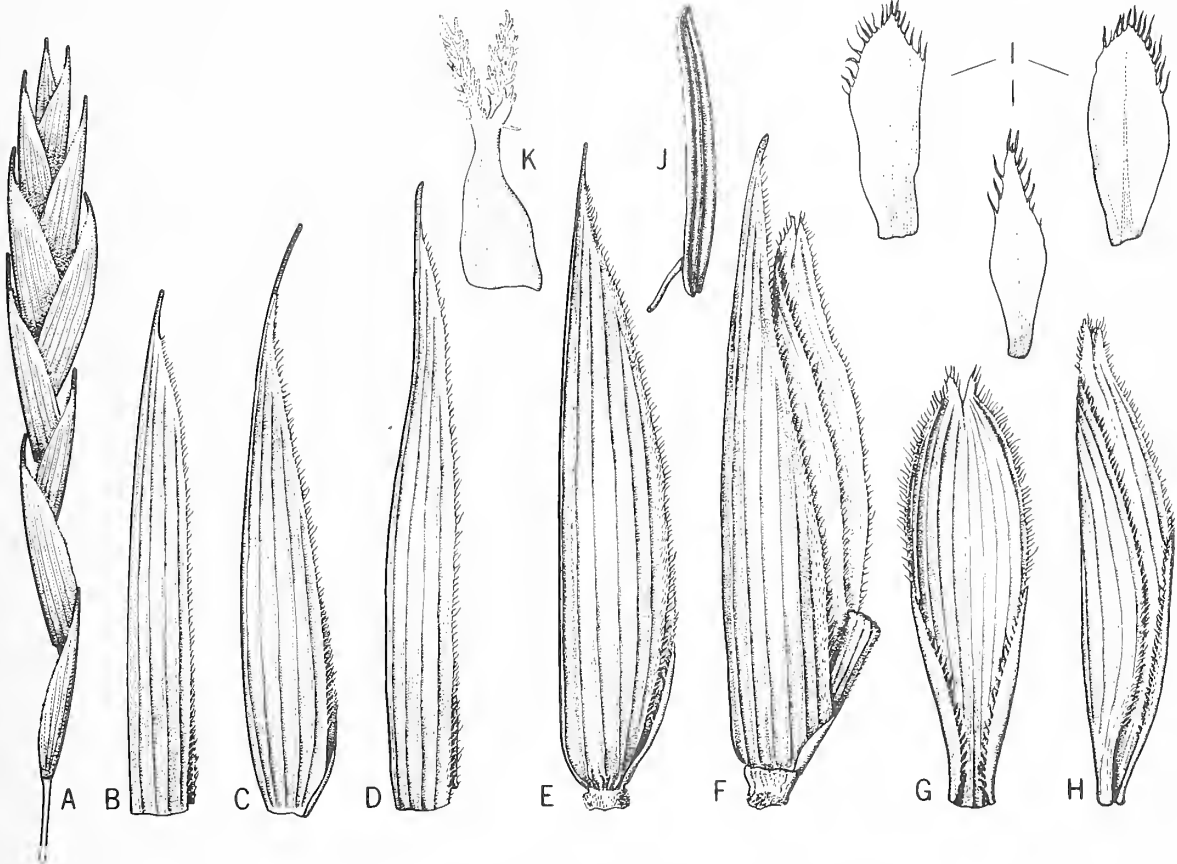


FIGURE 2.—*Apoclada arenicola* McClure. A, Spikelet,  $\times 1.2$ ; B, transitional glume I,  $\times 7.2$ ; C, transitional glume II,  $\times 7.2$ ; D, transitional glume III,  $\times 7.2$ ; E, lemma,  $\times 7.2$ ; F, floret,  $\times 7.2$ ; G, palea, abaxial view of distal portion,  $\times 7.2$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

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 ca 10 mm long, II ca 11 mm long, III ca 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 pergamineous, 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-semiovalate, 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. *Apocladia cannavieira* (Alvaro da Silveira) McClure, new combination

FIGURE 3

*Arundinaria cannavieira* Alvaro da Silveira, 1919:101, fig. 2.

TYPE-COLLECTION.—In campis arenosis siccisque in Serra do Caparaó (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. *Apocladia diversa*

FIGURE 4

*Apocladia diversa* McClure and Smith, in Reitz, ed., 1967:62, fig. 10z-e'.

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

## 4. *Apocladia simplex*

FIGURE 5

*Apocladia simplex* McClure and Smith, in Reitz, ed., 1967:59, fig. 10s-y.

FIGURE 3.—*Apocladia cannavieira* (Alvaro da Silveira) McClure. A, Upper portion of flowering culm,  $\times 0.6$ ; B, apex of leaf sheath and base of leaf blade,  $\times 12$ ; C, spikelet,  $\times 1.2$ ; D, diagram of longitudinal section of spikelet,  $\times$  ca. 2.4; E, transitional glume (sterile lemma),  $\times 3.6$ ; F, depauperate floret attached to rachilla segment (transitional glume [E], which subtended bud has been removed),  $\times 6$ ; G, floret,  $\times 2.7$ ; H, lemma,  $\times 2.7$ ; I, palea,  $\times 2.7$ ; J, stamen complement and lodicule complement,  $\times 3.6$ ; K, lodicule complement,  $\times 6$ ; L, stamen,  $\times 3.6$ ; M, gynoeceum,  $\times 14.4$ . All drawings based on *Alvaro da Silveira 644* (US).

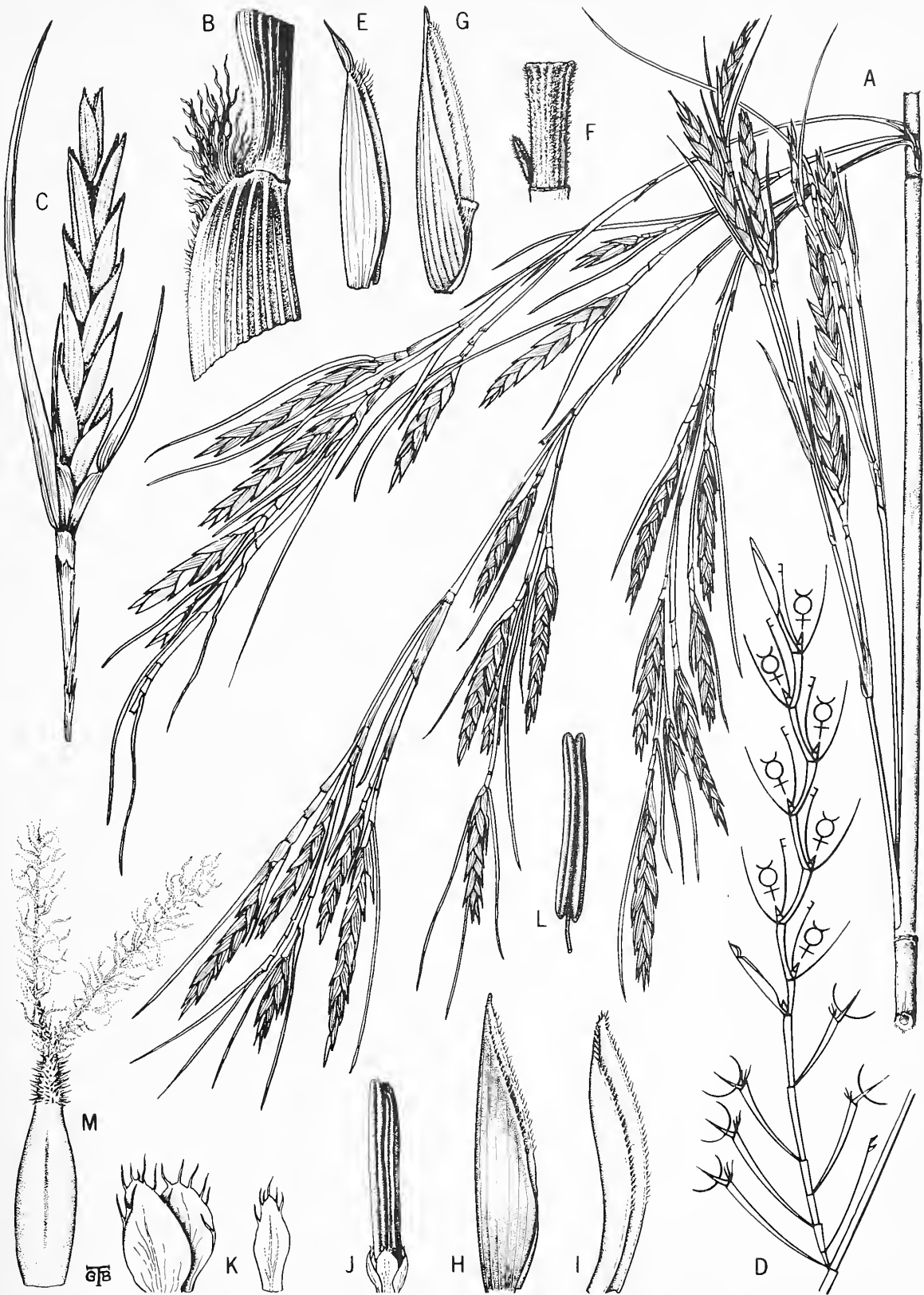






FIGURE 4.—*Apoclada diversa* McClure and L. B. Smith. A, Upper portion of leafless flowering culm,  $\times 0.6$ ; B, bud complement from node above midculm level,  $\times 3$ ; C, base of branch complement,  $\times 3$ ; D, spikelet with antecedent part of stem,  $\times 1.2$ ; E, bract that subtends flowering branches,  $\times 1.2$ ; F, floret,  $\times 7.2$ ; G, lemma,  $\times 7.2$ ; H, palea,  $\times 7.2$ ; I, lodicule complement,  $\times 15$ ; J, stamen,  $\times 15$ ; K, gynoeccium,  $\times 15$ ; L, fruit (juvenile),  $\times 15$ . All drawings based on Swallen 8271 (US).

TYPE-COLLECTION.—Brazil, Santa Catarina, Campos Novos, Palmares, pinhal, 900 m, 27 xii 1963, Reitz and Klein 16355 (holotype: US 2434535).

### *Arthrostylidium* Ruprecht

FIGURE 6

*Arthrostylidium* Ruprecht, 1839:27; 1840:117.—Hance, 1862: 235.—Munro 1868:39.—Doell, in Martius, 1880:172.—Bentham, in Bentham and Hooker, 1883:1208.—Hackel, in Engler and Prantl, ed., 1887:92.—Pilger, in Urban, ed., 1900-1901:336.—Hackel, 1903a:67.—Hitchcock, 1927b:307; 1936:243.—McClure, 1957:199.

Plants unicespitose, unarmed. Rhizomes pachymorph. Culms either self-supporting or clambering; each midculm node bearing a single initial (primary) branch bud, the prophyllum in some species elongating simultaneously with the germination of the bud, the primordium producing a single segmented, terete primary axis, this dominant over axes of higher orders that usually proliferate promptly from conventionally subtended buds typically present at its own proximal nodes; the base of the primary axis typically extending downward beyond the locus of insertion of the prophyllum or lowermost circumcinct sheath to form a low, downward-tapered promontory, this promontory naked in a few species (as in the available specimens of the type-species), elsewhere bearing usually two distichously inserted buds or branches each subtended by a small, noncircumcinct bract. Branch complement (when developed) at midculm nodes of either restricted or gremial insertion, the primary member typically strongly to weakly dominant; sometimes, however, apical growth in the initial primordium fails to take place, even after the precocious germination of buds at its proximal nodes. Sheaths at midculm nodes with or without a persistent girdle. Leaf blades with transverse veinlets not at all manifest to more or less clearly visible.

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 antheccium; 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 *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.

ETYMOLOGY.—The name *Arthrostylidium* (n.), derived from the Greek, *arthron*, joint, and *styli-dium*, 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.

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

RELATIONSHIPS.—Even after the exclusion of 23 of the 43 trivial names that have previously been associated with it, the image of the genus *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., *Arthrostylidium schomburgkii*) share such a feature with *Aulonemia queko*, *Glaziophyton mirabile*, *Rhipidocladum harmonicum*, and several species of *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

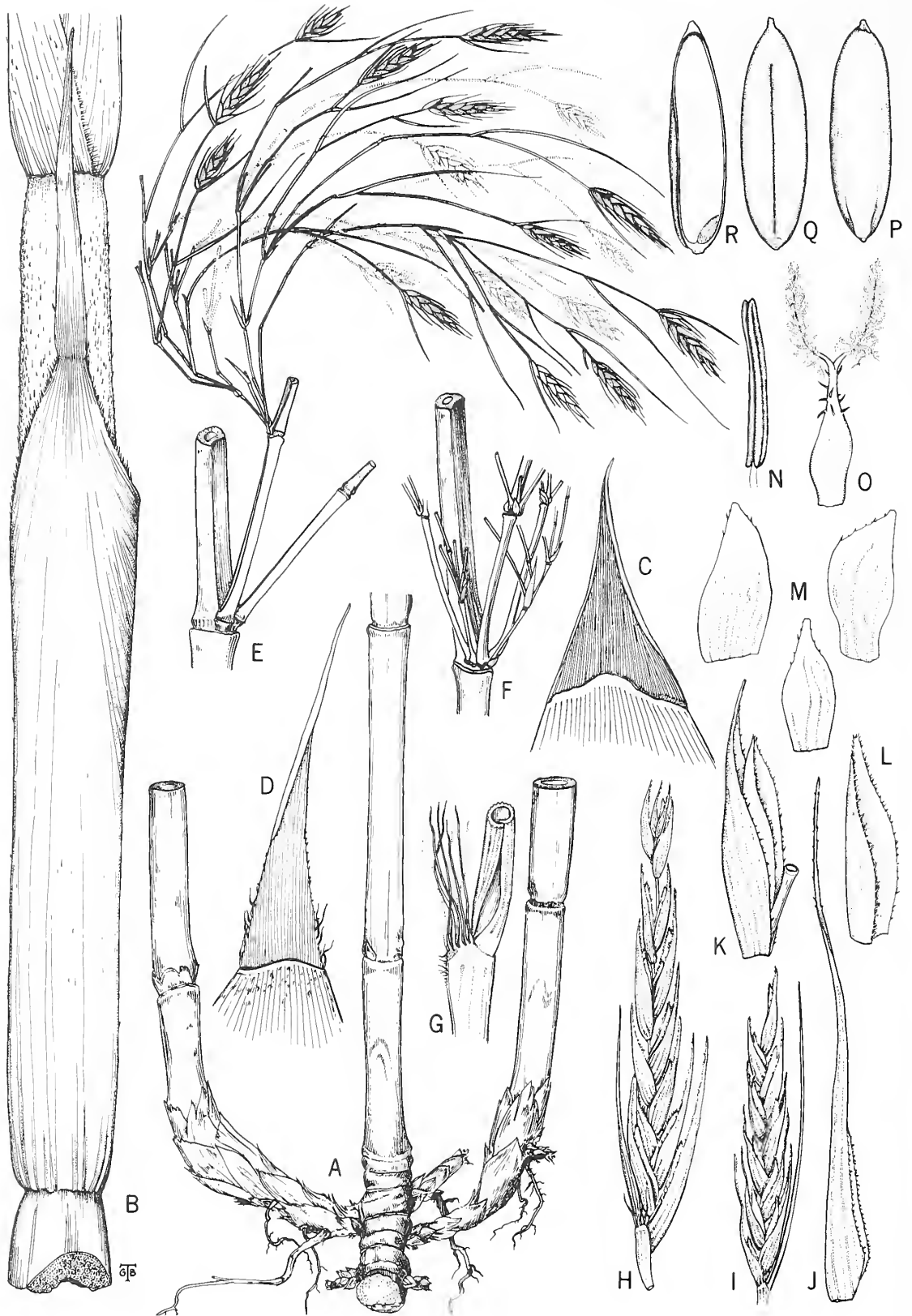


FIGURE 5.—*Apoclada simplex* McClure and L. B. Smith. A, Portion of clump showing rhizomes and base of culms,  $\times 0.12$ ; B, midculm internode, nodes and culm sheath,  $\times 0.6$ ; C, apex of sheath from lower culm node, adaxial aspect,  $\times 1.2$ ; D, apex of sheath from higher node, adaxial aspect,  $\times 1.2$ ; E, midculm complement of leafy flowering branches,  $\times$  ca. 0.6; F, variant of midculm branch complement,  $\times$  ca. 0.6; G, apex of leaf sheath and base of blade,  $\times$  ca. 4.8; H and I, spikelets, showing reduced laminiferous foliage leaf standing in place of a first transitional glume,  $\times 3$ ; 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),  $\times 6$ ; K, floret from middle of spikelet,  $\times 6$ ; L, palea,  $\times 6$ ; M, lodicule complement,  $\times$  ca. 18; N, stamen,  $\times 15$ ; O, gynoeceum,  $\times 15$ ; P, fruit, embryo side, showing weak indication of the position of the embryo,  $\times 7.2$ ; Q, fruit, hilum side, showing the sulcus,  $\times 7.2$ ; R, fruit, longitudinal section,  $\times 7.2$ . Drawings A, H based on Klein 4108 (US), B-F and I-R on Reitz and Klein 16,355 (US), and G on Klein 4657 (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 *Rhipidocladum 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-

mens of *A. cubense* the promontory lacks lateral buds; in *A. ekmanii* it sometimes bears one bud; in *A. capillifolium* it sometimes bears two buds; in *A. urbanii* it sometimes bears four buds. The buds that are borne on this outwardly unsegmented promontory are distichously inserted and subtended by noncircumcinct bract-like sheaths, while the buds that are borne more distally, on the proximal nodes of the segmented, terete primary axis that develops from the apical meristem of the initial primordium are subtended by circumcinct sheaths. As the number of buds on the unsegmented promontory increases, the number of circumcinct sheaths subtending buds on the proximal part of the primary axis decreases until, in *Arthrostylidium sarmentosum*, all the buds (excepting the uppermost one) are subtended by noncircumcinct bract-like sheaths. In some specimens of *Arthrostylidium sarmentosum* from Venezuela and Puerto Rico the development of the strongly dominant primary axis of the midculm branch complement is aborted immediately above the bud or branch at its uppermost proximal node. In other specimens, the dominance of the primary axis over the proximal secondary axes is greatly reduced. In such a specimen—as for example in *Soderstrom 1051* from Trinidad—the fully developed midculm branch complement is deceptively similar to that characteristic of all taxa I include in the genus *Rhipidocladum*. The persistence in arthrostylidioid taxa of the promontory (a feature that is entirely lacking in rhipidocladoid taxa), however, suggests that we have, in the vegetative cline observed in arthrostylidioid taxa, a case of evolution convergent toward *Rhipidocladum* with respect to the described feature complex. This convergence is weakly paralleled by the appearance, mentioned above, of a geniculate rachis in the inflorescence of *Arthrostylidium excelsum*, *A. venezuelae*, and *A. sarmentosum*, a feature shared by *Rhipidocladum* solely in *R. harmonicum*.

As initially delimited by Ruprecht, *Arthrostylidium* was already highly polymorphic. In the Latin notes that follow his brief formal description he (Ruprecht, 1840:117) says: "Genus Chusqueas et Arundinarias jungens." For years, I read this as meaning simply that *Arthrostylidium* is a genus that falls between *Chusquea* and *Arundinaria*. Although Ruprecht did not actually transfer any

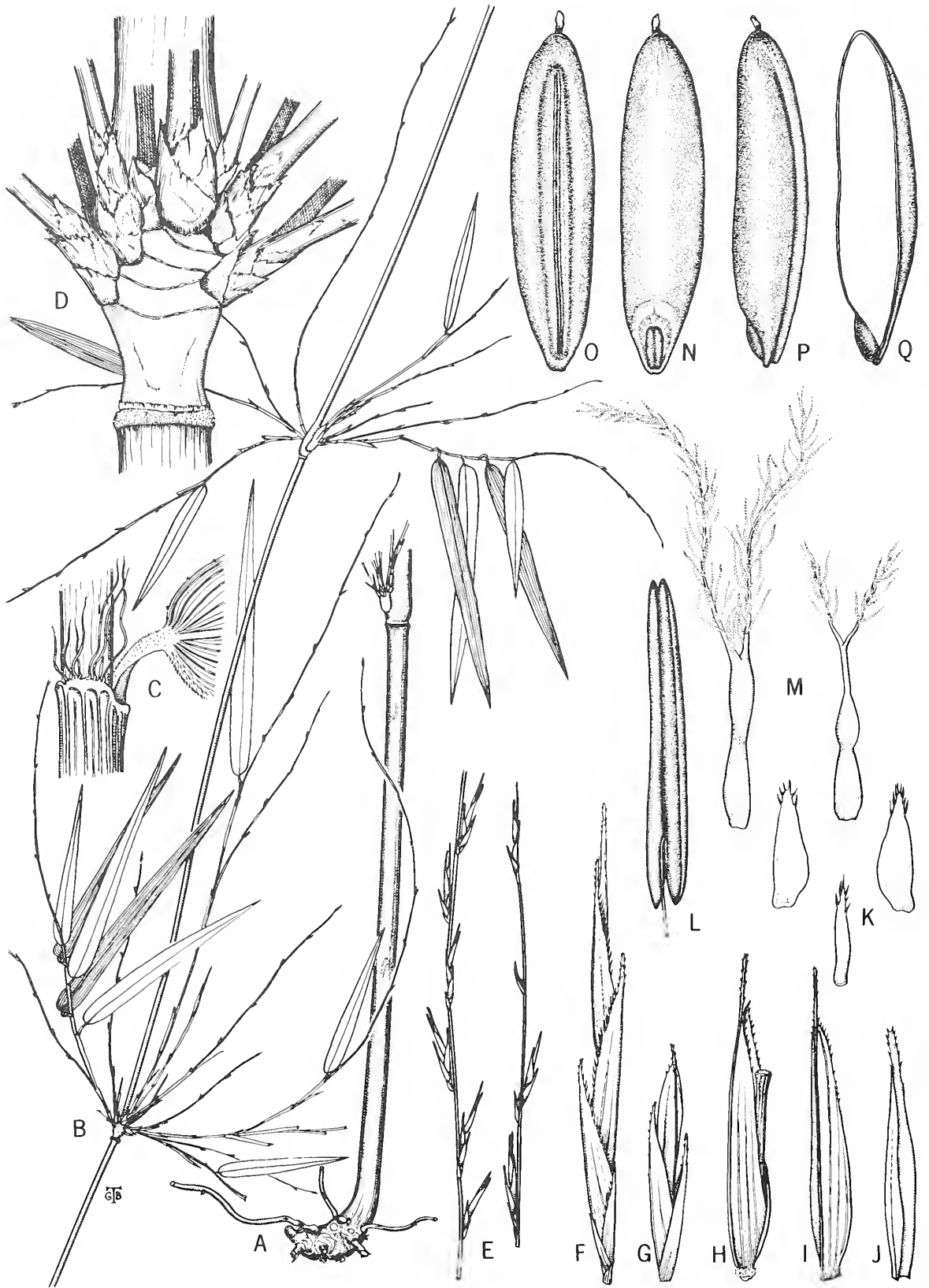


FIGURE 6.—*Arthrostylidium cubense* Ruprecht (A-M) and *Arthrostylidium multispicatum* Pilger (N-Q). A, Rhizome and lower part of culm,  $\times 0.6$ ; B, leafy flowering midculm nodes,  $\times 0.6$ ; C, apex of leaf sheath and base of blade,  $\times ca. 3$ ; D, insertion of components of midculm branch complement,  $\times 3$ ; E, inflorescence,  $\times 6$ ; F, spikelet,  $\times 6$ ; G, transitional glumes (3),  $\times 6$ ; H, floret,  $\times 6$ ; I, lemma,  $\times 6$ ; J, palea,  $\times 6$ ; K, lodicule complement,  $\times 15$ ; L, stamen,  $\times 15$ ; M, gynoeceum,  $\times 15$ ; N, fruit, embryo side,  $\times 12$ ; O, fruit, hilum side,  $\times 12$ ; P, fruit, oblique aspect,  $\times 12$ ; Q, fruit, longitudinal section,  $\times 12$ . Drawings A and H-M based on *Brother Leon 16214* (US), B-D on *Ekman 12649* (US), E-G on *Wright 3809* (US) and N-Q on *Leonard 3817* (US).

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. piniifolia*, *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 130 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: 336–337), 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 (1903[a]: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: 307) 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 unicespitate clump habit, a spikeate inflorescence with sessile or subsessile spikelets, and binate stigmas; while plants typical of *Arundinaria* possess leptomorph rhizomes, a diffuse or pluricespitate 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., 1964:3.
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: 531.
  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 sarmentosum* 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, 1854:337.

?*Arundinaria standleyi* Hitchcock, 1927a:79.

As illustrated by currently available herbarium specimens, *Arundinaria 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 *Rhipidocladum 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 *Colanthea 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 longifolium*. 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 *Aulonemia 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 parviflorum*.

#### *Arundinaria* Michaux

##### FIGURES 7-18

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

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

*Ludolfia* Willdenow, 1808:320.—McClure, 1957:204.

*Macronax* Rafinesque, 1808:353.—McClure, 1957:204.

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

*Pleioblastus* 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 *Arundinaria*—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 plurispitose 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 semelautant, 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 anthercia. 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 pericap thin, pergamineous 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, 1861:433) 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-SPECIES.—*Arundinaria gigantea* (Walter) Muhlenberg (1813).

As basionym, *Arundo gigantea* Walter (1788), takes precedence over *Festuca grandiflora* Lamarck (1791), and *Arundinaria macrosperma* Michaux (1803) at the species level, since both Lamarck'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 well-developed, sheath-like bracts by which the lower branches of each inflorescence are subtended.

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, a unicespitose clump habit, and binate stigmas; cf *Yushania* sg. *Otatea*, 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-



issippi, 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 *macrosperma* (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 macrosperma* Michaux, to a total of about 376, counting only binomials. The inclusion of trinomials swells the number of its published nomen-

clatural 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*, *Neosasamorpha*, *Oreocalamus*, *Pseudosasa*, *Sasa*, *Sasaella*, *Sasamorpha*, *Semiarundinaria*, *Sinarundinaria*, *Sinobambusa*, *Thamnocalamus*, 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 macrosperma* 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*  $\beta$  *pumila* Ruprecht, 1839:22.  
\**Arundinaria tecta*  $\gamma$  *distachya* Ruprecht, 1839:22.  
\**Arundinaria tecta*  $\delta$ ? *colorata* Ruprecht, 1839:22.  
\**Arundinaria macrosperma*  $\alpha$  *arborescens* Munro,  
1868:15.  
\**Arundinaria macrosperma*  $\beta$  *suffruticosus* Munro,  
1868:15.  
\**Arundinaria macrosperma*  $\beta$  *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-*

*naria 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 macrosperma* Michaux "Gramen altissimum ramosum a Virginia ad Floridam & in occidentalibus juxta fluviis ab Illinoensibus ad ostium Misissippi [sign for under-shrub]." 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. Lodicules typically subopaque, fringed with marginal cilia, and supplied with numerous vascular traces. Pistils lacking the uncinat 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 12b), 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. Lodicules 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.

that have been concerned with the clarification of the taxonomy of the New World components of the genus *Arundinaria*—including not only local floras and manuals, but such taxonomic treatises as

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, 1933: 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 3, 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*

FIGURES 7-11, 15A, 16A

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."

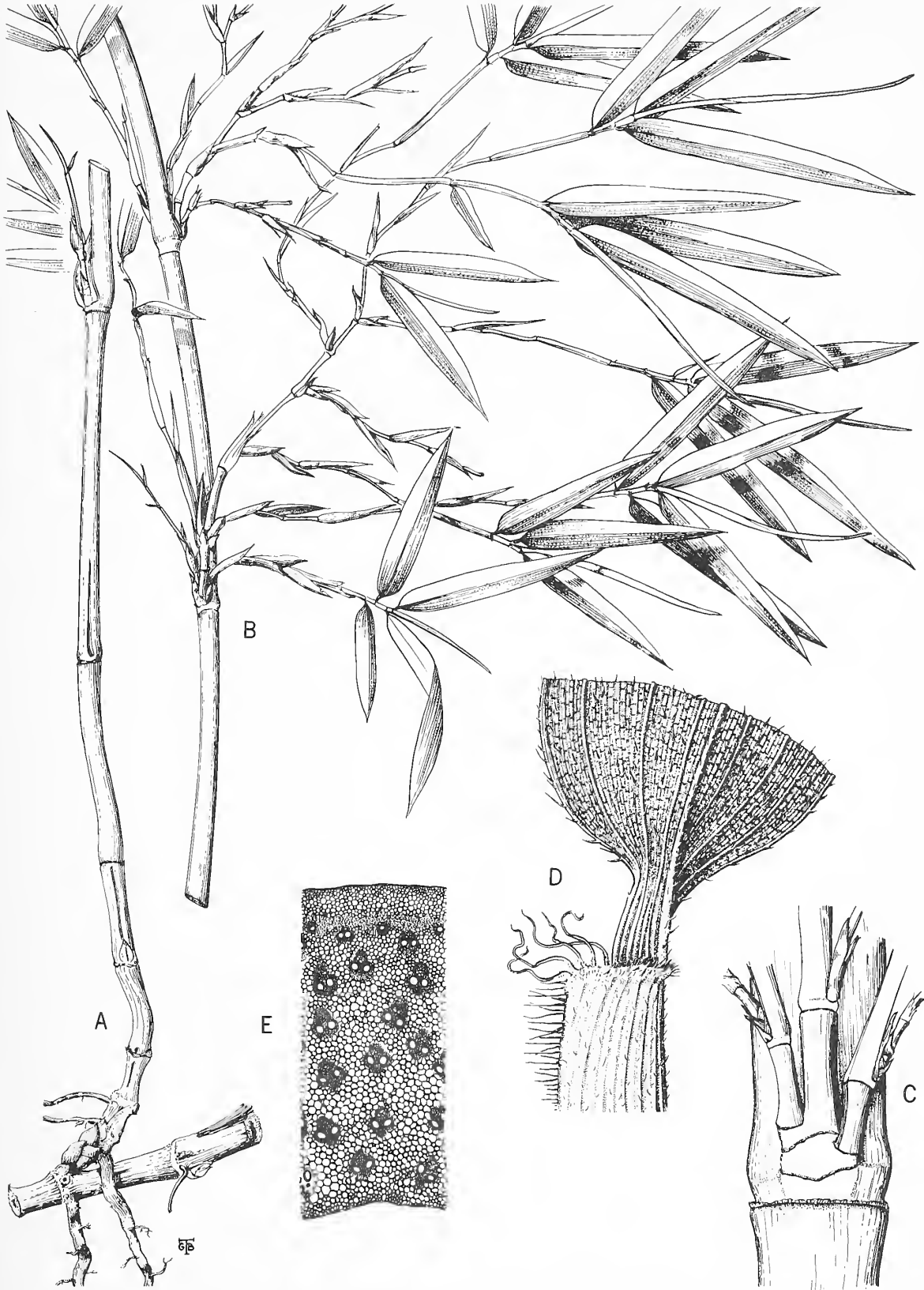
*Swallen* 6717 (US 2078084-2078089)—illustrated in Hitchcock, 1935 [1951, fig. 1], as *Arundinaria gigantea* (Walter) Muhlenberg—and *D. M. Moore, s.n.* (US 2206426-2206430) are relatively complete specimens that appear at first sight to represent typical *A. gigantea* ssp. *gigantea*. On closer examination, 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, 15B, 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,  $\times 0.6$ ; B, middle section of mature culm at end of first season,  $\times 0.6$ ; C, base of midculm branch complement,  $\times 2.4$ ; D, apex of leaf sheath with petiole and base of leaf blade,  $\times$  ca. 6; E, cross-section of rhizome, showing lack of air canals,  $\times$  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 anthechia. Two plants among those maintained under cultivation in my garden (about 20 miles from the natural stand) flowered and fruited freely. The production of fruits by these cultivated plants is a circumstance attributed to the absence of the parasitic insect at the latter site. In all observed cases of flowering, whether in wild plants or in those grown under cultivation, the culms that flowered died in the same season, along with the rhizomes that remained attached to them.

### 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'André Michaux." "Gramen altissimum ramosum  $\text{卍}$  [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 Misissipi  $\text{‡}$  [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 Desv.

*Arundo gigantea* Walter

M. Michaux le dit très différent de l'Arundo.

il a tout le port du Nastus de l'inde et paroît être la même plante, mais M. Michaux dit qu'il n'a que 3 étamines et pour l'ordinaire 3 styles ou peut-être un style divisé profondément en 3. Caroline et Rives du Mississipi jusqu'à l'Ohio. Donné par M. Michaux 1797.

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-

FIGURE 8.—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Midculm section of young culm,  $\times 0.6$ ; B, tip section of young culm,  $\times 0.6$ ; C, culm sheath from midculm node, with blade not reflexed,  $\times 3$ ; D, culm sheath from higher level, with blade reflexed,  $\times 3$ ; E, Walter's type of *Arundo gigantea* (from British Museum photo),  $\times$  ca. 0.4. All drawings based on *McClure Bamboo Garden specimen no. 2784* (US).



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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 *tecta* but differ in their much larger average size and in the infrequent incidence of the unciform 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 13E) 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

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FIGURE 9.—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Young leafy sterile culm with section of rhizome attached,  $\times 0.6$ ; B, young leafless flowering culm,  $\times 0.6$ ; C, whole sheath on midculm node of young culm shoot,  $\times 0.6$ ; D, apex and blade of culm sheath from upper node of young culm, showing reflexed sheath blade,  $\times$  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.

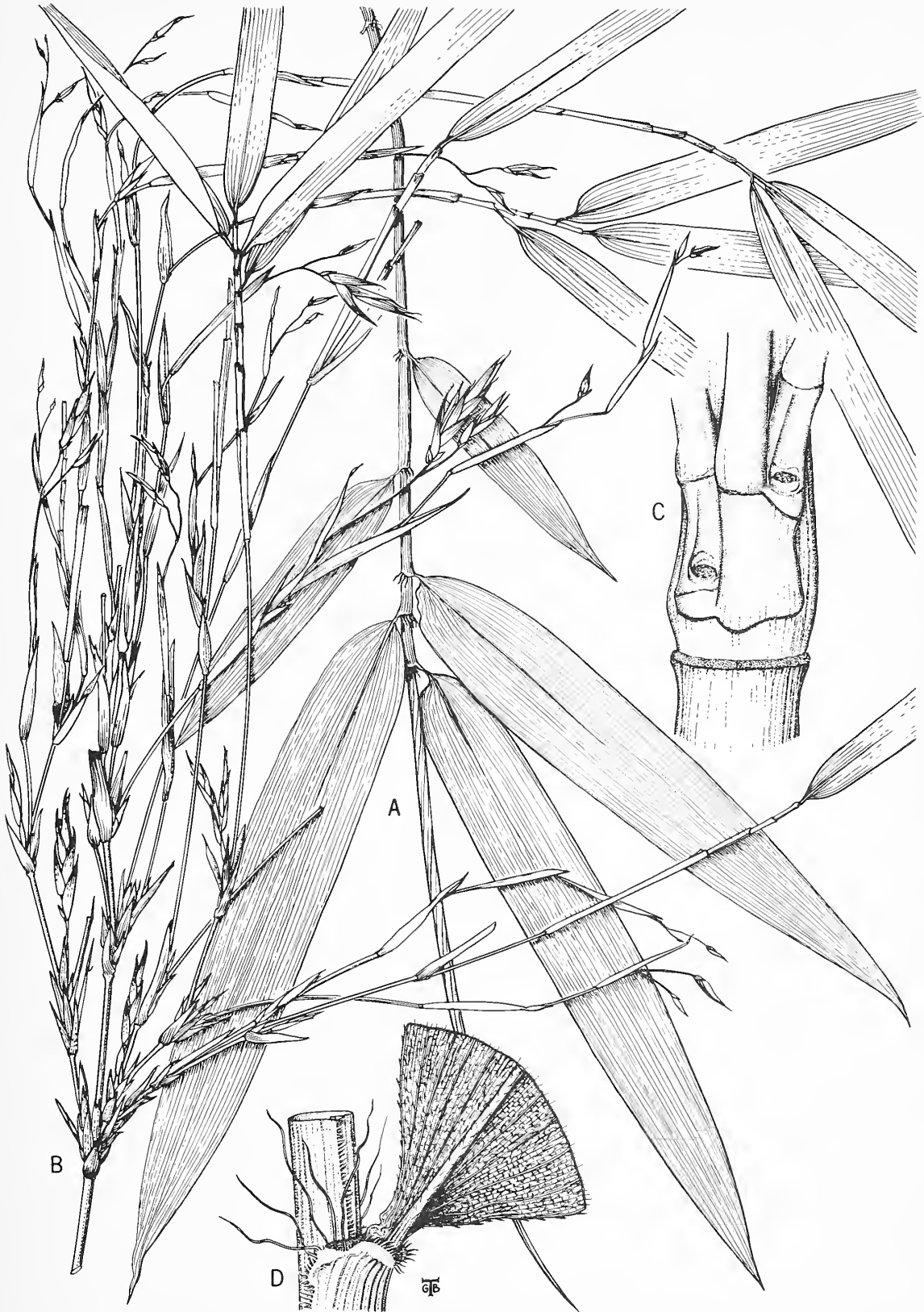
#### Observations Concerning the Taxonomic Utility of Certain Structures and Their Contrasting Features

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

FIGURE 10.—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Leafy culm tip,  $\times 0.6$ ; B, branch complement from node high on culm, with leafy and leafless flowering branches (with many spikelets shattered),  $\times 0.6$ ; C, base of midculm branch complement,  $\times 2.4$ ; D, apex of leaf sheath with petiole and base of leaf blade,  $\times$  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 (1929:317) 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. 1m] 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 phenotypic 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 possi-

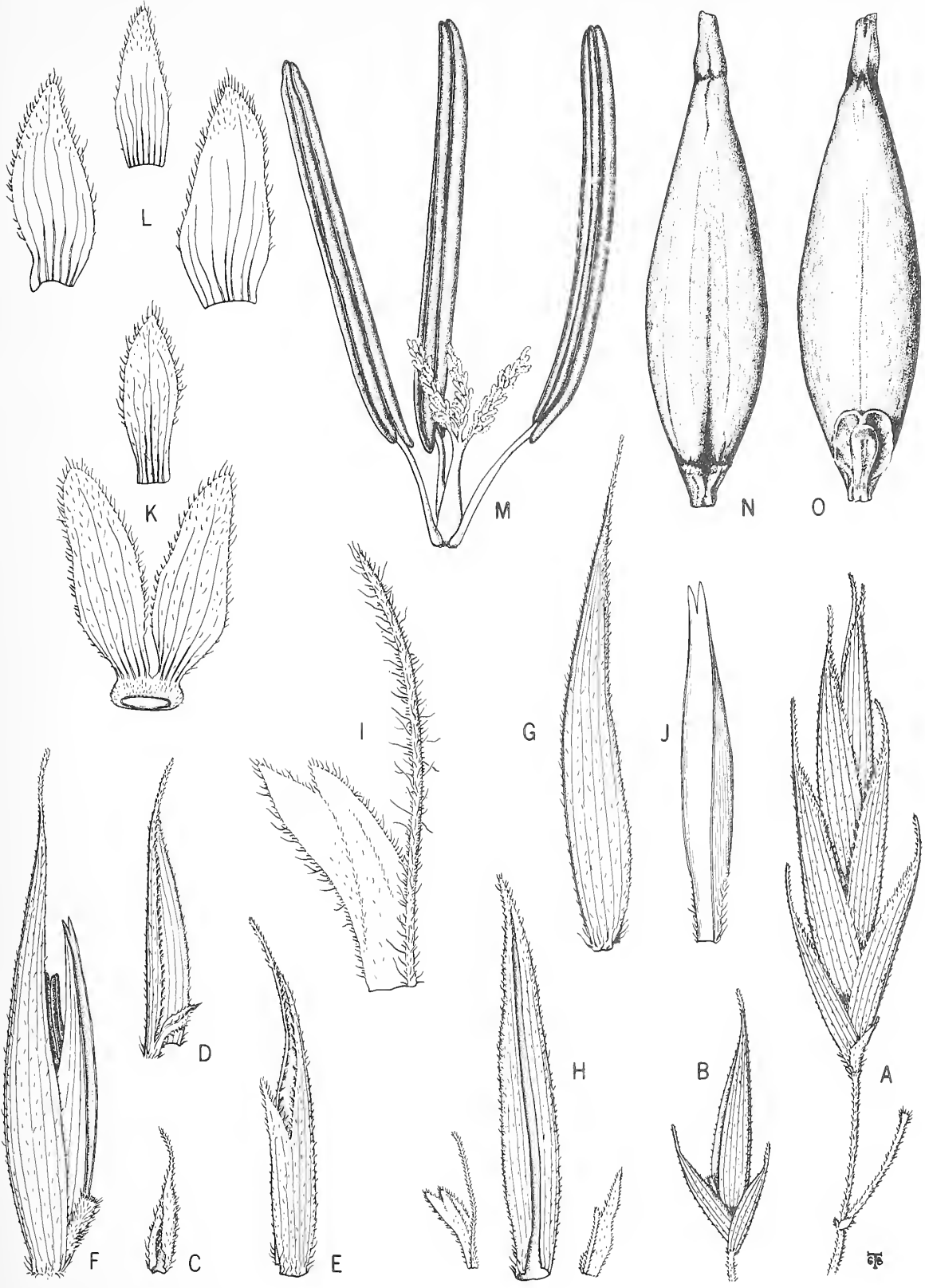
ble—even probable—that at least some of the plants with very tall culms may embody what is commonly known as hybrid vigor.

**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) supposedly 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. gi-*

FIGURE 11.—*Arundinaria gigantea* (Walter) Muhlenberg ssp. *gigantea*. A, Spikelet with pedicel and inflorescence branch subtended by a small bract,  $\times 1.8$ ; B, base of spikelet showing transitional glumes I and II and sterile lemma,  $\times 1.8$ ; C, transitional glume I (normal),  $\times 3.6$ ; D, transitional glume II (variant),  $\times 3.6$ ; E, transitional glume III (sterile lemma), variant,  $\times 3.6$ ; F, floret,  $\times 3.6$ ; G, fertile lemma (normal),  $\times 3.6$ ; H, fertile lemma with stipule-like appendages,  $\times 3.6$ ; I, stipule-like appendage,  $\times 10.8$ ; J, palea,  $\times 3.6$ ; K, lodicule complement showing dorsal surface,  $\times 7.2$ ; L, lodicule complement from another flower showing adaxial surface,  $\times 7.2$ ; M, gynoeccium and androeccium,  $\times 7.2$ ; N, fruit, hilum side,  $\times 7.2$ ; O, fruit, embryo side,  $\times 7.2$ . All drawings based on D. M. Moore, s.n., Arkansas, USA, 2 August 1947 (US).



*gantea* (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, I: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 STYLAR 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.

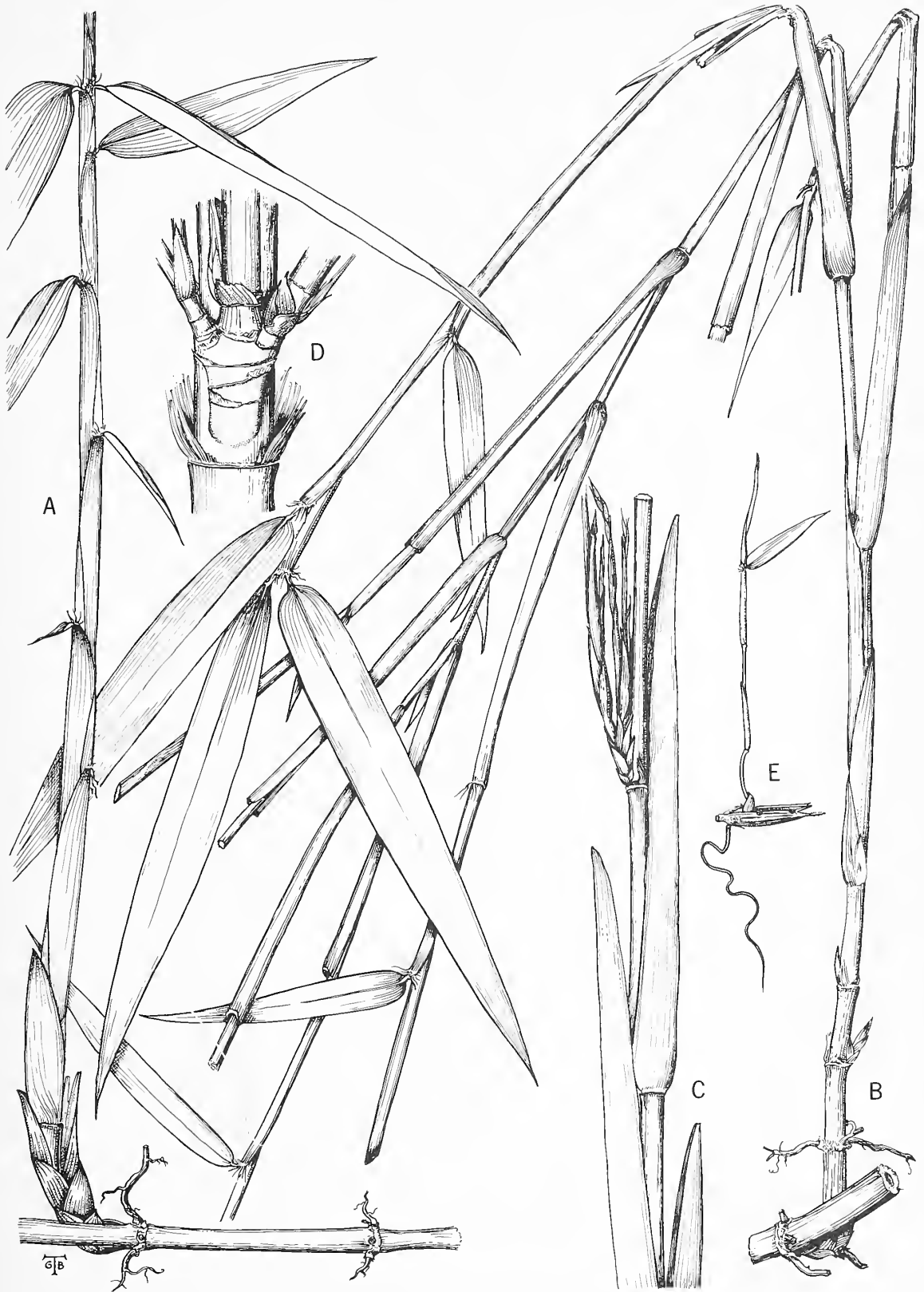
Reeder (1957, fig. 29) illustrated, in cross-section and sagittal section, the embryo of a fruit from a plant of bamboo native in Ann Arundel County, Maryland, documented under MBG 2762, and identified as *Arundinaria tecta*. Gould (1960:873) reported for a plant from a stand of bamboo native in Walker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

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FIGURE 12.—*Arundinaria gigantea* ssp. *tecta* (Walter) McClure. A, Young culm shoot with segment of rhizome,  $\times 0.6$ ; B, lower part of sterile leafy culm in the second season of its growth, with solitary leafy branches fully developed,  $\times 0.6$ ; C, midculm section of culm in its second season of growth, showing persistent sheaths and developing branch complement,  $\times 0.6$ ; D, base of unrestricted monoclade midculm branch complement,  $\times 1.2$ ; E, seedling with anthercium still attached,  $\times 1.2$ . All drawings from McClure *Bamboo Garden specimen no. 2762* (US).





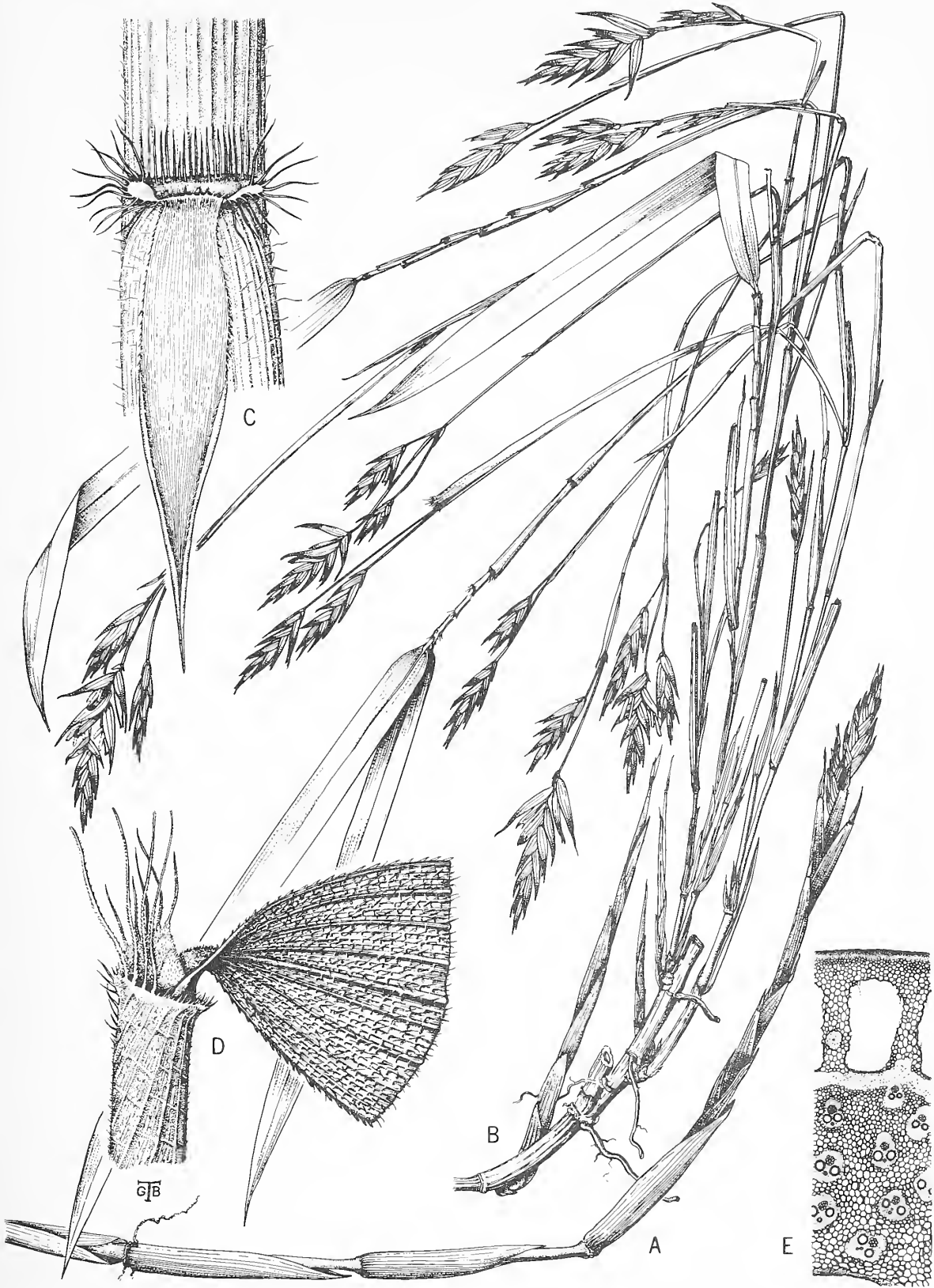
ventional circumscriptions of the genus *Arundinaria* that were published after that of Nees (1834) has postponed the recognition that, of the approximately fifty distinct neotropical taxa that have at one time or another been assigned to this genus, not one falls within its natural boundaries.

1. *Arundinaria acuminata*. See *Yushania acuminata*.
  2. *Arundinaria amplissima*. See *Aulonemia amplissima*.
  3. *Arundinaria aristulata*. See *Aulonemia aristulata*.
  4. *Arundinaria* ? *attenuata* Doell; species sedis mihi incertae etiam nunc manet.
  5. *Arundinaria burchellii*. See *Colanthesia burchellii*.
  6. *Arundinaria cannavieira*. See *Apoclada cannavieira*.
  7. *Arundinaria capillifolia* is *Arthrostylidium capillifolium* Grisebach.
  8. *Arundinaria cubensis* is *Arthrostylidium cubense* Ruprecht.
  9. *Arundinaria* ? *decalvata* Doell; species sedis mihi incertae etiam nunc manet.
  10. *Arundinaria deflexa*. See *Aulonemia deflexa*.
  11. *Arundinaria distans*. See *Colanthesia distans*.
  12. *Arundinaria effusa*. See *Aulonemia effusa*.
  13. *Arundinaria excelsa*. See *Arthrostylidium venezuelae*.
  14. *Arundinaria fimbriata* is *Arthrostylidium fimbriatum* Grisebach.
  15. *Arundinaria flabellata*; species sedis mihi incertae etiam nunc manet.
- The name *Arundinaria flabellata* (Fournier) McClure (in Maguire, Wurdack, et al., 1964:182) is based on *Guadua* ? *flabellata* Fournier 1881:131. The plant is known only by nonflowering specimens (*Liebmann 132* ["131"]) really too fragmentary for confident generic allocation at present. Since it clearly does not belong in *Arundinaria* (as the genus is defined herein) the taxonomic disposition of this plant awaits the realization of its thorough study and documentation, preferably at the type-locality.
16. *Arundinaria glaziovii*. See *Aulonemia glaziovii*.
  17. *Arundinaria glaziovii* var. *macroblephara*. See *Aulonemia ramosissima*.

18. *Arundinaria goyazensis*. See *Aulonemia goyazensis*.
19. *Arundinaria haenkei*. See *Aulonemia haenkei*.
20. *Arundinaria haitiensis* is *Arthrostylidium haitiensis* (Pilger) Hitchcock and Chase.
21. *Arundinaria herzogiana*. See *Aulonemia herzogiana*.
22. *Arundinaria hirtula*. See *Aulonemia hirtula*.
23. *Arundinaria humillima*. See *Aulonemia humillima*.
24. *Arundinaria leptophylla* is *Chusquea leptophylla* Nees.
25. *Arundinaria longiflora* is *Arthrostylidium longiflorum* Munro.
26. *Arundinaria longifolia*. See *Bambusa* (*Guadua*) *longifolia*.
27. *Arundinaria macrostachya*. See *Colanthesia macrostachya*.
28. *Arundinaria maculata*. See *Aulonemia parviflora*.
29. *Arundinaria microclada* is *Chusquea abietifolia* Grisebach.
30. *Arundinaria mirabilis* is *Glaziophyton mirabile* Franchet.
31. *Arundinaria mucronata*. See *Aulonemia aristulata*.
32. *Arundinaria multiflora* is synonym of *Arundinaria trianae*, q. v. infra.
33. *Arundinaria multispicata* is *Arthrostylidium multispicatum* Pilger.
34. *Arundinaria obtusata* is *Arthrostylidium obtusatum* Pilger.
35. *Arundinaria parviflora*. See *Rhipidocladum parviflorum*.
36. *Arundinaria patula*. See *Aulonemia patula*.
37. *Arundinaria pinifolia* is *Chusquea pinifolia* (Nees) Nees.
38. *Arundinaria pittieri*. See *Rhipidocladum pittieri*.
39. *Arundinaria prestoei*. See *Rhipidocladum prestoei*.

FIGURE 13.—*Arundinaria gigantea* ssp. *tecta* (Walter) McClure. A, rhizome turned upward apically and terminating in a simple inflorescence,  $\times 0.6$ ; B, leafy and leafless flowering branches from tip of rhizome,  $\times 0.6$ ; C, apex of sheath and reflexed blade from midculm node,  $\times 3$ ; D, apex of leaf sheath showing petiole and base of blade,  $\times 6$ ; E, cross-section of rhizome, showing one of the peripheral air canals,  $\times$  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 *Colantheia 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* Benth

FIGURES 19, 20

*Athroostachys* Benth, in Benth and Hooker, 1883:1208.—Hackel, in Engler and Prantl, 1887:93.—McClure, 1957:200.  
*Athroostachys* [sic] Benth, 1881:134 [nomen nudum].—McClure, 1957:199.

Plants unicespitate, 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 *Glaziov* 13325; illustrated in Figure 19B) 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 semelauclant, solitary, contracted, short-peduncled panicles of capitate or subcapitate form, each inserted at or near the apex of a

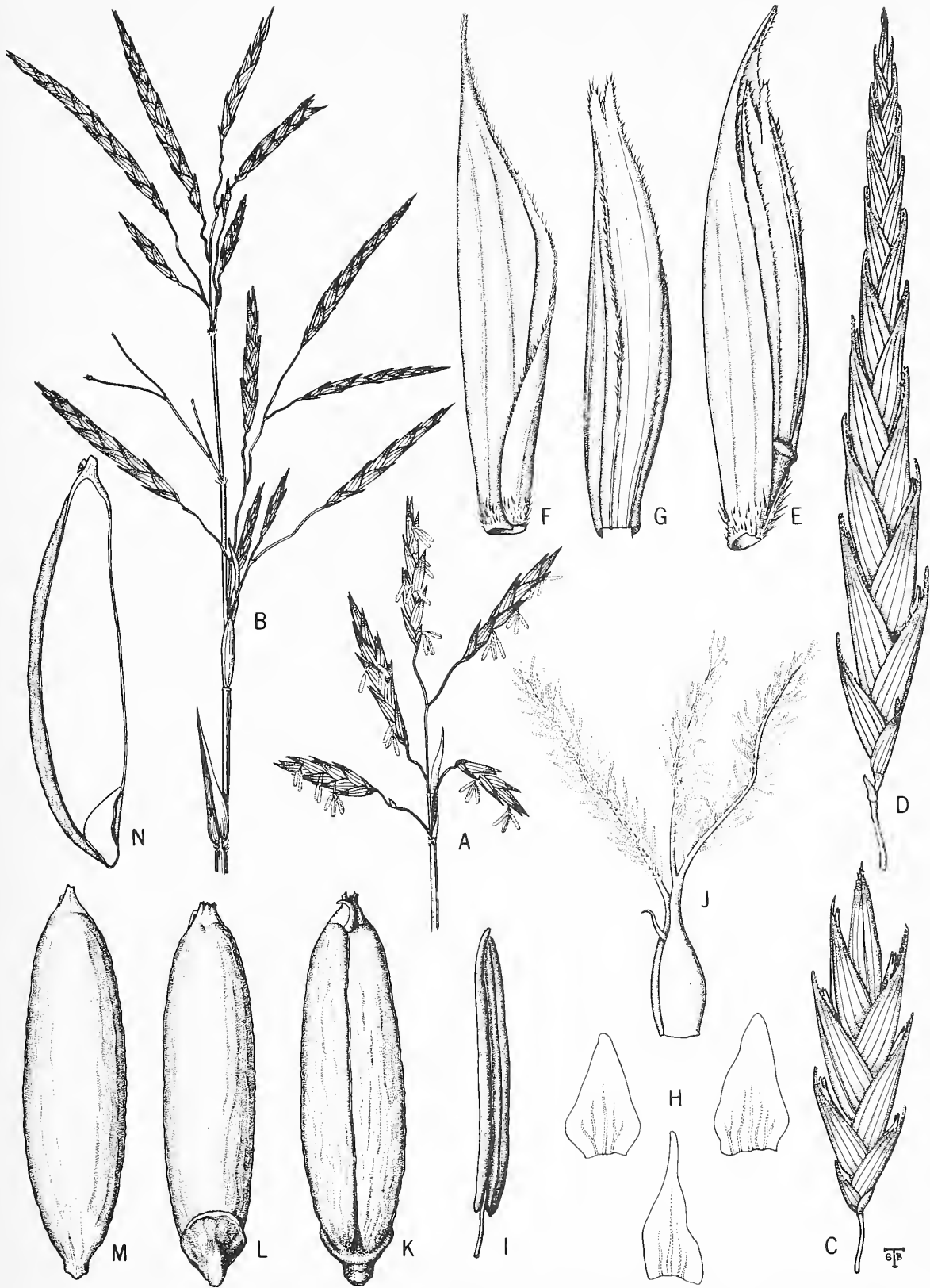
usually leafy twig, and subtended by a laminiferous sheath; the primary branches of the percurrent rachis inserted distichously in obscurely secund orientation, very short, not prophyllate, either unbranched or bearing one or two subequal short branches; the lowermost primary branches each subtended 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 subtend 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 depauperate sterile antherium. Lemma of perfect florets fully embracing its palea only basally at maturity. Palea gaping antically, narrowly sulcate and 2-keeled dorsally. Lodicules 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, *athroos*, crowded, and *stachys*, spike) ostensibly alludes to the condensed paniculate branching of the capitate inflorescence.

TYPE-SPECIES.—*Athroostachys capitata* (Hooker) Benth (in Benth 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 Benth in determining the categories to which to

FIGURE 14.—*Arundinaria gigantea* ssp. *tecta* (Walter) McClure. A, Inflorescence of racemose branching,  $\times 0.6$ ; B, inflorescence of paniculate branching,  $\times 0.6$ ; C, immature spikelet,  $\times 1.8$ ; D, abnormally elongate spikelet,  $\times 1.5$ ; E, floret,  $\times 7.2$ ; F, fertile lemma,  $\times 7.2$ ; G, palea,  $\times 7.2$ ; H, lodicule complement,  $\times 15$ ; I, stamen,  $\times 7.2$ ; J, gynoceum  $\times 7.2$ ; K, fruit, hilum side,  $\times 7.2$ ; L, fruit, embryo side,  $\times 7.2$ ; M, fruit, embryo side, the embryotegium inconspicuous,  $\times 7.2$ ; N, fruit, longitudinal section,  $\times 7.2$ . All drawings based on McClure Bamboo Garden specimen no. 2762 (US).



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: "spiculis . . . revera 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 steriles."

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:  $\alpha$  *latifolia* (presumably representing the typical form of the species) and  $\beta$  *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 19D), 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. Rhizomata non adhuc visa (?pachymorpha). Culmi in speciminibus suppetenibus haud satis representati; internodiis teretibus, vel inanibus vel fistulosis. Ramorum complementarum (in speciminibus suppetentibus) axes componentes primum proditi plures, ad circa libram inserti, unusquisque ex primordio distincto enascens (gemmis intactis primordios primos includentibus non adhuc visis); uno alios plus minusve valde dominantis; 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,  $\times 0.3$ ; ab, young culm, full height at age 3 months, showing branches already well developed,  $\times 0.15$ ; ac, cross-section of root from rhizome, to show air canals,  $\times 15$ ; ad, cross-section of root from culm base, to show air canals,  $\times 15$ ; ba, base of culm and section of rhizome, with roots,  $\times 0.6$ ; bb, young culm, full height, with branches not yet developed,  $\times 0.3$ ; bc, cross-section of root from rhizome, to show air canals,  $\times 30$ ; bd, cross-section of root from culm base, to show air canals,  $\times 30$ . Drawings aa–ad based on McClure Bamboo Garden specimen no. 2784 (US). ba–bd on McClure Bamboo Garden specimen no. 2762 (US).



plemento ubi plene evoluto composito-pleioclado. Foliorum lamina venulis transversis extus vel infirme vel haud manifestis.

Inflorescentiae iterauctantes, vel capitatae vel diffusae, earumdem ramorum insertione aut disticha aut sympodiali, rhachidum ramificationibus omnibus et bracteatis et prophyllatis, omnis rhachidis segmento terminali pro pedicello spiculae consistenti. Glumae transitionales ad basin spicularum vulgo praeditae hic nullae. Spiculae deciduae, infra et proxime locum lemmatis insertionis disarticulantes, unaequaeque flosculam perfectam solitariam habentes, rhachilla post paleam prolongata in setam gracilem anthecio rudimentario terminatam. Lemma fertile maturitate saltem paleam suam basi tantum circumplectans. Palea apice bifurcata, dorso sulco angustissimo instructa, antice leviter imbricata. Lodiculae 3, anteriores 2 sese aequales, plus minusve valde asymmetricae atque geminatae, posteriore symmetrica et anterioribus aliquanto minore. Stamina 3, filamentis filiformibus liberisque. Stigmata typice 2 (atypice et rarissime 3). Fructus maturus adhuc non inventus.

Plants of as yet unrecorded habit. Rhizomes not yet seen, ?pachymorph.<sup>1</sup> Culms not adequately represented in the available specimens; the internodes terete, either fistular or efistular. Branch complements (at least those seen) containing several initial components, each arising from a distinct initial primordium.<sup>2</sup> 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 manifest, externally.

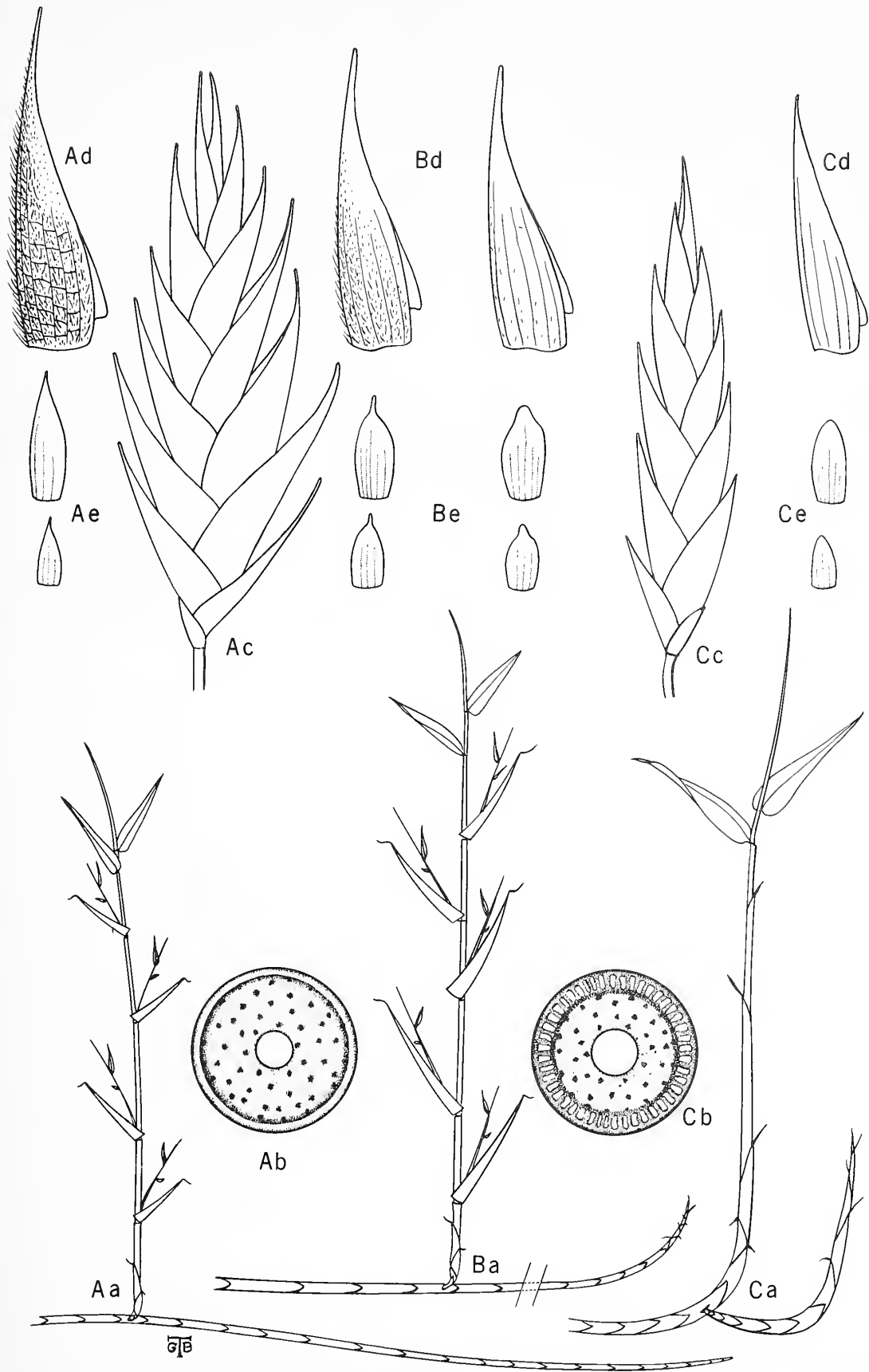
<sup>1</sup>The pachymorph character of the rhizomes (which are neither represented in the available specimens nor described by the collector) may be surmised from the strong resemblance of the inflated base of the primary axis of a branch complement (exemplified in the isotype specimen of *A. radiata*) to a pachymorph rhizome (see McClure 1966b:58, last paragraph).

<sup>2</sup>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 independent primary bud.

FIGURE 16.—*Arundinaria gigantea*, sensu lato. Semidiagrammatic sketches showing the extremes and intermediate expressions of the principal features that characterize the recognized components of the *Arundinaria gigantea* complex, including subspecies *gigantea* (A), subspecies *macrosperma* (B), and subspecies *tecta* (C), as to growth habit (a), rhizome in cross-section (b), spikelet (c), fertile lemma (d), and transitional glumes (e). Subspecies *gigantea* is characterized by the combination of expressions Aa, Ab, Ac, Ad, and Ae. Subspecies *tecta* is characterized by the combination of expressions ca, cb, cd, and ce of the same features. Nothomorphs of the presumed hybrid swarms (of which subspecies *gigantea* and subspecies *tecta* are the putative parents or grandparents) herein given the status subspecies *macrosperma*, show diverse combinations of the same contrasting expressions of these features, or of intermediate expressions of them. Some of these intermediate expressions are illustrated by Ba, Bd, and Be (transitional glumes) in the intermediate expression shown in the lectotype of *Arundinaria macrosperma* Michaux. The transitional glumes often vary more or less widely in size and shape within any given specimen, whether of otherwise typical subspecies *gigantea* or typical subspecies *tecta*, or of the polymorphic subspecies *macrosperma*. Moreover, in any given specimen of any one of the subspecies the lowermost transitional glume may be lacking entirely, or it may be inserted at some distance below the second one. A third transitional glume sometimes appears in the guise of a "sterile lemma."

Inflorescences iterauctant, of either capitate or diffuse form, their branching pattern either distichous or sympodial, each axis the bracteate and prophyllate rachis of a pseudospikelet, the terminal segment of each rachis serving as the pedicel of an abscissile spikelet. Transitional glumes at the base of each spikelet none.<sup>3</sup> Spikelets each made pedicellate by the segment of the rachis it terminates, each spikelet typically containing but a single perfect flower, and disarticulating promptly at maturity just below the locus of insertion of the lemma, the rachilla prolonged behind the palea in a bristle-like structure bearing a minute rudiment of a sterile anthecium. Lemma in functional florets embracing its palea only basally at maturity. Palea apically bifurcate, lightly imbricate antically, dorsally 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,

<sup>3</sup>The ostensible (approximate) position of the transitional glumes is here (and in *Elytostachys*, q.v.) occupied by what I now classify as bracts.



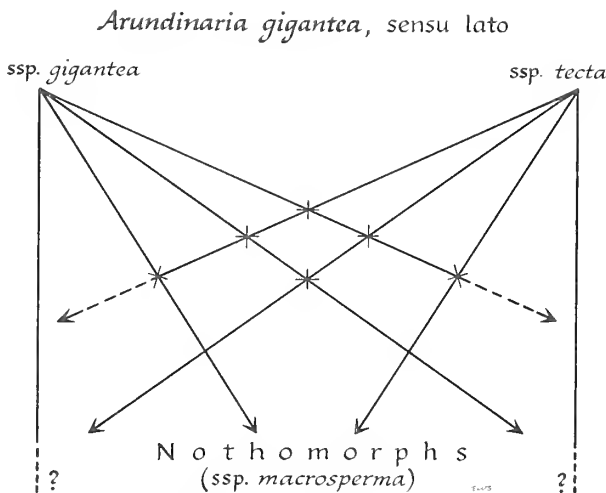


FIGURE 17.—*Arundinaria gigantea*, sensu lato. Diagrammatic representation of the putative phylogenetic relationships of the principal New World components of the genus *Arundinaria*. The arrows suggest putative contemporary potential for further introgression or hybridization. The question marks and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

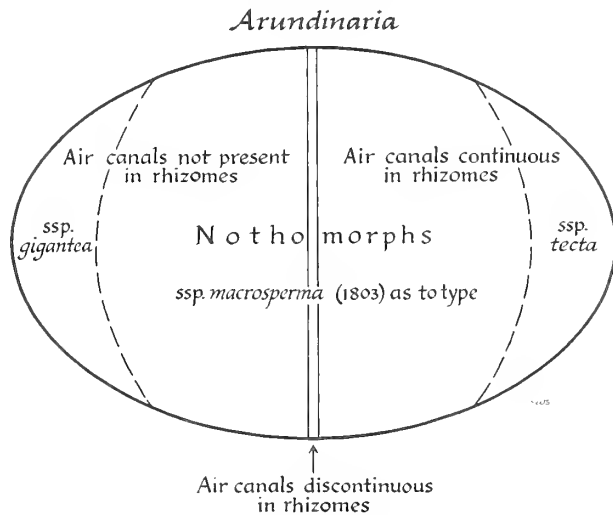


FIGURE 18.—*Arundinaria gigantea*, sensu lato. Schematic portrayal of some of the quantitative and qualitative relationships visualized as existing between the strongly divergent populations herein categorized as subspecies *gigantea* and subspecies *tecta*, respectively, and the populations of intermediates (putative nothomorphs) herein given taxonomic status as subspecies *macrosperma*, based on *Arundinaria macrosperma* 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 polymorphic species, and given the formal, comprehensive name, *Arundinaria gigantea*, sensu lato.

free. Stigmas typically 2 (atypically and very rarely 3 in *A. radiata*, q. v.). Mature fruit not yet found.

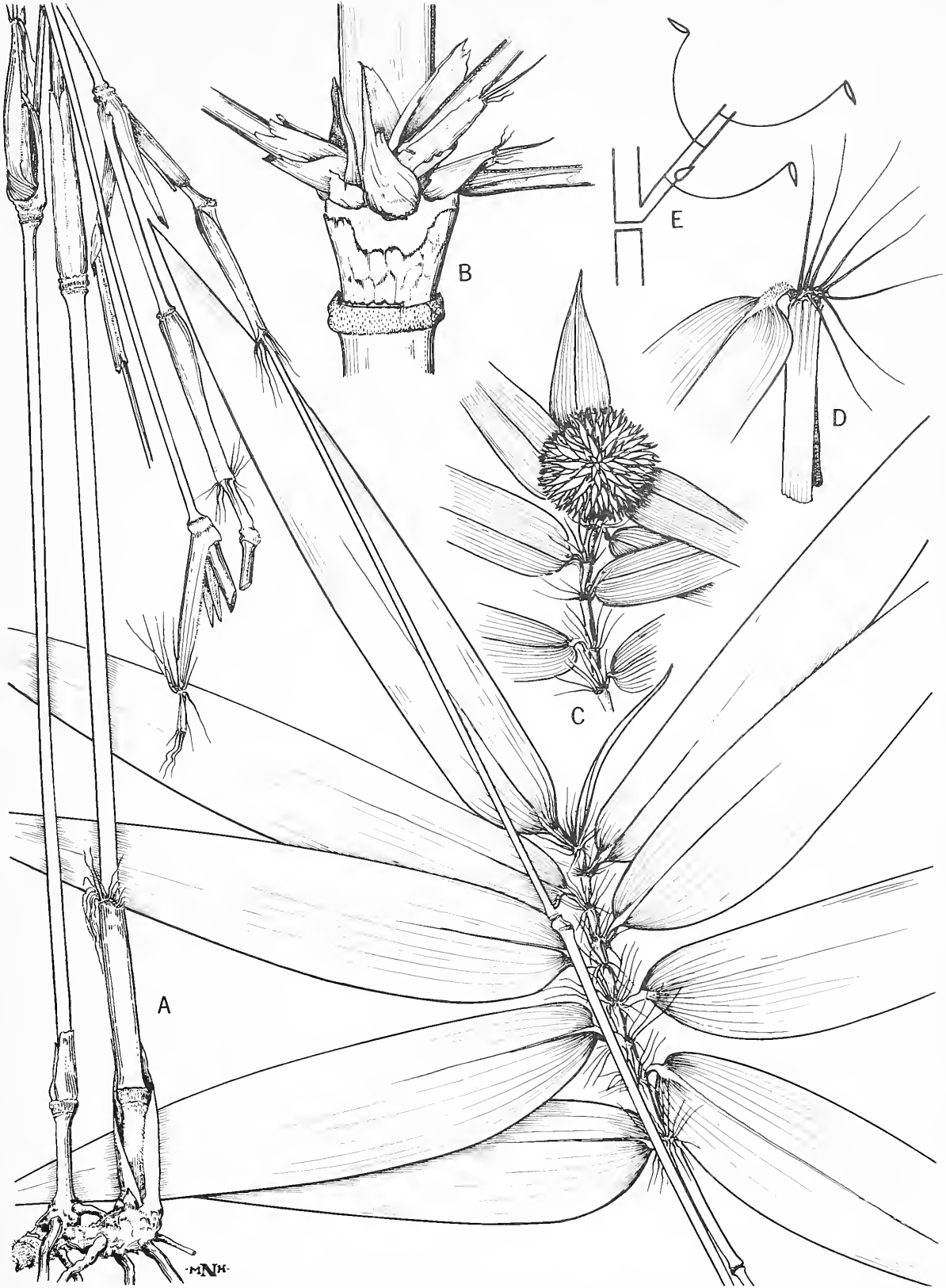
ETYMOLOGY.—The name *Atractantha* (f.) Greek *atraktos*, spindle, and *anthos*, flower, alludes to the spindle-like form of the anthercia.

TYPE-SPECIES.—*Atractantha radiata* McClure.

RELATIONSHIPS.—The obvious natural affinity of the known bamboos of the genus *Atractantha* is toward bamboos of the genus *Elytrostachys*, with which they share the following features: inflorescences are pseudospikelets 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 nodes that precede the elongated terminal segment of each rachis; each spikelet typically containing but a single perfect floret, which is followed by a rudiment of a sterile anthercium borne on the tip of a bristle-like prolongation of the rachilla. Insofar as currently available specimens inform us, bamboos of the genus *Atractantha* differ from bamboos of the genus *Elytrostachys* in the following respects: midculm branch complements containing several axes of primary order, each developed from one of several distinct initial branch primordia each with its own prophyllum; 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 anthercia; 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

FIGURE 19.—*Athroostachys capitata* (Hooker) Benth. A, Basal portion of young plant in the vegetative state, showing two culms and the rhizomes to which they are terminal,  $\times 0.6$ ; B, midculm node and branch complement showing three primary branches of independent origin, derived from the primordial meristem enclosed within the prophyllum of a solitary primary bud,  $\times 3$ ; c, tip of a leafy flowering branch with its terminal inflorescence,  $\times 0.6$ ; D, apex of leaf sheath which subtends a flowering branch and the base of its blade,  $\times 0.9$ ; E, base of a flowering branch (schematic). Drawing A based on *Glaziou 13325* (P), B, on *Weddell 152* (P), and c, D, E on *Glaziou 20155* (F).





MNH

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 *Atractantha* 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 *Atractantha*

- 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. *Atractantha falcata* McClure, new species

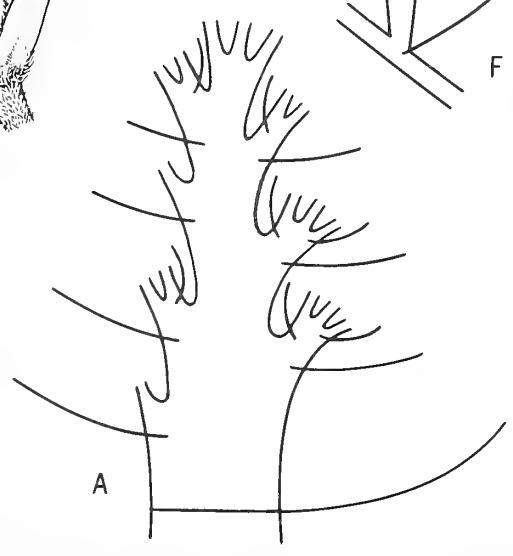
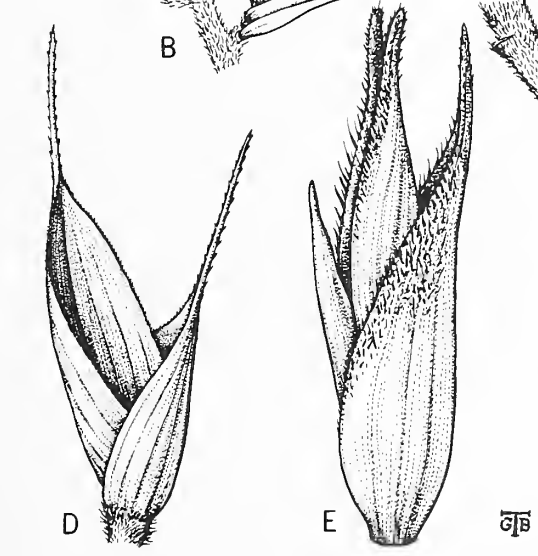
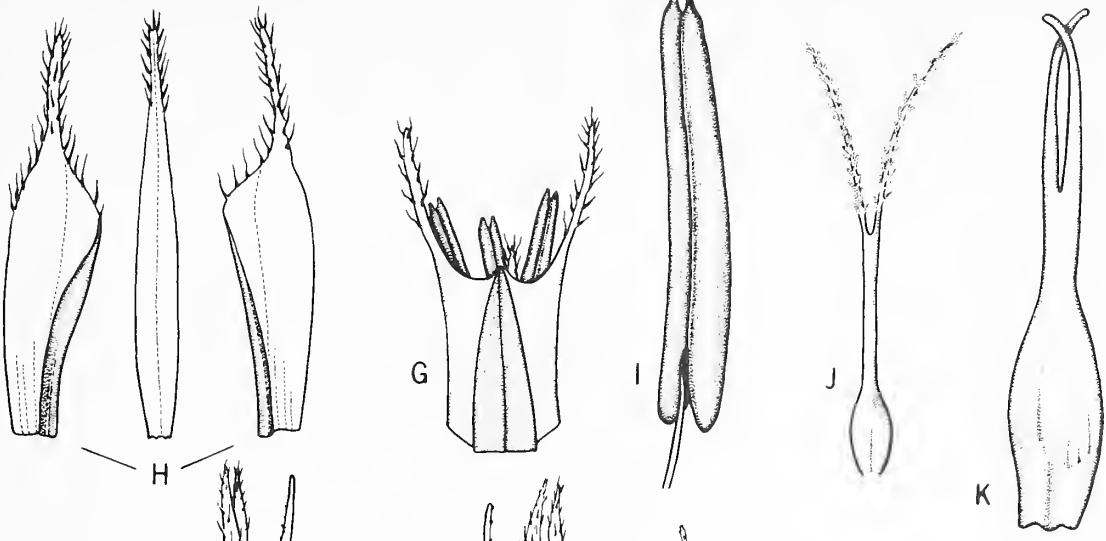
##### FIGURE 21

Plantarum habitus non adhuc relatus. Culmi in specimine suppetenti neque satis representati neque descripti, itaque ignoti. Vaginae culmi et vaginae ramorum primariorum in specimine 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 sparsissime et antrorse scaberulis, fragilissimis, vel mox vel postea effractis; ligula interiore subnulla, truncata; ligula exterior truncata, margine primo sparse et minutissime ciliolata denique glabrescenti integraque; petiolo vix 2 mm longo, pagina adaxiali hispidulo pagina abaxiali hirsuto; lamina usque 10.5 cm longa et 1.0 cm lata, lineari-lanceata, apice acuta, basi rotundata, basin versus utrinsecus sparse hirsuta, alibi utrinsecus primo antrorse hispidula, denique sensim glabrescenti; costa mediana et tribus paribus nervorum secundariorum pagina abaxiali sat prominulis; pagina adaxiali inter omnes nervos propinquos profunde et angustissime sulcata, prope marginem externam costa alata penitus instructa; venulis transversis extus haud manifestis.

Inflorescentiae ramos ramulosque vel foliigeros vel aphyllous terminantes, ob rhachidibus ramificationibus insertionis sympodialis falcatae diffusaeque. Bracteae e quoque rhachidi proditae

pleraeque 2, altera gemmam subtendenti altera vacua, approximatae, laminiferae, paucinerves, substantia indurata sed fragili, dorso sparsim puberulae. Spiculae usque 15 mm longae, maturitate cadentes; ubi unaquaque spicula delapsa relictum est segmentum terminale rhachidis a bractea persistenti fere omnino vestitum. Glumae transitionales nullae. Anthecia papyracea, glabra nitidaque, nervis extus vix vel haud manifestis. Lemma usque 15 mm longum, lanceatum, attenuate acuminatum. Palea lemmate brevior, secus margines sulci angustissimi antrorse ciliata. Lodiculae diaphanae, angustae, margine apicem versus sparsim ciliolatae. Antherae apice emarginatae, basi profunde divisae, ubi desiccatae brunneae. Ovarium vel omnino glabrum vel apice tantum hispidulum. Stylus antrorse hispidulus. Fructus maturus adhuc non visus.

FIGURE 20.—*Athroostachys capitata* (Hooker) Benth. 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,  $\times$  ca. 3; C, a secondary branch subtended by a bract and bearing a solitary spikelet,  $\times$  ca. 3; D, transitional glumes of a mature terminal spikelet,  $\times$  ca. 3; E, hermaphrodite floret and (at left) depauperate (sterile) antherium of a mature terminal spikelet,  $\times$  ca. 3; F, component structures of a secondary branch of the inflorescence (schematic); G, floral parts in immature state (gynoecium not visible),  $\times$  ca. 12; H, mature lodicule complement (the narrow symmetrical one is the posterior member),  $\times$  ca. 18; I, stamen,  $\times$  ca. 12; J, gynoecium, unmodified,  $\times$  ca. 12; K, gynoecium, immature fruit stage,  $\times$  ca. 12. All drawings based on *Glaziou 20155* (F).



गण

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 antrorsely scaberulous basally, very fragile, sooner or later broken off; the inner ligule truncate, not at all or barely exerted; the outer ligule truncate, sparsely ciliolate 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 antrorsely 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 subtending a bud, the other empty. Spikelets up to 15 mm long, falling away at maturity, each at length leaving the ca 5 mm long terminal segment of its rachis almost completely clothed in a persistent bract. Transitional glumes at the base of each spikelet none. Anthea 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. Lodicules 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 antrorsely hispidu-

lous apically. Style antrorsely 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).

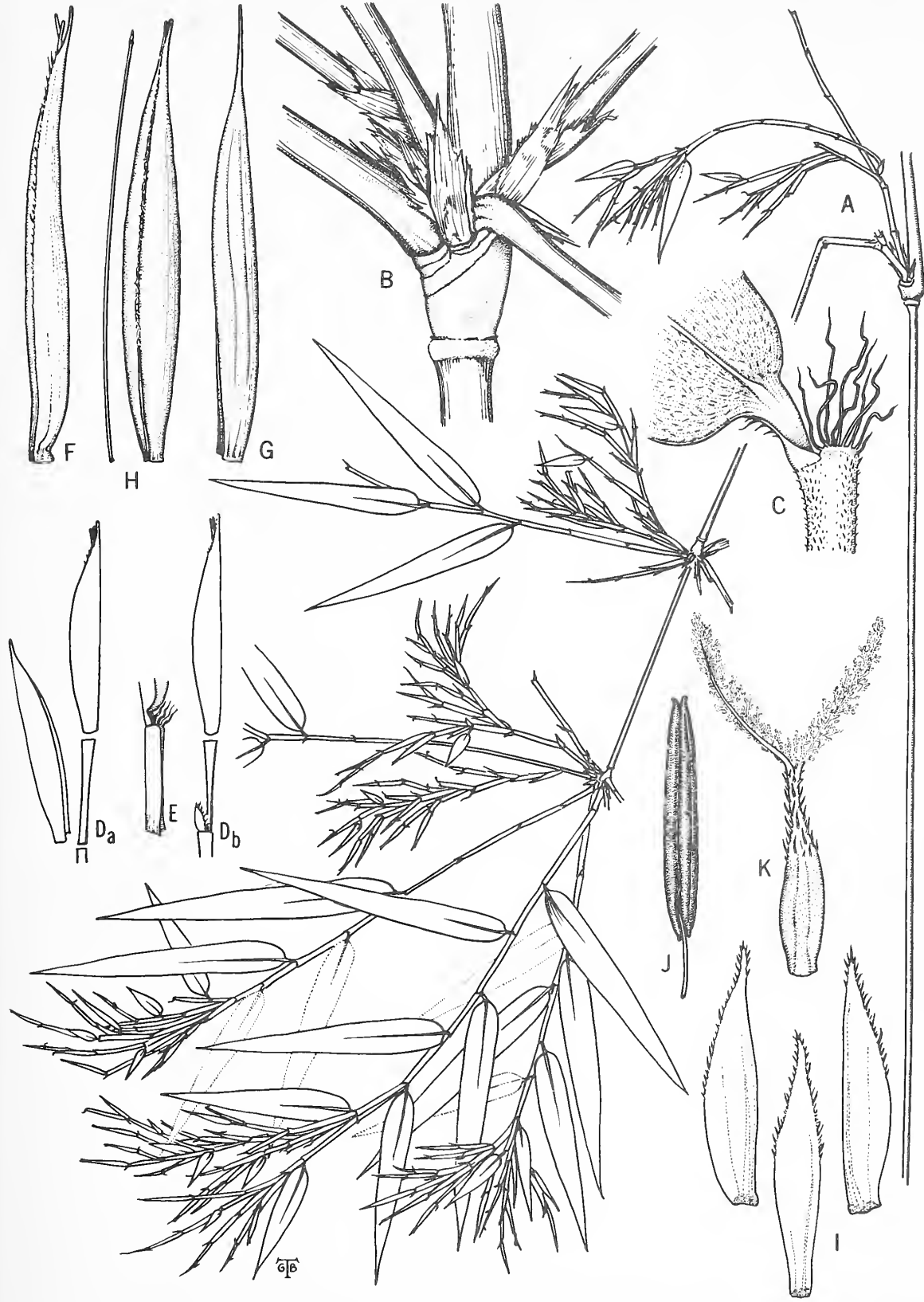
## 2. *Atractantha radiata* McClure, new species

FIGURES 22, 23

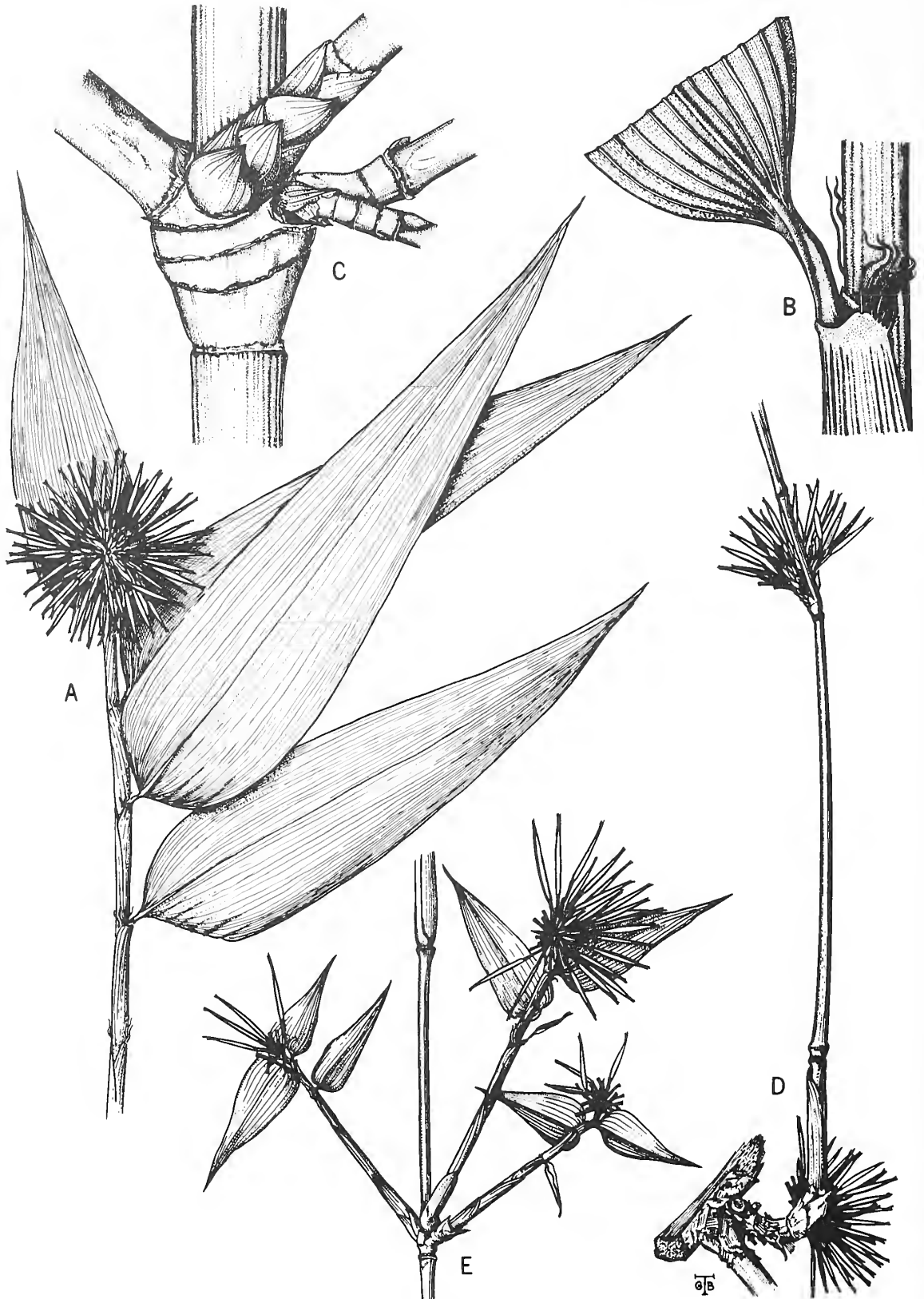
Plantarum habitus collectore neglectus. Culmi in specimine suppetenti neque satis representati neque descripti, ita ignoti. Vaginae culmi et vaginae ramorum primariorum in specimine suppetenti deficientes. Vagina foliorum arcta, dorso glabra, opaca, nervis vix aut haud manifestis; auriculis vel nullis vel ad lineam reductis; setis oralibus crebris, superne saltem anfractis, omnino glabris, propter substantiam fragilissimam mox effractis; ligula interiore 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, tertiariis a secundariis haud facile distinguendis, venulis transversis perpaucis inter se late distantibus.

Inflorescentiae capitatae, in ramis ramulisque 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,  $\times 0.6$ ; B, base of branch complement,  $\times$  ca. 3; C, apex of leaf sheath and base of leaf blade,  $\times$  ca. 6; D<sub>a</sub> and D<sub>b</sub> variations in structures forming terminal portion of a flowering twig, diagramatic; E, laminiferous bract from base of a branch of the inflorescence; F, floret,  $\times 6$ , G, lemma,  $\times 6$ ; H, palea (right) and prolongation of the rachilla (left),  $\times 6$ ; I, lodicule complement,  $\times 15$ ; J, stamen,  $\times 6$ ; K, gynoeccium,  $\times 30$ . All drawings based on *Pinto 0681* (US).



62



apice usque 1.0 mm diametro dilatatum, omnino glabrum laevigatum nitidumque. Bractee gemmam subtendentes in nodis basalibus omnis 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 apicaeque nuda. Glumae transitionales nullae. Anthechia papyracea, dorso glabra nitidaque, nervis extus haud 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. Antherae apice obtusae basi conspicue sagittatae, ubi desiccatae vinaceae. Ovarium 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 ciliate 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 veinlets few and far removed from each other.

Inflorescences capitate, terminal and lateral to leafy branches and leafy twigs, the branches (ra-

chises) 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. Anthechia 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 antrorse 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 Agrônomico do Norte, Belém, Pará, Brazil (IAN no. 15373).

### *Aulonemia* Goudot

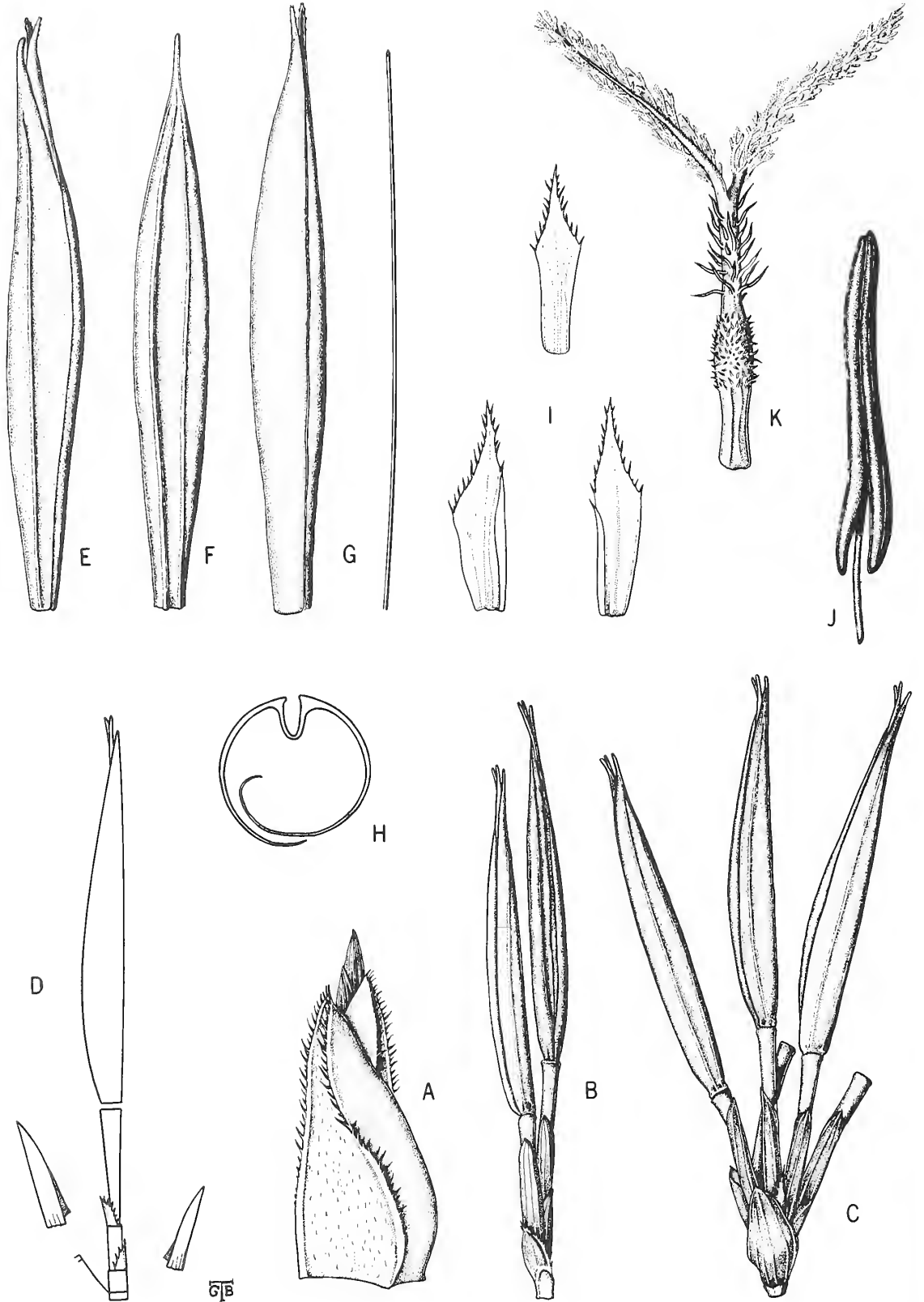
FIGURES 24–26

*Aulonemia* Goudot, 1846:75.

*Matudacalamus* Maekawa, 1961:344.

Plants unicespitate, 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

FIGURE 22.—*Atractantha radiata* McClure. A, Leafy flowering branch,  $\times 0.6$ ; B, apex of leaf sheath and base of leaf blade,  $\times 3$ ; C, base of branch complement,  $\times 4.8$ ; D, E, variants of flowering axes,  $\times 0.6$ . All drawings based on Fróes 19947 (US).





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 semelauclant, 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 antherium. 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 subfusiform, sulcate, apically mucronate 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 elongated culm internodes of plants of the type-species, and (2) the browse made accessible to herbivorous animals by the pendulous leafy culm 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 internode. This peculiarity—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-

FIGURE 23.—*Atractantha radiata* McClure. A, Primary pseudospikelet (early stage of development),  $\times 15$ ; B, two pseudospikelets, showing the prophyllum at the base of the one on the left,  $\times 3$ ; C, cluster of pseudospikelets, with two pedicels naked,  $\times 3$ ; D, diagram of a typical pseudospikelet; E, floret,  $\times 9$ ; F, lemma,  $\times 9$ ; G, palea (left) and prolongation of the rachilla (right),  $\times 9$ ; H, diagrammatic cross-section of palea,  $\times 18$ ; I, lodicule complement,  $\times 15$ ; J, stamen,  $\times 6$ ; K, gynoeceum,  $\times 15$ . All drawings based on Fróes 19947 (US).

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 *Colantheria 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; Venezuela, with three species at 1900–2760 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 Steyermark, 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.

*Siegingia 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.

*Arundinaria effusa* Hackel, 1903a:71.

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

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

*Arundinaria glaziovii* Hackel, 1903a:72.

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.

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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, gynoeceium,  $\times$  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 parviflora* (Presl) McClure, new combination.  
*Guadua parviflora*, J. S. Presl, in K. B. Presl, 1825–1835, I (4–5):257.  
*Bambusa parviflora* (Presl) J. A. and J. H. Schultes, in Roemer and Schultes, 1830, 7 (2):1350.  
*Arthrostylidium maculatum* Ruprecht, 1839:28.  
*Arundinaria maculata* (Ruprecht) Hackel, 1903a: 69.
13. *Aulonemia patula* (Pilger) McClure, new combination.  
*Arundinaria patula* Pilger, 1898:719.
14. *Aulonemia purpurata* (McClure) McClure, new combination.  
*Arthrostylidium purpuratum* McClure, 1942:170.
15. *Aulonemia queko* Goudot, 1846:76, pl. 4 (Figures 24–26).  
*Arthrostylidium queko* (Goudot) Hackel, in Engler and Prantl, 1887:93 [sphalm. quexo].  
*Arundinaria queko* (Goudot) Hackel, 1903a:74.

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 prickly-hairs 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 Quindío. I found no sign of either the original forest, or the bamboo described by Goudot as *Aulonemia queko*. The

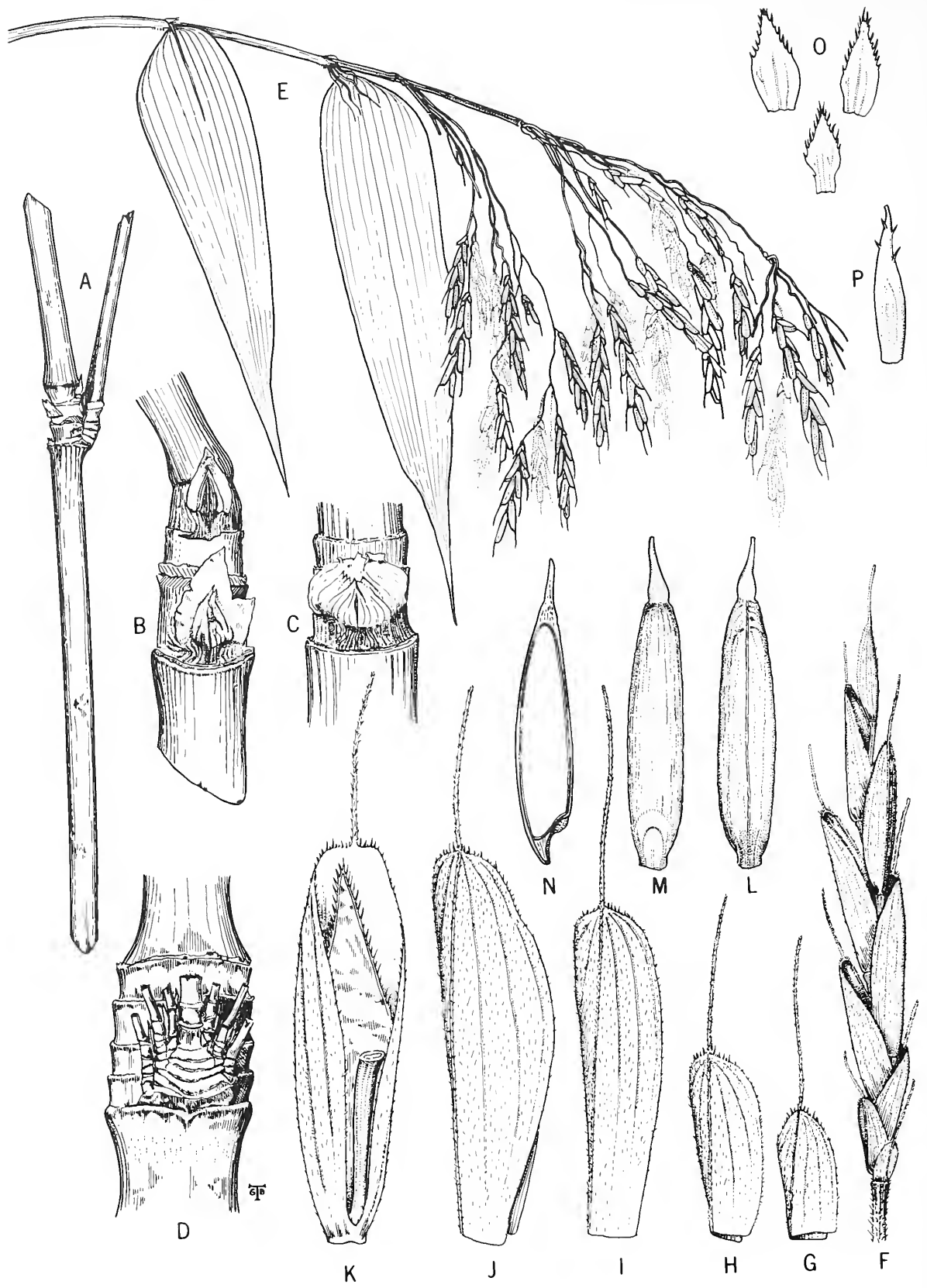
mountainside is clothed instead with a beautiful carpet of *Pennisetum clandestinum* Hochstetter ex Chiovanda, a grass native to Africa. I eventually decided that specimens of a plant I had collected in Ecuador (McClure 21429) and in Peru (McClure 21450) represent *Aulonemia queko*, in spite of minor 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 delimitation 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 (1839) broad circumscription of *Arthrostylidium*. Again, Hackel's (1903a) transfer of *Aulonemia 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 *Elytostachys* 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.  
*Arundinaria radiata* Ruprecht, 1839:25.
17. *Aulonemia ramosissima* (Hackel) McClure, new combination.  
*Arundinaria ramosissima* Hackel, 1903a:74.  
*Arundinaria glaziovii* var. *macroblephara* E.-G. Camus, 1913, I:41.
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, I: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* (Munro) McClure, new combination.

*Arundinaria trianae* Munro, 1868:25.

*Arundinaria multiflora* 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*

FIGURE 26.—*Aulonemia queko* Goudot. A, Upper culm nodes with buds and base of branch bud,  $\times 0.6$ ; B, buds enlarged,  $\times 1.2$ ; C, bud in advanced development,  $\times 1.2$ ; D, base of young branch complement,  $\times$  ca. 1.2; E, tip of leafy branch terminating in an inflorescence,  $\times 0.6$ ; F, spikelet,  $\times 2.4$ ; G, transitional glume I,  $\times 6$ ; H, transitional glume II,  $\times 6$ ; I, sterile lemma,  $\times 6$ ; J, fertile lemma,  $\times 6$ ; K, floret, showing palea,  $\times 6$ ; L, mature fruit (hilum side),  $\times$  ca. 15; M, mature fruit (embryo side),  $\times$  ca. 15; N, mature fruit, longitudinal section,  $\times$  ca. 15; O, lodicule complement,  $\times$  ca. 6; P, gynoeceum (without stigmas),  $\times$  ca. 6. All drawings based on McClure 21429 (US).

1. *Aulonemia cingulata*. See *Colanthesia cingulata*.

2. *Aulonemia intermedia*. See *Colanthesia intermedia*.

3. *Aulonemia lanciflora*. See *Colanthesia lanciflora*.

#### *Bambusa* Schreber, Subgenus *Guadua* (Kunth) Hackel

FIGURES 27–29

Genus *Guadua* Kunth, 1822a:150; 1822b:254.—Ruprecht, 1839:38 [1840:128].—Munro, 1868:70.—Doell, in Martius, 1880:176.—Bentham, in Bentham and Hooker, 1883:1210.—McClure, 1957:203.

*Bambusa* (*Guadua*) Nees, in Martius, 1829:532.

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

*Bambusa* (*Guadua*) Hackel, 1903c:194.

Plants typically unicespitate 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*) multifistular 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 iterant, 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 anthercia, or terminating abruptly in a single depauperate anthercium; 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 swalleniana*), the filaments filiform, free. Style terminating in 2 or 3 (rarely 4) stigmas or (exceptionally) undivided. Mature fruit an oblong or lagenoid, mucronate or subrostrate, in some species strongly dorsiventral caryopsis, the pericarp pergamineous or coriaceous, somewhat thickened apically, the sulcus and the basal position of the embryo clearly manifest.

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.

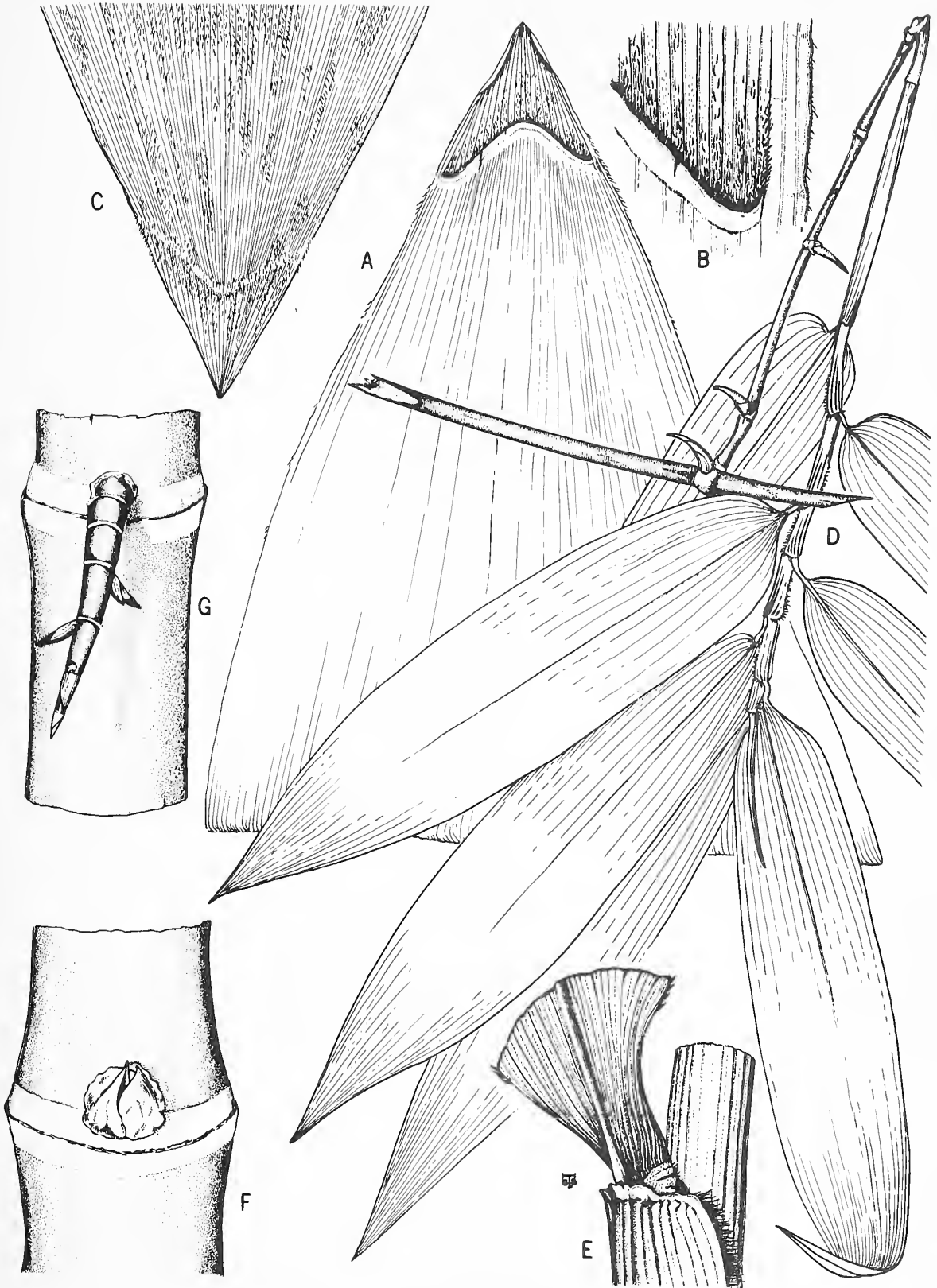
By 1829 Nees (in Martius, p. 532) had already made "*Guaduae*" an uncategorized division of the genus *Bambusa*. This proposal was more fully developed by Nees in *Linnaea* (1834:465).

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

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FIGURE 27.—*Bambusa guadua* Humboldt and Bonpland, sensu lato. A, culm sheath, adaxial aspect,  $\times 0.3$ ; B, same, detail at base of blade, enlarged; C, upper portion of culm sheath, abaxial aspect,  $\times 0.3$ ; D, portion of first-order branch bearing a leafy twig with thorns,  $\times 0.6$ ; E, apex of leaf sheath and base of blade,  $\times$  ca. 0.6; F, branch bud at culm node,  $\times$  ca. 0.6; G, short-shoot thorny branch at lower node of culm,  $\times$  ca. 0.6. Drawings A-D based on *Gutierrez and Barkley* 17 C 609 (US), and E-G on *Fosberg* 19831 (US).





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 475). 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, 1881:130.  
*Guadua aculeata* var. *liebmanniana* E.-G. Camus, 1913, I:112.

*Guadua inermis* Ruprecht ex Fournier, 1881:129.

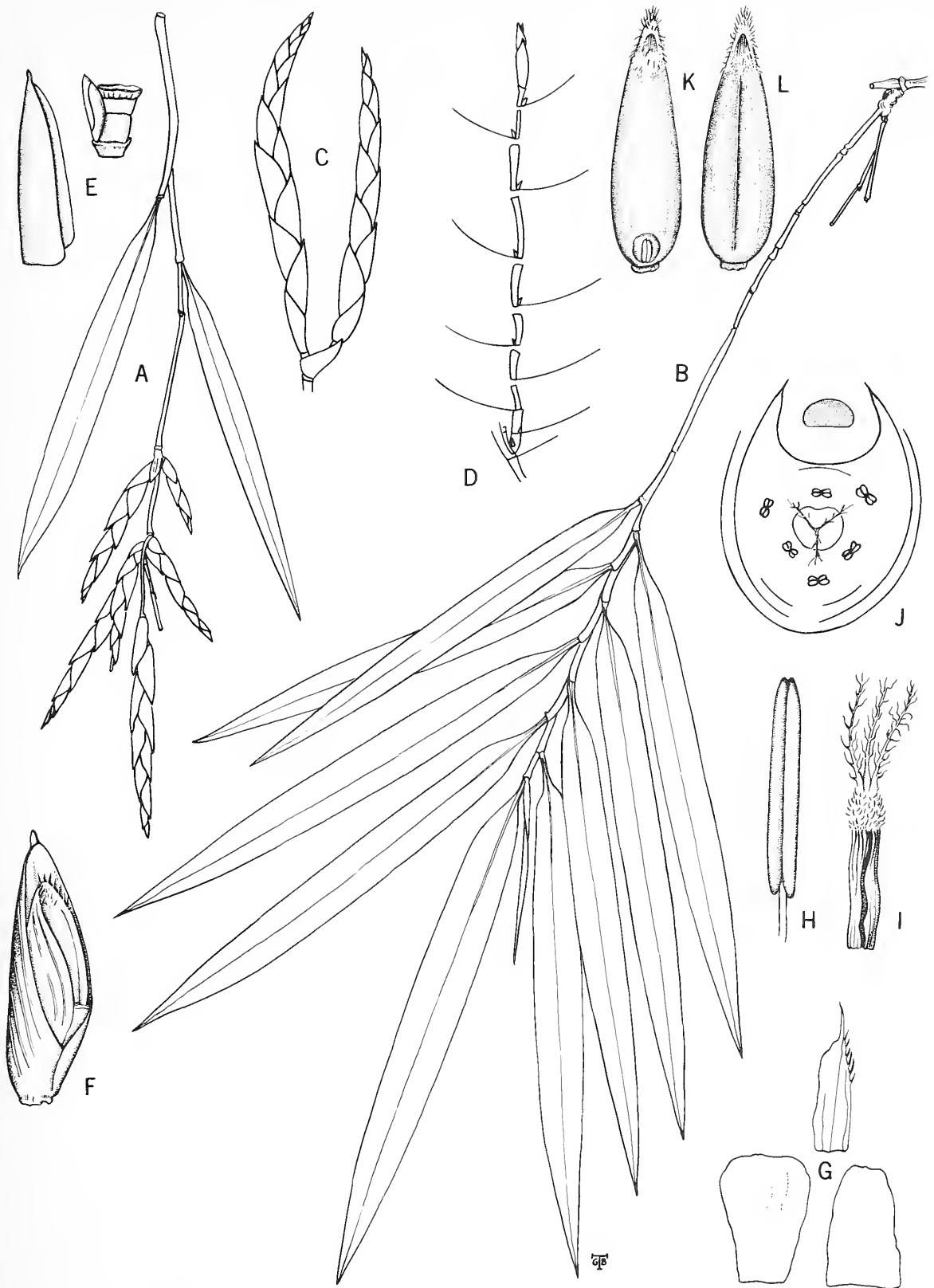
*Guadua intermedia* Ruprecht ex Fournier, 1881:130.

*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 lemmas 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 enveloppes 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 (1934:544ff; 1966b:100, 117) and Arber (1934:133). 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

FIGURE 28.—*Bambusa guadua* Humboldt and Bonpland (A-J) and *B. aculeata* Ruprecht ex Fournier (K-L). A, Leafy flowering twig,  $\times 0.6$ ; B, sterile leafy twig,  $\times 0.6$ ; C, pair of pseudospikelets,  $\times 1.2$ ; D, diagram of longitudinal section of pseudospikelet; E, bract and bud subtended by it at base of pseudospikelet,  $\times 1.8$ ; F, floret,  $\times 3$ ; G, lodicule complement,  $\times$  ca. 5.4; H, stamen,  $\times 6$ ; I, gynoeceium,  $\times$  ca. 6; J, diagram of cross-section of floret; K, fruit, embryo side,  $\times$  ca. 6; L, fruit, hilum side,  $\times$  ca. 6. Drawing A based on *Cobin 1167* (US), B-J on *McClure 21228* (US), and K, L on *McClure 21556-A* (US).



changes in sexual expression that become potential during the later stages of the ontogeny of indeterminate (iterarctant) 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 *Guadua*) for Brazilian collections of this species.

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

*Guadua distorta* (Nees) Ruprecht, 1839:131, pl. 16; fig. 59.

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

*Guadua glaziovii* (Hackel) E.-G. Camus [as *glaziowii*], 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 synonym 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.

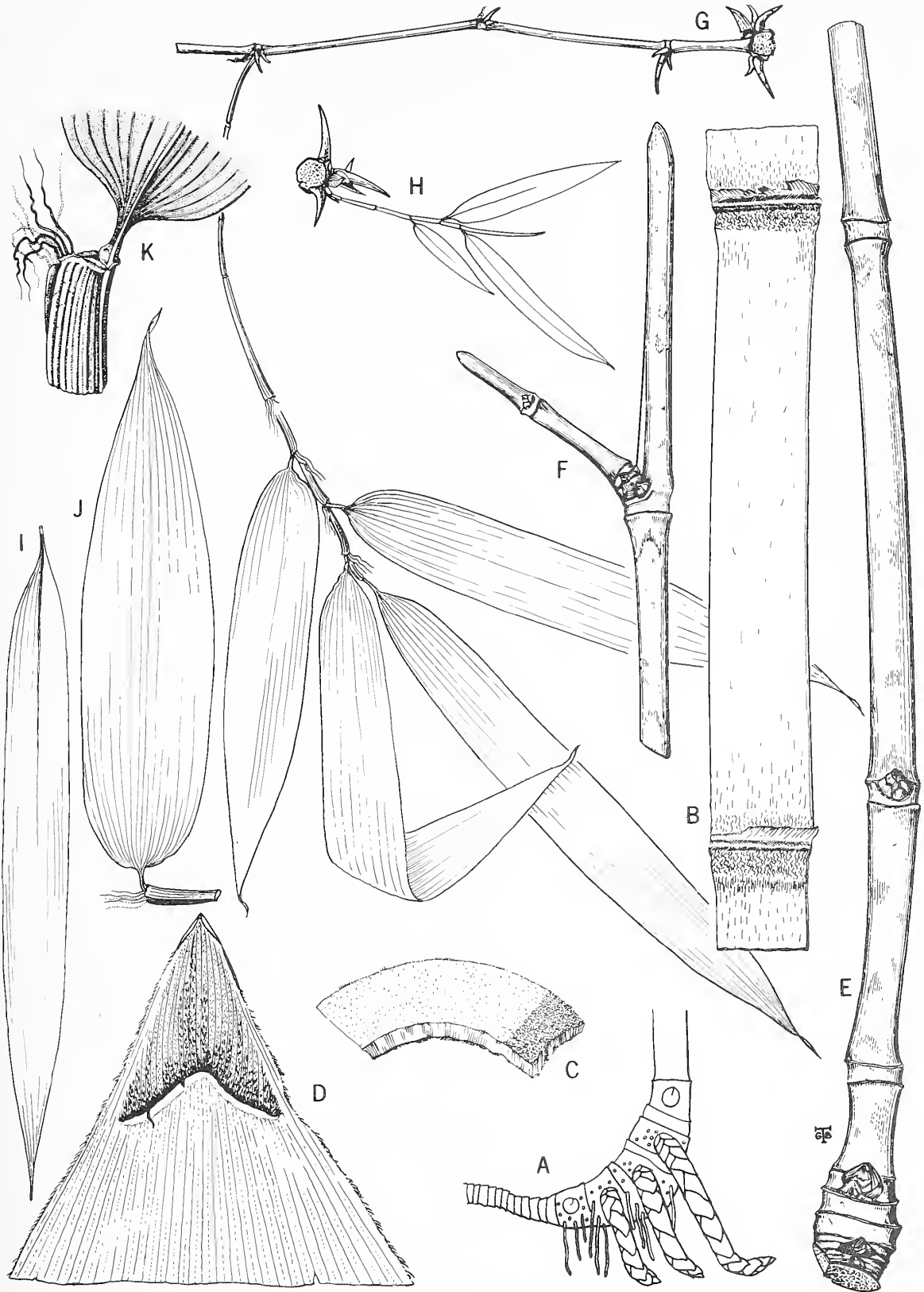
*Guadua longifimbriata* E.-G. Camus, 1913, I:113.

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

FIGURE 29.—*Bambusa guadua* Humboldt and Bonpland, sensu lato. A, Base of culm with its rhizome and the precociously developed necks that help the root system support the culm, which may be as much as 37 meters tall and 20 cm in diameter,  $\times ca. 0.06$ ; B, tangential slice from internode and nodes v and vi of a culm ca. 3.5 cm in diameter,  $\times 0.6$ ; C, sector of cross-section of culm wall at internode iv,  $\times 0.6$ ; D, apex of culm sheath, adaxial aspect,  $\times 0.6$ ; E, basal part of first-order branch from midculm node, with buds still intact,  $\times ca. 0.6$ ; F, second-order branch with buds still intact,  $\times ca. 0.6$ ; G, third-order branch showing spines and foliage,  $\times ca. 0.6$ ; H, thorn complement with leafy twig arising from proximal node of thorn,  $\times ca. 0.6$ ; I, J, examples of extreme forms of leaves,  $\times ca. 0.6$ ; K, apex of leaf sheath and base of blade, enlarged. Drawings A, B based on McClure 21232 (US) and C-K on McClure 21215 (US).



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, 1839:39, pl. 15: fig. 35.

*Guadua dioica* Steudel, 1854:334, teste Doell, in Martius, 1880:182.

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.

*Bambusa munroi* Hackel, 1909b:374.

Non invalidatus by *Bambusa paniculata* Willdenow ex Munro (1868:123) [nom. nud. ex sched.] as synonym of *Nastus borbonicus* Gmelin (cf. ICBN 1966, Art. 64).

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; I:112.

18. *Bambusa superba* (Huber) McClure, new combination.

*Guadua superba* Huber, 1904:479.

19. *Bambusa swalleniana* McClure, new name.

*Guadua spinosa* (Swallen) McClure, 1954:82 (not

*Bambusa spinosa* Roxburgh, 1832:198.)

*Arthrostylidium spinosum* Swallen, 1938:6.

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.

*Guadua trinii* var.  $\beta$  *scabra* Doell, in Martius, 1880:179.

*Bambusa tacuara* Arechavaleta, 1897:550, pl. 72; teste Parodi, 1936:239.

24. *Bambusa riograndensis* Dutra, 1938:147, fig. 1.

*Guadua riograndensis* (Dutra) Herter, 1941:49.

*Guadua ribbentropii* Herter, 1940:148 (based on *Bambusa tacuara* Arechavaleta).

25. *Bambusa venezuelae* (Munro) McClure, new combination.

*Guadua venezuelae* Munro, 1868:86.

26. *Bambusa virgata* Trinius, 1835:624.

*Guadua virgata* (Trinius) Ruprecht, 1839:40.

27. *Bambusa weberbaueri* (Pilger) McClure, new combination.

*Guadua weberbaueri* Pilger, 1905:152.

#### OLD WORLD BAMBOOS

28. *Bambusa philippinensis* (Gamble) McClure, new combination.

*Guadua philippinensis* Gamble, 1913:203.

#### 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:I113.

*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 *Yushmaniam* 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 tuldoidea* Munro (1868:93), an Old World species naturalized in Brazil.
4. *Guadua parviflora* J.S. Presl (in K. B. Presl, 1830:257). See *Aulonemia parviflora* (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.—Arechavaleta, 1897:542.—McClure, in Swallen, 1955:86; 1957:202.

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

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

Plants of unicespitate or multicespitate 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 capitate; 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 (–5, as sometimes in *C. bambusaeoides*): i and ii “empty glumes” (these in some species subobsolete), 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 (1834:493); specimens under McClure 21292 (*C. oxylepis* (Hackel) Ekman) commonly show an aborted floret in the axil of transitional glume iv (“sterile lemma” ii)—the rachilla

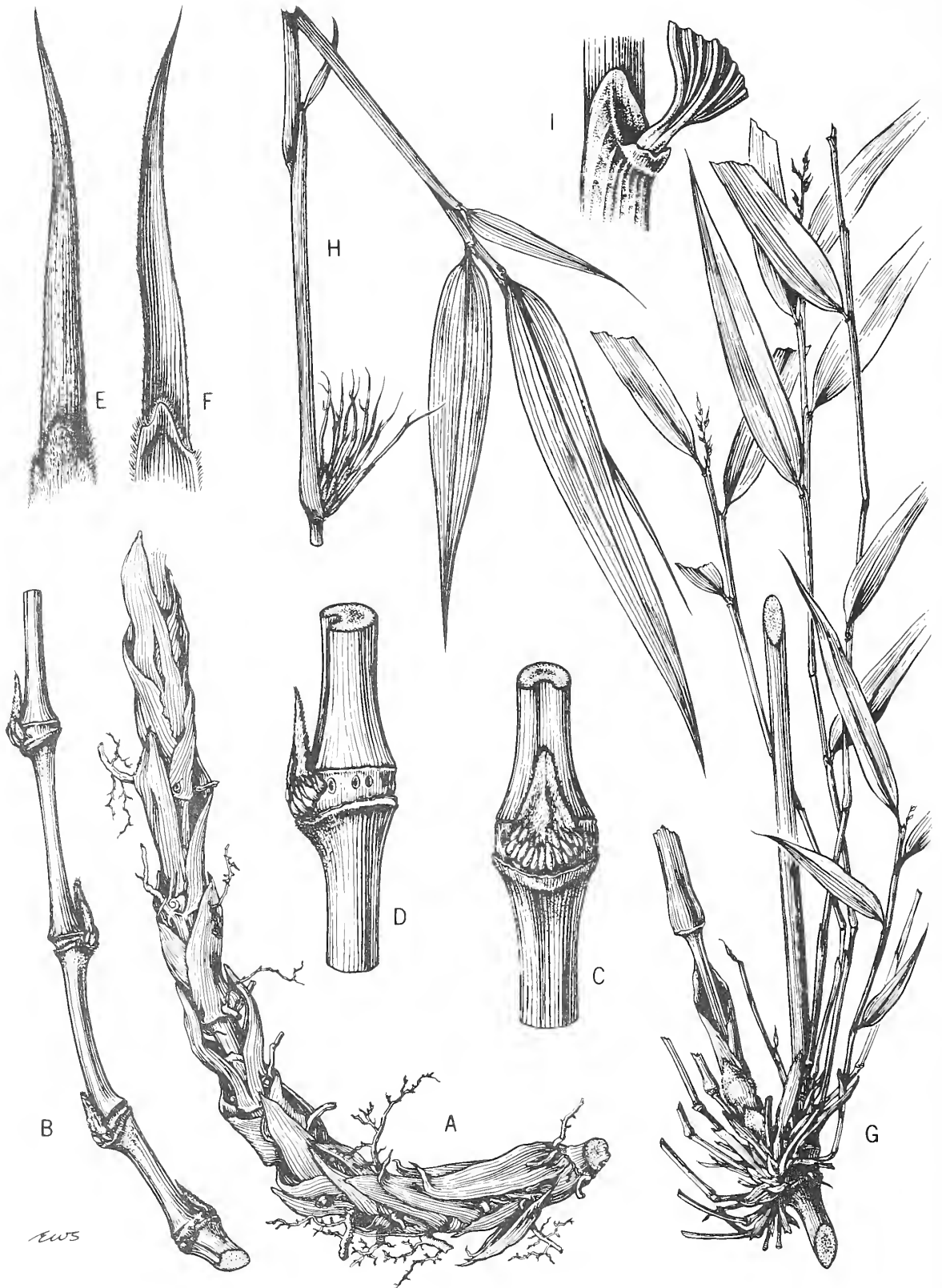




FIGURE 30.—*Chusquea scandens* Kunth. A, Leptomorph rhizome turning up to form a culm,  $\times 0.6$ ; B, lower segment of a small culm with buds,  $\times 0.6$ ; C, midculm node showing complement of branch buds, front view,  $\times 1.2$ ; D, same, in profile,  $\times 1.2$ ; E, apex of culm sheath, abaxial view,  $\times 1.2$ ; F, apex of culm sheath, adaxial view, showing ligule; G, midculm node with fully developed branch complement,  $\times 0.6$ ; H, auxiliary branch, showing leaves at apex, branch sheath, and a complement of branches emerging extravaginally,  $\times 0.6$ ; I, apex of leaf sheath with petiole and base of leaf blade,  $\times 12$ . All drawings based on *McClure 21414* (US).

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 cuspidulate or bicorniculate caryopsis with a pergamineous pericarp of uniform thickness, the sulcus and the embryotegium showing different degrees of conspicuousness in different species.

ETYMOLOGY.—The name *Chusquea* is the Latinized version of a vernacular term used by aboriginal natives of Ecuador and Colombia to designate plants of this genus.

TYPE-SPECIES.—*Chusquea scandens* Kunth (1822b: 254); *Nastus chusque* Humboldt, Bonpland, and Kunth (1816, I:201).

RELATIONSHIPS.—Although all members of the genus *Neurolepis* share a spikelet structure (Figure 41 C-L, N) that is basically similar to that universal in *Chusquea*, members of the latter genus diverge

conspicuously from *Neurolepis* by their bambusoid, deciduous leaf blades, their branched culms with fistulose internodes, and their more prominently developed rhizomes.

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) leptomorph 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) *Platonina* (Kunth) with *C. (Platonina) 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 *Platonina* Kunth (non *Platonina* Martius) was restored by Meisner

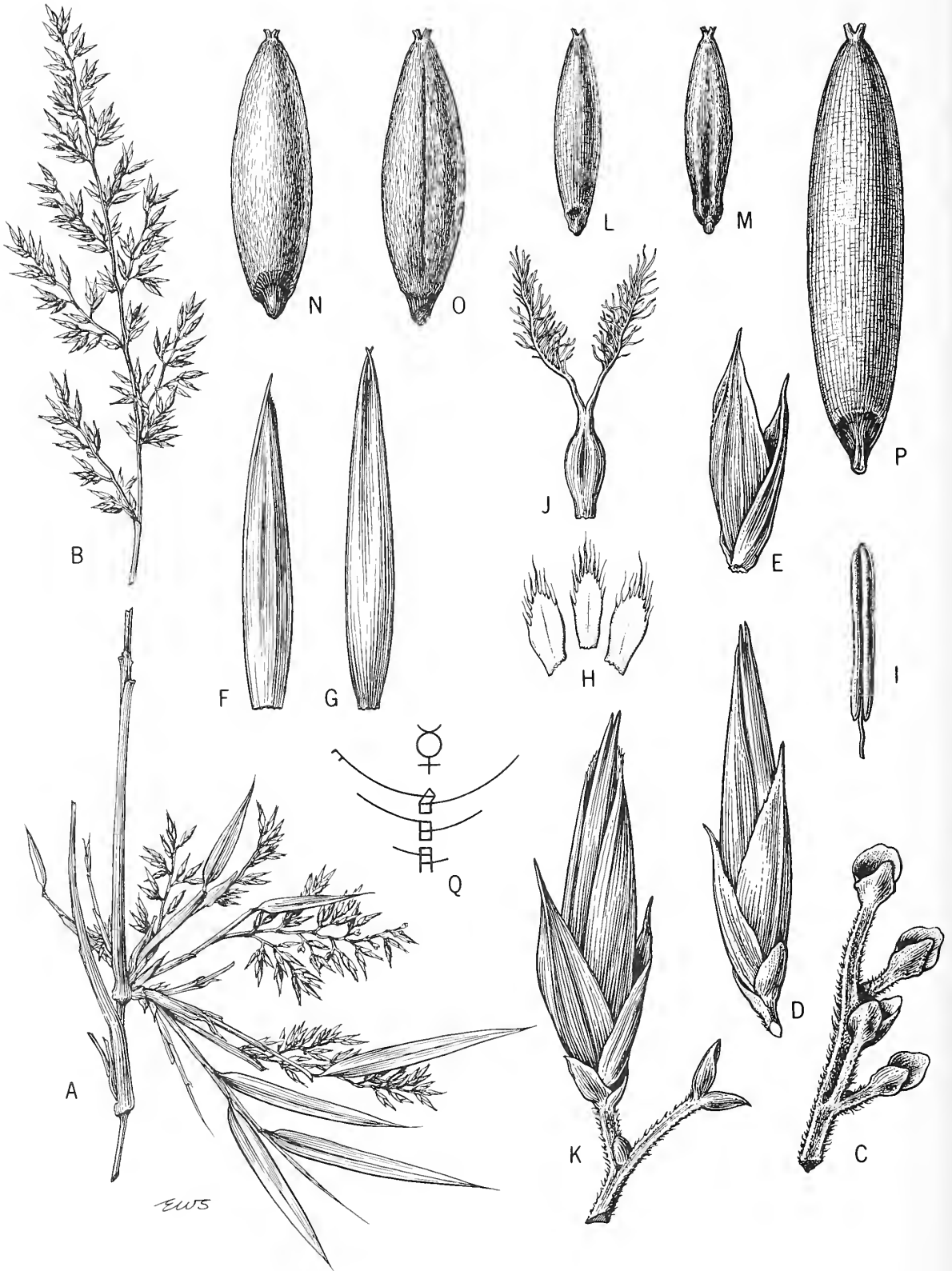


FIGURE 31.—*Chusquea scandens* Kunth (A-M) and *C. oxylepis* (Hackel) Ekman (N-P). A, Leafy flowering complement of branches of secondary order,  $\times 0.6$ ; B, inflorescence terminating a primary branch,  $\times 0.6$ ; C, terminal ramifications of inflorescence with persistent transitional glumes ("empty glumes" I and II),  $\times 7.5$ ; D, spikelet with its pedicel,  $\times 7.5$ ; E, transitional glumes III and IV ("sterile lemmas"),  $\times 7.5$ ; F, lemma,  $\times 7.5$ ; G, palea,  $\times 7.5$ ; H, lodicule complement,  $\times 9$ ; I, stamen,  $\times 7.5$ ; J, gynoeceum,  $\times 9$ ; K, terminal branches of inflorescence,  $\times 7.5$ ; L, fruit, embryo side,  $\times 7.5$ ; M, fruit, hilum side,  $\times 7.5$ ; N, fruit, embryo side,  $\times 7.5$ ; O, fruit, hilum side,  $\times 7.5$ ; P, fruit, embryo side,  $\times 7.5$ ; Q, diagram of spikelet. Drawing A-J based on McClure 2144 (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 *Rettbergia* as a monotypic genus. As observed by Nees (in Martius, 1829:536) a number of the features attributed to the type-species of *Rettbergia* 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, 1880:198)—that the type-species of *Rettbergia* does not fall outside the natural boundaries of the genus *Chusquea*. However, the trivial name of the type-species of *Rettbergia* (*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. baculifera* Alvaro da Silveira (1919:99), *C. heterophylla* Nees (1835:488) 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 laMontaña"); 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  
Bamboos 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 undesigned. Pilger's uncertainty as to the correct generic disposition of this taxon is patent.

2. *Chusquea acuminata* Doell, in Martius, 1880:204.  
*Chusquea tenuis* Glaziou ex E.-G. Camus, 1913, I:90.
3. *Chusquea affinis* Munro ex E.-G. Camus, 1913, I:80, pl. 60: fig. B.
4. *Chusquea andina* R. A. Philippi, 1858:103.  
[In rough notes McClure compares this species with *Chusquea culeou* Desvaux, perhaps indicating that it is synonymous with it. Munro (1868:58-59) expressed the opinion that this species is very probably only an alpine form of *C. culeou*.—T.R.S.]
5. *Chusquea anelythra* Nees, 1834:491.
6. *Chusquea anelytroides* Ruprecht ex Doell, in Martius, 1880:206.
7. *Chusquea argentina* Parodi, 1941:339, pl. 24: fig. 4.
8. *Chusquea bambusoides* (Raddi) Hackel, in Wettstein, ed., 1908:81.  
*Rettbergia bambusaeoides* Raddi, 1823:18, 57, pl. 1: fig. 1.  
*Chusquea gaudichaudii* Kunth, 1829:138. Nomen nudum.  
*Chusquea gaudichaudii* Kunth, 1830:331-332, pl. 78.
9. *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.
10. *Chusquea bambusoides* var. *minor* McClure and Smith, in Reitz, ed., 1967:25.
11. *Chusquea bilimekii* Fournier, 1881:132.
12. *Chusquea capitata* Nees, 1834:489.  
*Rettbergia capitata* Nees was cited as a synonym of *C. capitata* in Munro (1868:69) and Doell (in Martius, 1880:196). Nees had regarded *Rettbergia* as synonymous with *Chusquea* and published the species as *C. [R(ettbergia)] capitata*.
13. *Chusquea capituliflora* Trinius, 1835:613.  
The spikelets sometimes contain two florets in this species.
14. *Chusquea capituliflora* var. *pubescens* McClure and Smith, in Reitz, ed., 1967:28.
15. *Chusquea carinata* Fournier, 1881:132.
16. *Chusquea culeou* Desvaux, in Gay, 1854:450.

16. *Chusquea culeou* forma *longiramea* Parodi, 1941:343.
17. *Chusquea cumingii* Nees, 1835:487.  
*Chusquea parvifolia* R. A. Philippi, 1864:299.
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 dombeyana* 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. ligulata* Munro.]
26. *Chusquea galeottiana* Ruprecht ex Munro, 1868:59.
- Chusquea galeottiana* Ruprecht, in Galeotti, 1842:246. Nomen nudum.
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.  
*Chusquea pilgeri* E. -G. Camus, 1913, I:83. [Type cited as "*C. leibmanni* [sic!] Pilger . . . non Fournier," error for *C. lehmannii* Pilger which is valid, as is *C. liebmannii* Fournier.]
36. *Chusquea leptophylla* Nees 1835:489.  
*Arthrostylidium trinii* sensu Steudel, 1854:336, in part, non Ruprecht, 1839:119.  
*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 (3): 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 31N-P).  
*Chusquea bambusoides* (Raddi) Hackel subsp. *oxylepis* Hackel, in Wettstein, ed., 1908:81-82.
53. *Chusquea palenae* R. A. Philippi, 1896:350.
54. *Chusquea pallida* Munro, 1868:65.
55. *Chusquea parviflora* R. A. Philippi, 1896:349-350.
56. *Chusquea perligulata* (Pilger) McClure, new combination.  
*Guadua* (?) *perligulata* Pilger, in Diels, 1937:57-58.
57. *Chusquea peruviana* E. -G. Camus, 1913, I:88.  
*Chusquea ramosissima* Pilger, 1905:145, not Lindman 1900:24.
- Chusquea sandiensis* Pilger, 1920:29.
58. *Chusquea picta* Pilger, 1905:151.
59. *Chusquea pinifolia* (Nees) Nees, 1834:490.  
*Arundinaria pinifolia* Nees, in Martius, 1829:525.  
? *Ludolfia pinifolia* (Nees) A. Dietrich, 1833, II:25.  
*Chusquea heterophylla* Nees, 1834:488.  
*Chusquea heterophylla* var. *elongata* Doell, in Martius, 1880:207.  
*Chusquea heterophylla* var. *microphylla* Doell, in Martius, 1880:207.  
*Chusquea heterophylla* var. *squamosa* Doell, in Martius, 1880:207.  
*Chusquea pinifolia* var. *heterophylla* (Nees) Hackel, in Wettstein, ed., 1908 [1906:21].
60. *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 pubescens* Steudel, 1854:337.
63. *Chusquea pubispicula* Pilger, 1905:148-149.
64. *Chusquea purdieana* Munro, 1868:56.
65. *Chusquea quila* Kunth, 1830:329-330, pl. 77. *Nastus prolifer* Desvaux, 1831:211. *Coliquea quila* Steudel, in Bibra, 1853:115. *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, 1854:337. *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 sclerophylla* Doell, 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* Ernst, 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. *subcylindrica* 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, 1868:63.

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 simplissima*. 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 *Arthrostyloidium venezuelae*.
12. *Chusquea weberbaueri*. See *Swallenochloa weberbaueri*.

#### Invalid Species of *Chusquea*

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

#### *Colantheia* McClure and E. W. Smith, new genus

FIGURE 32

Plantae unicespitosae, inermes. Rhizomata pachymorpha. Culmi habitu staturaque late diversi, aut parum alti et erecti vel "decumbentes" (teste Hackelii sub *Arundinaria rhizantha*) aut "altissimi scandentes" (teste Trinii sub *Arundinaria distans*), nodis valde elevatis et anguste cristatis, nodo medio unoquoque juventute gemmam solitariam gerenti, prophylo gemmae et gemma ipsa in germinatione simul elongatis. Ramorum complementum ad nodos culmorum medianos axem ordinis primarii solitarium continens, idem basi vulgo mox proliferatum, ramis ordinis superioris axem primarium plus minusve valde superantibus. Vaginae internodia culmorum foventes basi cingulis latis post delapsam vaginarum persistentibus praeditae. Foliorum laminae venulae transversae extra vulga haud manifestae.

Inflorescentiae semelauctantes, in speciebus plerisque vel infirme paniculatae vel racemosae, formis intermediis variis in ipsa planta interdum praesentibus; prophylla omnino haud ulla, bracteis dempta infima vel parvis vel obsoletis.

Glumae transitionales vulgo 2, rarissime vel 1 vel 3. Spiculae raro pauciflorae (ut in *Colantheia lanciflora*) pleraeque pluriflorae, angustissimae et fragilissimae, apice in anthecio sterili plus minusve valde depauperato terminantes. Lemma fertile in maturitate paleam suam basi tantum circumplectans. Palea dorso 2-carinata et late sulcata, marginibus vix vel haud imbricatis. Rachillae segmenta ob fragilitas articulorum (nodorum) suorum in maturitate facilissime disarticulantia. Lodiculae

typice 3, duae anticae plus minusve asymmetricae atque geminatae, postica symmetrica et vulgo minore. Stamina 3, filamentis filiformibus liberisque. Stigmata 2. Fructus non adhuc suppetens.

Plants unicespitosae, unarmed. Rhizomes pachymorph. 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 prophyllum 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 transverse 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 typically 2, rarely 1 or 3. Spikelets usually pedicellate, typically many-flowered (few-flowered in *Colantheia 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 typically 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 *Colantheia* (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 noticeably to strongly manifested tendency toward a progressive reduction of the reproductive structures from weak panicles to simple racemes and, in some cases, even from whole flowering branches all the way to little more than solitary spikelets.







FIGURE 32.—*Colantheia cingulata* (McClure and L. B. Smith) McClure. A, Rhizome and culm bases,  $\times 0.6$ ; B, branch complement from midculm range, in flowering state,  $\times 1.2$ ; C, culm sheath from above midculm range, with developing branch complement,  $\times 0.9$ ; D, apex of leaf sheath and base of leaf blade,  $\times 7.2$ ; E, paniculate inflorescence terminating a leafy flowering branch,  $\times 0.6$ ; F, progressively depauperate leafy and leafless flowering branches,  $\times 0.6$ ; G, flowering branch terminating in an inflorescence with mixed paniculate and racemose branching,  $\times 0.6$ ; H, spikelet with its pulvinate pedicel,  $\times 2.4$ ; I, transitional glumes,  $\times 6$ ; J, floret,  $\times 6$ ; K, lamina,  $\times 6$ ; L, palea,  $\times 6$ ; M, lodicule complement,  $\times 12$ ; N, stamen,  $\times 6$ ; O, gynoeceum,  $\times 12$ . Drawings A-E, G-O based on Reitz and Klein 9679 (US), and F on Dusén 18011 (US).

TYPE-SPECIES.—*Colantheia 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 *Colantheia* 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 *Arthrostyloidium*. 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 *Colantheia*, 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 *Colantheia* (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 *Colantheia lanciflora*, all known mem-

bers 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 *Colantheia* 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 *Colantheia 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 *Colantheia*

1. *Colantheia burchellii* (Munro) McClure, new combination.  
*Arthrostyloidium burchellii* Munro, 1868:43.  
*Arundinaria burchellii* (Munro) Hackel, 1903a:69.
2. *Colantheia cingulata* (McClure and L. B. Smith) McClure, new combination (Figure 32).  
*Aulonemia cingulata* McClure and L. B. Smith, in Reitz, ed., 1967:50.
3. *Colantheia distans* (Trinius) McClure, new combination.  
*Arundinaria distans* Trinius, 1835:621.  
Trinius (1836, III:622) states, incorrectly, that a terminal rudiment is lacking in *Arundinaria distans* Trinius, q.v.
4. *Colantheia intermedia* (McClure and L. B. Smith) McClure, new combination.  
*Aulonemia intermedia* McClure and L. B. Smith, in Reitz, ed., 1967:52.
5. *Colantheia lanciflora* (McClure and L. B. Smith) McClure, new combination.  
*Aulonemia lanciflora* McClure and L. B. Smith, in Reitz, ed., 1967:47.
6. *Colantheia macrostachya* (Nees) McClure, new combination. *Arundinaria macrostachya* Nees, 1834:481.
7. *Colantheia rhizantha* (Hackel) McClure, new combination. *Arundinaria rhizantha* Hackel, 1909a:323.

#### *Elytrotachys* McClure

FIGURES 33-35

*Elytrotachys* 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 gremial insertion, unrestricted monoclade, 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 veinlets not at all or only weakly manifest externally; oral setae few, rigid, erect or spreading, slender except at the bulbous base, scabrous.

Inflorescences itercaucant, 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 on which the empty bracts are inserted serves as the pedicel of the spikelet that is terminal to it. Having noted this, we can confirm the lack of empty glumes by recalling that the natural loci of their insertion would be found immediately preceding, and close to, that of the first lemma.] Spikelets each made pedicellate by the segment of the rachis it terminates, and each typically containing but a single perfect flower (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 *elytro* (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,  $\times 0.6$ ; B, culm sheath at midculm node of young culm shoot,  $\times 0.6$ ; C, midculm node and basal part of a typical branch complement,  $\times 0.6$ ; D, leafy twig with terminal inflorescence,  $\times 0.6$ ; E, two nodes from upper part of leafless flowering culm,  $\times 0.6$ . All drawings based on McClure 21478 (US).



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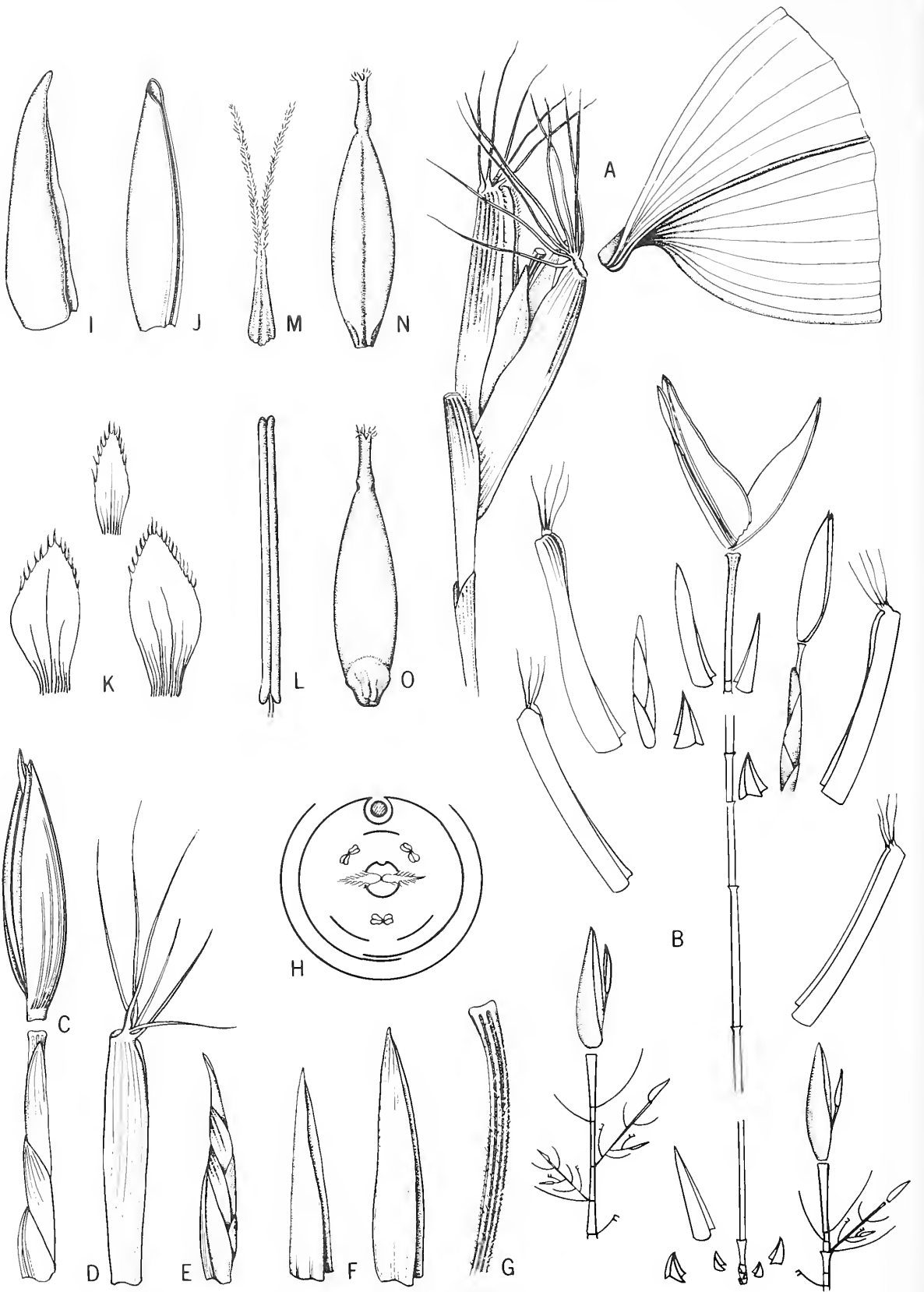


FIGURE 34.—*Elytostachys clavigera* McClure. A, Leafy twig with pseudospikelet after the leaf blades and the first spikelet have fallen away,  $\times 1.5$ ; B, diagrammatic array of the parts of a flowering branch, showing pseudospikelets in various stages of development; C, pseudospikelet with the terminal spikelet mature and disarticulated,  $\times 1.5$ ; D, laminiferous bract (blade lacking) that subtended a young pseudospikelet,  $\times 1.5$ ; E, young pseudospikelet; F, transitional glumes,  $\times 1.5$ ; G, pedicel of the one-flowered spikelet,  $\times 1.5$ ; H, diagram of cross-section of a floret; I, lemma, lateral aspect,  $\times 1.5$ ; J, palea, lateral aspect,  $\times 1.5$ ; K, lodicule complement,  $\times 3$ ; L, stamen,  $\times 3$ ; M, gynoeccium,  $\times 3$ ; N, mature fruit, hilum side showing sulcus,  $\times 1.5$ ; O, mature fruit, embryo side showing embryotegium,  $\times 1.5$ . All drawings based on McClure 21478 (US). For detailed caption for B, see McClure, 1942:178, fig. 6.

and oral setae of leaf sheaths not only much more conspicuously developed, but of different morphological configuration; in the presence of at least two empty bracts preceding the elongated terminal segment of each rachis; in the loosely convolute, more or less inflated form of the anthechia; and in the presence of twice as many stamens in each flower. As far as known to date, the respective geographical ranges of the two genera are widely disjunct.

DISTRIBUTION.—Of the two recognized species, *E. typica* has been reported only from the borders of a forest at the type-locality, El Limón, Venezuela. *Elytostachys clavigera* McClure has been collected in Colombia and all countries northward to Honduras, and from situations at reported elevations from 200 to 1500 m, described as river banks, old river terraces, wet ravines, crest of range, edge of forest, opening in forest. Both species are represented as flowering and fruiting freely.

branch complements of restricted or gremial insertion, each arising from a solitary branch bud containing but a single initial primordium; auricles

### Key to the Species of *Elytostachys*

- 1a. Leaf blades scabrous toward the base on the upper surface; laminiferous bracts silky-pubescent in part; bladesless 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 6.5 mm long and entirely glabrous; lemma to 23 mm long; ovary entirely glabrous ..... 2. *E. typica*

### *Glaziophyton* Franchet

FIGURE 36

*Glaziophyton* Franchet, 1889:277.—McClure, 1957:203.  
*Arundinaria* sect. *Glaziophyton* (Franchet) Hackel, in Engler and Prantl, 1897:46.—Lamson-Scribner, 1899:9.

Plants multicespitose, unarmed. Rhizomes pachymorph, the neck of an occasional one much elongated, 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, juncooid 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; juncooid 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 veinlets 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 appressed pleioclade complements each arising from a solitary 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 semelauctant, effusely branched panicles with a deliquescent rachis, the branches of all orders solitary, very slender and wiry, each subtended by a bract, and each bearing a 2-keeled

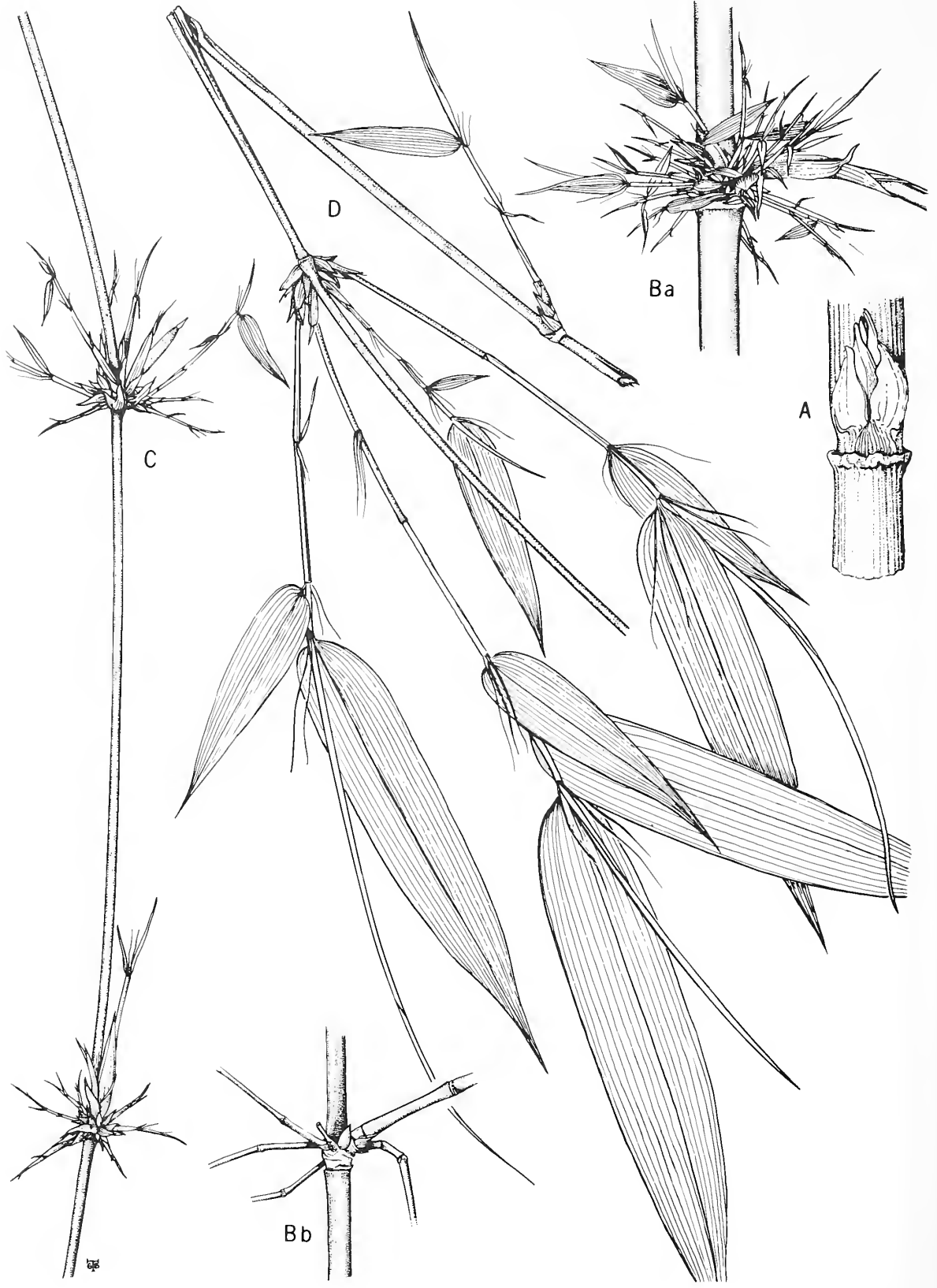


FIGURE 35.—*Elytostachys clavigera* McClure. A, Midculm branch bud in early stage of germination,  $\times 0.6$ ; Ba, basal portion of young midculm branch complement,  $\times 0.6$ ; bb, basal portion of mature branch complement at upper node of culm,  $\times 0.6$ ; c, branch complements at upper nodes of culm in early stage of development,  $\times 0.6$ ; D, middle portion of sterile leafy first-order axis of midculm branch complement,  $\times 0.6$ . All drawings based on McClure 21478 (US).

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 antherium (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-SPECIES.—*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 eifistular 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, juncooid 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 *Mero-stachys*, *Myriocladus*, and *Arthrostylidium*. The genus *Glaziophyton*, however, stands without any obviously close affinities among the bamboos.

Glaziou assumed the existence of juncooid 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 juncooid, 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 juncooid 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 36.—*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 diaphragms) and two young shoots, diameter  $\times 0.6$ , length  $\times ca. 0.9$ ; C, tip of leafless sterile culm, showing close-set budless nodes,  $\times ca. 3$ ; D, E, culm sheaths (apical portion only) from nodes 8 and 13 of sterile culm, abaxial and adaxial aspects, respectively,  $\times 4.8$ ; F, stumps of burned leafless plant, with leafy culms that developed by tillering, after burning,  $\times 0.6$ ; G, foliage leaf and part of its sheath, abaxial aspect,  $\times 1.8$ ; H, junction of foliage leaf and its sheath, adaxial aspect,  $\times 1.8$ ; I, portions of two mature flowering branch complements, the latter with an intact subtending sheath,  $\times 1.2$ ; J, bract subtending a middle-order branch of the inflorescence,  $\times 6$ ; K, prophyllum of a middle-order branch of the inflorescence,  $\times 9$ ; L, diagram of the structure, in longitudinal section, of the ultimate-order branching of the inflorescence. Each branch terminates in a spikelet. The axis of the flower proper is represented by a narrow cone, bearing the prophyllum-like palea; M, spikelet, showing extreme development in length and in number of functional florets. Spikelets with 2 or 3 functional florets are typical,  $\times ca. 2.4$ ; N, transitional glumes,  $\times ca. 12$ ; O, floret,  $\times 9$ ; P, diagram of floret structure in cross-section; Q, lemma,  $\times 9$ ; R, palea,  $\times 9$ ; S, lodicule complement,  $\times 9$ ; T, stamen,  $\times 9$ ; U, gynoceium,  $\times 15$ ; V, branch of stigma,  $\times ca. 120$ . Drawings A, B based on *Glaziou 8999* (A based on Glaziou's notes incorporated in Franchet's description of the plant), C-E on *Glaziou 14383* (P), and F-V on *Glaziou 17914* (P).

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

### *Merostachys* Sprengel

FIGURE 37

*Merostachys* Sprengel, 1825, II:132.—Endlicher, 1836-1840: 102.—Ruprecht, 1839:36.—Munro, 1868:46.—Doell, in Martius, 1880:207.—Bentham, in Bentham and Hooker, 1883: 1209.—Hackel, in Engler and Prantl, 1887:93.—McClure, 1957:205.

*Brasilocalamus* Nakai, 1933:10.—McClure, 1957:201.

Plants unicespitate, 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, fistulose 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 monoclade, with its primary element solitary, flat, unsegmented, roughly ovate or cordate to triangular in contour, thin, adnate to the surface of the culm; secondary branches slender, subequal, of apiculate insertion, arising from primordia formed on the margin of the primary element, and displayed in fan-shaped array. Leaves (blades of leaf sheaths) with transverse veinlets usually not manifest externally.

Inflorescences semelaucant, spicate racemes terminating usually leafy twigs, the rachis excurrent, bearing spikelets of solitary (in a few species paired or ternate) insertion and secund orientation, the distal 1 or more spikelets typically depauperate or rudimentary; bracts subtending spikelets (excepting the lowermost one) generally reduced, rudimentary, or obsolete. Transitional glumes usually 2 and very unequal, both usually empty, but one or the other sometimes subtending what appears to be a 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 antherium. 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 antherium more substantial than rudimentary.) Florets more or less strongly inflated, the lemma fully embracing the palea only basally at maturity, the palea gaping anticly, narrowly to broadly sulcate and 2-keeled dorsally. Lodicules 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-

cus and an embryotegium, the respective positions of the hilum and the embryo are not manifest externally.

ETYMOLOGY.—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, 42d). However, the form of the sheaths (Figures 37b, 42e) 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 secund, 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 antheridium 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

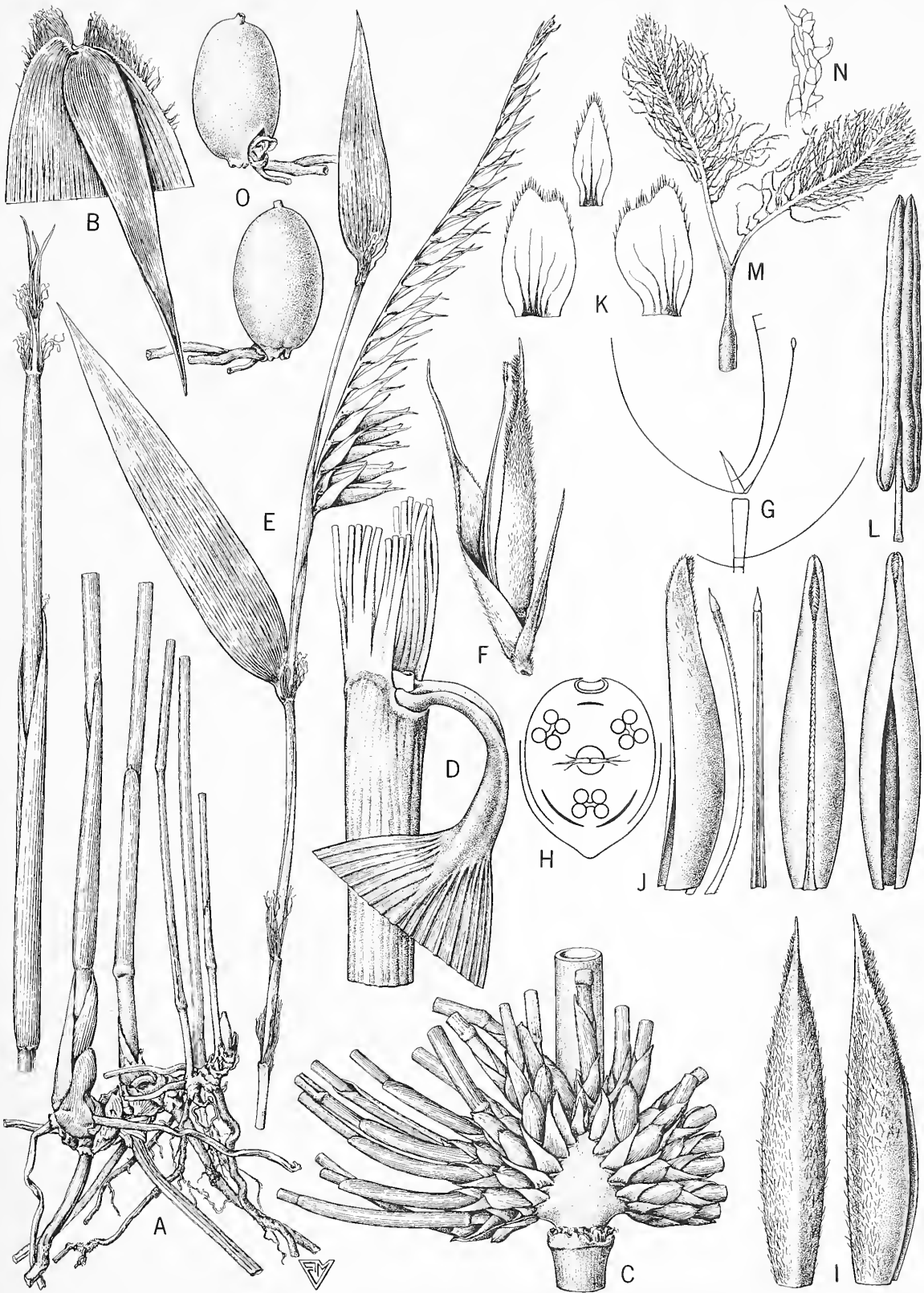
from Argentina to Guatemala and British Honduras, at moderate elevations and up to 1500 meters. As far as known today, the genus reaches its fullest development and greatest diversity in Brazil, where 20 described species are found. Outlying stands of single species have been reported from Argentina, 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 brevispica* Munro, 1868:49.
5. *Merostachys burchellii* Munro, 1868:51.

This species was initially described by Munro on

FIGURE 37.—*Merostachys* sp. (A, O) and *Merostachys speciosa* Sprengel (B–N). A, Seedling plant, basal part, showing caespitose clump habit and pachymorph rhizomes (tip of young culm shoot at left),  $\times 1.2$ ; B, culm sheath (apical portion only) from midculm node of mature culm,  $\times 0.6$ ; C, branch complement (base only of the component axes) at midculm node,  $\times ca. 0.9$ ; D, leaf sheath (apex only) showing ligule, base of oral setae, petiole, and base of leaf blade,  $\times 4.8$ ; E, flowering branch, terminating in a secund spicate inflorescence,  $\times 0.6$ ; F, single branch (a sessile spikelet) of the inflorescence,  $\times 2.4$ ; G, diagram in longitudinal section of a spikelet, showing two transitional glumes followed by a segment of the rachilla, a bristle-like prolongation of the rachilla (terminated by a rudiment), the lemma, palea, and the floral axis — the last shown as a narrow cone; H, diagram in cross-section of the floret; I, lemma in two aspects,  $\times ca. 3.1$ ; J, palea in three aspects, and the bristle-like prolongation of the rachilla in two aspects,  $\times ca. 3.1$ ; K, lodicule complement,  $\times 6$ ; L, stamen,  $\times 4.8$ ; M, gynoeceum,  $\times 6$ ; N, branch of a stigma, greatly enlarged; O, mature fruit (in two aspects,  $\times 3.6$ ) after it has produced a seedling plant (shown at A). Drawings A, O based on Swallen 8134 (US), B on Chase 9466 (US), C on Lofgren 1653 (US), D–F on Sellow 1286 (US ex B) and G–N on Reitz 2268 (US).



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*. 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. 12D-H.

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

? *Merostachys clausenii*  $\beta$  *mollior* Doell, in Martius, 1880:214.

Ekman (1913:64) expressed the opinion that Doell's type of  $\beta$  *mollior* is identical with Munro's type of *M. clausenii*. 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 in 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 affinibus distat; spicula brevi *M. Fischeriana* approximata."

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 "*Bambusa*" 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: "*Merostachys* sp. indescr. *M. pluriflora* nov. sp. *M. Kunthii* Rupr. affinis differt spiculae flosculis 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* Loddiges in Lindley (1835) which name appears (Camus, 1913, I:152) in a list of synonyms under *Dendrocalamus strictus*. In 1927 Pilger described *Merostachys 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[erostachys] 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 anthesis 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. *Merostachys polyantha* McClure, new species

Culmi 6-8 m alti (teste A. Lima); internodia teretia, cava, parietibus tenuibus, extus infra unum-

quidque nodum in zona angusta pilis albidis adpressis confertim vestita, alibi papillis retrorse aculeiferis praedita, demum luteo-viridia et punctis vinosis minutis elongatisque omnino variegata. Culmorum vaginae deciduae, tum ex omnibus cingulo pilis albidis retrorse adpressis vestito remanenti; auriculis et setis oralibus valde evolutis; ligula perbrevis, margine irregulatim denticulata ciliolataque; lamina decidua (non adhuc visa). Foliorum vagina striato-sulcata, secus marginem externam setis lustratis ornata, vaginis infimis dorso et ut videtur omnino glabris, supremis papillis retrorse uncinatis punctatis; auriculis et setis oralibus circa ut in vaginis culmorum evolutis; ligula interiore haud exserta, exteriori anguste lineari, margine vel subglabra vel dense ciliolata; petiolo usque 8 mm longo, compresso, vel omnino glabro vel utrinque dense scabro; lamina usque 150 x 35 mm, oblongo-lanceolata, basi asymmetricice vel rotundata vel cordata, apice asymmetricice et abrupte acuminata; laminis infimis et eis supremis in quoque axi florifero ovatis acuminatissimisque, omnibus utrinque concoloratis et fere glabris; nervis longitudinalibus omnibus in laminarum facie abaxiali tantum salientibus; costa tantum basin versus laminae distinguenda; nervibus secundariis utroque 5-8; tertiariis in quoque spatio costae contiguo usque 8, versus marginem laminae gradatim paucioribus ita in quoque spatio marginali saepius ad 2 redactis; venulis transversis in facie abaxiali tantum distinguendis, vicinis 1.5-4.0 mm sese distantibus.

Inflorescentiae e racemis spicatis secundisque sistentes, solitariae, axes saepius laminiferos terminantes; pedunculo vel haud vel parum exserto, apice dense canescenti; rhachidi 25-65 mm longa, curvula, dense antrorse-pubescenti; bractea spiculam basilarem subtendenti ovata, apice acuta apiculataque, multinervia et valde carinata, dorso marginibusque omnino glabra, usque 10 mm longa, succedentibus gradatim redactis, distalibus vel rudimentariis vel obsoletis. Spiculae compressulae, anguste triangulae, apice indeterminatae, insertione solitariae, confertae, alternae, distichaeque, pleraeque 1.5-2.0 mm (infimae usque 4.0 mm) sese distantes; spiculis in quoque racemo usque 26, infima 55 mm longa, sequentibus gradatim brevioribus, tum distalibus 7-8 vel depauperatis vel rudimentariis; pedicello sub-nil, latere externo prominenter pulvinato; glumis transitionalibus saepius

2, alia vel alia aliquando rudimentum (velut gemmam dormientem) foventi; I 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 tantum invalide ciliolata. Flosculi in spiculis proximalibus usque 10, eis in spiculis succedentibus gradatim paucioribus; flosculo terminali vel plus minusve depauperato vel etiam in statu rudimentario dirempto. Anthoeciorum elementae utraeque crustaceae, extus plus minusve dense strigosae, secus margines apicem versus antrorse-ciliatae. Rhachillae segmenta usque 4 mm longa, semiclaviformia, omnino molli-ter 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, sursum semper translucidae, 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 stigmata 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-

face of the auricles, lustrous, very sparsely and obscurely antrorse-scabrous throughout, crisped distally; ligule short, truncate or slightly arcuate apically, minutely and irregularly denticulate and ciliate on the margin; blade deciduous (not seen). Leaf sheaths proper (represented on flowering twigs only in the available specimens) minutely corrugated (quasi-plicate) longitudinally, densely fringed with lustrous hairs on and near the outer margin; the proximal sheaths in a given series glabrous, the distal ones strewn (on the exposed surface at least) with retrorsely uncinata 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 antrorse-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 internode 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 canescent 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 obsolete, each prominently pulvinate on the external side only; transitional glumes normally two, one or the other sometimes subtending a bud-like rudiment; *r* about 4 mm long, narrowly triangular, acuminate, prominently keeled, otherwise without visible nerves, weakly appressed hirtulous dorsally and strongly ciliate on the margins; *n* 6–9 mm long, ovate, acuminate, 5-nerved and strongly keeled, hirtulous dorsally and weakly ciliolate on the margin toward the apex only. Florets in the lowermost spikelets up to 10, progressively fewer and shorter in succeeding spikelets, the terminal floret either more or less strongly depauperate or stalled at a rudimentary stage in its development. Elements of the anthercia both crustaceous, more or less densely strigose on the outer surface, antrorse-ciliolate on the margins apically. Rachilla segments up to 4 mm long, semiclaviform, softly pubescent throughout with antrorse 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. Lodicules 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 Tórigo (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 Mon-

gaguá, pr. Praia Grande, Município Mongaguá, São Paulo, Brasil, a sombra da mata no alto da serra (100–120 m). 6–8 m. Fl. roxoescuro. Caule c/peq. 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, anthercia 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 anthercia; 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, Município São Paulo, Brasil. Its nearest known relative, *Merostachys pluriflora*, has been collected near Iguapé, State of São Paulo, and on the Island of Santa Catarina, State of Santa Catarina.

20. *Merostachys retrorsa* McClure, in Maguire, Wurdack, et al., 1964:6.
21. *Merostachys riedeliana* Ruprecht ex Doell, in Martius, 1880:213.
22. *Merostachys sellovii* Munro, 1868:51.
23. *Merostachys sparsiflora* Ruprecht, 1839:37, pl. 10: fig. 32.
24. *Merostachys speciosa* Sprengel, 1825:249 (Figure 37B-N).

Under this name Munro (1868:48) writes “I find in one of Sellow’s specimens the second hermaphrodite flower which I had first observed in *M. Clauseni*.”

25. *Merostachys speciosa* sensu Kunth, 1830:333, 334, pl. 79. [See *Merostachys kunthii*.]
26. *Merostachys speciosa* sensu Nees, in Martius, 1829:527–531. [See *Merostachys neesii*.]



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 *Athroostachys capitata*.]  
*Merostachys capitata*  $\alpha$  *latifolia* Doell, in Martius, 1880:217.  
*Merostachys capitata*  $\beta$  *angustifolia* Doell, in Martius, 1880:217.
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, unicespitate, unarmed. Rhizomes pachymorph. Culms self-supporting, the internodes terete, in some species hollow, in others efiistular, 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 sessile, the transverse veinlets usually obscure or invisible externally or (as in *M. paludicolus*) more or less conspicuously manifest on both surfaces.

Inflorescences semelauctant, 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 antherium. 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: I and II “empty glumes,” III 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. Lodicules 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.

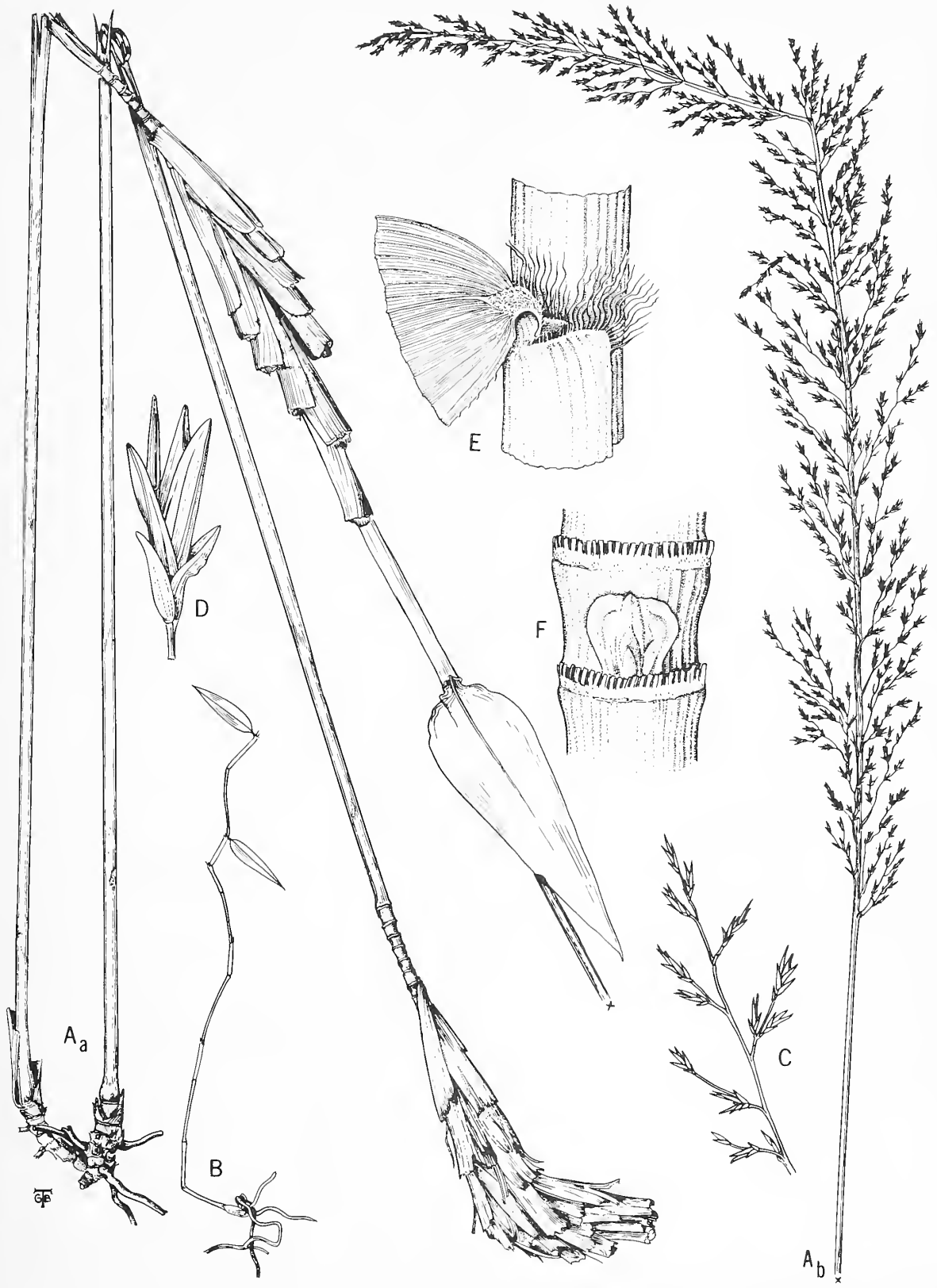
ETYMOLOGY.—The name *Myriocladus*, formed from the Greek, *myrios*, numberless, and *clados*, branch, ostensibly alludes to the profuse ramification of the inflorescences.

TYPE-SPECIES.—*Myriocladus virgatus* Swallen.

RELATIONSHIPS.—Certain of the striking generic features of *Myriocladus* are shared by individual

FIGURE 38.—*Myriocladus confertus* Swallen. Aa, Ab, Leafy flowering plant,  $\times 0.6$ ; B, seedling,  $\times 1.2$ ; C, first-order branch of inflorescence,  $\times 1.2$ ; D, spikelet,  $\times$  ca. 9.6; E, apex of leaf sheath and base of blade,  $\times 1.8$ ; F, two nodes of culm with shortened internode and an intact branch bud,  $\times$  ca. 6. All drawings based on Steyermark and Wurdack 1220 (US).





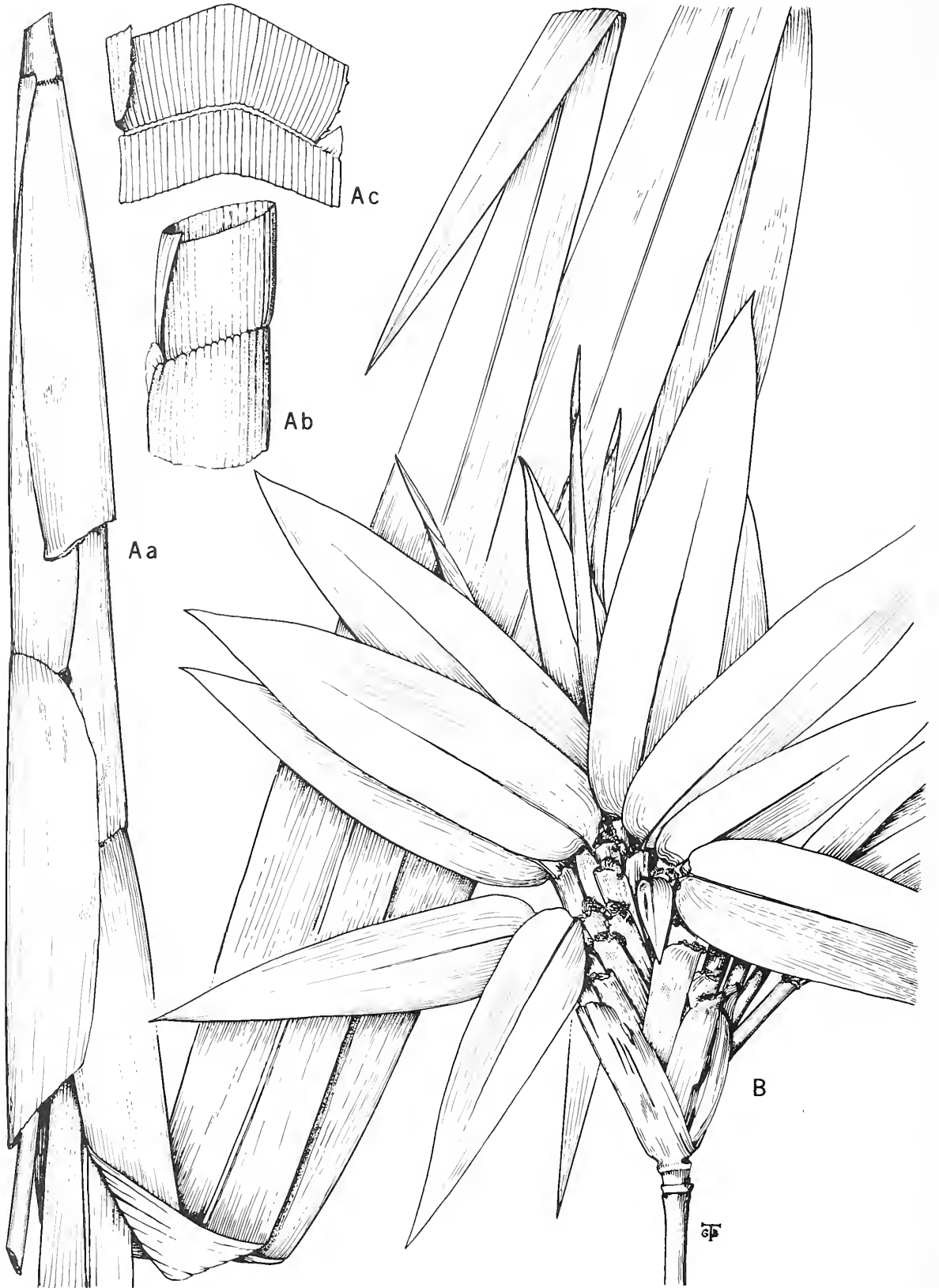


FIGURE 39.—*Myriocladus virgatus* Swallen (Aa–Ac) and *Myriocladus confertus* Swallen (B). Aa, Leafy tip of sterile culm,  $\times 0.6$ ; Ab, apex of leaf sheath and base of blade (abaxial aspect),  $\times 1.2$ ; Ac, apex of leaf sheath and base of blade (adaxial aspect),  $\times 1.2$ ; B, leafy tip of sterile culm,  $\times 0.6$ ; Drawing Aa based on Cowan and Wurdack 31376 (US), Ab, Ac on Steyermark 58293 (F), and B on Steyermark and Wurdack 1220 (US).

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 deflexa* 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 churunensis* Swallen, in Steyermark, 1967:132.
5. *Myriocladus distantiflorus* 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. 3h.
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 paruensis* 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. 3a; 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:325.—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 unicespitate, 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

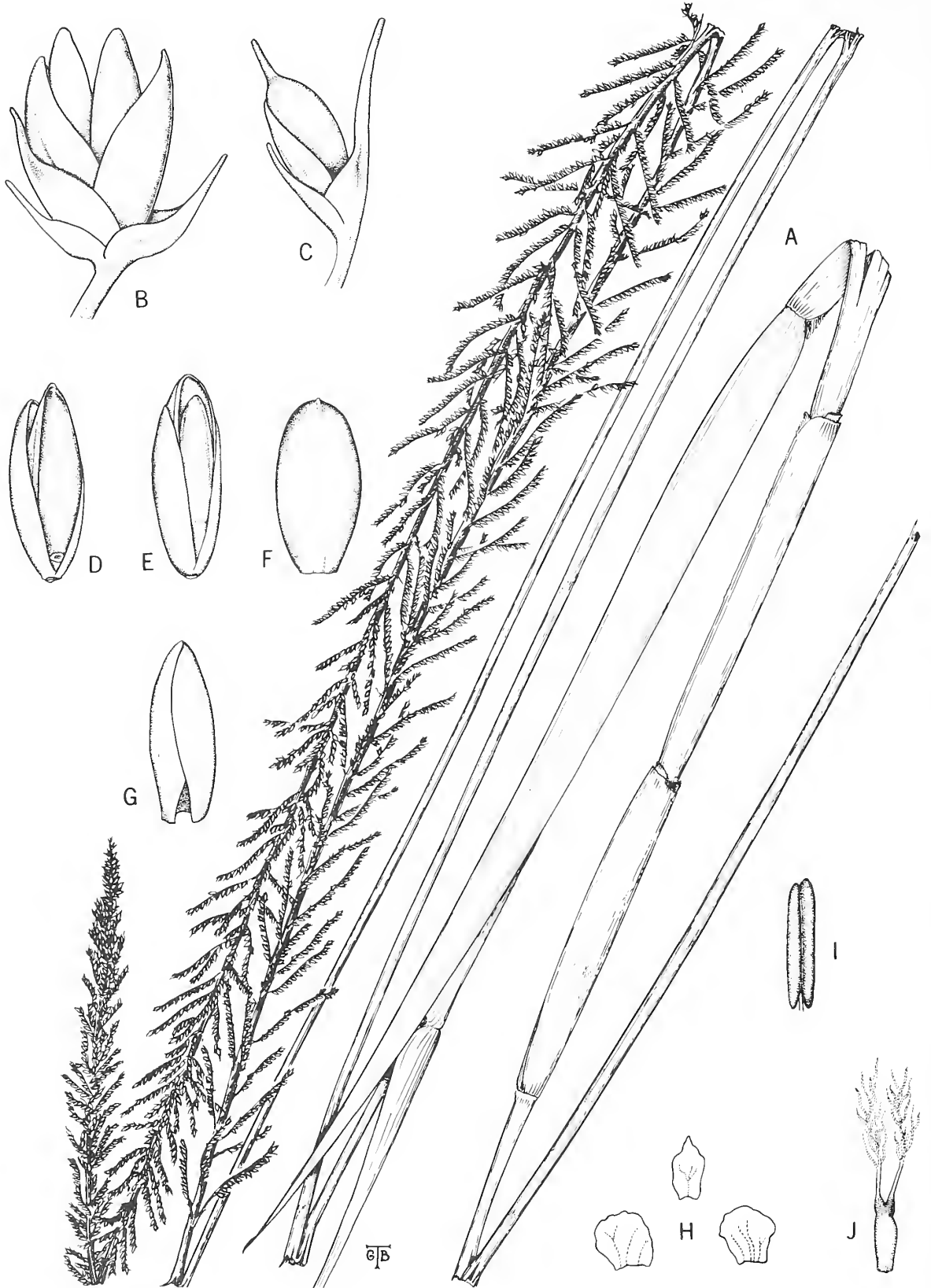


FIGURE 40.—*Myriocladus virgatus* Swallen. A, Tip of leafy flowering culm,  $\times 0.6$ ; B, spikelet,  $\times 12$ ; C, transitional glumes,  $\times 12$ ; D, floret I, showing dorsal aspect of palea,  $\times 12$ ; E, floret II, showing terminal depauperate floret lying in the sulcus of the palea,  $\times 12$ ; F, lemma I, dorsal aspect,  $\times 12$ ; G, palea, ventral aspect,  $\times 12$ ; H, lodicule complement,  $\times 12$ ; I, stamen,  $\times 12$ ; J, gynoeceium,  $\times 12$ . Drawing A based on Cowan and Wurdack 31376 (US), and B–J on Steyermark 58293 (F).

sheath, the transverse veinlets not at all visible to clearly manifest, externally.

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 secund 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 locus 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. Lodicules 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 *Cuatrecasas 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 Cuatrecasas (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 (1839:30), 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 valde a *Chusquea* distat.”

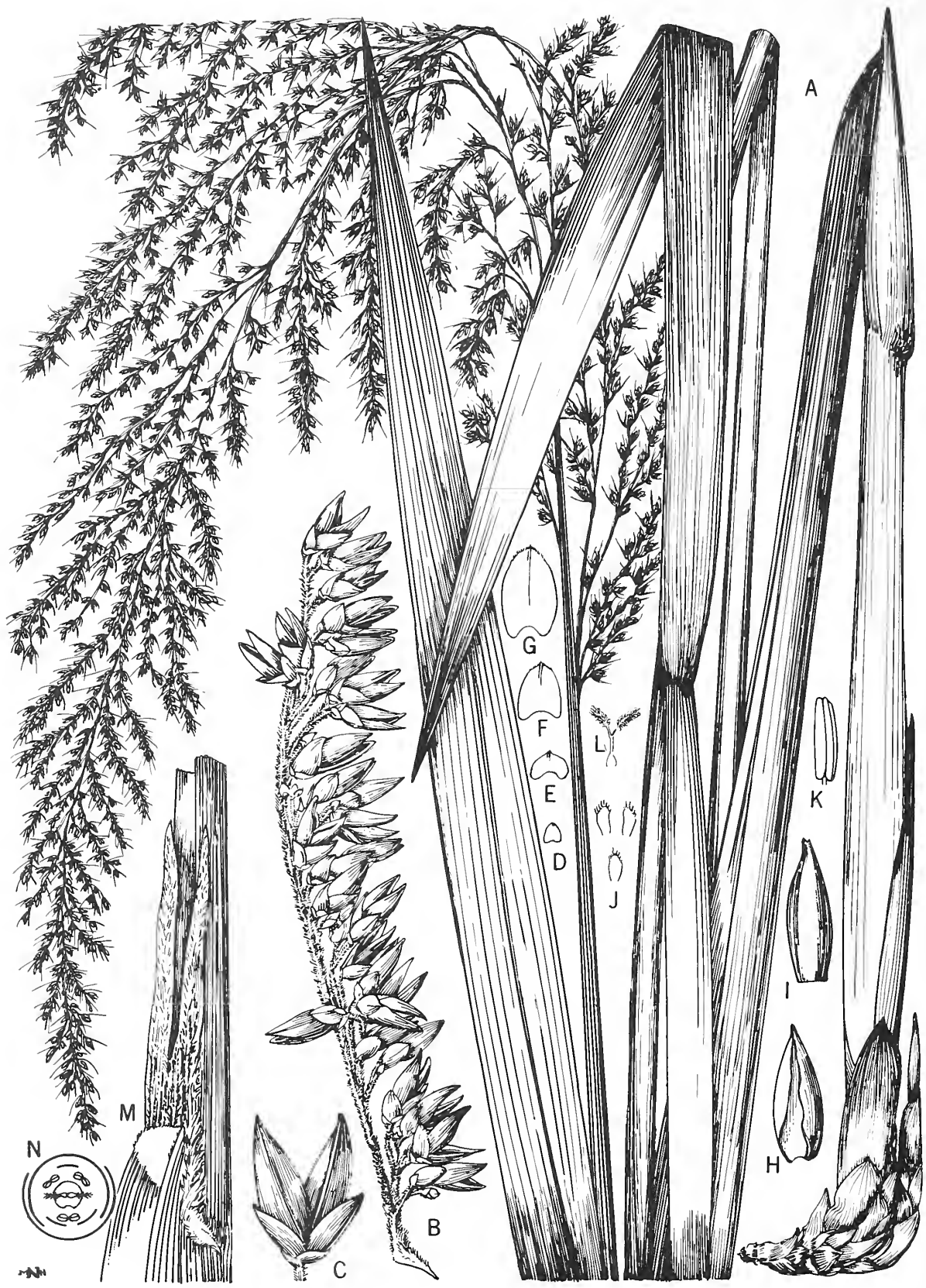


FIGURE 41.—*Neurolepis aristata* (Munro) Hitchcock (A) and *Neurolepis pittieri* McClure (B-N). A, Flowering plant,  $\times 0.6$ ; B, branch of an inflorescence,  $\times 2.4$ ; C, spikelet,  $\times 4.8$ ; D, E, transitional glumes,  $\times 4.8$ ; F and G, sterile lemmas,  $\times 4.8$ ; H, fertile lemma,  $\times 4.8$ ; I, palca,  $\times 4.8$ ; J, lodicule complement,  $\times 4.8$ ; K, stamen,  $\times 4.8$ ; L, gynoeccium,  $\times 4.8$ ; M, apex of leaf sheath,  $\times 1.2$ ; N, diagrammatic cross-section of floret. Drawing A based on *Cuatrecasas 14813* (US) and B-N on *Pittier 10067* (US).

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 aperta* Munro [= *Neurolepis aperta* (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.

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

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

*Planotia aperta* Munro, 1868:73.

*Planotia ingens* Pilger, 1898:721.

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

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

*Chusquea aristata* Munro, 1868:61.

*Planotia acuminatissima* Munro, 1868:72.

*Planotia stübelii* Pilger, 1898:720.

*Planotia tessellata* Pilger, 1898:720.

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

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

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

*Neurolepis weberbaueri* Pilger, 1921:446.

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

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

*Platonia elata* Kunth, 1830:327, pl. 76.

*Planotia elata* (Kunth) Munro, 1868:71.

*Planotia nobilis* Munro, 1868:72.

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

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

*Neurolepis nigra* Swallen, 1957b:400.

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

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

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

*Platonia virgata* Grisebach, 1864:530.

*Planotia virgata* (Grisebach) Munro, 1868:71.

#### *Rhipidocladum* McClure, new genus

FIGURE 42

Plantae unicaespitosae, inermes. Rhizomata pachymorpha. Culmi infra saltem medium sese sustinentes erecti, sursum vulgo vel scandentes vel



apice penduli; internodiis cylindratis, intus fistulosis. Ramorum complementum ad nodos medianos culmorum insertum; eiusdem axi primario appanato, subtriangulato, ad culmi superficiem appresso adnatoque, neque cylindrato neque segmentato; axibus secundariis numerosis, gracilibus, subaequalibusque, margine axis primarii insertis, ita ordinatione rhipidiforme sese ostendentibus. Foliorum lamina venulis transversis in speciebus plerisque extus vulgo haud manifestis, alibi plus minusve clare visibilibus.

Inflorescentiae semelauctantes, ramificatione typice racemosa, rachidi vel percurrenti vel deliquescenti; spiculae insertione et orientatione diversae; prophyllis bracteisque nullis. Glumae transitionales (glumae vecuae et lemmata sterilia) numero diversae atque nonnumquam inconstantes. Spiculae vel sessiles vel subsessiles vel pedicellatae, flosculos hermaphroditos vel paucos vel plures continentes, apice in anthesio depauperato sterilique terminantes. Lemma fertile maturitate saltem paleam suam basi tantum circumplectens. Palea dorso 2-carinata et late sulcata, antice hians. Lodiculae (nonnumquam -2, -1, -0) typice 3, duabus anterioribus plus minusve asymmetricis atque geminatis, posteriore symmetrica sat minoreque. Stamina 3, filamentis filiformibus liberisque. Stigmata 2. Fructus maturus caryopsidens; caryopsis oblonga sulcataque, leviter compressa, apice cuspidata; pericarpio vel pergamineo vel crustaceo, glabro, vel opaco vel nitido, crassitudine uniformi; sulco et embryotegio aut valde aut debiliter manifestis.

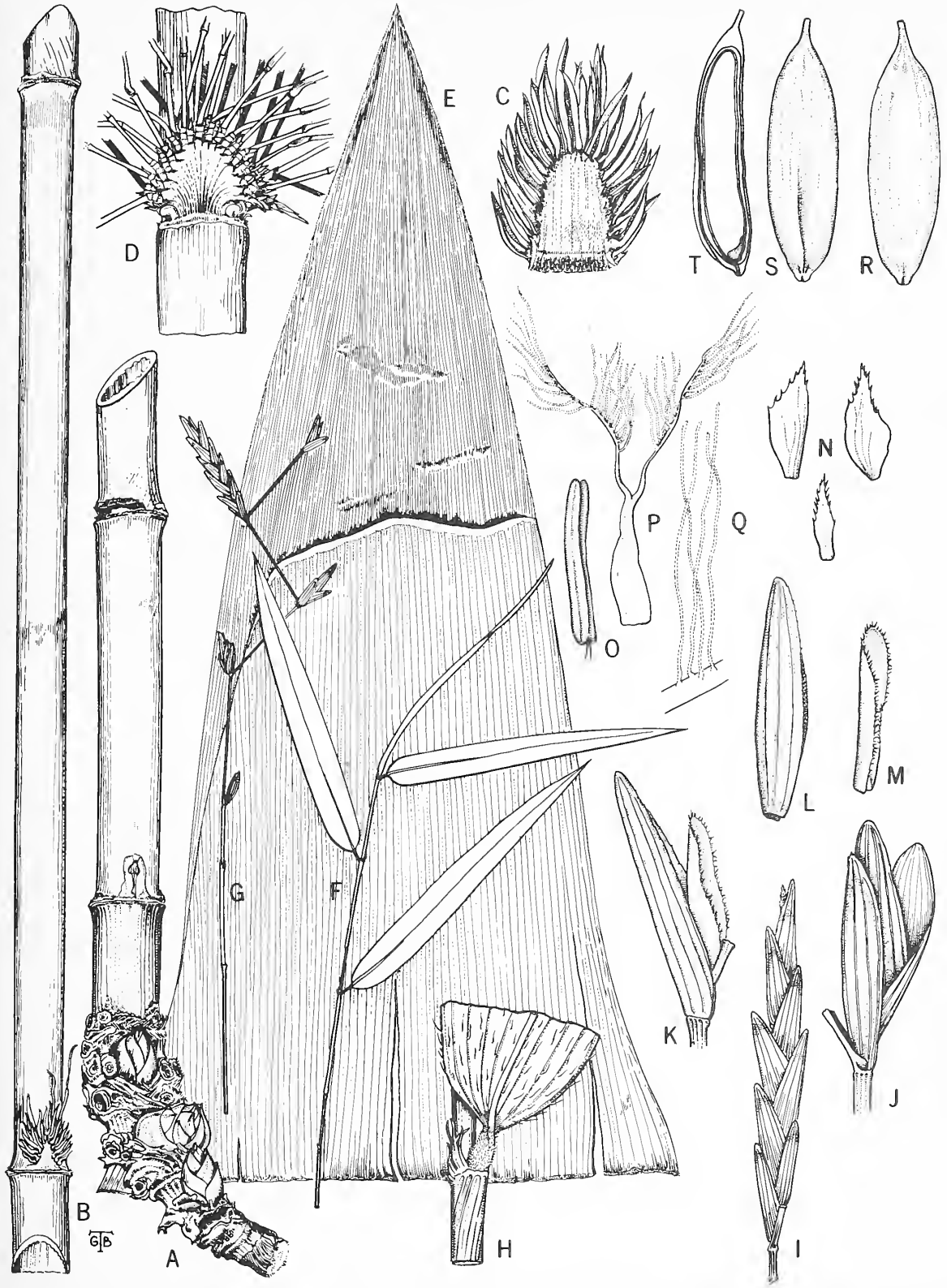
Plants unicespitose, unarmed. Rhizomes pachymorph. Culms self-supporting below, commonly either scandent or pendulous above, the internodes cylindrical, hollow. Primary branch buds (when present) at midculm nodes, solitary, each containing a single initial primordium. Branch complement at midculm nodes 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 lemmas) 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 anthesia. 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-

FIGURE 42.—*Rhipidocladum harmonicum* (Parodi) McClure (A-Q) and *Rhipidocladum verticillatum* (Nees) McClure (R-T). A, Rhizome and base of its culm,  $\times 0.6$ ; B, culm internode between nodes v and vi, showing first-order element of the branch complement with second-order elements developing from buds on its margin,  $\times 0.6$ ; C, first-order element of branch complement from B, removed and shown from the adaxial aspect,  $\times 1.8$ ; D, fully developed midculm branch complement, basal portion only, in situ,  $\times 0.48$ ; E, midculm sheath, adaxial aspect,  $\times 0.6$ ; F, sterile leafy twig,  $\times 0.6$ ; G, leafless flowering twig;  $\times 0.6$ ; H, apex of leaf sheath and base of blade,  $\times$  ca. 3; I, spikelet, sessile with portion of rachis attached,  $\times$  ca. 1.8; J, transitional glumes from I,  $\times$  ca. 6; K, floret,  $\times$  ca. 3.6; L, lemma,  $\times$  ca. 3.6; M, palea,  $\times$  ca. 3.6; N, lodicule complement,  $\times$  ca. 7.2; O, stamen,  $\times$  ca. 6; P, gynoeceum,  $\times$  ca. 14.4; Q, stigmatic processes, greatly enlarged; R, fruit, embryo side,  $\times 7.2$ ; S, fruit, hilum side,  $\times 7.2$ ; T, fruit, longitudinal section,  $\times 7.2$ . Drawings A, B based on McClure 21398 (US), C, E, F, H on McClure 21416 (US), D on Camp E-1613 (US), G, I-M on Killup and Smith 25622, N-Q on Sodiro s. n., Oct. 1900 (US), and R-T on Glaziou 22424 (P).





cal in the dorsiventral plane; pericarp pergaminous (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 morphology 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 42E) 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.

### Key to Recognized Species of *Rhipidocladum*

- |  |  |
|--|--|
| 1a. Rachis deliquescent; spikelets pedicellate .....   | 11. <i>R. verticillatum</i> , new combination  |
| 1b. Rachis excurrent; spikelets sessile or subsessile .....  | 2  |
| 2a. Spikelets inserted on the rachis in predominantly binate clusters .....  | 4. <i>R. geminatum</i> , new combination   |
| 2b. Spikelets of monate (solitary) insertion .....   | 3  |
| 3a. Rachis geniculate (at least in its distal portion); spikelets in distichous orientation.....                                   | 5. <i>R. harmonicum</i> , new combination  |
| 3b. Rachis not geniculate; spikelets in secund orientation.....  | 4  |
| 4a. Spikelets oriented within a single plane giving a banneret-like form to each inflorescence .....                               | 6. <i>R. maxonii</i> , new combination   |
| 4b. Spikelets not oriented within a single plane .....   | 5  |
| 5a. Spikelets 4-5 cm long; the rachilla not disarticulating promptly at maturity .....   | 1. <i>R. ampliflorum</i> , new combination   |
| 5b. Spikelets not exceeding 2.5 cm in length; the rachilla disarticulating promptly at maturity (the following six species): ..... | 2. <i>R. angustiflorum</i> , new combination;  |
|  | 3. <i>R. bartlettii</i> , new combination; 7. <i>R. parviflorum</i> , new combination; 8. <i>R. pittieri</i> , new combination; 9. <i>R. prestoei</i> , new combination; 10. <i>R. racemiflorum</i> , 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 synonymies 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).

*Arthrostylidium harmonicum* Parodi, 1944:479, fig. 1.—McClure, in Sohns and Swallen, 1955:133.  
HOLOTYPE.—*Vargas 3260* (Parodi herbarium).  
Specimens examined include *McClure 21416* (US); *Sodirol “25-Pilger”* (US ex Sodirol herbarium); *Vargas 3260* (US ex Parodi).

DISTRIBUTION.—Ecuador; Peru.

6. *Rhipidocladum maxonii* (Hitchcock) McClure, new combination.

*Arthrostylidium maxonii* Hitchcock, 1927a:80.

HOLOTYPE.—*Maxon 8154* (US). Specimens examined include the holotype and *Standley 33643, 33812, 39096, 39105, 39179, 39411* (US); *Standley and Torres 50981* (US); *Standley and Valerio 49781* (US).

DISTRIBUTION.—Costa Rica.

To the midculm branching habit that gives to the culms of all species of *Rhipidocladum* a strong merostachyoid appearance, *R. maxonii* adds another merostachyoid feature — the conspicuously secund orientation of the branches of its banneret-like inflorescence. Other less conspicuous but clearly divergent morphological features, however, testify (in the key) to the authenticity of a generic disjunction between *Rhipidocladum* and *Merostachys*.

7. *Rhipidocladum parviflorum* (Trinius) McClure, new combination.

*Arundinaria parviflora* Trinius, 1835:619.

HOLOTYPE.—“in sylvis pr. Ypenéma Bras.” [*Riedl 189*] (LE).

*Arthrostylidium trinii* Ruprecht, 1839:29.

HOLOTYPE.—“in sylvis Brasiliae pr. Ypenema 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, 1:40.

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.—*Ghiesbreght 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); *Ghiesbreght 234* (US ex LE, US ex P); *Liebmann 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, 1868:23.—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 unicespitosae, inermes. Rhizomata pachymorpha. Culmi sese sustententes, in speciebus plerisque adhuc saltem cognitis rigide erecti; internodiis fistulosis, supra locum insertionis vel ramorum vel gemmarum complementi tantum vel breviter vel prorsus sulcatis, alibi teretibus. Ramorum complementum ad nodos culmorum medianos insidens raro absens, nonnumquam monocladum, typice solutum pleiocladum, axibus primariis vulgo 3 (usque 5), ad libram confertissime insertis et ex gemmis discretis, unoquoque mox vel demum ex gemmis ad nodos proximos suos proliferanti. Foliolorum lamina venulis transversis in speciebus nonnullis haud 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 pleraeque florem perfectam unicam terminalemque continentes; rhachilla post paleam haud producta. Anthoeciorum fertiliium maturorum lemma paleam suam imo tantum circumnectans. Palea antice hians, saltem apicem versus vulgo et sulcata et nonnumquam plus minusve manifeste bicarinata, dorso alibi convexa. Lodiculae 3, duabus anterioribus aequalibus, plus minusve valde asymmetricis et congruenter geminatis, posteriore symmetrica et aliquanto 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,  $\times 0.6$ ; B, apex of leaf sheath and base of leaf blade,  $\times 3$ ; C, base of branch complement high on culm,  $\times 3$ ; D, tuft of ultimate branches of inflorescence with transitional glumes attached,  $\times 7.2$ ; E, spikelet,  $\times 7.2$ ; F, sterile lemma I,  $\times 7.2$ ; G, sterile lemma II,  $\times 7.2$ ; H, fertile lemma,  $\times 7.2$ ; I, palea,  $\times 7.2$ ; J, lodicule complement,  $\times 25$ ; K, stamen,  $\times 15$ ; L, gynoeccium,  $\times 30$ . 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-obsolete; 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. Lodicules 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 nu-

merous 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,  $\times 0.6$ ; B, sheath subtending flowering twigs (left) and detached blade (right),  $\times 1.2$ ; C, apex of leaf sheath and base of leaf blade,  $\times 7.2$ ; D, tuft of ultimate branches of inflorescence with transitional glumes attached,  $\times 7.2$ ; E, spikelet (without pedicel and transitional glumes),  $\times 7.2$ ; F, sterile lemma I,  $\times 7.2$ ; G, sterile lemma II,  $\times 7.2$ ; H, fertile lemma,  $\times 7.2$ ; I, palea, oblique aspect; J, palea, dorsal aspect,  $\times 7.2$ ; K, lodicule complement,  $\times 15$ ; L, stamen,  $\times 15$ ; M, gynoeceum,  $\times 30$ . 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.

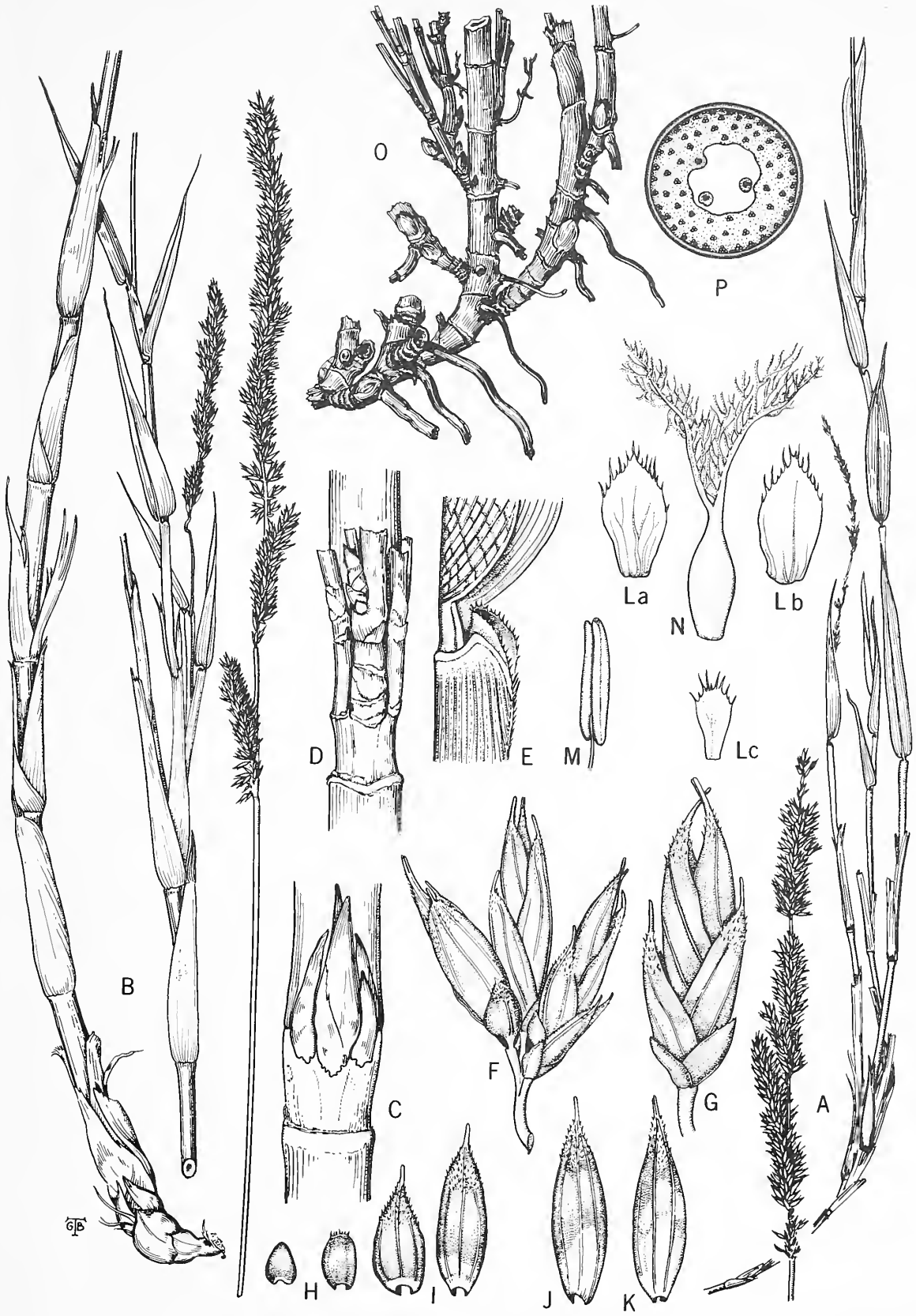
The genera *Chusquea*, *Neurolepis*, and *Swallenochloa* represent groups of species that are closely related in the essential features of the reproductive apparatus, members of *Chusquea* leading in the diversity of form expressed in the branching of the rhizomes, culms, and inflorescences. From the 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 fistulose 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

FIGURE 45.—*Swallenochloa tessellata* (Munro) McClure. A, Small leafy flowering culm,  $\times 0.6$ ; B, leafy flowering culm with its pachymorph rhizome,  $\times 0.6$ ; C, midculm complement of three branch buds,  $\times 3$ ; D, base of midculm complement of three independent primary branches,  $\times 3$ ; E, apex of leaf sheath and base of leaf blade,  $\times 6$ ; F, secondary branch of inflorescence, bearing three pedicellate spikelets,  $\times 3$ ; G, spikelet,  $\times 6$ ; H, two transitional glumes,  $\times 6$ ; I, two "sterile (empty) lemmas,"  $\times 6$ ; J, "fertile lemma,"  $\times 6$ ; K, palea,  $\times 6$ ; L a-c, lodicule complement,  $\times 12$ ; M, stamen,  $\times 6$ ; N, gynoecium,  $\times 24$ ; O, rhizome and base of culms,  $\times 0.6$ ; P, cross-section of rhizome,  $\times 5.4$ . Drawing A based on *Triana 306*, type-species (US); B, F-N on *Schultes 18771* (US), C, P on *García-Barriga 11643-A*; D, E on *García-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 2181972*) 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  $\frac{3}{4}$  as long as the lemma, and showing only one well-developed vein on each side of the midrib ..... 4. *S. tessellata*, new combination
- 4a. Anthercium dull; pale stramineous; awn of lemma glabrous ... 2. *S. spicata*, new combination
- 4b. Anthercium 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.

HOLOTYPE.—*Lechler 2154* (K) the principal element.

*Chusquea humilis* Lechler ex Munro, 1868:60.

HOLOTYPE.—*Lechler 2694* (K) the principal element.

*Chusquea simplicissima* Pilger, 1905:145.

HOLOTYPE.—*Weberbauer 2217* (B).

DISTRIBUTION.—Peru.

Hitchcock (1927b:310) made *Chusquea simplicissima* Pilger a synonym of *Chusquea spicata* Munro. I cannot with confidence verify this disposition of the matter on the basis of the documenting material available to me. Dr. Hitchcock's decision, however, was based on a study of the intact type-specimens of which I have seen only fragments in which the spikelets do not exemplify a clearly representative norm.

3. *Swallenochloa subtessellata* (Hitchcock) McClure, new combination (Figures 43, 44).

*Chusquea subtessellata* Hitchcock, 1927a:81.

HOLOTYPE.—*Tonduz 3367* (US).

DISTRIBUTION.—Costa Rica.

*Pittier 3069* (US) cited by Hitchcock (1927a:81) as belonging here deviates noticeably from the holotype in both vegetative and reproductive features (cf. Figure 44).

4. *Swallenochloa tessellata* (Munro) McClure, new combination (Figure 45).

*Chusquea tessellata* Munro, 1868:60.

TYPE-MATERIAL.—*Triana [306]* (K) and *Holton 97* (K).

DISTRIBUTION.—Colombia.

Munro gives the altitude at which Triana's collection was made at 3000 feet. In Triana's field notes the same figure is given in meters.

5. *Swallenochloa weberbaueri* (Pilger) McClure, new combination.

*Chusquea weberbaueri* Pilger, 1905:146.—*Fosberg, 1944:230*.

HOLOTYPE.—*Weberbauer 4415* (B).

DISTRIBUTION.—Colombia to Peru.

### *Yushania* K. H. Keng

FIGURES 46, 47

*Yushania* Keng f., 1957:355.

Plants unarmed, compactly unicespitate at first; mature clumps of pluricespitate 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 fused; 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 semelauctant, 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 caryopsis, the pericarp pergamineous, glabrous, of uniform thickness, the sulcus and the embryotegium clearly manifest.

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

*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 a 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.

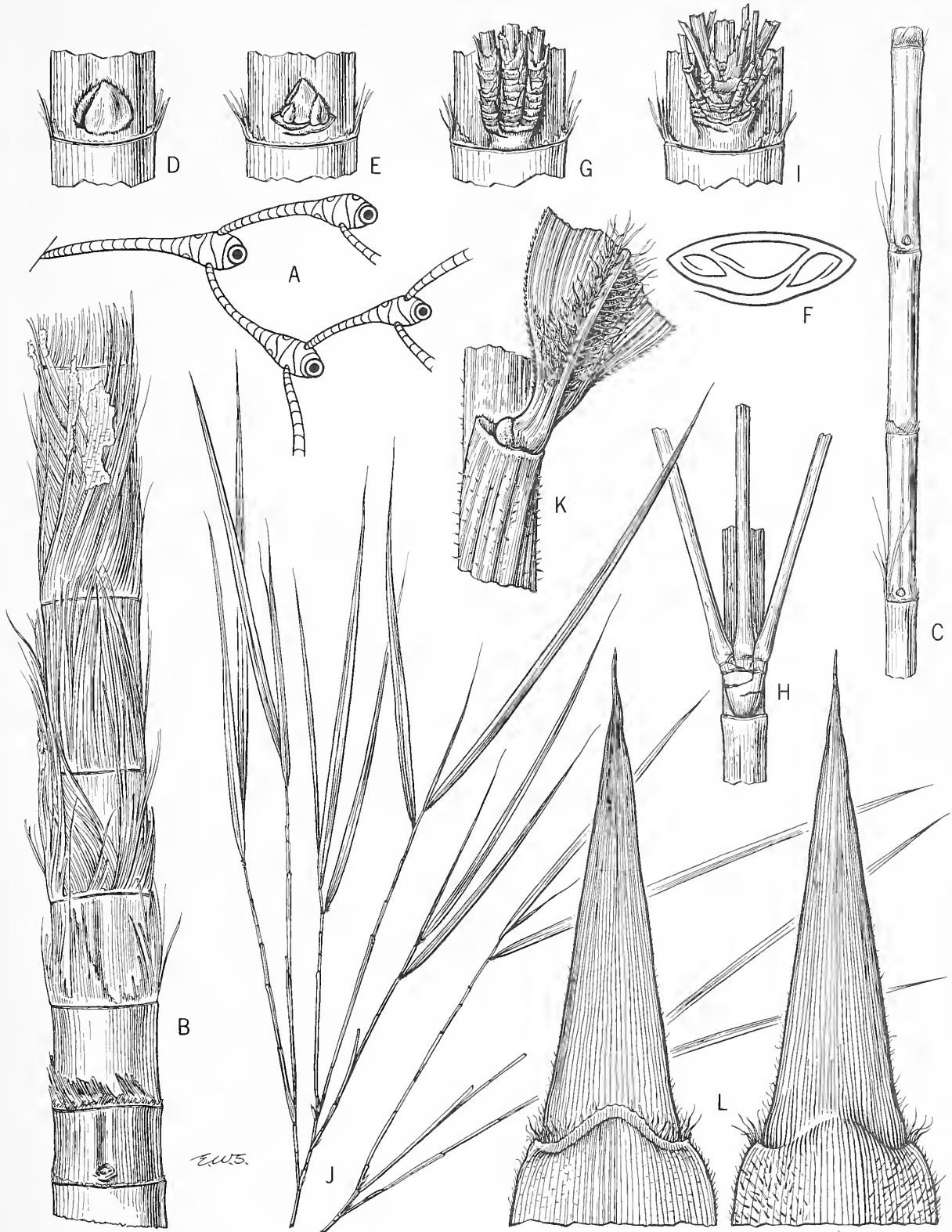
DISTRIBUTION.—In the Chinese text that follows his Latin diagnosis of the genus, K. H. Keng (1957: 356) says of the Old World component of *Yushania*: "Of this genus only the type species is known at present. It is native of Taiwan, and is found also on Luzon, P.I., and in the mainland Chinese provinces 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

### 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 ..... Subgenus *Yushania*
- 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 ..... *Otatea*, new subgenus

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 successive orders (generations) of rhizomes become progressively more elongated. [This feature has not yet, however, been established as generic in *Yushania*.] B, Basal portion of a culm, showing the characteristically short internodes and wire-like fibrovascular remains of the weathered, nonabscissile culm sheaths,  $\times 0.6$ ; 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,  $\times 1.5$ ; E, primary branch bud at a midculm node, with the prophyllum removed, revealing three growing points, each a prophyllate but unsubtended

bud,  $\times 1.5$ ; 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),  $\times 4.8$ ; G, base of a midculm branch complement, showing the initial components in an early stage of development, with sheaths removed,  $\times 0.9$ ; H, midculm branch complement with the initial components fully developed,  $\times 1.2$ ; 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,  $\times 1.2$ ; 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,  $\times 0.6$ ; K, leaf sheath apex with petiole and base of a narrow leaf blade,  $\times 7.2$ ; L, culm sheath from midculm range (apex only), adaxial aspect (left) and abaxial aspect (right),  $\times 0.9$ . 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 *Otatea* McClure and E. W. Smith,  
new subgenus**

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

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

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

**1. *Yushania (Otatea) aztecorum* McClure and  
E. W. Smith, new species**

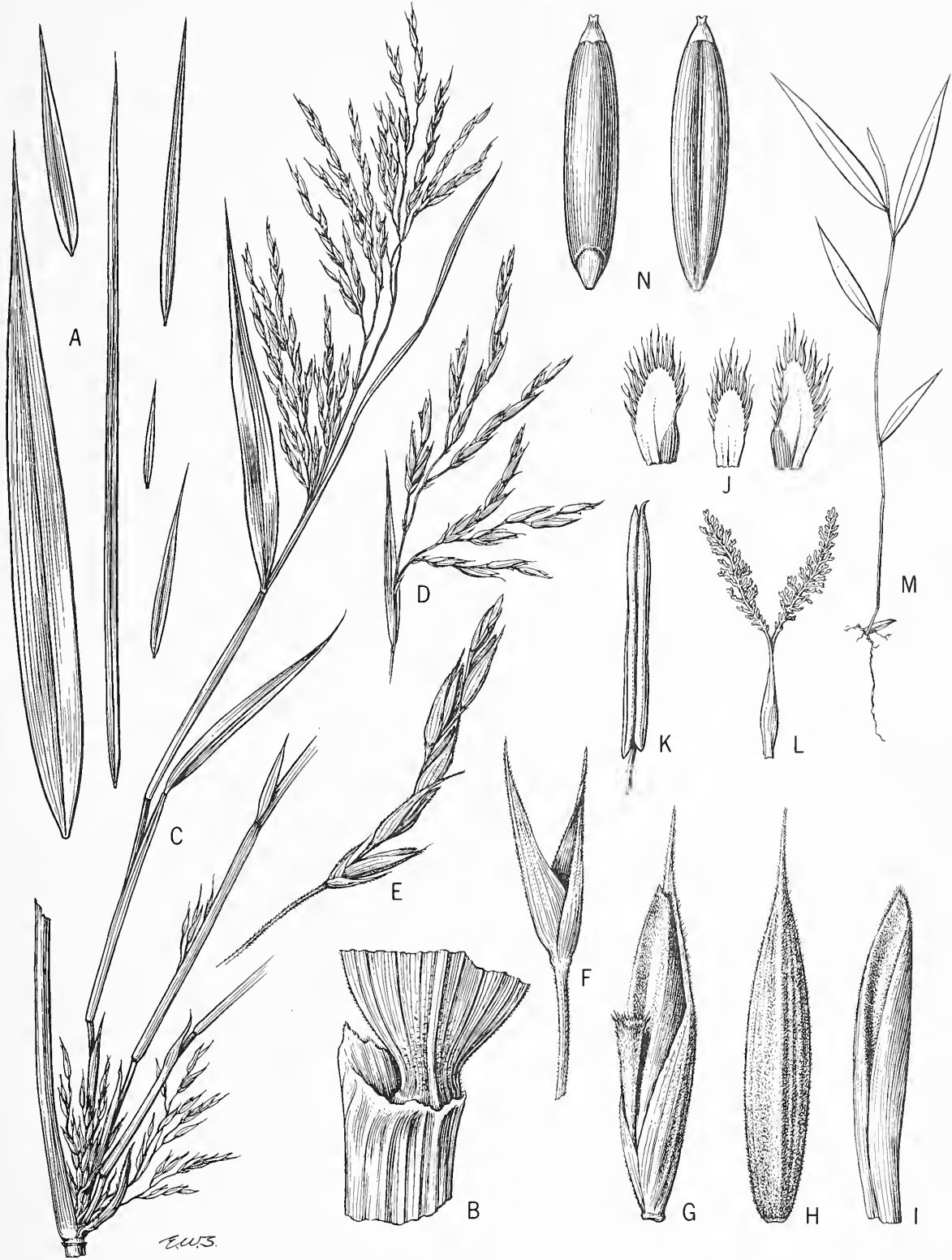
FIGURES 46, 47 A–M

Plantae initio conferte caespitose demum sensim aperientes. Rhizomatum collum initio (in plantis staturae juventae) rhizomate proprio suo brevius, demum (in plantis staturae adultae) rhizomate proprio multo longius. Culmi usque ad 6 m alti et 2.5 cm diametro; internodia glabra, in plantis juvenibus intus farcta, in plantis adultis fistulosa, ea supra nodos medianos ramiferos sulcata. Ramorum complementum ad nodos medianos oriens initio axes primarios 3 subequales subcoetaneosque vulgo capiens; axes ordinum superiorum a primarii valde superati. Vagina internodios culmi fovens dorso initio setis castaneis fragilis vel sparse vel dense vestita, demum calvescens sed papillis persistentibus conspersa; auriculae et setae orales vel nullae vel invalide evolutae; ligula arcuata, margine pro parte ciliata et pro parte crasse fimbriata; lamina appressa et late vel anguste triangula; vaginae ad nodos inferiores culmorum orientes haud deciduae, in situ demum fatiscentes.

Vagina foliorum prominenter nervoso-striata, inter nervos plus minusve dense usque haud papillata, vel omnino glabra vel hic illic vel omnino puberula; auriculae et setae orales vel vix ullae vel nullae; ligula interior et ligula exterior dimensionibus, forma, margine vesturaque maxime variabiles; lamina foliorum vel lanceolata cum nervis secundariis usque 3–4, vel lineari-lanceolata usque linearis et nervos secundarios vulgo 1–2 praebens; venulae transversae extus haud usque clare manifestae; pubescentia laminae caractere, crebretate, et distributione maxime variabilis.

Inflorescentiae ramos et ramulos vel foliiferos vel efoliatis terminantes; pedunculus, rhachis et radii scaberuli; bractee sat minimae nonnunquam obsoletae. Spiculae omnino pallide strigosae, laxae, usque ad 4 cm longae, flosculos 3–7 fungentos capientes, ubi maturae sat friabiles. Glumae transitionales typice 2, lanceolatae, valde carinatae, apice in aristam scabram ca 2.5 mm longam terminantes; I (dempta arista): 2.5–3.5 mm longa, nervos secundarios 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

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 vegetative 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,  $\times 0.6$ . B, Leaf sheath apex with petiole and base of a broad leaf blade,  $\times 7.2$ ; 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,  $\times 0.6$ ; 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,  $\times 1.2$ ; E, spikelet,  $\times 1.8$ ; F, transitional (empty) glumes,  $\times 6$ ; G, floret,  $\times 6$ ; H, lemma,  $\times 6$ ; I, palea,  $\times 6$ ; J, lodicule complement,  $\times 12$ ; K, stamen,  $\times 6$ ; L, gynoecium,  $\times 12$ ; M, seedling,  $\times 0.6$ ; N, fruit, embryo side, showing embryotegium (left), and hilum side (right), showing the sulcus (conventionally referred to as a hilum),  $\times 7.2$ . Drawings 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. Lodiculae 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 caespitose, 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 pallidly 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; 1 (without the awn): 2.5-3.5 mm long, with 1-2 secondary nerves; 11 (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. Lodicules subopaque, nervose, 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 exerted. 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, capitate; Dif, diffuse; Dig, digitate. *Infl Dev*: inflorescence development. S, scmelautant; I, iterautant. *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	Stamen	Spikelet Apex	Br Subt	Br Proph	Infl Br	Infl Dev	Genus	Rhizome	Midculm Prophyllum and Primordium	Initial (Primary) Branch	L/S Int
	3	3		0	0	Pan Rac	S	<i>Arundinaria</i>	L			0
	2	3		0	0	Con Ope Pan	S	<i>Chusquea</i>	L LP P			0
Not yet known	2	3		0	0	Sec Con Pan	S	<i>Swallenochloa</i>	P			0
	2	3		0	0	Pan	S	<i>Neurolepis</i>	P			0
	2	3		0	0	Pan or Sec Rac	S	<i>Myriocladus</i>	P			+ 0
Not yet known	2	3		0	0	Pan Rac Sol	S	<i>Colantheia</i>	P			0
	2	3		0	0	Pan	S	<i>Yushania (Otatea)</i>	P			0
	2	3		0	0	Pan	S	<i>Aulonemia</i>	P			+ 0
	2	3		0	0	Spi Rac (See descr)	S	<i>Arthrostylidium</i>	P			+ 0
	2	3		0	0	Div (See descr)	S	<i>Rhipidocladum</i>	P			+ 0
	2	3		0	0	Sec Spi	S	<i>Merostachys</i>	P			0
	2	3		+	+	Sol to Rac	S	<i>Apoclada</i>	P			0
Not yet known	2	3		+	0	Cap	S	<i>Athroostachys</i>	P			0
Not yet known	2	3		+	+	Dif Pan	S	<i>Glaziophyton</i>	P			+ 0
Not yet known	2	3		+	+	Cap or Dif	+	<i>Atractantha</i>	P			0
	2	6		+	+	Dif	I	<i>Elytrostachys</i>	P			0
	(4) 3 2 1	6 (3)		+	+	Dig to Cap	I	<i>Bambusa (Guadua)</i>	P			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; *morphē*, 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. *anastomōsis*, a new outlet). "Union of one vein with another, the connection forming a reticulation" (Jackson, 1949).

ANDROECIUM (Gr. *andros*, male; *oikos*, house). The stamen complement of a flower. I have not followed Arber (1934:152 et passim) in adopting the spelling (andraeceum) 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, anticously (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.

\*\*APOCLADA (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. apsis*, 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 *Rhipidocladum*, qq. vv. See CONSTELLATE; GREMIAL; LEVEL; RESTRICTED.

ASSIMILATION TISSUE. Mesophyll; the interior ground tissue of a leaf blade.

AWNED. Bearing a bristlelike apical appendage called an awn (OE). The empty glumes of the spikelet in the type and some other species of *Neurolepis* are awned. In *Streptochoeta* (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; *peto*, 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. Circumcinct bracts subtend branch buds and branches of the rachis in all bamboo genera with iterant 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 semelaucant inflorescences; in *Glaziophyton*, however, they are well developed and circumcinct.

\*\*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; PLURICESPITOSE; UNICESPITOSE.

**\*\*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 *Athrostachys*; 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. deliquescens*, 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.

**\*\*DEPAUPERATE** (*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**; **SEMELAUXTANT**. 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**; **TRIADELPHOUS**.

**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. *embryon*, a 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 prophyllum (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 agrastology. 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 prophyllum (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.

GREGARIOUS (L. *gregarius*, of or pertaining to a flock or herd). "Growing in company" (Jackson, 1949). Gamble (1896:viii) makes gregarious mean simultaneous, to describe the flowering behavior manifested when all of the members of a given generation of bamboo plants (from seeds of a common origin) enter the reproductive state at approximately the same time. Cf. SPORADIC.

\*\*GREMIAL (L. *gremialis*, of a lap or bosom). "Growing in a pollard-like cluster" (R. W. Brown, 1954); characterizes the mode of insertion of a tuft of subequal second-order axes that develop from buds on a decurrent extension of the primary (first-order) axis of an unrestricted monoclade branch complement (as in *Bambusa walleniana* [*Guadua spinosa*] and in numerous species of the genus *Arthrostylidium*). Cf. PROMONTORY.

GYNŌECIUM (Gr. *gynē*, female; *oikos*, house). The complete pistil, consisting of the ovary, the ovule(s), style(s), and the stigma(s), of a single flower. I have not followed Arber (1934:120 et passim) in adopting the spelling (gynaecium) advocated by Kraus (1908). Jackson (1949) and Nybakken (1959) both give gynœcium. Cf. ANDROECIUM.

HALM, haulm, haum (terms used in British agrostology). See CULM.

\*\*HERMAPHRODITE. Same as PERFECT, q.v.

\*\*HILUM (L. *hilum*, a trifle). "The scar left on a seed where formerly attached to the funicle or placenta" (Jackson, 1949). This definition confines the connotation of the term hilum to a scar on a deciduous seed that has been freed from its attachment on a dehiscent carpel. However, in the literature of agrostology, the term hilum is quite generally applied to the longitudinal furrow or groove that marks, on the exterior of the indehiscent gramineous caryopsis, the locus of attachment of the indeciduous seed that remains confined within an indehiscent pericarp. In the present treatise, this external furrow is referred to as a sulcus. See SULGATE.

IMBRICATE (L. *imbricatus*, covered with tiles). "Overlapping like roofing tiles and shingles" (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, iterant) 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 ITERAUCTANT; 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 semelauctant or iterauctant (q.v.) in its manner of development. The occurrence of individual features of an intermediate (incongruous) nature is rare. Cf. FLOWERING BRANCH; see also INFLORESCENCE, ITERAUCTANT; INFLORESCENCE, SEMELAUCTANT.

\*\*INFLORESCENCE, ITERAUCTANT. An inflorescence 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 inflorescence with peduncles proliferating (duplicating themselves indefinitely from nascent or dormant prophyllate 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, SEMELAUCTANT. An inflorescence in which typically the initiation of growth is simultaneous or nearly so in all axes, and the termination 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 respect 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.

\*\*ITERAUCTANT (L. *iterum*, again; *auctans*, growing). Embracing more than one grand period of growth, as the mode of development of the successive orders of the branches of an inflorescence composed (as in bamboos of the genera *Bambusa*, *Elytostachys*, and *Atractantha*) of pseudospikelets (q.v.). Cf. SEMELAUCTANT; 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 occasioned by its indiscriminate use in the literature. The word is commonly used by agrostologists, without modification or qualification, to refer to any one of the morphologically, anatomically, and functionally 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 bamboos 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 inserted). 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 ORGAN.

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

\*\*LEMMA (Gr., a husk). The glume that subtends a flower. Lemmas that subtend normally constituted and developed flowers are conventionally called fertile lemmas, to distinguish them from sterile lemmas, whose subtended flowers are depauperate or obsolete. See TRANSITIONAL GLUMES.

\*\*LEPTOMORPH (Gr., *leptos*, slender, and *morphē*, form). Characterizes the rhizomes proper (of a bamboo plant) when they are long and slender, and have the following associated characteristics: 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 narrow 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 fea-

tures 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 ap-

pendages 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 F<sub>1</sub>, 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 ellipsoid (Stearn, 1966; Webster, 1959).

**P.I.** Abbreviation of “Plant Introduction,” prefixed to a permanent identifying number assigned by the U.S. Department of Agriculture to each lot of living plant material (seeds, plants, or cuttings) accessioned in its record of plant introductions. These numbers are published, along with pertinent names and documenting notes, in a continuing series of “Plant Inventories.” See also MBG.

**\*\*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 dormant state asymmetrically dome-shaped, with a subcircular margin and an intramarginal apex. Cf. LEPTOMORPH.

**PALEA** (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.

**\*\*PÁRAMO** (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 pseudospikelets, 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 arbi-

trarily 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 pseudospikelet is terminal (instead of lateral) to a flowering branch. Here the peduncle is more elongate. Cf. PEDICEL; RACHIS.

**PEDUNCULATE**. Having a peduncle.

**\*\*PERCURRENT** (L. *percurrens*, passing through). Used here in a sense identical with that given EXCURRENT.

**\*\*PERFECT**. Signifies the presence, within an antheridium, of a flower containing a normally developed complement of sexual elements, both staminate and pistillate. Same as hermaphrodite.

**PERGAMINEOUS** (L. *pergamena*, 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 antorsely 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 GYNŌECIUM.

**\*\*PLEIOCLADE** (Gr. *pleiōn*, 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.

**PLEIOGENY** (Gr. *pleiōn*, 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.

**\*\*PLURICESPITOSE** (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. **UNICESPITOSE**.

**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.

**\*\*PRIMITIVE**. "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 (1949) differentiates as "The production of terminal or lateral leaf buds in a flower." An example of proliferation is cited under **DETERMINATE**. See also **PLEIOGENY**.

**\*\*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 *Arthrostylidium*. 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 trōpical organ (L. *trōpicus*, 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. *Athrostachys capitata* (Figure 19c) bears paniculate racemes in which all branches are relatively short. This gives the inflorescence a capitate 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 rhachilla vaguely as "a 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 nor-

mal 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. *rhizōma*, 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.

SENSU 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. *shethe*). 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 lamiferous 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. *scēotan*, 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 subsessile 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, 1937). 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 gynoeceum. 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 (gynoeceum) 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 subdistal, 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 sympodium; 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 sympodium 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). Elaborat-

ing 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."

**TERATIC** (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. **OBTERETE**.

**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.

**TRACANT** (Fr., running, creeping). Ranging widely and freely; a term used by the Rivières (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.

**TRIADELPHOUS** (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 pleio-clade 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. **PLURICESPITOSE**.

**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 pleio-clade) as possessing the potential for proliferating by way or buds at the proximal nodes of its component first-order member (s).

**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.

**\*\*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."

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